

Appendix C: Population and Habitat Viability Analysis

The PHVA Workshop was held 6-9 December 2004 at the Beatty's Guest Ranch in Miller Canyon near Sierra Vista, Arizona (Figures A1 and 2). The Workshop was led by Phil Miller and Juan Cornejo of CBSG and attended by 22 members of the Technical and Stakeholders Subgroups of the Recovery Team. Funding for CBSG was provided by the BLM – Arizona State Office and the Turner Endangered Species Fund. The Beatty's provided lodging and a venue for the workshop. After an introductory plenary session, the recovery team members were divided into three working groups: Population, Habitat, and Modeling. The Modeling group developed a population viability model that mathematically allowed testing of various management scenarios and identification of population parameters most important in determining population viability. Over the course of the four-day workshop, the working groups periodically reconvened into plenary sessions to assess progress and exchange ideas.

The Population and Habitat groups identified issues surrounding recovery relevant to populations or habitats of the Chiricahua leopard frog, then prioritized those issues, listed all information about the issues, and prioritized the uncertainty of that information. The two groups then developed goals for resolving high priority issues. Issues corresponded to threats and goals were equivalent to recovery strategy elements in part 1 of this recovery plan. The groups then cross-checked threats and strategy elements, as well as recovery actions in the draft plan to make sure it contained all necessary background and actions needed to address the issues. If deficiencies were found, the groups recommended changes to the plan. The PHVA provided a forum for recovery team members to work together in small groups over four days and discuss and explore issues and solutions to a degree that had not been possible in previous meetings lasting only five or six hours. The Beatty's Guest Ranch, where most team members stayed, also provided a casual venue for after-hours discussions and reflection on the day's proceedings.

The Population and Habitat groups produced a report by the end of the meeting with their findings and recommendations. The Modeling group finished with recommendations for Phil Miller to run additional scenarios. Dr. Miller completed the modeling and the group's report, a summary of which is included below with summaries of the Population and Habitat groups' report. A key finding from the latter two groups was that administrative and political barriers and a lack of cultural value ascribed to the Chiricahua leopard frog were threats or barriers to recovery that needed to be described in the "Reasons for Listing/Threats" section in part 1 of the plan. To address these challenges, the groups recommended expansion of recovery action 7 "Develop and implement public outreach and conduct broad-based community planning to promote public support and understanding of recovery actions" and added detail below on how to implement that action. Additional recommendations were made regarding funding and priority levels for recovery actions, emphasizing the need for agency cooperation, and the need to enhance bankline and streamside vegetation at habitat sites. The Modeling group's key findings were that population viability is particularly sensitive to juvenile survivorship, the extent of female reproductive success (defined as the proportion of adult



Figure A1: Habitat group at Beatty's Guest Ranch. From right to left: Doug Powers (BLM), Sheridan Stone (Fort Huachuca), Anna Magoffin (Magoffin Ranch, Malpai Borderlands Group), Stefanie White (San Carlos Apache Tribe), Trevor Hare (Sky Island Alliance), and Jeanmarie Haney (The Nature Conservancy).

females that were able to produce metamorphs) and the average number of metamorphs per successful female.

Population viability declines rapidly in populations of less than 60 adults, or less than 40-50 adults in habitats resistant to drought; moreover, small populations (~10 adults) do not contribute much to viability of metapopulations and may serve as population sinks. Also, to properly assess the likelihood of population persistence, monitoring should occur over a period of more than 15 years. The complete findings and recommendations of the three groups are summarized here. The full text of the Population and Habitat groups' reports are memorialized in the administrative record for this recovery plan. Note that their findings were based on internal drafts available in December 2004. The current version has been revised in accordance with these findings and recommendations.



Figure A2: **Deliberations on the population viability modeling, Betty's Guest Ranch.**

Population Group's Summary Findings and Recommendations for the Draft Recovery Plan

Issue Statement

The following primary issues were identified and ranked as to their importance:

- 1) Administrative and political barriers to recovery (High)
- 2) Metapopulation dynamics (extent, distribution, and suitability of habitat) (Medium)
- 3) Disease (Very High)
- 4) Predators and competition (Very High)
- 5) Lack of resources for artificial enhancement of populations (Low)
- 6) Maintenance of regional genetic diversity (Medium)
- 7) The frog lacks cultural value in our society (High)
- 8) Direct anthropogenic effects (Low)

Threats to the frog and its habitat include direct anthropogenic activities, such as human population increases, demands for food, land conversion, road construction, pollution, and increased wildland interface and recreation. This results in fragmentation and conversion of additional habitat. It converts land uses near urban populations centers from rural ranch lands

that contain frogs. Use of frogs for food items in parts of the range (Mexico) may be locally significant. In addition, some collection for backyard pond and pet trade may occur. Management of non-native species, policies that create barriers to reestablishment of native species, air-borne and water-borne contaminants, and habitat fragmentation due to roads, subdivisions, and mining are additional challenges.

The frog lacks social or cultural value. In general the value of this organism to society is unknown. Why would society in general decide to conserve a species for which it does not understand the significance? Finally, we are lacking knowledge in many aspects of frog biology that will make recovery even more challenging.

Strategies for overcoming administrative and political barriers and building support for recovery through outreach

The Populations Group examined the draft recovery plan to see if it adequately addressed the issues identified above. The group found that the plan needed to be strengthened in regard to identifying as threats to recovery administrative and political barriers and a lack of cultural value. Once identified in Part I of the plan, these issues then needed to be reflected in the recovery strategy and recovery actions in Part II. The following concepts were outlined for building broad-based community support for recovery. It was thought that if communities and individuals on a local level support recovery, administrative and political factors are less likely to be significant barriers to progress. The group also endorsed the Habitat Group's recommendations for comprehensive education and outreach to address the cultural value issue (see below).

- Keep working groups on a scale that is manageable, but with communication and coordination among groups
 - Regional
 - Statewide-coordinate regional groups
 - Public outreach- keep process transparent to avoid an 11th hour catastrophe
 - Use phone, email, website, emails-common thread so all can be involved
 - Look for incentives to conduct recovery (i.e. Beatty's Guest Ranch and ecotourism)
 - Selling/marketing the project to the cooperators
- Build coalitions
 - Need to be broad group that includes stakeholders and scientists, community-based planning
 - Should include opposing viewpoints
 - Persistence
 - Bring meetings to the community, insist on participation by all at meetings
 - Design early win-win situation to create bonding among members - people see they can work together - and then build momentum to address more difficult issues
 - Define roles and methods of resolving conflicts, and employ a good facilitator to identify problems and move to solutions
 - Keep decision-makers aware of progress of coalition and give feedback so group performs to their expectations
- Identify sources of funding and capture funding

- All cooperators need to make effort to secure funding from sources that they are aware of but are not necessarily known to the group at whole
- Commitment from all participants to seek funding
- Coordinator to oversee process and ensure that things are moving forward and funds are being secured
- Decision-makers are aware of available funding
- Amplify efforts by expanding coalitions to include other species, ecosystems, and issue resolution
 - Restoration of a natural assemblage approach

Based on these concepts, the Population Group then wrote text for the recovery plan to be inserted at specified locations that addressed the issues not covered adequately, and that further developed recovery strategies and actions relevant to these issues. This draft recovery plan has incorporated that text.

Habitat Group's Summary Findings and Recommendations for the Draft Recovery Plan

Education/Outreach (1st priority)

Issue Statement

- Target specific user groups - ranchers, sportsmen, off-highway vehicle users, K-12
- Target specific geographic areas near extant populations of Chiricahua leopard frogs
- Use professionals to develop education and outreach materials and messages
- Need a more basic level of education, and more law enforcement, signing, deterrents

Need more funding for the following three recovery actions dealing with public outreach in the Recovery Plan step-down narrative:

- 7.2 Post and maintain signs to inform the public of land use restrictions (*with American Flags*)
- 7.2 Develop outreach materials to inform the public and build support for frog recovery
- 7.4 Continue momentum through Stakeholder and Recovery Groups

Need additional education/outreach activities. General sense is that past education-outreach efforts have not been enough to adequately gain public and user group support for frog recovery.

Recommendations

Specific suggestions for additional education/outreach activities and information resources:

- Sub-contract with Environmental Education Exchange or other contractor TREE, Project WILD, Project WET, ALIAE
- Develop curricula for Douglas school system and other targeted areas
- Hopkins/NRCD resource center – working with specific sites with extant leopard frogs
- Arizona Partners in Amphibian and Reptile Conservation (PARC) – are developing curriculum for 4th graders on reptile and amphibian conservation. Dovetail with frog conservation.
- Based on environmental education research, target 4th graders

- K-12 teachers often eager to have visitor presentations in class. Develop a speakers' bureau to give presentations to classrooms.
- Hire a public relations firm to develop a message about endangered species/Chiricahua leopard frogs, which may include logos, phrases, mottos, branding – public relations professionals have skills that scientists do not.
- Conduct coordination meetings with targeted land users groups, including:
 - o Grazing permittees – USFS, BLM – including developing habitat and population protection specifications for inclusion into grazing permits
 - o Special use permits – horseback riders, etc – develop information that would accompany their permit
 - o Range conservationists and maintenance workers – train/educate them to collect information on frogs in the course of their work
 - o Targeted geographic areas and user groups plus opportunistic education
 - o Use volunteers from non-profit conservation organizations to accomplish recovery work (e.g. Sky Island Alliance, Audubon, Arizona Riparian Council, Native Plant Society)
 - o Develop educational materials to target off-highway vehicle dealerships and user groups
 - o Develop materials and presentations for BLM and USFS Resource Advisory Councils and other public agency advisory groups
 - o Inject need for frog recovery into Forest Plan Revisions, for which public meetings are beginning

Bald Eagle outreach has successfully used pamphlets and Bald Eagle Nest Watch Program as educational outreach. Investigate using this as a model for Chiricahua leopard frog recovery, e.g. “Pond Watchers” could be used to collect frog data.

Agency Cooperation/Coordination (2nd priority)

Findings and Recommendations

- Continuing education and professional development is needed for agency staff in regard to techniques for riparian restoration and frog management.
- Need additional accountability of agency managers to implement recovery plan actions - there is a statutory responsibility within section 7(a)(1) and elsewhere in the ESA regarding this.
- Within the plan, clear identification is needed of which agency is responsible for which actions (need clear statement in the Implementation Schedule). Each agency should designate an individual representative responsible for overseeing frog recovery. Agencies should report in a written document what has been accomplished on an annual basis (see recovery action 7.4).
- Small projects with a low risk and costs will be easier to gain cooperation from user groups and build trust for future actions.
- Coordination in New Mexico is easier than in Arizona due to more people/agencies/organizations with which one needs to coordinate. As a result, agency coordination is a larger issue in Arizona.

Habitat Restoration (3rd priority) and Habitat Protection (4th priority)

Findings and Recommendations

Vegetation cover at pond and stream sites provides protection for juveniles from predation; populations are very sensitive to juvenile mortality (from the Modeling group). Therefore, a primary focus of habitat management actions should be recovery of bankline and streamside vegetation. In addition, habitat heterogeneity should allow for greater reproduction, recruitment, and juvenile survival. A major impediment to management for bankline and streamside vegetation is the multiple use mandate on most BLM and USFS public lands. Willing private landowners may provide opportunities good opportunities for recovery actions.

Solutions:

- Safe Harbor Agreements (private lands)
- Application of the 4d rule (non-Federal lands)
- Outreach to alleviate land owner uncertainty
- Messaging – obtain assistance from professionals (see Education/Outreach recommendations above)

Add an additional Appendix to Recovery Plan:

Non-native aquatic species removal/control

Include stakeholder involvement in identification of potential re-establishment sites

Need Data Roll-up:

Need data synthesis, analysis, and presentation and information in a manner to document/justify/prioritize land protection (including land acquisition)

The solutions are political and educational:

Insufficient funding for appropriate management of public lands

Insufficient funding for conservation easements/acquisitions of private lands

(For the above two items, the Population Management group has good thoughts in their notes on Administration/Institutional Barriers)

Additional Recommendations for the Recovery Plan

Semlitsch (2003) has relevant references on protection of watershed and riparian biodiversity. In the Implementation Schedule add funding for education/outreach

In this Participation Plan, address specifically “who to call” for instance, when a pond with frogs is drying

Modeling Group’s Report

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Introduction

The Chiricahua leopard frog occurs at elevations of 3,281 to 8,890 feet in central and southeastern Arizona; west-central and southwestern New Mexico; and northern Sonora and the Sierra Madre Occidental of Chihuahua and northern Durango, Mexico. The range of the species is split into two disjunct parts - the northern populations along the Mogollon Rim in Arizona east into the mountains of the west-central New Mexico, and the southern populations in southeastern Arizona, southwestern New Mexico, and Mexico. Threats to this species include predation by non-native organisms, especially American bullfrogs, fish, and crayfish; a fungal disease - chytridiomycosis; drought; floods; degradation and loss of habitat as a result of water diversions and groundwater pumping, poor livestock management, a long history of fire suppression that has resulted in scouring of montane creek bottoms and cienegas, mining, development, and other human activities; disruption of metapopulation dynamics; increased chance of extirpation or extinction resulting from small numbers of populations and individuals existing in dynamic environments; and probably environmental contamination (such as runoff from mining operations and airborne contaminants from copper smelters). Loss of Chiricahua leopard frog populations fits a pattern of global amphibian decline, suggesting other regional or global causes of decline may be important as well, such as elevated ultra-violet radiation, pesticides or other contaminants, and climate change.

To date (December 2004), the internal draft Recovery Plan has not included an intensive and detailed quantitative risk assessment, based on the concepts of population viability analysis (PVA). An analysis of this type, particularly when combined with public involvement in the interpretation of PVA results and their use in the construction of integrated and achievable species and habitat management alternatives, 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 Chiricahua leopard frog in its wild habitat in the southwestern United States. *VORTEX*, a simulation software package written for population viability analysis, was used here as a tool to study the interaction of a number of leopard frog 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.

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

- What is our depth of understanding of the population biology of the Chiricahua leopard frog?
- Based on this understanding, what do we see as the primary drivers of leopard frog population growth? To which parameters is our demographic model most sensitive?
- How vulnerable are small, fragmented Chiricahua leopard frog populations to local extinction in the absence of demographic interaction with other populations?

- Is the current Recovery Plan definition of a “robust population” adequate in terms of relative risk of population extinction?
- What is the relative risk to leopard frog population viability posed by drought in lentic vs. lotic habitats?
- What are the relative levels of importance of subpopulation size and dispersal rate within a given metapopulation in terms of metapopulation viability?
- Under what set of subpopulation characteristics (e.g., population size, dispersal rates, and management intensity) can we observe a functioning metapopulation?

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 inputs 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 Chiricahua leopard frog in 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).

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

Throughout the discussion of our demographic model, it is important to recognize that we have slightly modified our definition of “reproduction” in order to account for the reproduction biology of Chiricahua leopard frogs within the constraints of the *VORTEX* modeling environment. In order to more effectively deal with the breeding biology of this amphibian, we are defining

“reproduction” as the production of metamorphs, age approximately six months, that have then survived an additional six weeks or so to reach the full juvenile stage.

Baseline population model

Breeding System: We assume that Chiricahua leopard frogs demonstrate a polygynous mating system. Frogs can breed year-round, but do so only in hot springs. For this model, we are assuming that adult females breed once per annual cycle, although it may be possible for them to occasionally breed more frequently. Since we might expect springs to have more similar birth and death patterns than they do with the fall of the same year, then maybe it is better to model on an annual cycle. We are therefore setting our *VORTEX* time-step as equal to one year.

Age of First Reproduction: *VORTEX* considers the age of first reproduction as the age at which metamorphs are produced, not simply the onset of sexual maturity. Observational data indicate that Chiricahua leopard frogs will be a little more than one year old at the time of offspring metamorphosis, so we set the age of first reproduction at one year for both males and females.

Age of Reproductive Senescence: In its simplest form, *VORTEX* assumes that animals can reproduce (at the normal rate) throughout their adult life. Maximum known age for Chiricahua leopard frogs is 10 years based on skeletochronology at Ramsey Canyon (Platz *et al.* 1997). Phil Fernandez has a population of this species in a greenhouse at

Grand Canyon University. Those frogs, although we assume they are unnaturally old, continue breeding. Although the age reported by Platz seems unrealistic, this is only being used to set ages at which a female can reproduce, if she lives that long. Discussion of this parameter led to an agreed maximum reproductive age equal to nine years.

Offspring Production: Data from Platz suggest that all adult females reproduce in a given year, with some perhaps double-clutching in both the spring and fall, while other habitats may experience substantially fewer females breeding. Initial discussion of this parameter led to an early estimate of no more than about 50 percent of females successfully producing metamorphs in a given year. Some group members saw this estimate as highly pessimistic, perhaps more reflective of breeding propensities in high-density situations. After lengthy discussion, the group concluded that metamorph production would be density-dependent, with as few as 50 percent of the adult females successfully producing metamorphs at high population density and as many as 100 percent reproducing successfully at low density. We assumed that the relationship between reproductive rate and population density would be linear; in other words, 100 percent of adult females would breed at low (optimal) density, about 75 percent of adult females would produce metamorphs at intermediate density, and only 50 percent would produce metamorphs at high density (near carrying capacity, K).

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 metamorphs within a given year. While no data are available for this parameter, we propose that annual variance would be relatively high. We therefore set the standard deviation in the percentage of adult females breeding at 13 percent.

Based on the number of juveniles in April (or August) at Big Springs, Arizona (the species was *Rana yavapaiensis*, which was used as a surrogate species) in a ratio with the number of adults in the previous interval, we estimated there were 3.2 metamorphs per adult female. However, some group members have seen as many as 20 times more juveniles in the fall than the number of adults, or 40 times the number of adult females. Moreover, in any given year some proportion of the total pool of adult females will fail to produce metamorphs (although many may actually lay eggs). Non-reproducing females will include those that fail to lay eggs or those that do lay eggs but experience total clutch failure. Taking all of this information into account, we assumed for our model that, on average, approximately 10 eggs laid by a given breeding female would survive to the metamorph – early juvenile stage.

The full distribution of metamorph production per successful female is given below.

Number of metamorphs	percent
1	0.05
2	0.23
3	0.76
4	1.89
5	3.78
6	6.31
7	9.01
8	11.26
9	12.51
10	12.51
11	11.37
12	9.48
13	7.29
14	5.21
15	3.47
16	2.17
17	1.28
18	1.42

This distribution yields an average of 9.99 metamorphs per successfully breeding female. The overall population-level sex ratio among metamorphs is assumed to be 50 percent.

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 about 30 percent of adult males are successful in siring offspring (metamorphs). Based on a Poisson distribution of breeding success among males, we therefore assume that about 44 percent of adult male Chiricahua leopard frogs are available for breeding each year.

Mortality: The only data source for estimating mortality for adults and juveniles is the Big Springs population from 1991 through 1996. Mortality was available from one within-year interval to the next, so the annual survivorship was generated by multiplying the seasonal interval survivorship estimates. Survivorship was assumed to follow a binomial distribution, so the demographic, within-year variability estimated using the binomial distribution was added to the between-year, environmental variability in survivorship. We then estimated the proportion of total variability due to environmental (between-year) effects.

Using this technique, our initial estimate of adult mortality was 66.5 percent per year, with 29.1 percent of the total variability in this parameter due to environmental effects (EV). These data also indicated that the entire cohort of juveniles died between one year and the next in four of the six years considered: annual mortality was therefore estimated to be 97.6 percent with 5.5 percent due to EV. Using these data directly resulted in an extremely rapid rate of population decline and extinction within about a decade. In order to better understand our data and the biology of the leopard frog, we revisited these mortality estimates with the assumption that baseline population mortality should, at least initially, exclude natural or anthropogenic impacts that should be added later as, perhaps, catastrophic effects of incremental additions to more “natural” mortality. Coupled with the direct historical observation of persistence of leopard frog populations for extended periods of time, we refined our mortality estimates to 80 percent mortality for juveniles (EV = 5.5 percent) and 50 percent for adults (EV = 14.5 percent). Moreover, we ultimately assumed that juvenile mortality was density-dependent around a mid-point value of 80 percent at intermediate densities. At low population density, juvenile mortality was assumed to be 75 percent, with an increase to 85 percent mortality at high density. As in the case of density-dependent reproductive success, we assumed that mortality showed a linear relationship with density.

Catastrophes: Catastrophes are singular environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival. Natural catastrophes can be 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.

While drought may well be considered an extreme of normal climate in the Southwest, we wanted to investigate the impact of severe rainfall deficit on the persistence of threatened Chiricahua leopard frog populations. We would like to highlight the negative impacts of drought, so maybe we stay with a narrow range of precipitation, with droughts as exceptions to the pattern.

For those models in which drought was included, we assumed that such an extreme event occurs, on average, every 20 years. It is important to note, however, that these events are essentially independent over time so that multiple events could occur within a much shorter time interval. It is also important to consider the relative impacts of drought on lentic and lotic systems. For

example, springs do not generally experience a drought-based catastrophe like more isolated lentic systems (e.g., cattle tanks), since they don't dry completely. In general, lotic systems are likely to be impacted to a lesser degree than their lentic counterparts. Therefore, we set the following severity parameters for drought in each of these habitats:

Habitat	Frequency	Severity	
		Reproduction	Survival
Lentic	5 percent	0.33	0.2
Lotic	5 percent	0.66	0.4

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 Chiricahua leopard frog populations were not available for this analysis, the strong evidence for the deleterious impacts of inbreeding in many different types of species suggests that it can be a real factor in the persistence of small populations of vertebrates. We therefore elected to include this process in some of our models, with a genetic load of 1.0 or 3.0 lethal equivalents and approximately 50 percent of this load expressed as lethal genes.

Initial Population Size: We chose to initialize our baseline model with 100 individuals, age one year and older. Subsequent sensitivity and risk assessment models were initialized with different numbers of individuals in order to address specific questions related to management of frog populations (see below).

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 .

Carrying capacity is typically extremely difficult to estimate in the field for any species. For the purposes of our modeling effort here, we will assume that the vast majority of Chiricahua leopard frog populations across their range are close to their ecologically sustainable maximum as they occupy increasingly smaller and more fragile habitats. Therefore, we set all values of carrying capacity equal to 1.6 times the initial population size. This "artificial" inflation of K will allow the population, through the action of density dependence for both reproductive success (metamorph production) and juvenile mortality, to maintain a long-term population size average that is close to the initial size entered into the model. For example, an initial population size of 100 individuals would include an estimated carrying capacity equal to 160 individuals.

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.

Demographic sensitivity analysis

During the development of the baseline input dataset, it quickly became apparent that a number of demographic characteristics of Chiricahua leopard frog populations 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 identified a selected set of parameters from

Table 1. Demographic input parameters for the baseline *VORTEX* model for the Chiricahua leopard frog in the southwest US. See accompanying text for more information.

Model Input Parameter	Baseline value
Breeding System	Polygynous
Age of first reproduction (♀ / ♂)	1 / 1
Maximum age of reproduction	9
Inbreeding depression?	No
Annual percent adult females reproducing (SD)	100.0 – [50.0*(N/K)] (13)
Maximum metamorph clutch size	18
Mean clutch size [†]	10.0
Overall offspring sex ratio	0.5
Adult males in breeding pool	44 percent
percent annual mortality (SD) [‡]	
0 – 1	75.0 + [10.0*(N/K)] (5.5)
1 +	50.0 (14.5)
Catastrophe?	Drought
Annual frequency of occurrence	5 percent
Severity: Reproduction [Lentic/Lotic]	0.33 / 0.66
Severity: Survival [Lentic/Lotic]	0.2 / 0.4
Initial population size	100
Carrying Capacity (K)	250

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

[‡] No sex-based differences in annual mortality rates.

Table 1 whose estimates we saw as considerably uncertain. We then developed 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 Chiricahua leopard frog populations in the southwestern United States. 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 (AFR)		1	2
Inbreeding Depression (#Leth Equiv)	0.0	1.0	3.0
percent Adult Females Reproducing	50	75	100
Average Brood Size	6	10	15

percent Juvenile Mortality	56	80	88
EV (Juvenile Mortality)	3.85	5.5	8.25
percent Adult Mortality	35	50	55
EV (Adult Mortality)	10.15	14.5	21.75
Drought Severity	None	Lotic	Lentic

For each of the 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 nine 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 17 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 whose initial size and carrying capacity is equal to that of the original baseline model, i.e., 100 and 250 individuals, respectively.

Metapopulation input parameters

A major component of our risk assessment effort centered around the development of metapopulation models. In these models, we constructed four separate subpopulations with different size categories, drought regimes, and dispersal rates. Specifically, our metapopulation models were parameterized as follows:

- General dispersal characteristics: Both sexes disperse, and may do so as soon as they reach adulthood. All individuals are assumed to be capable of dispersing throughout their lives. In our models, we assumed that all dispersal-mediated mortality is included in our general estimate of age-sex-specific mortality. Therefore, we did not include any cost to dispersal as defined by increased mortality.
- Rates of dispersal: We assumed three different levels of dispersal, defined here as being from one single population to another single population: Low (one percent), Medium (four percent), and High (eight percent). Therefore, under a Low dispersal scenario, and given four total subpopulations per metapopulation, a total of three percent of the individuals are assumed to disperse away from any one subpopulation while 97 percent are assumed to remain in the subpopulation. We made no attempt at being spatially explicit in our estimates of dispersal distances, as we are currently not modeling precise examples of natural subpopulation aggregations on the southwestern U.S. landscape but are rather exploring the dynamics of somewhat more arbitrary Chiricahua leopard frog metapopulations in order to gain insight into management options required for persistence of local populations.
- Subpopulation size: We classified subpopulations as either Small (10 individuals), Medium (40 individuals), or Large (100 individuals). This range of sizes represents a reasonable description of the subpopulation types currently present across Chiricahua leopard frog habitat. Metapopulation models were constructed that differed in the distribution of various subpopulation types in an attempt to provide insight into the minimum subpopulation distribution type that would lead to an acceptable level of

viability. As with all models, we assumed that the carrying capacity was equivalent to 1.6 times the initial subpopulation size.

- **Drought regime:** We modeled the following types of scenarios when incorporating drought into our metapopulation models:
 - No drought in any subpopulation
 - All Small populations experience the more severe lentic drought, while the Medium and Large populations experience the lesser lotic drought. This was used to simulate the higher risk posed by drought on the more ephemeral pond populations, while the larger subpopulations would perhaps be more resistant in spring-fed or lotic habitats.
 - All subpopulations experience lotic drought, with one of the Small populations showing full resistance to drought. This scenario type is used to simulate a more aggressive strategy of drought management.

Results of Simulation Modeling

Baseline simulation

Where appropriate, the results that are reported here for each modeling scenario include:

\bar{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.

$P(E)_{15/50/100}$ – Probability of population extinction after the specified time interval, 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.

$N_{15/50/100}$ – Mean population size after the specified time interval, averaged across all simulated populations, including those that are extinct.

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 Chiricahua leopard frogs in the southwest United States is hereafter referred to as our *baseline model*. In this case, our baseline model simulates the predicted trajectory of a relatively large population of leopard frogs that is free of the impacts of drought and genetic sources of mortality (i.e., inbreeding depression). The results of this analysis are presented in Figure 1. The average population growth rate is 0.042, and the extinction probability over 100 years is 0.2 percent (0 percent over 15 years).

It is important to observe and appreciate the amount of annual variation in population size across the iterations. The initial size of our simulated population was 100 individuals, but the population fluctuates in size to a minimum of just 15 – 20 animals up to the maximum carrying capacity of 250 individuals. This is also reflected in the high standard deviation in baseline model stochastic

growth rate (0.446). Even though our carrying capacity was set at 250 individuals, the imposition of density dependence in both

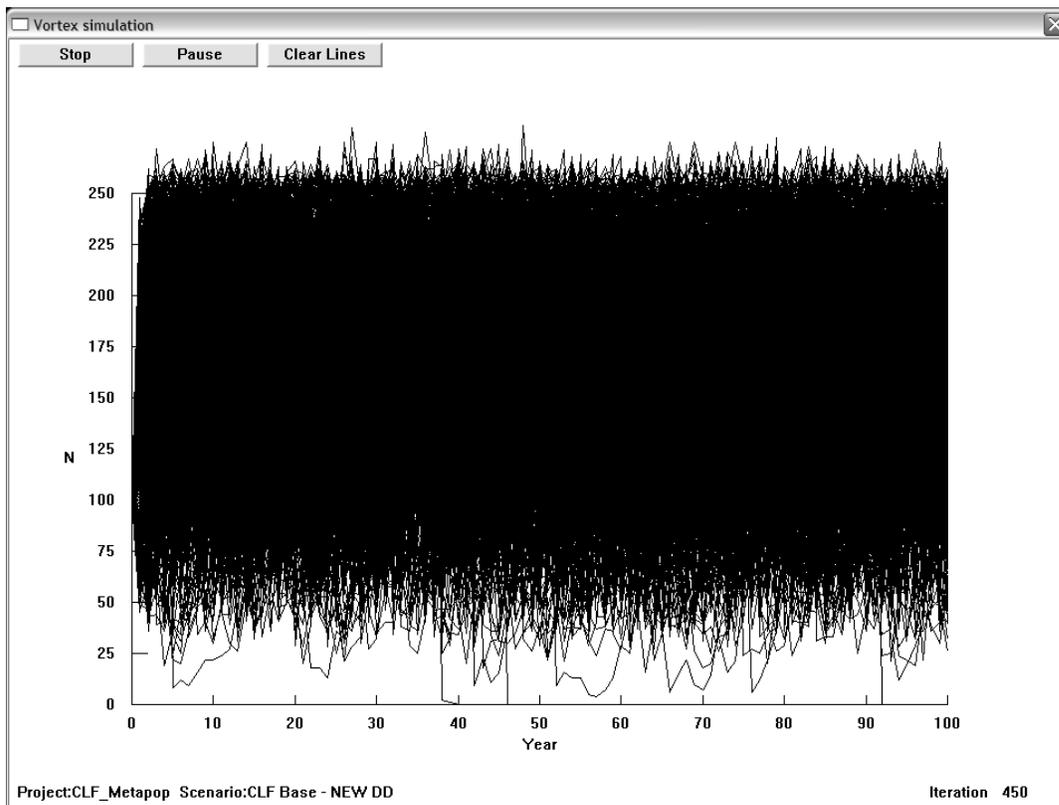


Figure 1. Plot of 500 individual iterations of the baseline *VORTEX* simulation model of Chiricahua leopard frog population dynamics. The average rate of population growth across these iterations is 0.042, with a very small risk of population extinction. Note the level of variance in the model's population growth rate as defined by both demographic and environmental sources of stochasticity. See text for accompanying details.

reproductive success (metamorph production) and juvenile mortality generates a simulated population that stabilizes at approximately 165 individuals. Our description of density dependence is, therefore, having the desired effect of dampening the approach to carrying capacity.

Our group thought that the simulation of leopard frog population dynamics was acceptably accurate, both in its mean trajectory and in its manifestation of annual variability in demography and subsequent population growth. We therefore felt comfortable with proceeding into the demographic sensitivity analysis phase of our work with the baseline model unchanged. It is important to note that, despite our sense of comfort with this model, we see this baseline projection as merely a starting point for deeper analysis of Chiricahua leopard frog population viability. In other words, we do not see this single model as precisely descriptive of the predicted fate of any one population or class of populations currently known to exist in the southwestern United States.

Generalized demographic sensitivity analysis

The results of our initial demographic sensitivity analysis are shown graphically in Figures 2a and 2b.

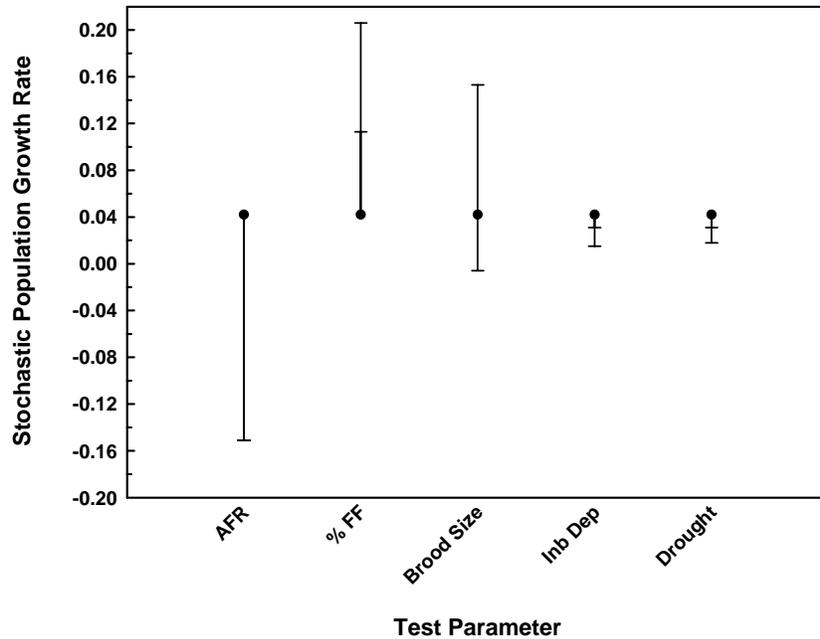


Figure 2a. Generalized demographic sensitivity analysis of a simulated Chiricahua leopard frog population. Stochastic population growth rate for a set of models in which the specific parameter is varied across a range of biologically plausible values. The baseline model growth rate of 0.042 is given by the central data point for each parameter. The general model of leopard frog population dynamics is most sensitive to uncertainty in those parameters giving the widest range in simulated population growth rates. See Table 2 for additional details.

Our initial analysis indicates that our model is highly sensitive to uncertainty in the age of first reproduction (AFR), female reproductive success (percent adult females producing metamorphs), and average brood size. While our estimate of the age of first reproduction may not have the same degree of uncertainty as other parameters analyzed here, it is instructive for our general understanding of leopard frog demography to observe the dramatic decrease in population growth brought about by a single year's delay in reproductive output for adult females. Given the rather high levels of mortality we see in this simulated population, a single year's delay in reproductive output decreases a given female's total reproductive potential by a sizeable amount. For example, the probability of a given female metamorph reaching five years of age is just 1.25 percent. Therefore, a delay in one year in reproductive ability will reduce her lifetime reproductive output by approximately 25 percent.

Using stochastic population growth rate as our metric to test model sensitivity may not give us the whole picture that can emerge from such an analysis. This is shown in Figure 2b, where we see that uncertainty in the type of drought affecting a given population may have a dramatic effect on the risk of population extinction – even if the overall effect on stochastic population growth rate is relatively minimal (Figure 2a). This result demonstrates the significant effect that a catastrophic event like drought can have on a

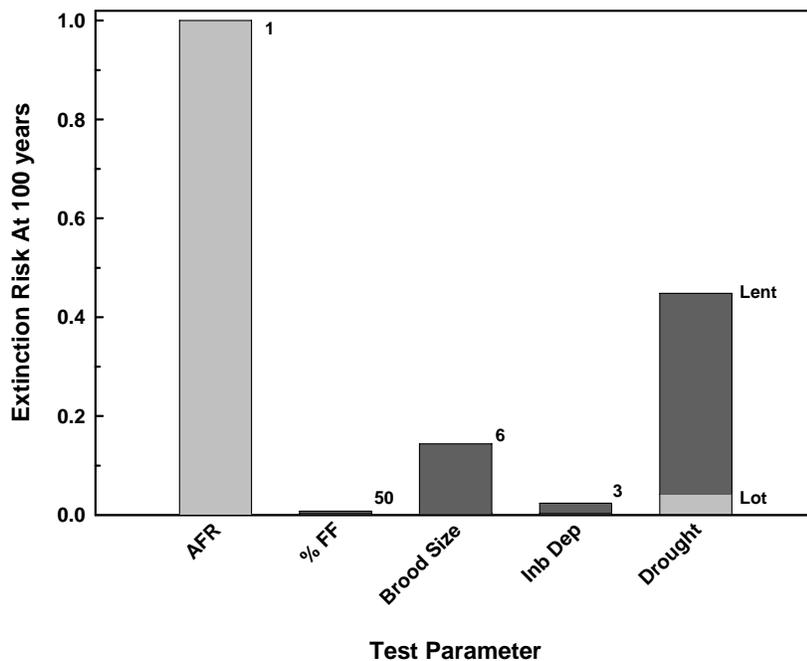


Figure 2b. Generalized demographic sensitivity analysis of a simulated Chiricahua leopard frog population. Probability of population extinction at 100 years for a set of models in which the specific parameter is varied across a range of biologically plausible values. Labels associated with each bar give the parameter values corresponding to the specific risk estimate. See Table 2 for additional details.

population that is relatively stable in the long-term but is susceptible to periodic stochastic reductions in population size.

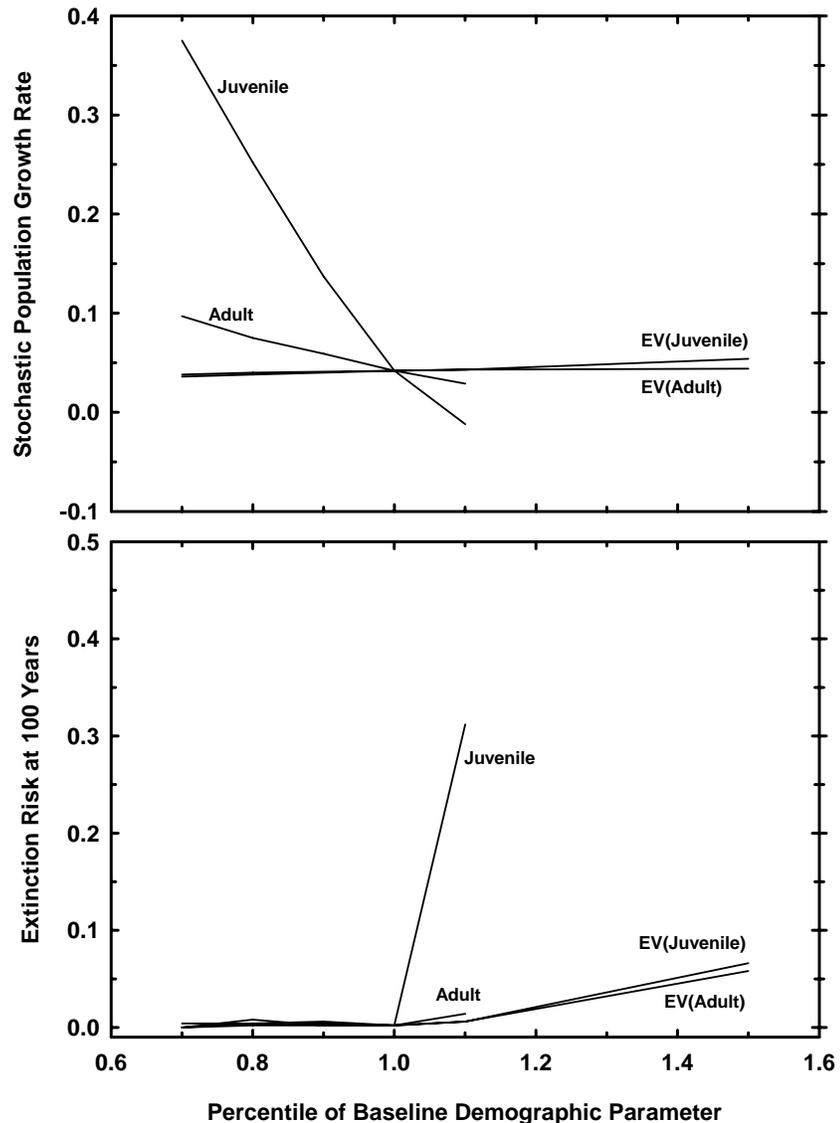
Mortality sensitivity analysis

We undertook a more detailed investigation of the sensitivity of our baseline model to changes in age-specific mortality rates and the magnitude of environmental variability (EV) around these rates. These results are shown in Figure 3.

When compared on a unit-change basis, our Chiricahua leopard frog model appears to be considerably more sensitive to uncertainty in juvenile mortality relative to adult mortality – both in terms of average stochastic population growth and in population extinction risk. This is generally the result with many “r-selected” species that are the subject of such an analysis, which reflects the large increase in overall population reproductive potential brought about by small changes in juvenile stage survival.

The results of this type of analysis help to identify the primary drivers of Chiricahua leopard frog population dynamics, and can assist in the prioritization of both research and management activities related to species conservation management. In this situation, broad management actions related to maximizing survival of juveniles can be viewed as priority recommendations. At a more detailed level, research directed towards better estimates of juvenile survival rates in the wild can help conservation biologists refine their models of Chiricahua leopard frog population biology, which will subsequently improve our ability to predict the response of populations to anthropogenic threats.

Figure 3. Mortality sensitivity analysis of a simulated Chiricahua leopard frog population in terms of stochastic growth rate (top) and probability of population extinction at 100 years (bottom). Values for age-specific mortality and associated environmental variability (EV) are varied in proportional units for more direct comparison of results. See Table 2 for additional details.



Risk analysis I: Population size, drought, and extinction risk

We were interested in looking at relative extinction risk as a function of population size, with and without the impact of catastrophic drought. This analysis may help us to identify a sort of population size threshold, below which the risk of extinction is likely to be unacceptably high. More specifically, we can begin to address the validity of the current definition of a “robust” leopard frog population.

To conduct this analysis, we developed a suite of models in which the baseline demographic parameters were employed, and then increased the initial population size from 10 to 100 in increments of 10. Our first set of ten models did not include drought. This first set of models was then repeated, but with the inclusion of a lotic-style drought. Next, a third set of models was constructed where the lotic drought was replaced with a more severe lentic drought. Finally, this

entire set of 30 models was itself repeated with the inclusion of inbreeding depression (arbitrarily set at 3.0 lethal equivalents) to test the impact of genetic instability on population viability.

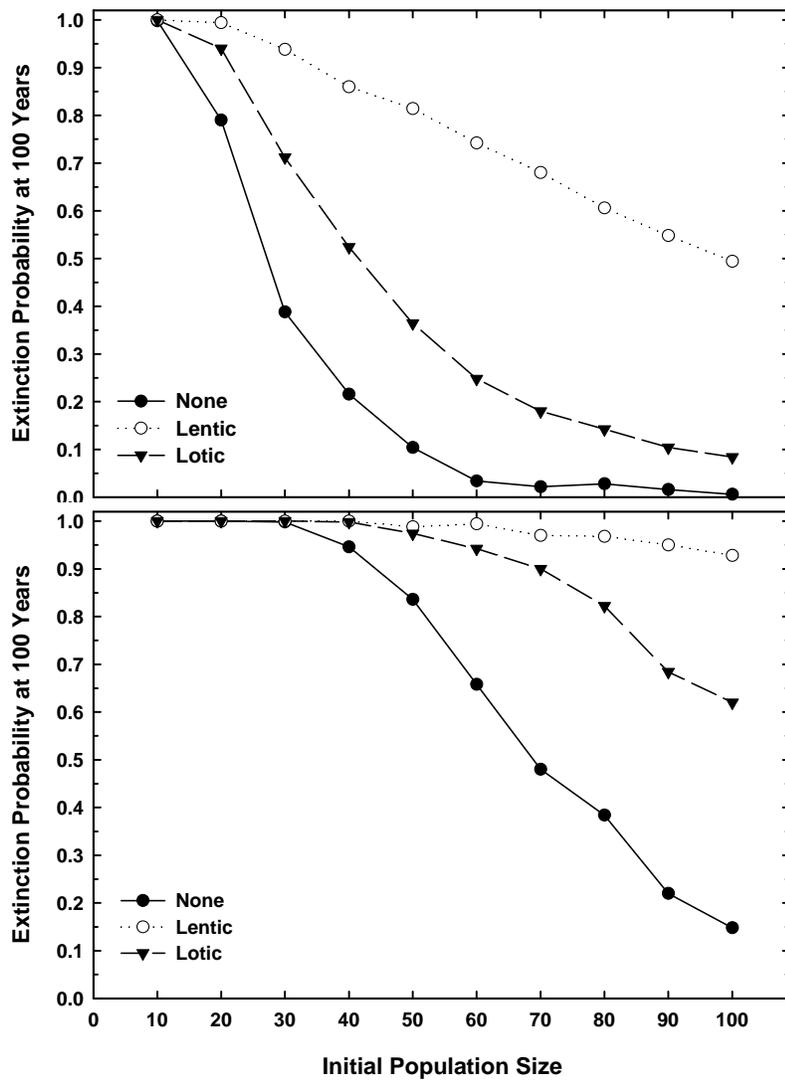


Figure 4. Risk analysis of a simulated Chiricahua leopard frog population. Extinction risk at 100 years as a function of initial population size and drought regime in the absence (top panel) or presence (bottom panel) of inbreeding depression for juvenile survival (3 lethal equivalents). See text for accompanying details.

The results of our risk analysis are presented graphically in Figure 4, in which the risk of population extinction is presented over the entire 100-year timeframe of the PVA simulation. In the absence of inbreeding depression, we can draw the following conclusions from these results:

- Immediately clear from these graphical results is the very high probability of extinction in the smallest populations (e.g., $N_0 \leq 20$ individuals), and the relative stability exhibited by populations starting with 60 or more individuals.
- The largest populations (e.g., $N_0 \geq 80$ individuals) appear to be largely unaffected by the less severe lotic drought. On the other hand, intermediate population sizes (e.g., $30 \leq N_0 \leq 70$) show a strong sensitivity to this event, with an often marked increase in extinction risk in the presence of this milder catastrophe.
- Lentic drought is seen to be a major catastrophic event. Even in the largest populations, extinction risk increases dramatically, with no discernible threshold effect with respect to population size.

When inbreeding depression is included in the model, nearly all populations are significantly affected. Only the largest populations in the absence of drought show little effect of this additional destabilizing force. Interestingly, we see a very dramatic change in the extinction risk profile under conditions of lotic drought: Even the largest populations show a large increase in extinction risk as inbreeding depression reduces overall population size to a point where periodic drought can render the population extinct with much greater frequency. This analysis demonstrates the common but complicated ways in which different processes can interact to put small populations of threatened wildlife at risk.

Of course, we have no data on the mode of action of inbreeding depression in wild Chiricahua leopard frog populations, or even if inbreeding depression exists at all. Therefore, we are unable to make specific predictions about the role this process plays in frog populations that exist currently. However, these analyses clearly demonstrate the additional risk that detrimental genetic processes can impose on small populations, and the sometimes subtle ways in which different processes whose individual impacts are relatively mild can interact to greatly increase extinction risk. Because of this, additional study of leopard frog population genetics may be warranted so that greater confidence can be placed on the inclusion of such factors into future PVA models.

Table 3 provides a more detailed look at the time course of extinction. These data are important as they help to evaluate the relative risk of extinction over a shorter time frame – in this case, we look at 15 and 50 years in addition to the standard 100-year timeframe. The 15-year period has been explicitly included in operational definitions of viability and recovery for Chiricahua leopard frogs. Note that the extinction risk increases over time, and the population size typically decreases as more extinctions occur over the time course of the computer simulation – even in the presence of a positive long-term stochastic growth rate. For example, a population initialized with 40 individuals in the absence of drought has only a 2.2 percent probability of extinction in 15 years, but this risk increases to 9.6 percent in 50 years and 21.6 percent in 100 years. The operation of stochastic demographic fluctuations serves to destabilize populations over time and therefore increases their risk of significant decline and possible extinction. When evaluating the results of population viability analyses, it is important to project far enough into the future so that processes with longer time horizons have a chance to influence the course of the projection. This is particularly important in this Chiricahua leopard frog analysis, where drought occurs on average only once in a 20-year period. A time horizon for analysis that is significantly shorter than this period will be unable to resolve the longer-term impacts of drought – an impact that we can see as profound indeed. While a time horizon of 100 years may in some instances be impractical for realistic management recommendations, it may be necessary to revise the timeframe definition of viability of

Table 3. Results of Chiricahua leopard frog population size risk analysis models under different drought regimes. In all simulations, lotic drought is assumed to display only 50 percent of the severity of lentic drought. Extinction risk and population size estimates are given for 15, 50 and 100-year time periods. The rows with initial population size of 40 individuals is highlighted as this represents the current Recovery Plan definition for “robust” population. See page 9 for definitions of column headings.

N_0	Drought	r_s (SD)	P(E)	N	T(E)
			15 / 50 / 100	15 / 50 / 100	

10	None	0.028 (0.548)	0.584 / 0.966 / 0.998	4.25 / 0.37 / 0.01	16
20		0.028 (0.516)	0.184 / 0.512 / 0.790	16.16 / 10.32 / 4.48	41
30		0.034 (0.490)	0.054 / 0.194 / 0.388	30.57 / 25.68 / 18.68	50
40		0.035 (0.484)	0.022 / 0.096 / 0.216	41.87 / 37.62 / 31.95	53
50		0.037 (0.471)	0.010 / 0.056 / 0.104	52.95 / 49.26 / 46.36	52
60		0.039 (0.461)	0.006 / 0.016 / 0.034	63.54 / 62.87 / 61.32	51
70		0.038 (0.461)	0.002 / 0.008 / 0.022	75.14 / 72.87 / 70.54	53
80		0.037 (0.455)	0.008 / 0.018 / 0.028	84.95 / 79.56 / 84.25	39
90		0.038 (0.456)	0.000 / 0.006 / 0.016	94.78 / 94.99 / 92.88	59
100		0.038 (0.450)	0.000 / 0.002 / 0.006	107.14 / 105.35 / 110.12	53
10	Lotic	0.014 (0.561)	0.710 / 0.986 / 1.000	3.22 / 0.16 / --	13
20		0.008 (0.565)	0.310 / 0.762 / 0.940	13.44 / 4.80 / 0.82	30
30		0.017 (0.551)	0.140 / 0.438 / 0.712	24.54 / 15.95 / 8.18	43
40		0.021 (0.544)	0.088 / 0.286 / 0.524	33.44 / 27.64 / 18.55	47
50		0.021 (0.538)	0.072 / 0.200 / 0.364	43.22 / 38.18 / 30.76	46
60		0.023 (0.531)	0.032 / 0.140 / 0.248	55.88 / 47.64 / 43.02	48
70		0.025 (0.524)	0.014 / 0.098 / 0.180	65.64 / 61.09 / 56.52	49
80		0.027 (0.518)	0.022 / 0.086 / 0.142	74.99 / 71.17 / 69.07	46
90		0.027 (0.523)	0.016 / 0.048 / 0.104	85.14 / 82.24 / 75.57	56
100		0.027 (0.516)	0.010 / 0.036 / 0.084	97.22 / 93.41 / 90.11	52

10	Lentic	0.010 (0.563)	0.740 / 0.994 / 1.000	2.68 / 0.09 / --	11
20		0.002 (0.587)	0.446 / 0.926 / 0.994	10.86 / 1.46 / 0.09	21
30		0.004 (0.608)	0.368 / 0.790 / 0.938	17.83 / 5.78 / 1.72	28
40		0.005 (0.628)	0.256 / 0.648 / 0.860	27.37 / 12.97 / 4.85	35
50		0.006 (0.626)	0.218 / 0.560 / 0.814	37.04 / 19.86 / 8.51	38
60		0.006 (0.631)	0.136 / 0.476 / 0.742	46.16 / 28.13 / 12.79	42
70		0.009 (0.632)	0.132 / 0.400 / 0.680	58.53 / 38.16 / 22.02	44
80		0.008 (0.636)	0.110 / 0.368 / 0.606	64.08 / 45.67 / 29.03	44
90		0.011 (0.627)	0.088 / 0.314 / 0.548	72.20 / 58.88 / 38.18	47
100		0.012 (0.631)	0.078 / 0.290 / 0.494	78.66 / 64.51 / 45.65	45

Chiricahua leopard frog populations to longer than just 15 years.

Note that a population initiated with 40 individuals shows a minimum level of extinction risk in the absence of drought, as expected. This risk increases as drought severity increases and over the time period of the simulation. What may appear to be relatively immune from extinction in 15 years shows a considerably higher risk over longer time periods. The time course of extinction under the three drought regimes for a population initiated with 40 individuals is shown in Figure 5.

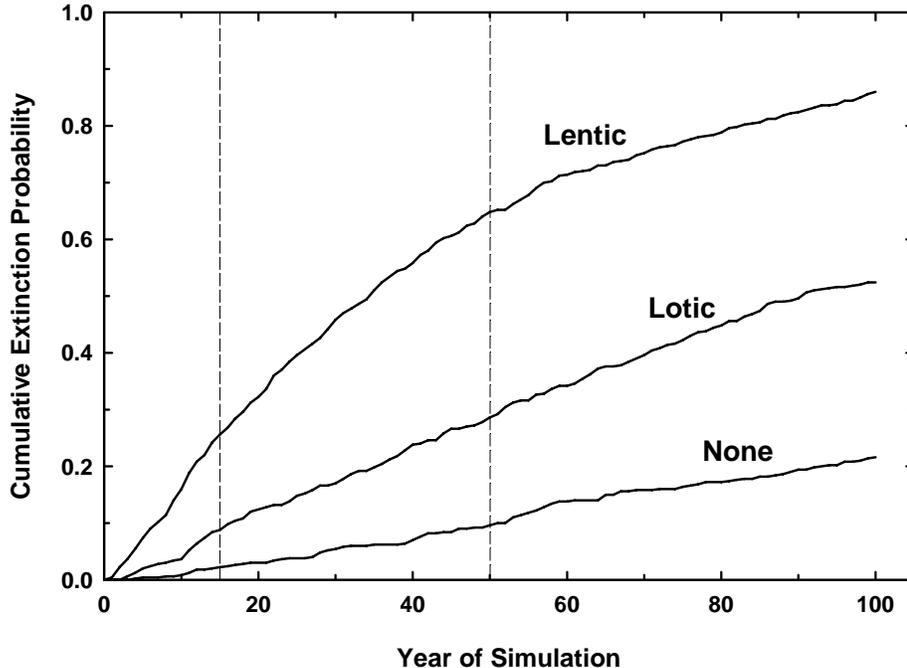


Figure 5. Cumulative population extinction risk as a function of time for a simulated Chiricahua leopard frog population initiated with 40 individuals and subjected to three different drought regimes. The vertical dashed lines correspond to 15 and 50 years of elapsed time in the simulation. See text for accompanying details.

Risk analysis II: Metapopulation viability

In order to be “recovered” under the conditions set forth in the Draft Chiricahua Leopard Frog Recovery Plan, the species “...must reach a population level and have sufficient habitat to provide for the long-term persistence of metapopulations in each of the eight recovery units (RUs), even in the fact of local losses (e.g., extirpation).” Given this recovery goal, a population viability analysis must consider selected elements of metapopulation dynamics in the context of Chiricahua leopard frog persistence.

To begin our metapopulation analysis, we wanted to investigate the relative importance of increasing subpopulation size as compared to increasing rates of dispersal between subpopulations as a means of increasing the likelihood of metapopulation persistence, given a constant number of subpopulations per metapopulation. We therefore constructed a set of models with the following characteristics:

- Each metapopulation consisted of four subpopulations, and each subpopulation was initialized with either 10, 40, or 100 individuals (giving a total metapopulation size of 40, 160, or 400). Carrying capacity was equal to 1.6 times initial population size in all cases.
- For each metapopulation, dispersal rates were fixed at one, four, or eight percent between any one subpopulation and each of its neighbors. Therefore, the total dispersal rate for any one subpopulation was three, 12, or 24 percent for any one specific dispersal scenario.

- Drought was either absent or present for any given scenario. When present, we randomly selected two populations to experience a more severe lotic drought, while the other two populations suffered through a milder lotic drought. Because the metapopulation as a whole was symmetric with respect to both subpopulation size and dispersal rates, the choice of drought regime for a given subpopulation was arbitrary. The intent here was to simulate some systems within a metapopulation that would be, through natural or artificial means, differentially resistant to a given drought event.

This combination of characteristics yielded 18 different scenarios for analysis. The results of our models are presented in Figure 6 and Table 4.

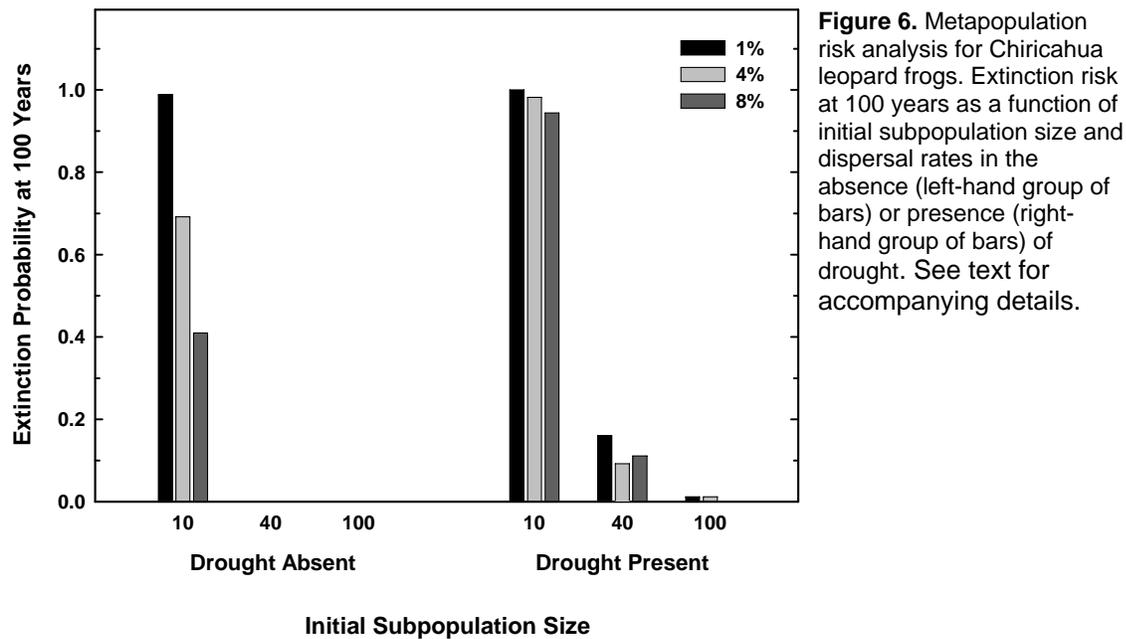


Figure 6. Metapopulation risk analysis for Chiricahua leopard frogs. Extinction risk at 100 years as a function of initial subpopulation size and dispersal rates in the absence (left-hand group of bars) or presence (right-hand group of bars) of drought. See text for accompanying details.

Once again, these results reinforce the severe impact that drought – of even a relatively milder form when lotic drought is included here – can have on the viability of small leopard frog populations. However, of greatest importance in this analysis is the dramatic effect of increasing subpopulation size when compared to increases in dispersal rate. In the absence of drought, an eight-fold increase in dispersal frequency in a metapopulation composed solely of the smallest subpopulations ($N_0 = 10$) shows a fairly significant reduction in the risk of overall metapopulation extinction within 100 years (left-most set of bars, Figure 6). But just a four-fold increase in the initial size of each metapopulation to 40 individuals, even under conditions of low dispersal frequency, eliminates extinction risk completely. Although the identical risk is not eliminated completely in the presence of mixed drought, the effect of increasing subpopulation size remains substantial (right-hand set of bars, Figure 6). Taken together, these results suggest that overall metapopulation stability may be more closely linked to the size of each component subpopulation, and less to the degree of connectivity between them.

Table 4. Results of Chiricahua leopard frog metapopulation risk analysis models. Each metapopulation was initialized with four subpopulations of the specified size, and differential dispersal between each subpopulation ranged from 1 percent to 8 percent. When drought was present, two subpopulations were assigned the more severe lentic drought, while the remaining two subpopulations were subjected to the milder lotic drought. All P(E) and N results are for the metapopulation as a whole. The bold line of data refers to discussion in the accompanying text. See page 9 for definitions of column headings.

N _{0,i}	Dispersal	r _s (SD)	P(E)	N	T(E)
			15 / 50 / 100	15 / 50 / 100	
Drought Absent					
10	1 percent	0.007 (0.441)	0.124 / 0.756 / 0.988	20.85 / 4.12 / 0.18	37
40		0.055 (0.301)	0.000 / 0.000 / 0.000	167.84 / 170.87 / 168.27	–
100		0.051 (0.293)	0.000 / 0.000 / 0.000	441.82 / 434.14 / 430.64	–
10	4 percent	0.027 (0.380)	0.088 / 0.432 / 0.692	29.48 / 18.32 / 10.03	45
40		0.048 (0.304)	0.000 / 0.000 / 0.000	174.29 / 174.46 / 174.94	–
100		0.045 (0.295)	0.000 / 0.000 / 0.000	450.91 / 446.26 / 458.51	–
10	8 percent	0.038 (0.357)	0.036 / 0.190 / 0.410	35.99 / 30.35 / 22.60	54
40		0.041 (0.305)	0.000 / 0.000 / 0.000	181.91 / 180.47 / 178.34	–
100		0.038 (0.297)	0.000 / 0.006 / 0.000	464.19 / 461.17 / 459.35	–
Drought Present					
10	1 percent	-0.028 (0.511)	0.342 / 0.944 / 1.000	13.15 / 0.73 / –	23
40		0.030 (0.459)	0.022 / 0.074 / 0.160	135.60 / 117.37 / 104.50	55
100		0.036 (0.442)	0.004 / 0.012 / 0.012	368.22 / 370.14 / 355.47	29
10	4 percent	-0.020 (0.487)	0.288 / 0.834 / 0.982	20.37 / 4.21 / 0.59	30
40		0.031 (0.451)	0.004 / 0.046 / 0.092	148.94 / 143.04 / 132.95	50
100		0.031 (0.449)	0.002 / 0.002 / 0.012	389.42 / 386.40 / 377.25	59

10	8 percent	-0.012 (0.479)	0.025 / 0.726 / 0.944	25.17 / 9.96 / 1.50	34
40		0.026 (0.454)	0.004 / 0.056 / 0.112	155.27 / 145.75 / 143.21	52
100		0.027 (0.448)	0.000 / 0.000 / 0.002	407.52 / 391.73 / 401.99	97

The more detailed results in Table 4 once again emphasize the importance of looking at population viability beyond a simple 15-year time horizon. For example, in the absence of drought, a metapopulation composed of small subpopulations connected by four percent dispersal (the bold line in the Table) exhibits just 8.8 percent risk in 15 years – but this risk jumps to 43.2 percent in 50 years. The shorter time horizon might show a tolerable level of risk to the population manager, but this acceptance of risk ignores the danger looming in the coming decades.

Moreover, the results presented here suggest that a single population composed of 40 individuals is considerably more stable than four linked subpopulations of 10 individuals. The bold line in Table 4 shows a 43 percent probability of metapopulation extinction at 50 years when these small subpopulations are linked by an intermediate level of dispersal in the absence of drought. This can then be compared to a drought-free isolated population of 40 individuals that displays a 10 percent risk at the same time interval (see Figure 5). Even when linked together by significant dispersal, small populations cannot sustain themselves in the face of stochastic fluctuation in basic demographic determinants of population growth.

The intriguing results from this rather simple analysis led to the development of more sophisticated models, designed to shed some light on the conditions necessary to provide for some level of metapopulation stability. To address this question, we constructed four different population configurations:

- A Three populations of 10 individuals, and one population of 40 individuals;
- B Two populations of 10 individuals, and two populations of 40 individuals;
- C One population of 10 individuals, and three populations of 40 individuals;
- D One population of 10 individuals, two populations of 40 individuals, and one population of 100 individuals.

In addition, we constructed three different drought regimes:

- No – No drought;
- Lentic/Lotic – All populations of 10 individuals experience lentic drought, while the larger populations experience lotic drought. This is designed to simulate the natural tendency for the smaller populations to frequently occupy more ephemeral sites that are particularly prone to drought-induced dessication;
- Lotic/Immune – All populations experience the milder lotic drought, with the exception of a single randomly-selected population of 10 individuals that is immune to the effects of drought. This regime is designed to simulate a more aggressive management regime where there is partial to full mitigation of the effects of drought, with the efficacy of mitigation largely determined by subpopulation size.

In addition, we assumed the standard levels of dispersal rate considered in earlier metapopulation viability models. This combination of characteristics yielded 36 different scenarios for analysis. The results of these analyses are presented in Figure 7 and Table 5.

In general, metapopulation configuration A shows the lowest degree of viability among all such configurations tested. This is not surprising, particularly in light of the results of the previous metapopulation analyses (Figure 6, Table 4). In the absence of drought, configurations B, C and D all show little to no extinction risk over the full 100 years of the simulation, with average annual population growth rates approaching 7.0 percent. These results serve to reinforce the conclusion reached in earlier analyses – very small populations, even when linked with relatively high levels of dispersal, will not be capable

Table 5. Results of Chiricahua leopard frog metapopulation risk analysis models. For each of four different subpopulation configurations, models combined different levels of dispersal (D) with drought regime. All P(E) and N results are for the metapopulation as a whole. See page 9 for definitions of column headings, and accompanying text for more model details.

D (percent)	Drought	r _s (SD)	P(E)	N	T(E)
			15 / 50 / 100	15 / 50 / 100	
Metapopulation Type A: 3x10, 1x40					
1	None	0.044 (0.388)	0.014 / 0.076 / 0.190	60.84 / 52.95 / 48.14	57
4		0.055 (0.345)	0.004 / 0.044 / 0.082	67.78 / 63.61 / 61.59	48
8		0.065 (0.337)	0.002 / 0.014 / 0.040	66.01 / 64.88 / 63.65	62
1	Len/Lot	0.016 (0.502)	0.080 / 0.304 / 0.538	47.51 / 32.73 / 21.64	48
4		0.021 (0.479)	0.104 / 0.342 / 0.598	53.48 / 38.82 / 22.67	45
8		0.025 (0.483)	0.088 / 0.368 / 0.658	52.16 / 35.32 / 18.28	47
1	Lot/Imm	0.025 (0.449)	0.038 / 0.270 / 0.506	51.17 / 36.74 / 24.76	51
4		0.037 (0.405)	0.032 / 0.156 / 0.312	60.12 / 48.52 / 41.61	51
8		0.046 (0.387)	0.014 / 0.116 / 0.278	60.38 / 51.32 / 41.38	55
Metapopulation Type B: 2x10, 2x40					

1	None	0.052 (0.337)	0.000 / 0.004 / 0.024	99.19 / 95.04 / 92.52	64
4		0.057 (0.325)	0.000 / 0.000 / 0.002	102.12 / 101.95 / 99.63	89
8		0.069 (0.320)	0.000 / 0.000 / 0.002	97.49 / 99.13 / 97.62	56
1	Len/Lot	0.020 (0.507)	0.062 / 0.224 / 0.444	74.74 / 54.54 / 38.34	50
4		0.028 (0.487)	0.052 / 0.202 / 0.382	79.40 / 66.56 / 50.97	49
8		0.033 (0.494)	0.062 / 0.272 / 0.466	78.39 / 59.17 / 46.16	48
1	Lot/Imm	0.035 (0.417)	0.010 / 0.076 / 0.208	85.50 / 74.20 / 61.80	60
4		0.045 (0.387)	0.006 / 0.026 / 0.068	89.01 / 86.62 / 83.33	59
8		0.056 (0.380)	0.012 / 0.042 / 0.074	88.45 / 83.05 / 40.61	51

Metapopulation Type C: 1x10, 3x40

1	None	0.054 (0.318)	0.000 / 0.000 / 0.002	132.58 / 132.53 / 134.42	78
4		0.054 (0.312)	0.000 / 0.000 / 0.000	135.68 / 136.93 / 137.63	–
8		0.060 (0.314)	0.000 / 0.000 / 0.000	136.74 / 135.60 / 135.62	–
1	Len/Lot	0.022 (0.503)	0.034 / 0.166 / 0.342	99.29 / 79.80 / 64.80	53
4		0.027 (0.493)	0.044 / 0.148 / 0.306	112.26 / 94.60 / 78.90	52
8		0.032 (0.497)	0.032 / 0.172 / 0.328	105.99 / 95.17 / 75.60	52
1	Lot/Imm	0.039 (0.394)	0.002 / 0.040 / 0.082	115.63 / 107.68 / 99.64	52
4		0.044 (0.380)	0.002 / 0.008 / 0.016	125.48 / 122.18 / 123.71	53
8		0.051 (0.375)	0.002 / 0.006 / 0.018	124.89 / 119.95 / 122.37	54

Metapopulation Type D: 1x10, 2x40, 1x100

1	None	0.052 (0.326)	0.000 / 0.000 / 0.000	201.55 / 198.01 / 198.54	–
4		0.059 (0.319)	0.000 / 0.000 / 0.000	200.70 / 196.82 / 199.95	–

8		0.074 (0.314)	0.000 / 0.000 / 0.000	191.66 / 189.10 / 190.72	-
1	Len/Lot	0.033 (0.475)	0.004 / 0.028 / 0.066	159.82 / 159.49 / 150.65	54
4		0.040 (0.467)	0.008 / 0.042 / 0.080	164.36 / 165.71 / 147.31	49
8		0.051 (0.470)	0.010 / 0.066 / 0.134	162.91 / 152.28 / 135.01	53
1	Lot/Imm	0.041 (0.400)	0.000 / 0.006 / 0.012	180.84 / 177.36 / 174.17	51
4		0.048 (0.389)	0.002 / 0.006 / 0.016	176.43 / 174.44 / 182.63	57
8		0.062 (0.380)	0.000 / 0.002 / 0.004	171.33 / 169.42 / 166.17	64

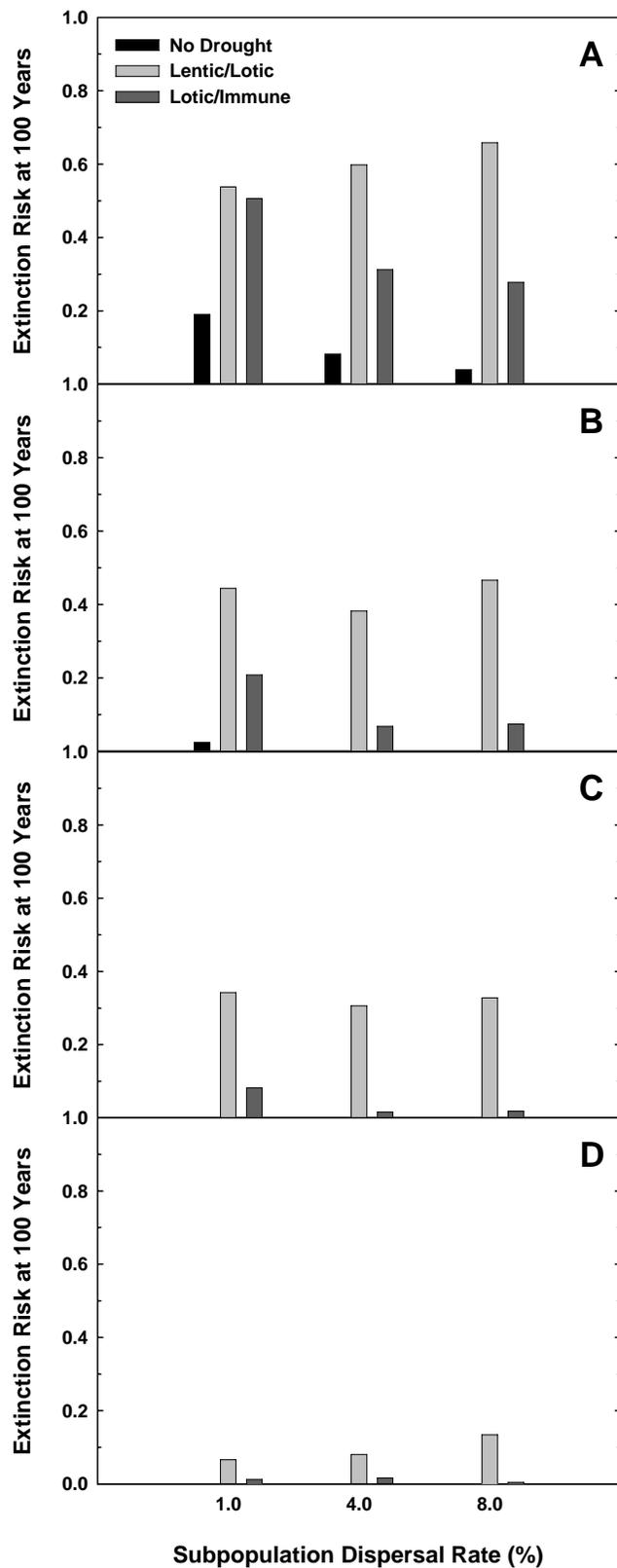


Figure 7. Metapopulation risk analysis for Chiricahua leopard frogs. Extinction risk at 100 years as a function of metapopulation configuration and dispersal rates under three different drought regimes.

Metapopulation configurations, defined as number of individuals per subpopulation, include:

A – 3 x 10, 1 x 40;

B – 2 x 10, 2 x 40;

C – 1 x 10, x 0;

D – 1 x 10, 2 x 0, 1 x 100.

“Lentic/Lotic” drought simulates lentic drought conditions among the smallest subpopulations and lotic drought among the remaining larger subpopulations. “Lotic/Immune” drought simulates lotic drought in all subpopulations with one small population immune from drought through active habitat management. See text for accompanying details.

by themselves of maintaining overall metapopulation viability. Having said this, it may be possible to compose a metapopulation with enough small subpopulations and sufficiently high dispersal to attain an acceptable level of metapopulation viability. For example, if each subpopulation were linked to each of its neighbors with four percent dispersal probability, it would require eight subpopulations of 10 individuals to achieve a metapopulation extinction probability of 0.08 in the absence of drought (model results not presented elsewhere in this report). One must remember, however, that each of these subpopulations will become extinct numerous times during a 100-year simulation, with frequent recolonization from nearby subpopulations necessary to achieve metapopulation “stability” for a given period of time. This level of quasi-stability may not be sufficient within the bounds drawn up within the Chiricahua leopard frog Recovery Plan.

Deeper analysis of the results in Figure 7 and Table 5 reveal interesting evidence of source-sink dynamics in selected metapopulations. For example, a look at panel A in Figure 7 shows that in the case of the lentic/lotic drought regime, an increase in the dispersal rate actually leads to an **increase** in the metapopulation extinction risk. In this configuration, the smallest populations are being driven to rapid extinction by a combination of stochastic small population dynamics and drought. The single medium-sized population then supplies individuals to these smaller populations for local subpopulation re-establishment, but the smaller recipient subpopulations are not able to supply dispersers to bolster the number of individuals in the larger subpopulation. In other words, the smaller populations become demographic “sinks” to the medium-sized population “source”. This same phenomenon is seen to a lesser degree in metapopulation configuration D where, under conditions of lentic/lotic drought, the single large subpopulation of 100 individuals plays the role of source to the smaller demographic sinks to which it is linked through dispersal. When the subpopulations are more evenly matched in size, as in metapopulation configurations B and C, these types of more complicated dynamics are less obvious to detect.

Overall, inspection of these results indicates that, within the constraints of our best understanding of Chiricahua leopard frog population biology and ecology, metapopulations need to include at least one large, healthy subpopulation (e.g., at least 100 adults) in order to achieve an acceptable level of viability as a larger unit. If drought can be managed effectively so that small, lentic habitats have a good chance of persistence, overall metapopulation viability may be achievable with a smaller number of individuals per subpopulation (e.g., 40 – 50 adults).

Directions for Future PVA Efforts

As discussed earlier within this document, it is unwise to use the results of a population viability analysis by themselves to determine precise and quantitative recovery targets for endangered species conservation and the strategies necessary for their achievement. The uncertainties surrounding our understanding of Chiricahua leopard frog biology, genetics, and ecology are too great for such precise predictions to be made. Nevertheless, we can gain considerable insight into the *relative response* of different frog populations to human activities, and thereby gain insight into how to best manage these populations to achieve a given level of security.

Although we are satisfied with the insights gained from this preliminary analysis, there are other factors and processes we see as potentially important to the future viability of Chiricahua leopard frog populations, but were unable to include in the models discussed here. Their omission from the current analysis reflects our lack of basic understanding of the processes involved, and/or our inability to precisely measure their impacts on frog populations. Such processes or factors include:

Impacts of non-native predators

We are currently unable to quantify the effects of different densities of non-native predators on leopard frog mortality. We would like to be able to more adequately model this impact in different habitats to identify those that are at particular risk.

Impacts of disease (chytrid fungus)

Chytrid fungus infection is seen by many herpetologists as a primary factor in global amphibian decline, and all indications are that Chiricahua leopard frogs are not immune to its dangers. We are currently unable to precisely describe the mode of action of chytrid fungus on leopard frog populations, although we recognize that any level of infection is likely to be catastrophic to many populations. Given this recognition, detailed modeling of its ecology and quantitative impact on frog populations may not be necessary.

Additional catastrophic processes

Our group engaged in very preliminary discussions on the impacts of other natural processes on Chiricahua leopard frog populations. For example, there is some suggestion that severe floods may have catastrophic impacts on local populations, although we are currently unable to describe these processes and their consequences in sufficient detail.

Optimal augmentation strategies

In addition to natural means of population augmentation through dispersal, would it be possible to boost the viability of local populations through augmentation? What would be the source of such individuals? Which populations within a given metapopulation should be the targets of augmentation in order to achieve the highest levels of metapopulation stability? What should be the optimal frequency and extent of augmentation? What types (i.e., age classes) of individuals should be used for augmentation? These questions may be of critical importance to the proper management of Chiricahua leopard frog populations, but we were unable to properly address them in this analysis.

Subsequent analyses of Chiricahua leopard frog population viability would greatly benefit from detailed discussions of these factors, in addition to those that were identified in the current analysis as both important in their contribution to population stability, yet also uncertain in their measurement.

Conclusions

We may conclude our preliminary analysis of Chiricahua leopard frog population viability by returning to the original set of questions that provided the foundation for our study. As a prelude, however, it may be worthwhile to discuss the general concept of extinction risk analysis and its

use in endangered population management. Without specific guidance from the US Endangered Species Act on consistent and quantitative definitions of threatened species categories, individual Recovery Teams are left to develop their own definitions. In the case of the Chiricahua leopard frog, delisting may occur under the following conditions (text taken directly from the draft species Recovery Plan):

At least two metapopulations in different drainages (defined here as USGS 10-digit Hydrologic Units) plus at least one isolated and robust population in each Recovery Unit (RU) exhibiting long-term persistence. Evidence of long-term persistence will be provided via a scientifically acceptable population monitoring program for at least a 15-year period, which is approximately 8-12 generations of the Chiricahua leopard frog.

The analyses presented here suggest that a 15-year window of observation may be inadequate to demonstrate viability of a relatively small population or metapopulation of Chiricahua leopard frogs that can be negatively impacted by human activities across the landscape. This is largely due to the fact that some processes and their effects, such as drought, often occur on time scales that are longer than the monitoring period set forth by the draft Plan. Consequently, dynamic and largely unpredictable processes that are very important in determining longer-term population performance are not taken into account to the extent necessary when making a decision on whether or not a species can be suitable for recovery.

Based on the above considerations, it may be recommended that specific and quantitative definitions of such important terms as “viability” and “robust population” be explicitly articulated within this species Recovery Plan. These terms are often linked to risk assessments that stem directly from an analysis like a PVA. Such a process has been used very effectively by the IUCN in its global Red List assessment of threatened species (IUCN 2001; available online at www.iucn.org/themes/ssc/redlists/redlistcatsenglish.pdf).

In addition, it may be important to recognize that “long-term persistence”, in and of itself, is not a satisfactory condition for population stability and, by extension, recovery. Persistence does not speak to the magnitude, variability, or even the average direction of change in abundance over time. As a result, a population may be present in a given locality for the required time interval, but may actually show a discernible negative trend in abundance. Such an observation clearly would not reasonably allow the taxon to be recovered. A revised definition of recovery that expands on the notion of long-term persistence – to include concepts related to sustained increases in population size as observed through intensive monitoring programs – may be in order.

- *What is our depth of understanding of the population biology of the Chiricahua leopard frog?*

A significant amount of effort has gone towards developing a quantitative understanding of Chiricahua leopard frog biology and ecology. Because of this work, we were able to develop a detailed preliminary demographic model of frog demography that proved extremely useful in our analysis.

- *Based on this understanding, what do we see as the primary drivers of leopard frog population growth? To which parameters is our demographic model most sensitive?*

Our demographic sensitivity analysis revealed that juvenile survivorship is an extremely important determinant of Chiricahua leopard frog population dynamics. As such, priority should be given to both additional research aimed at developing a better quantitative estimate of this parameter under a suite of different ecological settings, as well as to any management activity that would likely result in the reduction of natural or anthropogenic threats to juvenile survival. Other factors demonstrating particular importance in our model were the extent of female reproductive success (defined here as the proportion of adult females that were able to produce metamorphs) and the average number of metamorphs per successful female.

- *How vulnerable are small, fragmented Chiricahua leopard frog populations to local extinction in the absence of demographic interaction with other populations?*

Given our best estimates of Chiricahua leopard frog population biology and ecology, our models suggest that populations of fewer than 50 – 60 individuals are at a significantly elevated risk of extinction compared to larger populations. There appears to be a type of threshold effect at this population size, above which the risk of local population extinction remains low.

- *What is the relative risk to leopard frog population viability posed by drought in lentic vs. lotic habitats?*

Overall, drought is seen as a potentially severe risk to Chiricahua leopard frog populations. In particular, frogs occupying lentic habitats may be at considerably greater risk of catastrophic population decline and extinction due to the more severe impact of drought in these more ephemeral habitats. As a result, it may be prudent to develop specific management actions that reduce drought risk in lentic habitats (e.g., stock tank connections to windmills or pipelines, stock tank deepening, berm repair, etc.).

- *Is the current Recovery Plan definition of a “robust population” adequate in terms of relative risk of population extinction?*

Given the results discussed above, the current definition of a “robust population” may be inadequate in the context of population extinction risk. As discussed above, the current definition is highly subjective and is ultimately dependent on a more precise articulation of risk tolerance over a specific time frame. In the absence of such a definition, these preliminary analyses suggest that increasing the population size threshold to approximately 60 individuals may be more appropriate. This number represents the minimum necessary and may have to set to a higher level if the impacts of drought or other threat factors are not adequately addressed. Note that this definition refers to an isolated population; when such a population is linked to neighboring populations through dispersal, the subpopulation size threshold could be reduced to 40 – 50 individuals under our current level of species biology and demography.

- *What are the relative levels of importance of subpopulation size and dispersal rate within a given metapopulation in terms of metapopulation viability?*

Under the conditions modeled here, metapopulation stability is achieved much more effectively through increasing subpopulation size. Even when connectivity through dispersal is relatively low, larger subpopulations are relatively more immune to the destabilizing effects of stochastic demographic fluctuations. This increase in local subpopulation stability directly translates to a higher degree of overall metapopulation stability.

- *Under what set of subpopulation characteristics (e.g., population size, dispersal rates, management intensity) can we observe a functioning metapopulation?*

A precise answer to this question (and, to a similar degree, all of the previous questions discussed here) is highly dependent on the underlying demographics of the component subpopulations. Nevertheless, our analyses indicate that very small populations of Chiricahua leopard frogs can often act as demographic “sinks” – draining larger “source” populations of their animals without providing sufficient levels of reciprocal dispersal to achieve overall metapopulation stability. This “source – sink” dynamic can have marked negative consequences for metapopulation persistence. Moreover, this dynamic can be even more pronounced when catastrophic drought is present, through significantly increased risk of local extinction of the smallest populations.

Appendix to 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 (see Lacy and Miller (2002), Nyhus et al. (2002) and Westley and Miller (2003) for more details).

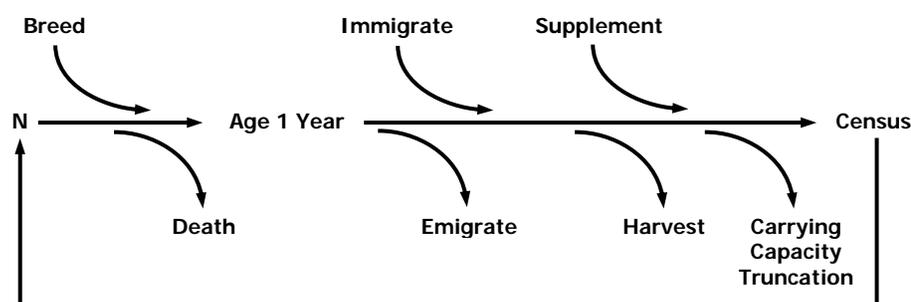
The *VORTEX* Population Viability Analysis Model

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 Simulation Model Timeline



Events listed above the timeline increase N, while events listed below the timeline decrease N.

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 above.) 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 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.

Results

Results reported for each scenario include:

Deterministic r – The deterministic population growth rate, a projection of the mean rate of growth of the population expected from the average birth and death rates. Impacts of harvest, inbreeding, and density dependence are not considered in the calculation. When $r = 0$, a population with no growth is expected; $r < 0$ indicates population decline; $r > 0$ indicates long-term population growth. The value of r is approximately the rate of growth or decline per year.

The deterministic growth rate is the average population growth expected if the population is so large as to be unaffected by stochastic, random processes. The deterministic growth rate will correctly predict future population growth if: the population is presently at a stable age distribution; birth and death rates remain constant over time and space (i.e., not only do the probabilities remain constant, but the actual number of births and deaths each year match the expected values); there is no inbreeding depression; there is never a limitation of mates preventing some females from breeding; and there is no density dependence in birth or death rates, such as a Allee effects or a habitat “carrying capacity” limiting population growth. Because some or all of these assumptions are usually violated, the average population growth of real populations (and stochastically simulated ones) will usually be less than the deterministic growth rate.

Stochastic r – The mean rate of stochastic population growth or decline demonstrated by the simulated populations, averaged across years and iterations, for all those 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. Usually, this stochastic r will be less than the deterministic r predicted from birth and death rates. The stochastic r from the simulations will be close to the deterministic r if the population growth is steady and robust. The stochastic r will be notably less than the deterministic r if the population is subjected to large fluctuations due to environmental variation, catastrophes, or the genetic and demographic instabilities inherent in small populations.

P(E) – The probability of population extinction, determined by the proportion of, for example, 500 iterations within that given scenario that have gone extinct in the simulations. “Extinction” is defined in the VORTEX model as the lack of either sex.

N – The mean population size, averaged across those simulated populations which are not extinct.

SD(N) – The variation across simulated populations (expressed as the standard deviation) in the size of the population at each time interval. SDs greater than about half the size of mean N often indicate highly unstable population sizes, with some simulated populations very near extinction. When SD(N) is large relative to N , and especially when SD(N) increases over the years of the simulation, then the population is vulnerable to large random fluctuations and may go extinct even if the mean population growth rate is positive. SD(N) will be small and often declining relative to N when the population is either growing steadily toward the carrying capacity or declining rapidly (and deterministically) toward extinction. SD(N) will also decline considerably when the population size approaches and is limited by the carrying capacity.

H – 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 (Lacy 1993b), with a 10 percent decline in gene diversity typically causing about 15 percent decline in survival of captive mammals (Ralls et al. 1988). Impacts of inbreeding on wild populations are less well known, but may be more severe than those observed in captive populations (Jiménez et al. 1994). Adaptive response to natural selection is also expected to be proportional to gene diversity. Long-term conservation programs often set a goal of retaining 90 percent of initial gene diversity (Soulé et al. 1986). Reduction to 75 percent of gene diversity would be equivalent to one generation of full-sibling or parent-offspring inbreeding.

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