

**Preliminary Population Viability Assessment for the
Ocelot (*Leopardus pardalis*)
In South Texas and Northern Tamaulipas**

Report prepared by:
Philip S. Miller
IUCN / SSC Conservation Breeding Specialist Group

In collaboration with

**Members of the
U.S. Fish and Wildlife Service Bi-National Ocelot Recovery Team**



Conservation Breeding Specialist Group

Species Survival Commission / IUCN - World Conservation Union

Facilitating Endangered Species Survival

12101 Johnny Cake Ridge Road, Apple Valley, MN 55124-8151, USA

Tel: 1-612-431-9325 Fax: 1-612-432-2757

E-mail: office@cbsg.org World Wide Web: www.cbsg.org

**Preliminary Population Viability Assessment for the
Ocelot (*Leopardus pardalis*)
In South Texas and Northern Tamaulipas**

**Philip Miller, Conservation Breeding Specialist Group
and
U.S. Fish and Wildlife Service Bi-National Ocelot Recovery Team Members**

TABLE OF CONTENTS

Introduction.....	1
Baseline Input Parameters for Stochastic Population Viability Simulations.....	2
Results of Baseline Simulations.....	7
Demographic Sensitivity Analysis.....	8
Risk Analysis I: Population Size, Road Mortality, and Extinction Risk	12
Risk Analysis II: Translocation and Metapopulation Viability	15
Future Directions for Additional Analysis.....	17
Conclusions.....	17
References.....	18
Appendix I: Simulation Modeling and Population Viability Analysis.....	20

**Preliminary Population Viability Assessment for the
Ocelot (*Leopardus pardalis*)
In South Texas and Northern Tamaulipas**

**Philip Miller, Conservation Breeding Specialist Group
and
U.S. Fish and Wildlife Service Bi-National Ocelot Recovery Team Members**

Introduction

In 1990, Harwell and Siminski published *The Listed Cats of Texas and Arizona Recovery Plan (With Emphasis on the Ocelot)* through the United States Fish and Wildlife Service. While considerable progress was made over the last decade in conducting ocelot research, there are a number of recovery actions that have received little attention following the publication of this important document. In addition the geographic, economic, and political landscapes in south Texas and northern Tamaulipas have changed considerably since 1990, thereby necessitating a review and probably revision of the Plan's information and recommended actions. In response to this need, an Ocelot Recovery Team was formed in May 2003 for the purpose of revising the outdated plan. The team is composed of both a Technical and an Implementation subgroup with representation from the United States and Mexico.

The first Recovery Plan (Harwell and Siminski 1990) recommended some major demography-related activities for ocelot recovery, namely “determining the precise population sizes and habitat sizes required for viability and the necessary spatial arrangement of habitat, and determining the impact of disease and other factors on the population; increasing ocelot numbers in Texas, in part by protecting at least 20,000 hectares of prime ocelot habitat in Texas (either in a single block or continuous blocks connected by corridors).” Population viability analysis (PVA) has been identified by the Recovery Team as a valuable tool for determining the likely fate of the ocelot populations currently distributed throughout south Texas and northern Tamaulipas, and to assist in the process of identifying the most promising recovery actions.

PVA can be an extremely useful tool for investigating current and future risk of wildlife population decline or extinction. In addition, the need for and consequences of alternative management strategies can be modeled to suggest which practices may be the most effective in managing populations of the ocelot in its wild habitat in south Texas and northern Tamaulipas. *VORTEX*, a simulation software package written for population viability analysis, was used here as a mechanism to study the interaction of a number of ocelot life history and population parameters treated stochastically, to explore which demographic parameters may be the most sensitive to alternative management practices, and to test the effects of selected management scenarios.

The *VORTEX* package is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild 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 stepping through the series of events that describe the typical life cycles of sexually reproducing, diploid organisms.

PVA methodologies such as the *VORTEX* system are not intended to give absolute and precise “answers”, since they are projecting the interactions of many randomly-fluctuating parameters used as model input

and because of considerable measurement uncertainty we observe in typical wildlife population demography datasets. Because of these limitations, many researchers have cautioned against the sole use of PVA results 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 the output depends upon our knowledge of the biology of the ocelot in this portion of its habitat, the environmental conditions affecting the species, and possible future changes in these conditions. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Appendix I, Lacy (2000) and Miller and Lacy (2003).

Specifically, we were interested in using this preliminary analysis to address the following questions:

- What is our best estimate of stochastic population dynamics of the ocelot within its current range in south Texas and northern Tamaulipas?
- What are the primary factors that drive population growth dynamics of ocelots in south Texas and northern Tamaulipas?
- How vulnerable are small, fragmented populations of ocelots in south Texas and northern Tamaulipas to local extinction in the absence of demographic interaction with other populations?
- What are the benefits to the ocelot of increasing range and connectivity in the landscape?
- How successful might translocation be as a conservation management strategy for smaller populations of ocelots in south Texas?
- How many individuals could be removed from a given source population such as northern Tamaulipas for translocation into smaller populations in south Texas at risk of extinction without negatively impacting the persistence of the source?

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.

Baseline Input Parameters for Stochastic Population Viability Simulations

The relatively scarce data on the population biology and ecology of the ocelot in the northern extreme of its global range comes primarily from Tewes and Schmidly (1987), Laack (1991), Caso (1994), and López Gonzalez et al. (2003). Moreover, the recent analyses of A. Haines (Texas A&I, Kingsville) proved valuable in the development of appropriate model input parameters. Discussion of baseline model input focused on our understanding of the ocelot population within the Laguna Atascosa National Wildlife Refuge, Cameron County, Texas. Where data were absent, we utilized similar information from captive populations and from studies focused on other geographic areas.

Breeding System: Ocelots will often form stable breeding groups that remain intact over more than one year. Therefore, we used the “long-term polygyny” option within *VORTEX* to model this breeding system. Under this option, a set of adult females are therefore randomly selected each year to breed with a given male. Pairs that are produced in a given year are then retained in future years until one of the mates dies.

Age of First Reproduction: *VORTEX* considers the age of first reproduction as the age at which the first kittens are born, not simply the onset of sexual maturity. All available information indicates wild female ocelots produce their first offspring no earlier than about 30 months of age. We therefore set this parameter at 3 years. In order to test the sensitivity of our models to uncertainty in this parameter, we ran additional models with this variable set to either 2 years or 4 years of age. Because males must typically wait for the opportunity to fill vacancies within a given territory, their age of first reproduction is typically older. We set this parameter to 4 years in all models.

Age of Reproductive Senescence: In its simplest form, *VORTEX* assumes that animals can reproduce (at the normal rate) throughout their adult life. There are no real data available on senescence in ocelots. Captive animals have lived up to 15-17 years, but it is quite likely that this cannot be achieved under much more competitive conditions in the wild. We therefore estimated that ocelots could live up to 11 years in the wild. In reality, achieving this age is unlikely given mortality rates (see below). In order to test the sensitivity of our models to uncertainty in this parameter, we ran additional models with this variable set to either 9 years or 13 years of age.

Offspring Production: Based on our knowledge of ocelot life history, we have defined reproduction in these models as the production of kittens observed in the field. Indirect evidence suggests that ocelots often breed every other year, but there are no direct data of this type in south Texas / northern Tamaulipas. Our best “guesstimate” of the average percentage of adult females that successfully breed per year was therefore set at 50%. There are some data (Laack et al, in press) to suggest that this value is an underestimate, although data to the contrary are sparse and difficult to interpret conclusively. In order to test the sensitivity of our models to uncertainty in this parameter, we ran additional models with this variable set to a higher value of 75%.

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 kittens within a given year. While no data are available for this parameter, we propose that annual variance is relatively low. We therefore set the standard deviation in the percentage of adult females breeding at 5%.

Many studies have cited an average ocelot litter size of about 1.4 – 1.5 kittens per successful female. We developed the following distribution of possible litter sizes for a given successful female:

Number of kittens	%
1	66.0
2	33.0
3	1.0

This distribution yields an average litter size of 1.35 kittens. Litters of 3 individuals are thought to be possible but quite rare. In order to test the sensitivity of our models to uncertainty in this parameter, we ran additional models with a reversed distribution of litters of size 1 and 2, thereby giving a new average litter size of 1.68. The overall population-level sex ratio among newborns is assumed to be 50%.

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.

At this time, there are no data to support density dependence in reproduction in ocelot populations occupying this portion of their range. Consequently, this option was not included in the models presented

here. It is possible that population decreases could actually stimulate higher levels of reproductive success through reduce in intraspecific competition; the detailed mode of action of this relationship, however, was not determined for this analysis.

Male Breeding Pool: 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. Within any given year, we assume that all adult male ocelots are equally capable of siring offspring; This is not to say, however, that all adult males actually meet with the same level of success during a given breeding season.

Mortality: Age-sex-specific mortality rates for this PVA are based on new analyses by Aaron Haines. When developing a mortality schedule for ocelots in south Texas, it is vitally important to separate out the impact of road-kill mortality from background mortality. Vehicle impacts are a major source of mortality in this geographic area, especially among subadult individuals that are attempting to disperse to new territories. From the available field and Haines’ analysis, we have developed the following schedules, with and without the effect of vehicle-impact mortality:

Age Class	% Mortality (SD) (Road mortality excluded)		% Mortality (SD) (Road mortality included)	
	Females	Males	Females	Males
0 – 1	30.0 (6.0)	30.0 (6.0)	33.0 (7.0)	33.0 (7.0)
1 – 2	15.0 (3.0)	15.0 (3.0)	15.0 (3.0)	15.0 (3.0)
2 – 3	16.0 (4.0)	30.0 (6.0)	30.0 (7.0)	37.0 (8.0)
3 – 4	8.0 (2.0)	13.0 (3.0)	13.0 (3.0)	13.0 (3.0)
4+	8.0 (2.0)	8.0 (2.0)	13.0 (3.0)	13.0 (3.0)

Note the high levels of mortality among 2-3 year-olds, especially among males. In addition, Haines’ analysis indicates the significant effect that vehicle impacts have on the mortality of dispersing females in this same age class. Under these conditions, the probability of a female reaching reproductive age is about 50% in the absence of road mortality, but this drops to 40% when road mortality is included. Similarly, the probability of a female reaching the maximum age drops from about 24% in the absence of road mortality to about 12% in the presence of road mortality.

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 are imposed during the single year of the catastrophe, after which time the demographic rates rebound to their baseline values.

We suspected that a drought event could severely affect the reproductive capability of adult females. Therefore, we included a drought catastrophe in many of our models. Calculations by Haines at the workshop suggested that such a severe event would occur approximately once every 9-10 years, so we assumed that the annual probability of such an event occurring was 11%. We also assumed that such a drought would reduce the population-level measure of reproductive success (percentage of adult females breeding each year) by 50%. In other words, if approximately 50% of adult females bred successfully in a year without drought, only about 25% would be expected to do so during a serious drought. In order to test the sensitivity of our models to uncertainty in this parameter, we ran additional models with the drought event removed from the analysis.

Inbreeding Depression: *VORTEX* includes the ability to model the detrimental effects of inbreeding, most directly through reduced survival of offspring through their first year. While specific data on inbreeding depression in either captive or wild ocelot 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 of ocelots. We therefore elected to include this process in our models, with a genetic load of 3.14 lethal equivalents and approximately 50% of this load expressed as lethal genes. In order to test the sensitivity of our models to uncertainty in this parameter, we ran additional models with inbreeding depression removed from the analysis.

Initial Population Size: Current estimates put the total ocelot population size within the Laguna Atascosa National Wildlife Refuge (LANWR) in Cameron County at approximately 30 individuals, while the population occupying the lands in Willacy and Kenedy Counties is considered to be slightly larger (i.e., around 40 individuals). The closest population in Mexico, approximately 130km to the south in Tamaulipas, is thought to be about 200 animals. These values were used for specific models designed to evaluate the risk of extinction of existing populations.

Because of the uncertainty in these estimates, and because of a greater interest in the more general results that can be obtained from a systematic analysis of population size and its influence on persistence in the face of random demographic fluctuations in ocelot populations, we decided to also focus on a set of population size classes throughout the analysis. The size classes studied were:
 $N_0 = 30, 40, 50, 60, 75, 100, 150, 200$

VORTEX distributes the specified initial population among age-sex classes according to a stable age distribution that is characteristic of the mortality and reproductive schedules described previously.

Carrying Capacity: The carrying capacity, K , for a given habitat patch defines an upper limit for the population size, above which additional mortality is imposed randomly across all age classes in order to return the population to the value set for K .

All observations suggest that, through the action of habitat alteration and destruction by local human activities, ocelot populations in south Texas and northern Tamaulipas are at or very near their ecological carrying capacity within existing habitat. Therefore, we initialized all our models with K equal to the appropriate initial population size.

Metapopulation Analysis: An important issue for management of ocelot in the northern extent of their range is the feasibility of “linking” the three populations mentioned above by artificial dispersal, i.e., translocation. Natural dispersal has not been observed in this part of their range and does not appear to be a realistic expectation at this time. To evaluate artificial dispersal as a conservation tool, we developed a set of simulations that involved the removal of four 2-year-old animals (equal sex ratio) – those that have the highest probability of mortality through natural dispersal and associated vehicle impacts – from the Tamaulipas population every other year and distributing them into the two United States populations. During this process, we assume a 50% loss of individuals during transport, so that only one ocelot is being added to each of the LANWR and Willacy-Kenedy populations during the process. Moreover, we assume that this process can not last forever, so we continue the process at 2-year intervals for either 30 or 60 years. In addition to assessing the efficacy of this procedure for potential “rescue” of the much smaller United States populations, we also want to evaluate the impact that such a rate of removal might have on the source Mexican population.

Iterations and Years of Projection: All population projections (scenarios) were simulated 500 times. Each projection extends to 100 years, with demographic information obtained at annual intervals. All simulations were conducted using *VORTEX* version 9.45 (June 2004).

Table 1 below summarizes the baseline input dataset upon which all subsequent *VORTEX* models are based.

Table 1. Demographic input parameters for the baseline *VORTEX* models for populations of ocelot in south Texas and northern Tamaulipas. See accompanying text for more information.

Model Input Parameter	Baseline value
Breeding System	Long-term polygynous
Age of first reproduction (♀ / ♂)	3 / 4
Maximum age of reproduction	11
Inbreeding depression?	Yes
Lethal equivalents	3.14
Annual % adult females reproducing (SD)	50
Density dependent reproduction?	No
Maximum litter size	3
Mean litter size [†]	1.35
Overall offspring sex ratio	0.5
Adult males in breeding pool	100%
% annual mortality, ♀ / ♂ (SD)	
0 – 1	33.0 / 33.0 (7.0) [‡]
1 – 2	15.0 / 15.0 (3.0)
2 – 3	30.0 / 37.0 (8.0)
3 – 4	13.0 / 13.0 (3.0)
4 – +	13.0 / 13.0 (3.0)
Catastrophe?	Drought
Annual frequency of occurrence	11%
Severity: Reproduction	0.5
Severity: Survival	1.0
Initial population size / K	
Laguna Atascosa (LANWR)	30 / 30
Willacy – Kenedy Counties	40 / 40
Tamaulipas, Mexico	200 / 200

[†] Exact probability distribution of individual clutch size specified in input file.

[‡] Includes road mortality; see text for specification of natural mortality levels.

Results of Baseline Simulation

Results reported for each modeling scenario include:

r_s (SD) – The mean rate of stochastic population growth or decline (standard deviation) demonstrated by the simulated populations, averaged across years and iterations, for all simulated populations that are not extinct. This population growth rate is calculated each year of the simulation, prior to any truncation of the population size due to the population exceeding the carrying capacity.

$P(E)_{100}$ – Probability of population extinction after 100 years, determined by the proportion of 500 iterations within that given scenario that have gone extinct within the given time frame. “Extinction” is defined in the *VORTEX* model as the absence of either sex.

N_{100} (SD) – Mean (standard deviation) population size at the end of the simulation, averaged across all simulated populations, including those that are extinct.

GD_{100} – The gene diversity or expected heterozygosity of the extant populations, expressed as a percent of the initial gene diversity of the population. Fitness of individuals usually declines proportionately with gene diversity.

$T(E)$ – The average time to population extinction, in years.

The set of demographic, genetic, and ecological input data that represents our best understanding of the life history of ocelots in south Texas is hereafter referred to as our *baseline model*. This model simulates the predicted trajectory of a small population inhabiting Laguna Atascosa NWR when all sources of mortality – both natural and anthropogenic – are included. The results of this analysis are presented in Figure 1. The average population growth rate is -0.082, and the extinction probability over 100 years is 100%.

It is clear from this Figure that, under our best estimates of ocelot population biological parameters, the population currently occupying Laguna Atascosa NWR is expected to decline rapidly toward extinction within the next 50 years. The high rate of decline seen in the model is no doubt due at least in part to pessimistic estimates of certain key demographic parameters, such as the age of first reproduction or the percentage of adult female breeding success. In other words, we may be assuming that females begin breeding at an age that is older than the real situation in the wild, and we may be underestimating the rate of breeding success among adult females. However, this decline also surely results from a more accurate portrayal of other tangible consequences of ocelot biology and local anthropogenic activity, including:

- Habitat loss around LANWR that leads to a very small suitable area and an associated small ocelot population subjected to stochastic demographic fluctuations;
- “Frustrated dispersal”, with a significant proportion of dispersing individuals killed while attempting to move across compromised habitat in search of new territories; and
- Increased mortality through vehicle impacts.

The working group developing this model concludes that, while perhaps more severe in absolute magnitude compared to the actual situation in the wild, our simulation model of ocelot population dynamics within LANWR is a fairly accurate simulation of the likely fate of this population in the absence of intensive management.

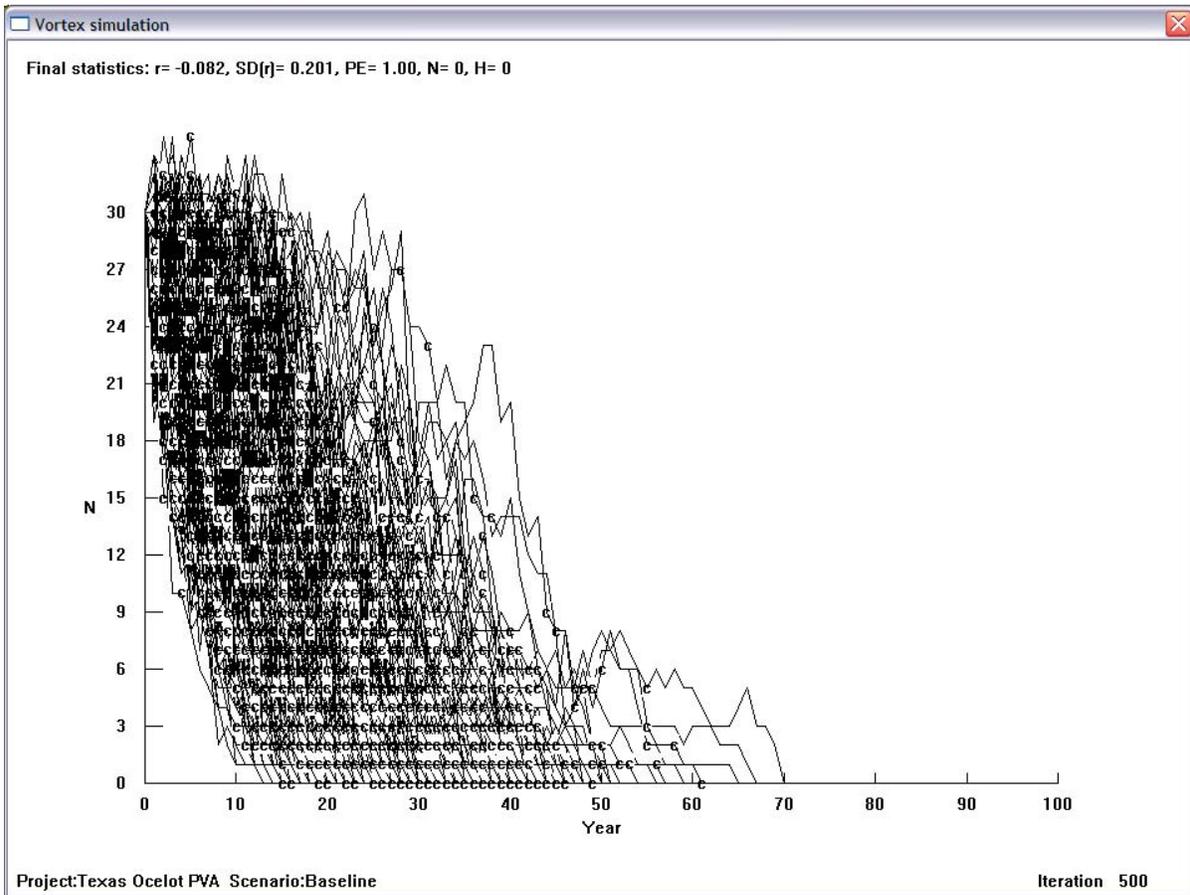


Figure 1. Plot of 500 individual iterations of the baseline *VORTEX* model of predicted ocelot population dynamics in Laguna Atascosa National Wildlife Refuge, Texas. The average rate of population growth across these iterations is -0.082, indicating a considerable rate of decline with extinction occurring within 40 years. Note the level of variance in the model as defined by both demographic and environmental sources of stochasticity included in the model. See text for accompanying details.

Demographic Sensitivity Analysis

During the development of the baseline input dataset, it quickly became apparent that a number of demographic characteristics of ocelot populations in south Texas and northern Tamaulipas were being estimated with varying levels of uncertainty. This type of measurement uncertainty, which is distinctly different from the annual variability in demographic rates due to extrinsic environmental stochasticity and other factors, impairs our ability to generate precise predictions of population dynamics with any degree of confidence. Nevertheless, an analysis of the sensitivity of our models to this measurement uncertainty can be an invaluable aid in identifying priorities for detailed research and/or management projects targeting specific elements of the species' population biology and ecology.

To conduct this demographic sensitivity analysis, we identify a selected set of parameters from Table 1 whose estimate we see as considerably uncertain. We then develop biologically plausible minimum and maximum values for these parameters (see Table 2).

Table 2. Uncertain input parameters and their stated ranges for use in demographic sensitivity analysis of simulated ocelot populations in south Texas and northern Tamaulipas. Values in bold are those used in the baseline model. See accompanying text for more information.

Model Parameter	Minimum	Estimate	
		Midpoint	Maximum
Age of First Reproduction	2	3	4
Maximum Age	9	11	13
Inbreeding Depression	No	Yes	
% Adult Females Reproducing		50	75
Average Litter Size		1.35	1.68
Road Mortality	No	Yes	
Drought	No	Yes	

For each of these parameters listed above we construct multiple simulations, with a given parameter set at its prescribed minimum and/or maximum value, with all other parameters remaining at their baseline value. With the seven parameters identified above, and recognizing that the aggregate set of baseline values constitute our single baseline model, the table above allows us to construct a total of 10 additional, alternative models whose performance (defined, for example, in terms of average population growth rate) can be compared to that of our starting baseline model. For the entire suite of sensitivity analysis models, we will consider a population very similar to that occupying Laguna Atascosa NWR, i.e., initial population size and ecological carrying capacity equal to 30 individuals.

The results of the sensitivity analysis are shown graphically in Figure 2 and in tabular form in Table 3.

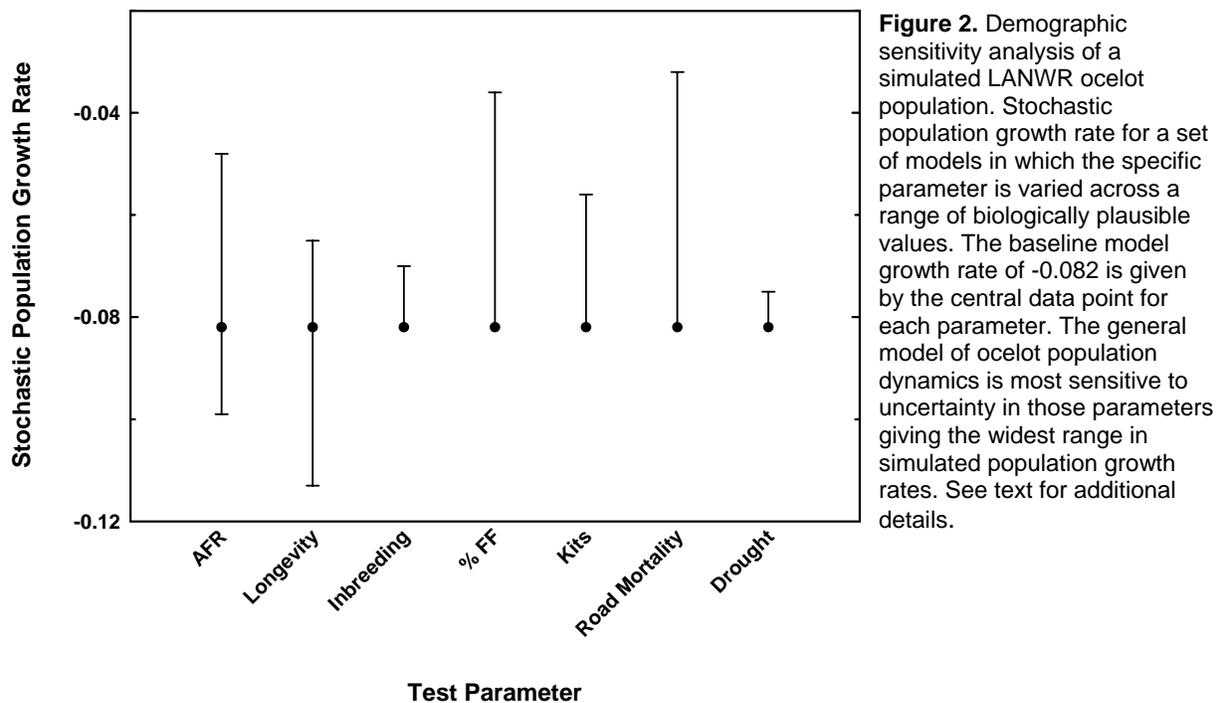


Table 3. South Texas / northern Tamaulipas ocelot PVA. Output from demographic sensitivity analysis models. See text for additional information on model construction and parameterization.

Model conditions	r, (SD)
Baseline	-0.082 (0.201)
Age of First Reproduction	
2	-0.048 (0.188)
4	-0.099 (0.205)
Maximum Breeding Age	
9	-0.113 (0.209)
13	-0.065 (0.191)
Inbreeding Depression	
No	-0.070 (0.204)
% Adult Females Breeding	
75	-0.036 (0.186)
Litter Size	
1.68	-0.056 (0.198)
Road Mortality	
No	-0.032 (0.168)
Drought	
No	-0.075 (0.195)

It is clear from the analysis that our model of ocelot population dynamics is most sensitive to uncertainty in adult female reproductive success (defined here as the percentage of adult females that successfully produce a litter) and to additional mortality of ocelots through vehicle impacts. Uncertainty in reproductive lifespan also leads to significant model response, but not to the level of that seen among the aforementioned variables. While in exclusion of inbreeding depression does not significantly alter the results of our baseline model, we are reluctant to discount its potential impact in small or isolated populations of ocelots in the periphery of the species' range. There is an abundance of evidence suggesting that small populations of mammals can suffer markedly from the impacts of inbreeding depression; there are simply too many other factors conspiring to drive this population into rapid decline for us to be able to discern the precise action of this genetic factor in our particular model.

Once the generalized sensitivity analysis was successfully completed, we set out to develop a set of models with the goal of more precisely identifying the relative contributions of adult and juvenile mortality to the overall growth dynamics of our simulated ocelot population. This was done in order to provide a better understanding of species population dynamics, to define a broad set of minimal conditions necessary to increase the chances of population persistence, and to gain additional insight into the magnitude of any detrimental impact of proposed major mortality factors. This type of analysis can provide a simple benchmark to which wild population management and associated field monitoring efforts can then be directed.

A total of 50 individual models were constructed that provided all possible combinations of two levels of reproductive success, five levels of juvenile mortality, and five levels of adult mortality. This was done in order to more effectively address the relationship between reproductive success and age-specific mortality required for population growth.

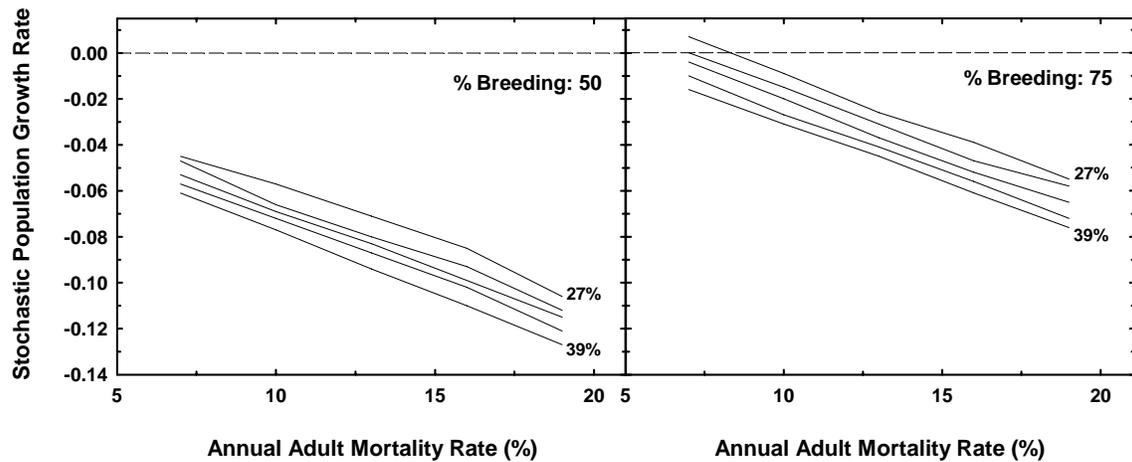


Figure 3. South Texas / northern Tamaulipas ocelot population mortality analysis. Plots give average stochastic population growth rate (r_s) as a function of annual mortality rate of adults with individual lines corresponding to different levels of juvenile mortality. Two panels correspond to variable levels of adult female reproductive success (see text for additional details on the determination of success). Initial population size for all simulations is set at 30 individuals.

The results of this mortality analysis are shown in Figure 3. It is clear that, under the conditions modeled here, only a very small number of combinations of juvenile and adult mortality can result in a population that is expected to grow over time (i.e., $r > 0.0$). Inspection of these graphs lead to the following additional conclusions:

- Nearly all simulated populations have negative growth rates, with many showing high rates of decline. Based on our understanding of the growth dynamics exhibited in the baseline model described earlier in this section, this poor level of population performance most likely reflects the high mortality present in small, isolated ocelot populations subjected to abnormal levels of vehicle impacts.
- Higher levels of reproductive success result in considerably higher levels of stochastic population growth under the same suite of mortality values. Nevertheless, the relatively high levels of vehicle-impact mortality present in the subadult (dispersing) stages included here reduce overall growth rates so that population growth is possible only under the most optimistic mortality schedule.
- A given percentage change in ocelot adult mortality results in a proportionally much larger change in mean population growth rate compared to a change in juvenile mortality of the same magnitude. In other words, the results of our simulation models are considerably more sensitive to adult mortality.

While it is very instructive to investigate the sensitivity of our model to uncertainty in demographic input, it is also important to recognize that detecting mortality rates to the level of precision discussed here is rather impractical at best. For example, statistical power analyses conducted on typical types of field demographic and survey data (e.g., Forcada 2000) suggest that either large sample sizes (say, in the hundreds of individuals) or long periods of observation (10 – 15 years) are necessary to detect meaningful changes in population numbers in the short term with reasonable levels of precision. Similarly, very large

and detailed field studies would be required to successfully differentiate between, for example, juvenile mortality rates of 27% and 30%. Consequently, the analysis presented here should typically be used at a more “strategic” level. When faced with the need for population management in the face of measurement uncertainty and limited institutional resources, research and/or management prioritization can be accomplished through a comparative study of sensitivity analysis data. Having said this, it is also important to note that those parameters to which a demographic model is most sensitive may **not** be the same parameters that are most directly affected by human activities and are therefore putting the population at risk. Successful conservation requires careful additional study to identify the specific risks the populations face and to develop appropriate remedial actions. In the case of the ocelot in south Texas, however, we may in fact have a more direct relationship between the primary demographic drivers influencing population growth dynamics and the anthropogenic factors leading to population endangerment. The next section will explore these relationships in greater detail.

Risk Analysis I: Population Size, Road Mortality, and Extinction Risk

With our demographic sensitivity analysis complete, our next task was to investigate the relationship between the size of an ocelot population and its vulnerability to extinction in the presence of significant anthropogenic disturbance. To do this, we ran simulations for each initial population size discussed in the Input Parameters section across each of three alternative values of female reproductive success, deemed to be one of the most sensitive parameters in our model. This yields a total of 24 different model scenarios. To investigate the impact of road mortality, we then repeated this set of models but removed the additional mortality brought about through vehicle impacts – thereby producing a grand total of 48 models for analysis.

Essentially, our goal in this analysis is to identify, for a given scenario of assumed ocelot demography, the minimum population size necessary to reduce the risk of extinction below a defined threshold. Unfortunately for us biologists, the identification of this extinction threshold is based more on political and social factors than on anything else. The agreement upon a threshold must be done within a more participatory framework that includes a diversity of perspectives among those involved in the management and utilization of the taxon under study.

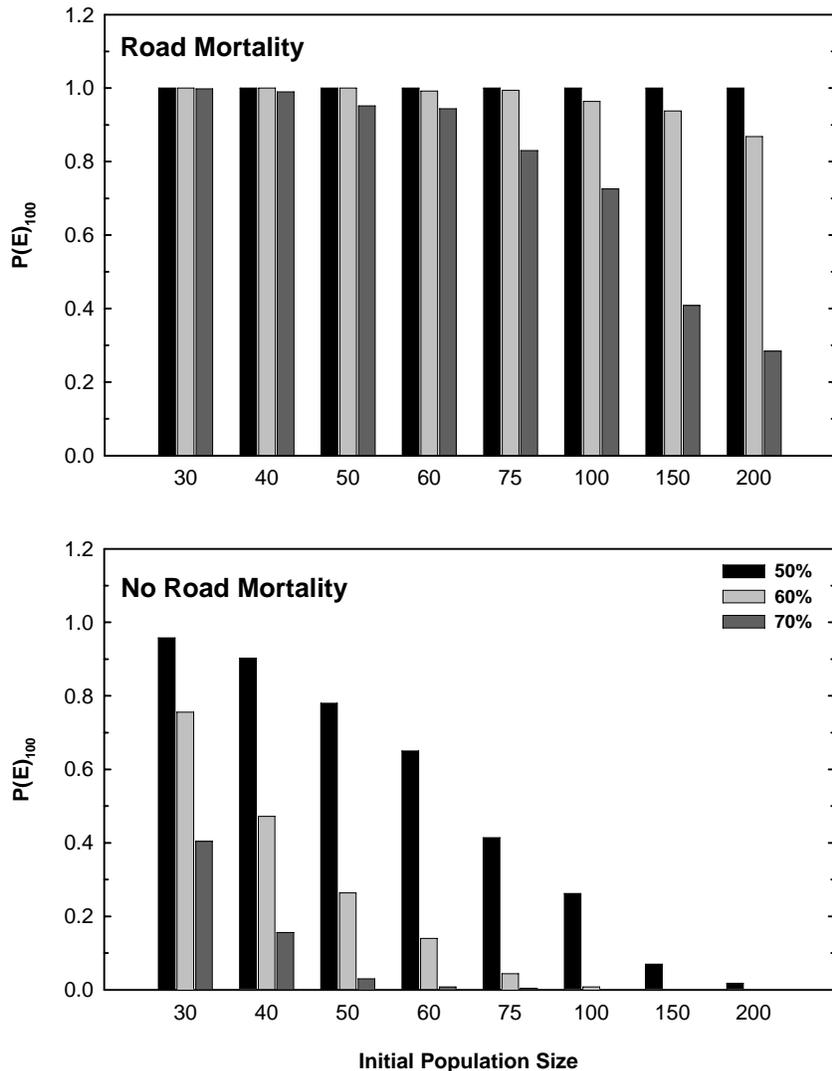
Table 4 and Figure 4 present the aggregate results of this analysis. Examination of these results lead us to the following conclusions:

- Road mortality has a considerable impact on the estimated viability of our simulated ocelot populations. When this additional mortality source is included, even the largest populations experience rapid population decline and very high extinction probabilities over the 100-year timespan of the simulations. Average time to extinction varies from 25 – 50 years. When this additional mortality source is removed, overall population growth rates rebound markedly.
- In the absence of road mortality, small ocelot populations still have a considerable risk of extinction. This results from the detrimental impact of stochastic variability in demographic rates, leading to a general level of population instability and a subsequent reduction in growth potential.
- Under conditions of low reproductive success – i.e., when only 50% of adult females successfully produce a litter in any given year – ocelot populations have a significantly lower growth potential. In fact, inspection of these data indicate that when road mortality is present, the risk of population extinction in 100 years drops below 50% only under the most favorable conditions modeled here: a relatively large population of 150 – 200 individuals with the highest level of female reproductive success (70%). Even here, however, the average growth rate is about -0.025 and the final population size is reduced from the initial value by approximately 80%.

Table 4. South Texas / northern Tamaulipas ocelot PVA. Results of population size risk analysis models in the presence (top half) and absence (bottom half) of road mortality and under alternative conditions of underlying female reproductive success. See page 7 for definitions of column headings.

% ♀♀	N ₀	r _s (Obs) (SD)	P(E) ₁₀₀	N ₁₀₀ (SD)	GD ₁₀₀	T(E)
Road Mortality						
50	30	-0.082 (0.199)	1.000	–	–	25
	40	-0.085 (0.199)	1.000	–	–	29
	50	-0.084 (0.192)	1.000	–	–	32
	60	-0.082 (0.182)	1.000	–	–	34
	75	-0.080 (0.175)	1.000	–	–	38
	100	-0.078 (0.168)	1.000	–	–	43
	150	-0.078 (0.160)	1.000	–	–	48
	200	-0.077 (0.156)	1.000	–	–	52
60	30	-0.062 (0.195)	1.000	–	–	31
	40	-0.061 (0.187)	1.000	–	–	37
	50	-0.059 (0.179)	1.000	–	–	41
	60	-0.057 (0.173)	0.992	6 (2)	0.436	47
	75	-0.057 (0.167)	0.994	9 (6)	0.596	51
	100	-0.056 (0.163)	0.964	7 (5)	0.446	57
	150	-0.053 (0.152)	0.938	12 (15)	0.543	69
	200	-0.050 (0.146)	0.868	13 (11)	0.653	78
70	30	-0.047 (0.194)	0.998	2 (–)	0.000	39
	40	-0.042 (0.180)	0.990	8 (2)	0.354	48
	50	-0.039 (0.170)	0.952	10 (7)	0.544	58
	60	-0.038 (0.165)	0.944	13 (9)	0.573	65
	75	-0.034 (0.157)	0.830	14 (11)	0.590	73
	100	-0.033 (0.150)	0.726	18 (16)	0.608	83
	150	-0.026 (0.131)	0.408	31 (28)	0.729	80
	200	-0.023 (0.123)	0.284	44 (39)	0.780	82
No Road Mortality						
50	30	-0.033 (0.169)	0.958	8 (4)	0.379	50
	40	-0.030 (0.159)	0.902	11 (9)	0.476	61
	50	-0.026 (0.148)	0.780	15 (11)	0.547	79
	60	-0.023 (0.139)	0.650	17 (13)	0.609	73
	75	-0.019 (0.127)	0.414	21 (17)	0.645	76
	100	-0.014 (0.114)	0.262	35 (25)	0.731	81
	150	-0.007 (0.096)	0.070	64 (40)	0.830	87
	200	-0.003 (0.087)	0.018	102 (53)	0.879	92
60	30	-0.011 (0.160)	0.756	11 (7)	0.465	64
	40	-0.002 (0.143)	0.472	20 (11)	0.566	74
	50	0.003 (0.128)	0.264	28 (14)	0.648	77
	60	0.007 (0.117)	0.140	35 (17)	0.693	79
	75	0.014 (0.105)	0.044	52 (21)	0.762	83
	100	0.019 (0.095)	0.008	77 (23)	0.827	81
	150	0.025 (0.087)	0.000	130 (24)	0.888	–
	200	0.028 (0.083)	0.000	180 (25)	0.917	–
70	30	0.013 (0.150)	0.404	18 (8)	0.497	71
	40	0.023 (0.131)	0.156	28 (11)	0.599	77
	50	0.032 (0.115)	0.030	40 (11)	0.684	89
	60	0.036 (0.109)	0.008	50 (12)	0.731	84
	75	0.041 (0.102)	0.004	70 (11)	0.795	74
	100	0.045 (0.095)	0.000	93 (11)	0.838	–
	150	0.050 (0.090)	0.000	144 (10)	0.892	–
	200	0.052 (0.087)	0.000	194 (12)	0.918	–

Figure 4. South Texas / northern Tamaulipas ocelot PVA. 100-year extinction probabilities for simulated populations of different initial sizes in the presence (top panel) and absence (bottom panel) of road mortality and under alternative conditions of adult female reproductive success (indicated by bar shading; see legend in bottom panel). See text for additional model information.

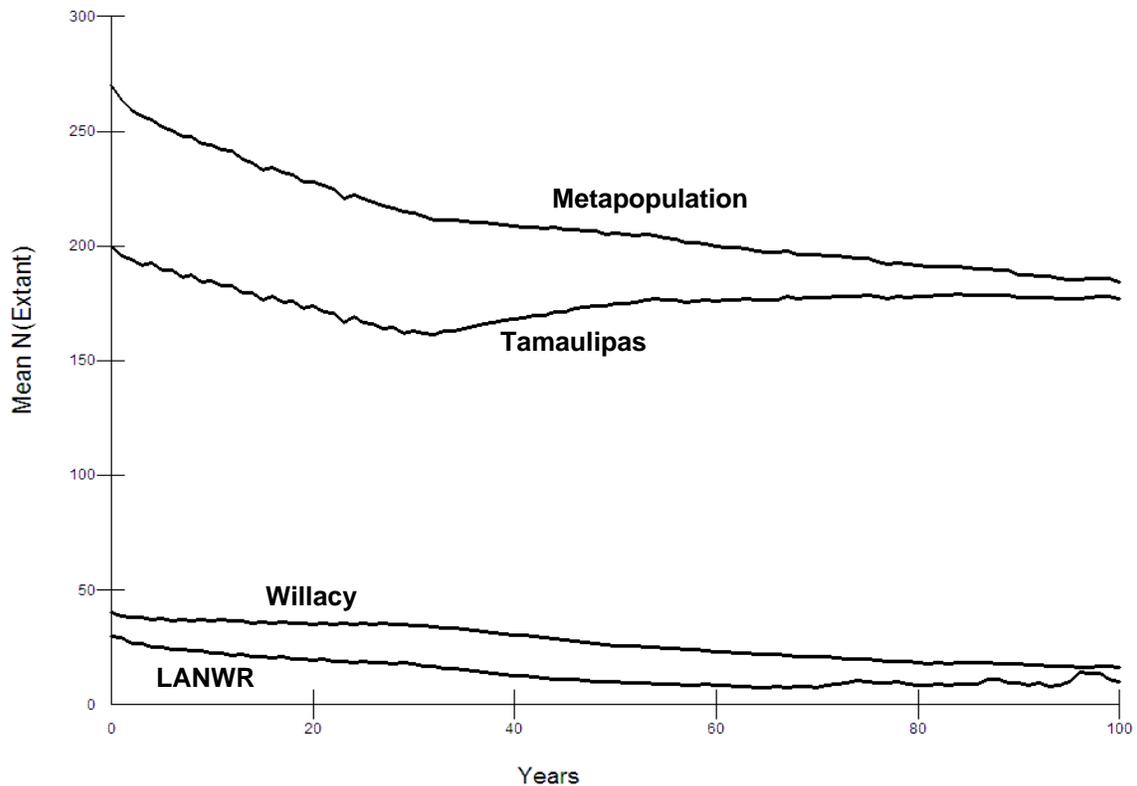


Taken together, these data reinforce the results obtained in our earlier demographic sensitivity analysis: uncertainty in our understanding of intrinsic ocelot breeding rates, and in our understanding of the quantitative impact of road-kill mortality, impairs our ability to make more precise predictions of the fate of ocelot populations subject to human activities. Nevertheless, models like these are invaluable in pointing out the relative importance of these factors in determining the persistence of these populations as humans encroach on their habitat with greater frequency and severity.

Risk Analysis II: Translocation and Metapopulation Viability

A representative population trajectory for each of the metapopulation components is presented in Figure 5, while the full results of the metapopulation analysis are presented in Table 5.

Figure 5. South Texas / northern Tamaulipas ocelot PVA. Representative translocation / metapopulation projection for 100 years, with translocation from Tamaulipas to the two U.S. populations occurring every other year for 30 years. Road mortality is included in this particular model, with a medium level of adult female reproductive success (60% of adult females are assumed to produce a litter each year). See accompanying text for additional model details.



Examination of these data lead us to the following conclusions:

- Even when translocation is used as a conservation strategy, the smaller South Texas populations are at a very high risk of population extinction when road mortality is included in the models. Bi-annual translocations from Tamaulipas are not sufficient to counteract the loss of individuals from vehicle impacts and the population decline resulting from stochastic fluctuations in demographic rates that is characteristic of small populations. When road mortality is removed from the analysis, and we assume a medium level of female reproductive success, all population growth rates are positive and extinction risks are greatly reduced.

Table 5. South Texas / northern Tamaulipas ocelot PVA. Results of metapopulation risk analysis models in the presence (top half) and absence (bottom half) of road mortality and under alternative conditions of underlying female reproductive success. See page 7 for definitions of column headings.

Years	% ♀♀	Population	r_s (Obs) (SD)	$P(E)_{100}$	N_{100} (SD)	GD_{100}	$T(E)$
30	50	LANWR	-0.048 (0.194)	1.000	–	–	42
		Wilacy	-0.023 (0.154)	0.910	9 (8)	0.487	71
		Tamaulipas	-0.022 (0.109)	0.288	64 (51)	0.796	75
		Metapop	-0.023 (0.099)	0.270	64 (51)	0.798	81
60	50	LANWR	-0.032 (0.195)	0.994	4 (3)	0.268	56
		Wilacy	-0.011 (0.143)	0.566	13 (8)	0.628	86
		Tamaulipas	-0.054 (0.137)	0.824	24 (26)	0.698	60
		Metapop	-0.034 (0.114)	0.458	18 (19)	0.669	88
30	60	LANWR	-0.033 (0.188)	0.996	10 (8)	0.612	50
		Wilacy	-0.004 (0.145)	0.568	16 (11)	0.578	79
		Tamaulipas	0.018 (0.082)	0.004	177 (33)	0.909	97
		Metapop	0.016 (0.075)	0.004	184 (35)	0.915	97
60	60	LANWR	-0.022 (0.188)	0.958	7 (4)	0.481	73
		Wilacy	0.012 (0.131)	0.152	20 (11)	0.683	90
		Tamaulipas	0.003 (0.096)	0.112	149 (60)	0.875	66
		Metapop	0.007 (0.080)	0.014	152 (74)	0.883	94
30	70	LANWR	-0.022 (0.183)	0.978	6 (4)	0.340	58
		Wilacy	0.019 (0.135)	0.224	23 (11)	0.614	80
		Tamaulipas	0.046 (0.083)	0.000	194 (10)	0.919	–
		Metapop	0.042 (0.076)	0.000	212 (18)	0.928	–
60	70	LANWR	-0.009 (0.177)	0.816	10 (6)	0.528	77
		Wilacy	0.034 (0.125)	0.048	28 (10)	0.712	92
		Tamaulipas	0.039 (0.085)	0.000	194 (11)	0.919	–
		Metapop	0.037 (0.075)	0.000	222 (17)	0.933	–
30	50	LANWR	-0.011 (0.163)	0.874	10 (7)	0.473	69
		Wilacy	-0.014 (0.151)	0.772	12 (8)	0.559	74
		Tamaulipas	-0.024 (0.116)	0.320	63 (52)	0.795	69
		Metapop	-0.019 (0.099)	0.212	60 (53)	0.781	85
60	50	LANWR	0.001 (0.153)	0.546	11 (7)	0.598	86
		Wilacy	0.000 (0.139)	0.388	15 (10)	0.665	89
		Tamaulipas	-0.052 (0.140)	0.824	40 (42)	0.750	60
		Metapop	-0.019 (0.101)	0.178	27 (27)	0.746	93
30	60	LANWR	0.008 (0.157)	0.636	13 (8)	0.496	77
		Wilacy	0.010 (0.140)	0.342	21 (11)	0.601	80
		Tamaulipas	0.018 (0.090)	0.008	175 (36)	0.908	61
		Metapop	0.020 (0.079)	0.000	192 (43)	0.918	–
60	60	LANWR	0.026 (0.147)	0.272	17 (8)	0.636	89
		Wilacy	0.027 (0.127)	0.076	26 (10)	0.706	90
		Tamaulipas	0.005 (0.102)	0.130	155 (57)	0.881	71
		Metapop	0.016 (0.079)	0.002	172 (76)	0.905	93
30	70	LANWR	0.029 (0.150)	0.288	19 (8)	0.540	80
		Wilacy	0.034 (0.131)	0.102	28 (10)	0.642	83
		Tamaulipas	0.046 (0.090)	0.000	194 (12)	0.918	–
		Metapop	0.046 (0.079)	0.000	232 (21)	0.935	–
60	70	LANWR	0.048 (0.141)	0.088	21 (8)	0.656	91
		Wilacy	0.049 (0.125)	0.014	31 (10)	0.723	94
		Tamaulipas	0.038 (0.092)	0.002	192 (16)	0.916	64
		Metapop	0.043 (0.078)	0.000	241 (24)	0.940	–

- Longer periods of translocation can improve the viability of the South Texas ocelot populations, but at the expense of the Tamaulipas population: longer translocation programs actually *increase* the risk of extinction in the source population. The Tamaulipas population, despite the absence of appreciable mortality from vehicle impacts, is not large enough to demographically withstand the removal of four females bi-annually. This conclusion, however, is dependent on the assumption that the source population in Tamaulipas is just 200 individuals, distributed relatively close to the border with the United States. This assumption may be unrealistic; the source population may in fact be considerably larger – perhaps up to 1000 individuals – if we base our population size estimate across the entire state. In this case, the removal of a relatively small number of ocelots will have a much smaller demographic impact. Care must be given in determining the total source population size before setting quantitative targets for translocation to smaller population in south Texas.

All in all, a carefully-designed translocation strategy appears to have considerable promise as a means of improving the viability of small remnant populations of ocelots on south Texas. Such a strategy, however, cannot be so aggressive as to compromise the demographic and genetic health of the source population in Tamaulipas. Vigilant monitoring of a program like this would be necessary, combined with improved transport protocols designed to minimize transit mortality, in order for long-term program success to be a realistic goal.

Future Directions for Additional Analysis

Impacts of habitat loss

Our models do not currently include a simulation of gradual erosion – or, for that matter, recovery – of ocelot habitat in south Texas and northern Tamaulipas. This is certainly a real possibility as the burgeoning human population expands into more and more urban areas. We need to better understand the nature of this expansion, and its specific impacts on both quantity and quality of ocelot habitat.

Impacts of disease

Preliminary discussions during baseline model development included the possibility of disease epidemics impacting ocelot populations in this area. While recognizing the potential risks, we were unable to parameterize a disease model with any real confidence at this time. Further discussions would be necessary to understand this process in greater detail.

Density-dependent survival

There was concern among workshop participants that we were not accurately modeling density dependent mortality in ocelot populations. It is quite likely that as population size decreases, rates of fecundity and survival may actually increase as competition for space, food and mates is reduced. This needs to be studied in more detail so that more accurate models can be developed.

Conclusions

We may conclude our preliminary analysis of south Texas / northern Tamaulipas ocelot population viability by returning to the original set of questions that provided the foundation for our study.

- *What is our best estimate of stochastic population dynamics of this species in its current range?*

Based on our current understanding of the demographics of ocelot populations occupying south Texas and northern Tamaulipas, these populations – particularly those in south Texas – appear to be at a considerable risk of extinction through the action of intrinsic, stochastic fluctuations in demographic rates that are the hallmark of very small, isolated populations of wildlife. Moreover, this risk is directly tied to the activities of humans in the area, namely the construction and use of roads throughout ocelot habitat.

- *What are the primary factors that drive population growth dynamics of ocelots in south Texas and northern Tamaulipas?*

Our preliminary set of PVA models discussed here show that ocelot growth dynamics is largely driven by adult female reproductive success – defined here as the proportion of adult females successfully producing a litter in a given year. Moreover, the additional levels of mortality brought about by vehicle collisions is a primary factor in determining the future growth dynamics of any given population subjected to such activity.

- *How vulnerable are small, fragmented populations of ocelots in south Texas and northern Tamaulipas to local extinction in the absence of demographic interaction with other populations?*

Small populations of ocelots – for example, those numbering less than 100 individuals – have an elevated risk of extinction compared to their larger counterparts. When additional anthropogenic mortality is included in our analyses, even larger populations do not appear to be able to tolerate this kind of additional demographic stress.

- *What are the benefits to the ocelot of increasing range and connectivity in the landscape?*

Because of the risk of extinction through isolation discussed above, range increase through habitat improvements may result in greater levels of ocelot population increase and, as a result, a reduced risk of extinction. This, of course, also depends on the success of mitigating human-mediated processes such as road mortality. As an alternative conservation measure, connecting small ocelot populations through the use of landscape corridors may provide an additional buffer against extinction risk. However, this strategy will meet with the greatest level of success when 1) individual subpopulations are increased in size in a way that approaches some level of viability in the absence of connectivity; 2) dispersal rates – whether natural or artificial – are sufficiently high to maintain a functioning metapopulation; and 3) anthropogenic sources of mortality are reduced to acceptable levels.

- *How successful might translocation be as a conservation management strategy for smaller populations of ocelots in south Texas?*

Our models indicate that, based on our best understanding of the demographics of ocelots in this portion of their range, the input of a relatively small number of individuals can have a significant positive impact on the viability of endangered recipient populations. Preliminary analyses indicate

that just 1-2 females injected into a population on a bi-annual basis may be enough to compensate for the destabilizing effect of stochastic demography operating on small populations.

- *How many animals could be removed from a given source population such as northern Tamaulipas for augmentation of smaller populations in south Texas at risk of extinction without negatively impacting the persistence of the source?*

It appears that careful consideration must be given to the extent of removal of ocelots from the source population in Tamaulipas. Removing four subadult females every other year – comprising approximately 4% of the total female population – may put the population at some risk if translocations last longer than 40 – 50 years. A smaller number of individuals could no doubt be removed more easily, but the assumed transit mortality would lead to a greatly reduced demographic benefit to the recipient populations. These conclusions are strongly dependent on our assumptions of overall ocelot population size in the source regions of Tamaulipas; risks to this population may be reduced substantially if our estimates of total population size are increased.

References

- Beissinger, S.R., and D.R. McCullough, eds. 2002. *Population Viability Analysis*. Chicago: University of Chicago Press.
- Caso, A. 1994. Home range and habitat use of three neotropical carnivores in northeast Mexico. Unpublished M.S. thesis, Texas A&M University, Kingsville, TX, 78 pp.
- Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. *Conservation Biology* 16:258–261.
- Forcada, J. 2000. Can population surveys show if the Mediterranean monk seal colony at Cap Blanc is declining in abundance? *Journal of Applied Ecology* 37:171-181.
- Harwell, G., and D.P. Siminski. 1990. *Listed Cats of Texas and Arizona Recovery Plan (with Emphasis on the Ocelot)*. Albuquerque, NM: U.S. Fish and Wildlife Service. 131 pp.
- Laack, L.L. 1991. Ecology of the ocelot (*Felis pardalis*) in south Texas. Unpublished M.S. thesis, Texas A&I University, Kingsville, Texas, 113 pp.
- Laack, L.L., M.E. Tewes, A.H. Haines, and J.H. Rappole. In press. Reproductive ecology of ocelot (*Leopardus pardalis*) in southern Texas. In *Current Research of the Caesar-Kleberg Wildlife Institute 2004 – 2005* (Fedynich, A.M., ed.). Kingsville, TX: Texas A&M University – Kingsville.
- Lacy, R.C. 2000. Structure of the *VORTEX* simulation model for population viability analysis. *Ecological Bulletins* 48:191-203.
- López Gonzalez, C. A., D. E. Brown, and J. P. Gallo-Reynoso. 2003. The ocelot *Leopardus pardalis* in north-western Mexico: ecology, distribution and conservation status. *Oryx* 37:358-364.
- Lotts, K.C., T.A. Waite, and J.A. Vucetich. 2004. Reliability of absolute and relative predictions of population persistence based on time series. *Conservation Biology* 18:1224-1232.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310.
- Miller, P.S., and R.C. Lacy. 2003. *VORTEX: A Stochastic Simulation of the Extinction Process. Version 9 User's Manual*. Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).

- Reed, J. M., L. S. Mills, J. B. Dunning Jr., E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M. Anstett, and P.S. Miller. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16:7–19.
- Tewes, M.E., and D.J. Schmidly. 1987. The neotropical felids: jaguar, ocelot, margay, and jaguarundi. Pp 695-712 in *Wild Furbearer Management and Conservation in North America* (M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, eds.). Ontario: Ministry of Natural Resources.

Appendix I

Simulation Modeling and Population Viability Analysis

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model which incorporates the processes which cause fluctuations in the population, as well as those which control the long-term trends in population size (Shaffer 1981). Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in "Population Viability Analysis" (PVA) (Lacy 1993/4). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are

intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which of the factors that were analyzed are most important to the population dynamics. PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models probably underestimate the threats facing the population. Finally, the models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed.

The *VORTEX* Population Viability Analysis Model

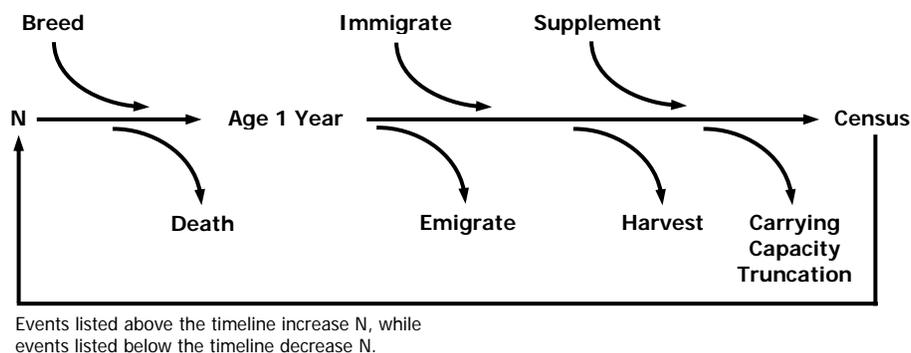
For the analyses presented here, the *VORTEX* computer software (Lacy 1993a) for population viability analysis was used. *VORTEX* models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. *VORTEX* also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations.

Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional mortality is imposed across all age classes to bring the population back down to the carrying capacity. The carrying capacity can be specified to change linearly over time, to model losses or gains in the amount or quality of habitat. Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size.

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. During the simulation, *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or “expected heterozygosity”) relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

VORTEX is an *individual-based* model. That is, *VORTEX* creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. (See figure below.) Events occur according to the specified age and sex-specific probabilities. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

VORTEX Simulation Model Timeline



VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each

pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

Further information on *VORTEX* is available in Lacy (2000) and Miller and Lacy (2003).

Dealing with Uncertainty

It is important to recognize that uncertainty regarding the biological parameters of a population and its consequent fate occurs at several levels and for independent reasons. Uncertainty can occur because the parameters have never been measured on the population. Uncertainty can occur because limited field data have yielded estimates with potentially large sampling error. Uncertainty can occur because independent studies have generated discordant estimates. Uncertainty can occur because environmental conditions or population status have been changing over time, and field surveys were conducted during periods which may not be representative of long-term averages. Uncertainty can occur because the environment will change in the future, so that measurements made in the past may not accurately predict future conditions.

Sensitivity testing is necessary to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the pronghorn population. If alternative plausible parameter values result in divergent predictions for the population, then it is important to try to resolve the uncertainty with better data. Sensitivity of population dynamics to certain parameters also indicates that those parameters describe factors that could be critical determinants of population viability. Such factors are therefore good candidates for efficient management actions designed to ensure the persistence of the population.

The above kinds of uncertainty should be distinguished from several more sources of uncertainty about the future of the population. Even if long-term average demographic rates are known with precision, variation over time caused by fluctuating environmental conditions will cause uncertainty in the fate of the population at any given time in the future. Such environmental variation should be incorporated into the model used to assess population dynamics, and will generate a range of possible outcomes (perhaps represented as a mean and standard deviation) from the model. In addition, most biological processes are inherently stochastic, having a random component. The stochastic or probabilistic nature of survival, sex determination, transmission of genes, acquisition of mates, reproduction, and other processes preclude exact determination of the future state of a population. Such demographic stochasticity should also be incorporated into a population model, because such variability both increases our uncertainty about the future and can also change the expected or mean outcome relative to that which would result if there were no such variation. Finally, there is “uncertainty” which represents the alternative actions or interventions which might be pursued as a management strategy. The likely effectiveness of such management options can be explored by testing alternative scenarios in the model of population dynamics, in much the same way that sensitivity testing is used to explore the effects of uncertain biological parameters.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination, and death with a pseudo-random number generator. For each life event, if the random value sampled from a specified distribution falls above the user-specified probability, the event is deemed to have occurred, thereby simulating a binomial process. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), based on the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s , are obtained by first determining the integral number of binomial trials, N , that would produce the value of s closest to the specified value, according to:

$$N = \frac{p(1-p)}{s^2}$$

N binomial trials are then simulated by sampling from the uniform 0-1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N , s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modeled as binomial distributions. Environmental variation in carrying capacity is modeled as a normal distribution. Environmental variation in demographic rates can be correlated among populations.

Catastrophes

Catastrophes are modeled in *VORTEX* as random events that occur with specified probabilities. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors 50% for the year. Such a catastrophe would be modeled as a random event with 0.02 probability of occurrence each year, and severity factors of 0.75 for survival and 0.50 for reproduction. Catastrophes can be local (impacting populations independently), or regional (affecting sets of populations simultaneously).

Genetic Processes

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical neutral (non-selected) genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. Each offspring created during the simulation is randomly assigned one of the alleles from each parent. *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or “expected heterozygosity”) relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

Inbreeding depression is modeled as a loss of viability of inbred animals during their first year. The severity of inbreeding depression is commonly measured by the number of “lethal equivalents” in a

population (Morton et al. 1956). The number of lethal equivalents per diploid genome estimates the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due entirely to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual, it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles which equate in effect with one lethal allele per individual.

VORTEX partitions the total effect of inbreeding (the total lethal equivalents) into an effect due to recessive lethal alleles and an effect due to loci at which there is heterozygote advantage (superior fitness of heterozygotes relative to all homozygote genotypes). To model the effects of lethal alleles, each founder starts with a unique recessive lethal allele (and a dominant non-lethal allele) at up to five modeled loci. By virtue of the deaths of individuals that are homozygous for lethal alleles, such alleles can be removed slowly by natural selection during the generations of a simulation. This diminishes the probability that inbred individuals in subsequent generations will be homozygous for a lethal allele.

Heterozygote advantage is modeled by specifying that juvenile survival is related to inbreeding according to the logarithmic model:

$$\ln(S) = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is the portion of the lethal equivalents per haploid genome that is due to heterozygote advantage rather than to recessive lethal alleles. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at loci in which the heterozygote has higher fitness than both homozygotes, because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under heterozygote advantage, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.

Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects apparently varies considerably among species (Falconer 1981; Ralls et al. 1988; Lacy et al. 1992) and even among populations of the same species (Lacy et al. 1996). Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterozygote advantage), PVAs must make assumptions about the effects of inbreeding on the population being studied. If genetic effects are ignored, the PVA will overestimate the viability of small populations. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3.14 lethal equivalents per diploid) reported in the survey by Ralls et al. (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0.90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5.62 lethal equivalents). In the few species in which inbreeding depression has been studied carefully, about half of the effects of inbreeding are due recessive lethal alleles and about half of the effects are due to heterozygote advantage or other genetic mechanisms that are not diminished by natural selection during generations of inbreeding, although the proportion of the total inbreeding effect can vary substantially among populations (Lacy and Ballou 1998).

A full explanation of the genetic mechanisms of inbreeding depression is beyond the scope of this manual, and interested readers are encouraged to refer to the references cited above.

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned

to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

Deterministic Processes

VORTEX can incorporate several deterministic processes, in addition to mean age-specific birth and death rates. Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional mortality is imposed across all age classes to bring the population back down to the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation. The carrying capacity can be specified to change over time, to model losses or gains in the amount or quality of habitat.

Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size. The default functional relationship between breeding and density allows entry of Allee effects (reduction in breeding at low density) and/or reduced breeding at high densities.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodeled) population. The numbers of additions and removals are specified according to the age and sex of animals.

Migration Among Populations

VORTEX can model up to 50 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. Migration among populations can be restricted to one sex and/or a limited age cohort. Emigration from a population can be restricted to occur only when the number of animals in the population exceeds a specified proportion of the carrying capacity. Dispersal mortality can be specified as a probability of death for any migrating animal, which is in addition to age-sex specific mortality. Because of between-population migration and managed supplementation, populations can be recolonized. *VORTEX* tracks the dynamics of local extinctions and recolonizations through the simulation.

Output

VORTEX outputs: (1) probability of extinction at specified intervals (e.g., every 10 years during a 100 year simulation), (2) median time to extinction, if the population went extinct in at least 50% of the simulations, (3) mean time to extinction of those simulated populations that became extinct, and (4) mean size of, and genetic variation within, extant populations.

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction is reported by *VORTEX* as:

$$SE(p) = \sqrt{\frac{p(1-p)}{n}}$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Sequence of Program Flow

- (1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.
- (2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.
- (3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

$$K_{\max} = (K + 3s)(1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size.

- (4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{\max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{\max} . Because N_{\max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.
- (5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.
- (6) Iterative simulation of the population proceeds via steps 7 through 26 below.
- (7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.
- (8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *VORTEX* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum (p_i^2)$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed

heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *VORTEX* is the mean inbreeding coefficient of the population.

- (9) For each of the 10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to $0.1 \times$ the mean number of lethal alleles per individual.
- (10) Years are iterated via steps 11 through 25 below.
- (11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).
- (12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) for the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.
- (13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.
- (14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.
- (15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

- (16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal A , and another existing animal, B , is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j , M is the mother of A , and P is the father of A . The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_A = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

- (17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is multiplied by

$$e^{-b(1-\text{Pr}[Lethals])F}$$

in which b is the number of lethal equivalents per haploid genome, and $\text{Pr}[Lethals]$ is the proportion of this inbreeding effect due to lethal alleles.

- (18) The age of each animal is incremented by 1.
- (19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.
- (20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *VORTEX* continues but reports that harvest was incomplete.
- (21) Dead animals are removed from the computer memory to make space for future generations.
- (22) If population supplementation is to occur in a particular year, new individuals of the specified age-class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.
- (23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.
- (24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying

capacity truncation is set to $(N - K)/N$, so that the expected population size after the additional mortality is K .

- (25) Summary statistics on population size and genetic variation are tallied and reported.
- (26) Final population size and genetic variation are determined for the simulation.
- (27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.

Literature Cited

- Ballou, J.D. 1983. Calculating inbreeding coefficients from pedigrees. Pages 509-520 in: Schonewald-Cox, C.M, S.M. Chambers, B. MacBryde, and W.L. Thomas (eds.). *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Menlo Park, California: Benjamin/Cummings.
- Crow, J.F. and Kimura, M. 1970. *Introduction to Population Genetics Theory*. New York: Harper and Row.
- Falconer, D.S. 1981. *Introduction to Quantitative Genetics*. 2nd ed. New York: Longman.
- Gilpin, M.E., and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19 – 34 in: Soulé, M.E. (ed.). *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer Associates.
- Jiménez, J.A., K.A. Hughes, G. Alaks, L. Graham, and R.C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266:271-273.
- Kirkpatrick, S, and Stoll, E. 1981. A very fast shift-register sequence random number generator. *Journal of Computational Physics* 40:517.
- Lacy, R.C. 1993b. Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biology and Medicine* 36:480-496.
- Lacy, R.C. 1993/1994. What is Population (and Habitat) Viability Analysis? *Primate Conservation* 14/15:27-33.
- Lacy, R.C. 2000. Structure of the *VORTEX* simulation model for population viability analysis. *Ecological Bulletins* 48:191-203.
- Lacy, R.C. 1992. The effects of inbreeding on isolated populations: Are minimum viable population sizes predictable? Pages 277-296 in: P.L. Fiedler and S.K. Jain (eds.). *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management*. New York: Chapman and Hall.
- Lacy, R.C. and J.D. Ballou. 1998. Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution* 52:900-909.
- Latour, A. (1986). Polar normal distribution. *Byte* (August 1986):131-2.
- Maier, W.L. (1991). A fast pseudo random number generator. *Dr. Dobb's Journal* (May 1991):152-7.

- Miller, P.S., and R.C. Lacy. 2003. *VORTEX: A Stochastic Simulation of the Extinction Process. Version 9 User's Manual*. Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).
- Morton, N.E., Crow, J.F., and Muller, H.J. 1956. An estimate of the mutational damage in man from data on consanguineous marriages. *Proceedings of the National Academy of Sciences, USA* 42:855-863.
- Ralls, K., J.D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* 2:185-193.
- Ricklefs, R.E. 1979. *Ecology*. 2nd ed. New York: Chiron.
- Shaffer, M.L. 1981. Minimum population sizes for species conservation. *BioScience* 1:131-134.
- Soulé, M., M. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: How long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101-113.