

**Preliminary Population Viability Assessment for the
Gopher Tortoise (*Gopherus polyphemus*)
in Florida**

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

and

**Participants in PVA Workshop, Tallahassee, FL
11 – 12 September 2001**



Conservation Breeding Specialist Group

Species Survival Commission / IUCN - World Conservation Union

Facilitating Endangered Species Survival

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

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

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

Preliminary Population Viability Assessment for the Gopher Tortoise in Florida

**Philip Miller, Conservation Breeding Specialist Group
and
Participants in PVA Workshop, Tallahassee, FL
11 – 12 September 2001**

TABLE OF CONTENTS

Report Summary	i
Introduction.....	1
Baseline Input Parameters for Stochastic Population Viability Simulations.....	2
Results from Simulation Modeling	
Demographic Sensitivity Analysis.....	10
Population Risk Analysis.....	12
Summary	26
Conclusions.....	27
References.....	29
Appendix I: Simulation Modeling and Population Viability Analysis.....	30
Appendix II: Florida Gopher Tortoise GIS Habitat Analysis and Population Size Estimates	35
Appendix III: Sample <i>VORTEX</i> Output File.....	41

9 December, 2001

Preliminary Population Viability Assessment for the Gopher Tortoise in Florida

**Philip Miller, Conservation Breeding Specialist Group
and
Participants in PVA Workshop, Tallahassee, FL
11 – 12 September 2001**

REPORT SUMMARY

A workshop was held in Tallahassee, Florida 11 – 12 September 2001 to address the issue of population viability of the gopher tortoise (*Gopherus polyphemus*) in the state of Florida. Biologists from the Florida Fish and Wildlife Conservation Commission asked Philip Miller of the IUCN / SSC Conservation Breeding Specialist Group to conduct the analysis and produce this report. The analysis was requested as part of a larger Biological Status Report that will greatly assist local conservation agencies in the management of this species. The Commission put forth a series of detailed questions concerning the predicted viability of the gopher tortoise in Florida, and these questions became the focus of the analysis that follows.

During the workshop, the seven Commission biologists in attendance – most with extensive gopher tortoise field experience – engaged in intense discussions centered around the population biology and ecology of the tortoises across the state. This information was then used to parameterize models using the *VORTEX* software package for population viability analysis (PVA). Data on age-specific mortality and fecundity were refined for use in the model, as was voluminous information on spatial analysis of real and potential tortoise habitat using GIS methodologies. Because much of these data are estimated with high levels of uncertainty, demographic sensitivity analysis was employed to evaluate the impact of this measurement error on model performance. Additional information was used to develop models that assessed the potential impact of Upper Respiratory Tract Disease (URTD), recently discovered in selected populations and considered by some to be a significant threat to the future local persistence of the species.

Demographic sensitivity analysis indicates that the PVA models developed here are highly sensitive to uncertainty in mortality rates of both juvenile (up to one year of age) and adult females. In other words, these parameters are primary drivers of overall growth dynamics in gopher tortoise populations. Consequently, future research efforts and broad management actions could be directed preferentially at these aspects of the species' life history.

A detailed risk assessment was conducted to evaluate the probability of persistence of gopher tortoise populations across Florida. Using GIS and other data analysis tools, nearly 300 sites known to or suspected to harbor tortoise populations were categorized into 10 size classes that became the fundamental unit of analysis. The growth rate among these population classes was found to be strongly tied to regional location: southern populations enjoy a longer growing season each year and, consequently, reach reproductive age much earlier than their counterparts farther northward. As a result, central and Panhandle populations are more sensitive to the negative impacts of human activities that act to either reduce habitat availability or increase mortality. Specifically, the introduction of URTD into a population can have severe consequences, particularly if the population is small (i.e., 50 – 200 individuals). It is difficult, however, to draw precise conclusions from these disease models as they are based on very little quantitative epidemiologic and/or demographic data from infected populations in the

field. Nevertheless, the analyses point out the need to better understand URTD in the context of proper identification and management.

Overall, our analyses suggest that the gopher tortoise is not imminently threatened with extinction in Florida, either when considering the entire statewide population or only those populations occupying FWC or public lands. There are, however, plausible scenarios (such as widespread and severe infection with URTD, or the recognition of general mortality rates that are higher than those currently estimated) that could put these populations at considerably greater risk. Smaller populations are particularly vulnerable to extinction through the combined action of direct interaction with humans and the unpredictable (and usually deleterious) nature of random variability in demographic rates imposed by a variable local environment. Despite the uncertainty associated with our understanding of gopher tortoise population biology, and an incomplete understanding of the ways in which human activities impact tortoise population dynamics, the PVA conducted here is based on the best information available, and was discussed and developed by those with the greatest knowledge of and experience with gopher tortoise biology and conservation management in Florida. As such, the set of conclusions drawn in this report should be considered a valuable tool in the larger decision-making process with respect to gopher tortoise conservation in Florida.

Preliminary Population Viability Assessment for the Gopher Tortoise in Florida

**Philip Miller, Conservation Breeding Specialist Group
and
Participants in PVA Workshop, Tallahassee, FL
11 – 12 September 2001**

Introduction

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

The *VORTEX* package is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild populations. *VORTEX* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or random variables that follow specified distributions. The package simulates a population by stepping through the series of events that describe the typical life cycles of sexually reproducing, diploid organisms.

VORTEX is not intended to give absolute answers, since it is projecting stochastically the interactions of the many parameters used as input to the model and because of the random processes involved in nature. Interpretation of the output depends upon our knowledge of the biology of the gopher tortoise, 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 Miller and Lacy (1999) and Lacy (2000).

Specifically, we were interested in addressing the following questions:

- Does the gopher tortoise have a $\geq 20\%$ probability of extinction in Florida over the next 100 years (3 generations)?
- Does the gopher tortoise have a $\geq 10\%$ probability of extinction in Florida over the next 100 years (3 generations)?
- Does the gopher tortoise have a $\geq 20\%$ probability of extinction in Florida over the next 100 years (3 generations) considering only populations on public lands? On lands where FWC is the lead manager?

- Does the gopher tortoise have a $\geq 10\%$ probability of extinction in Florida over the next 100 years (3 generations) considering only populations on public lands? On lands where FWC is the lead manager?
- What is the smallest-sized population of long-term (ca. 100+ yrs) conservation value by habitat/geographic strata (acreage and number of mature individuals)?
- Is the current relocation / restocking program an effective component of the statewide tortoise conservation program?
- What are the characteristics and consequences of the upper respiratory tract disease (URTD) now infecting gopher tortoise populations across Florida?

Baseline Input Parameters for Stochastic Population Viability Simulations

Much of the demographic data discussed here comes from the original work of J.L. Landers (Landers 1980; Landers et al. 1980, 1982). More recently, Joan Berish and Paul Moler have extended these datasets by assembling and analyzing new information on gopher tortoise populations across the state of Florida.

It is important to note here that, because of the large number of rather isolated tortoise populations distributed across Florida, a complete statewide demographic analysis of gopher tortoise population viability is beyond the computational scope of the *VORTEX* individual-based approach. Moreover, because of the highly fragmented nature of the species' distribution, the complexity of a statewide metapopulation model would also be effectively beyond the scope of PVA packages using a population-based approach. Consequently, I have approached this problem by categorizing the large number of populations across the state into a much smaller number of population size classes, with each class amenable to its own separate demographic evaluation (see below for more information). Using this technique, we can identify the smallest size classification that meets the viability criteria identified above. A simplification of PVA methodology such as this does not appreciably limit the value of the modeling effort.

Breeding System: Polygynous

Age of First Reproduction: *VORTEX* considers the age of first reproduction as the age at which the first clutch of eggs is laid, not simply the onset of sexual maturity. There is significant latitudinal variation in the length of the growing season in Florida. As a result, tortoises in the southern portions of the state grow more rapidly than those in the north. Since sexual maturity is largely a function of size in tortoises, animals in the south will attain breeding status earlier in life than their northern counterparts. A general breakdown of the age of first breeding is as follows:

Region	Females	Males
South	11	11
North-Central	16	11
Panhandle	20	17

Age of Reproductive Senescence: In its simplest form, *VORTEX* assumes that animals can reproduce (at the normal rate) throughout their adult life. While data of this type based on annual

scute counts are difficult to obtain, current estimates for reproductive longevity approach 60 years.

Offspring Production: Based on the depth of our knowledge of gopher tortoise life history, we have defined reproduction in these models as the deposition of a clutch of eggs by a female. On average, about 95% of adult females are believed to produce a clutch of eggs every year. The maximum number of eggs per clutch has been set at 10; while 15 or even 25 eggs has been observed on individual occasions, these are taken to be anomalous events and are not considered when developing data on the distribution of clutch sizes among breeding females.

Annual environmental variation in female reproduction is modeled in *VORTEX* by specifying a standard deviation (SD) for the proportion of adult females that successfully lay a clutch of eggs within a given year. Based on a presumed range of about 90% - 100% of adult females reproducing each year, we set the standard deviation in female reproductive success at 1.5%.

Given that an adult female lays a clutch of eggs, the distribution of clutch size was set as follows:

Number of eggs	%
4	3.2
5	12.0
6	30.4
7	28.8
8	14.4
9	7.2
10	4.0

This distribution yields an average clutch size of 6.77 eggs. While individual clutches may show strong temperature-dependent sex bias, the overall population-level sex ratio among eggs is assumed to be 50%.

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

At this time, there are no data to support density dependence in reproduction in gopher tortoise populations in Florida. Consequently, this option was not included in the models presented here.

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. This is not an issue in gopher tortoise populations, so we have assumed that all adult males are equally capable of breeding in any given year of a simulation.

Mortality: Data going back to Landers (1980) indicates that mean annual mortality does not change appreciably once a tortoise reaches three years of age. However, younger tortoises experience age-specific mortality rates according to the following schedule:

Age Class	% Mortality (SD)	
	Females	Males
0 – 1	94.9 (3.5)*	94.9 (3.5)
1 – 2	27.1 (3.0)	27.1 (3.0)
2 – 3	8.4 (1.0)	8.4 (1.0)
3 - +	3.3 (0.5)	3.3 (0.5)

$$\begin{aligned}
 * \text{ Mortality} &= 1 - [(\text{Hatching rate})(\text{Hatchling survival})] \\
 &= 1 - [(0.105)(0.49)] \\
 &= 0.949
 \end{aligned}$$

Note the high mortality rate of the 0-1 year age class. Because of our definition of reproduction as the deposition of eggs, we must include both an estimate of hatching success and the mortality rate from hatching to one year of age. Also note that environmental variation in annual mortality is based on expert opinion of those providing information on model parameterization.

Finally, it is important to note that selected age-specific mortality rates will be modified to simulate the potential impacts of upper respiratory tract disease (URTD; see below).

Inbreeding Depression: *VORTEX* includes the ability to model the detrimental effects of inbreeding, most directly through reduced survival of offspring through their first year. Because of the complete absence of information on the effects of inbreeding on the demography of gopher tortoises in Florida, this option was not included in our models.

Demographic impact of URTD: An upper respiratory tract disease has been observed in captive and wild gopher tortoise populations in Florida for about the last decade (Diemer Berish et al. 2000). Several pathogens of the genus *Mycoplasma* (*M. agassizii*, *M. mysteriousa*, *M. sp.*) appear to be the causal agents. The highly contagious disease is characterized by such symptoms as intermittent nasal and/or ocular discharge, recessed eyes, or dull skin. Clinical signs may appear within one or two weeks after exposure, but it takes six to eight weeks for an exposed gopher tortoise to develop a detectable immune response.

In a recent study of 386 tortoises across 53 sites, Diemer Berish et al. (2000) found that nearly 40% of the individuals tested showed one or more clinical signs of URTD, with 30% coming up seropositive in 14 locations scattered across the state and another 5% considered suspect. At the present time, it is unclear whether the pathogen is indigenous to the area with greater incidence of disease resulting from higher levels of anthropogenic stress, or if the pathogen is a recent introduction from outside the region, perhaps from captive animals. The latter hypothesis appears to be a viable explanation for the appearance of URTD in desert tortoise (*Gopherus agassizii*) populations in the southwestern United States.

While it is clear that the mycoplasmid is relatively common in tortoise populations across Florida, its demographic impact is a source of considerable debate. The Oldenburg Mitigation

Park is a classic case in point: a total of 87 tortoises in various stages of decomposition were found in a 28-hectare area during a 1998 survey. While 76% of the living animals tested by Diemer Berish et al. (2000) were seropositive, the cause of death of these 87 individuals is unknown. Because of the habitat in which the dead tortoises were found, questions have been raised about the possible illegal release of animals that may have been highly stressed from associated capture, transport and introduction.

In the face of this uncertainty, tortoise biologists at this PVA workshop felt that it was important to investigate the potential negative impacts of URTD infection in gopher tortoise populations across Florida. A general scenario was then developed in which the disease was manifest demographically in two distinct forms:

- A chronic increase in mortality of individuals greater than two years of age. This effect is based on direct mortality data presented by Joan Berish at Oldenburg Mitigation Park for 1998-2001. Data are summarized below.

Year	Number at Risk	Number Dead	% Mortality
1998 – 1999	46	4	8.7
1999 – 2000	41	3	7.3
2000 – 2001	35	1	2.9
		Average	6.3

Because of the very low levels of baseline adult mortality expected in healthy gopher tortoise populations (Landers et al. 1980, 1982), the researchers concluded that URTD played at least a supporting role in determining much of the additional mortality seen in these data. Therefore, models that include URTD have age-specific mortality increased from 3.3% to 6.3%.

- An infrequent catastrophic event with significant associated mortality. Catastrophes are singular environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival. Natural catastrophes can be tornadoes, floods, droughts, disease, or similar events. These events are modeled in *VORTEX* by assigning an annual probability of occurrence and a pair of severity factors describing their impact on mortality (across all age-sex classes) and the proportion of females successfully breeding in a given year. These factors range from 0.0 (maximum or absolute effect) to 1.0 (no effect), and are imposed during the single year of the catastrophe, after which time the demographic rates rebound to their baseline values. Although there are no direct data to substantiate this type of event, workshop participants see this as a real possibility that merits additional analysis. We assumed that a severe local outbreak of URTD occurs only once every 50 years or so, although the stochastic nature of events such as this tells us that it could happen more frequently during specific shorter time intervals. Moreover, for simplicity we are assuming that an outbreak will last a single year. When a local outbreak occurs, we will simulate a severe outbreak of URTD that slightly compromises the ability of adult females to successfully reproduce, and generates significant additional mortality among all animals aged 3 years and older. Specifically, we assume that there is a 10%

reduction in the percentage of adult females that breed during that year, and there will be a 25% reduction in the survival rate of all animals aged 3 years and older.

Initial Population Size: The Florida Fish and Wildlife Conservation Commission (FWC) has developed a list of 294 sites that meet the GIS habitat evaluation criteria for potential gopher tortoise habitat (Appendix II). The analytical steps used to generate tortoise population size estimates for each conservation land are described below.

- GIS analysis of Landsat TM (1985 – 1989) data by FWC biologists was used to estimate the extent of potential gopher tortoise habitat for each of these sites (Column F). The primary factor defining suitable habitat in this analysis was the presence of well-drained xeric soils and/or xeric community types. When available, ground-based habitat survey data were given preference in the development of a best estimate for total suitable tortoise habitat (Column G).
- Direct ground-based population surveys are not available for most of the listed conservation lands, but where available burrow counts (McCoy and Mushinsky 1992) were used to generate an initial estimate of tortoise abundance in each site (Column I). In addition, researchers have detailed information on population numbers for a small number of sites that takes precedence over habitat or burrow count analyses (Column J). For the remaining lands where surveys or other data were not available, we applied a density multiplier of 0.345 adult tortoises per acre. This multiplier was derived from an analysis of 30 sites where McCoy and Mushinsky (1992) provided tortoise population estimates. Specifically, the total acreage of suitable habitat based on GIS analysis (116,371 acres, excluding Apalachicola National Forest) was divided by the estimate of the total number of adult tortoises surveyed across those same lands analyzed by GIS (40239 tortoises). The density multiplier therefore is 0.345 surveyed adult tortoises per GIS acre of suitable habitat. This gives us our preliminary tortoise population estimate (Column K).
- Field researchers recognize that about 70% of the burrows counted in ground surveys are actually adult burrows. In addition, preliminary *VORTEX* modeling was used to estimate the age structure of a simulated tortoise population as it approached demographic equilibrium. This analysis suggests that a stable population of gopher tortoises is composed of about 40% adults. Taking these two observations together, we can estimate the total population size for a given conservation land (Column L) as

$$N_{Tot} = \frac{(N_{Init})(0.7)}{0.4} = 1.75N_{Init} .$$

Because of the impracticality of detailed assessment of each of the 294 conservation lands presented in Appendix II, we have chosen to subdivide these lands into discrete population size classifications that can then become the unit of analysis. In making this simplification, we have excluded those conservation lands known to be devoid of gopher tortoises, those with less than two acres of suitable habitat as well as those lands with an estimated total population size greater than 20,000 individuals as this approaches the maximum number of individuals that *VORTEX* can manipulate. This truncation reduces the total number of conservation lands from 294 to 284. The following table gives the size classifications and their relative abundances.

Population Size Class	N_{Tot} Range	Abundance
A	4 – 50	39
B	51 – 100	50
C	101 – 250	55
D	251 – 500	49
E	501 – 750	19
F	751 – 1000	12
G	1001 – 2500	28
H	2501 – 5000	19
J	5001 – 10000	8
L	10001 - 20000	4

This classification shows us that 144 (51%) of the conservation lands have estimated tortoise populations that do not exceed 250 individuals.

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

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

Ground survey data from the USF ERA indicates that tortoises can reach a density of 8 individuals per acre. Using this as a maximum operational density, the carrying capacity for each conservation land was calculated by multiplying this maximum density by the best estimate of total suitable tortoise habitat (Appendix II, Column G). When these calculations are made, we find that the mean value of K for each population size classification is typically about 10 times the value of the best current population estimate. This value will therefore be used as the appropriate carrying capacity estimate for each size classification.

Iterations and Years of Projection: All population projections (scenarios) were simulated 250 times. Each projection extends to 100 years, with demographic information obtained at ten-year intervals. All simulations were conducted using *VORTEX* version 8.41 (June 2000).

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

Table 1. Demographic input parameters for the baseline *VORTEX* gopher tortoise model. See accompanying text for more information.

Model Input Parameter	Baseline Value
Breeding System	Polygynous
Age of First Reproduction (F / M)	
South	11 / 11
North-Central	16 / 11
Panhandle	20 / 17
Maximum Age of Reproduction	60
Annual % Adult Females Reproducing	95
Maximum Clutch Size	10
Mean Clutch Size [†]	6.77
Overall Offspring Sex Ratio	0.5
All Adult Males in Breeding Pool?	Yes
% Annual Mortality (SD) [‡]	
0 – 1	94.9 (3.5)
1 – 2	27.1 (3.0)
2 – 3	8.4 (1.0)
3 - +	3.3 (0.5)
URTD Mortality (Adults)	3% above baseline
URTD Catastrophe	
Annual Probability	2%
Effect on Reproduction (multiplier)	0.90
Effect on Adult Mortality (multiplier)	0.75
Initial Population Size / Carrying Capacity	
Size Class A	50 / 5000
B	100 / 1000
C	250 / 2500
D	500 / 5000
E	750 / 7500
F	1000 / 10000
G	2500 / 25000
H	5000 / 32000
J	10000 / 32000
L	20000 / 32000

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

[‡] Mortality rates assumed to be equal across sexes.

Additional Model Input Information

Demographic Sensitivity Analysis

During the development of the baseline input dataset, it quickly became apparent that a number of demographic characteristics of gopher tortoise 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 identify a selected set of parameters from Table 1 whose estimate we see as considerably uncertain. We then develop biologically plausible minimum and maximum values for these parameters (see Table 2).

Table 2. Uncertain input parameters and their stated ranges for use in demographic sensitivity analysis. See accompanying text for more information.

Model Parameter	Minimum	Estimate	
		Baseline	Maximum
Maximum Age	50	60	70
% Adult Females Reproducing	90	95	100
% Mortality ₍₀₋₁₎	92.9	94.9	96.9
% Mortality ₍₁₋₂₎	25.1	27.1	29.1
% Mortality ₍₂₋₃₎	6.4	8.4	10.4
% Mortality _(Adult)	1.3	3.3	5.3

For each of these parameters we construct two simulations, with a given parameter set at its prescribed minimum or maximum value, with all other parameters remaining at their baseline value. With the seven parameters identified above, and recognizing that the aggregate set of baseline values constitute our single baseline model, the table above allows us to construct a total of 14 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 North-Central population of 1000 individuals.

Results from Simulation Modeling

Results reported for each modeling scenario include:

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_{100} -- mean population size at the end of the simulation, averaged across those simulated populations that are not extinct.

$SD(N_{100})$ -- 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_{100} -- the gene diversity or expected heterozygosity of the extant populations, expressed as a percent of the initial gene diversity of the population. Fitness of individuals usually declines proportionately with gene diversity (Lacy 1993b), with a 10% decline in gene diversity typically causing about 15% 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 (Miller, 1994; 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% of initial gene diversity (Soulé et al. 1986). Reduction to 75% of gene diversity would be equivalent to one generation of full-sibling or parent-offspring inbreeding.

Demographic Sensitivity Analysis

Figure 1 and Table 3 show the results of the demographic sensitivity analysis.

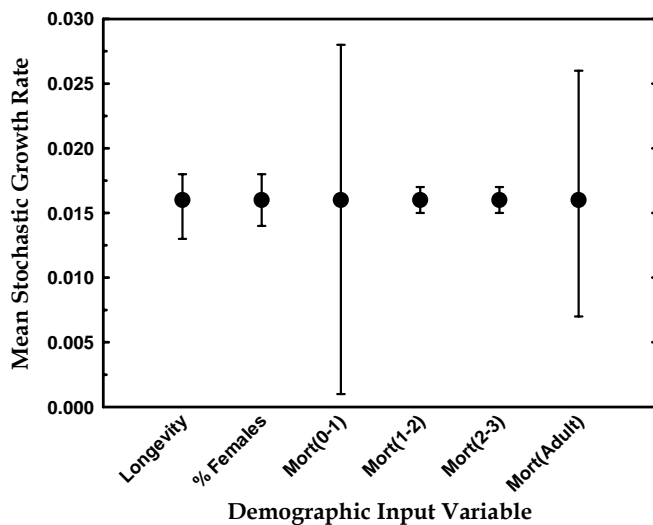


Figure 1. Demographic sensitivity analysis of a simulated Florida gopher tortoise population. Stochastic population growth rate for a set of models in which the specific parameter is varied across a range of biologically plausible values. The baseline model growth rate of 0.016 is given by the central data point for each parameter. The general model of gopher tortoise population dynamics is most sensitive to uncertainty in those parameters giving the widest range in simulated population growth rates. See text for additional details.

Table 3. Stochastic growth rate for Florida gopher tortoise demographic sensitivity analysis models. Boxed data indicate those parameters to which the baseline model is most sensitive.

Model conditions	rs (SD)
Baseline	0.016 (0.052)
Maximum age = 50 years	0.013 (0.051)
Maximum age = 70 years	0.018 (0.052)
Females breeding = 90%	0.014 (0.050)
Females breeding = 100%	0.018 (0.053)
Mortality ₍₀₋₁₎ = 92.9%	0.028 (0.049)
Mortality ₍₀₋₁₎ = 96.9%	0.001 (0.067)
Mortality ₍₁₋₂₎ = 25.1%	0.017 (0.051)
Mortality ₍₁₋₂₎ = 29.1%	0.015 (0.052)
Mortality ₍₂₋₃₎ = 6.4%	0.017 (0.051)
Mortality ₍₂₋₃₎ = 10.4%	0.015 (0.052)
Mortality _(Adult) = 1.3%	0.026 (0.051)
Mortality _(Adult) = 5.3%	0.007 (0.052)

It is clear from the analysis that our model of gopher tortoise population dynamics is most sensitive to uncertainty to mortality of both juveniles (age class 0 – 1) and adults, with slightly greater sensitivity per unit change in mortality among juveniles. In comparison, the model is rather insensitive to a similar unit change in mortality rates among what we may call the “subadult” age classes 1 – 2 and 2 – 3. However, this difference is understandable either in terms of both the number of individuals resident in each age class or the duration an individual may reside in a given age class. Because of the relatively large number of offspring produced per adult female, a small change in mortality among these newborn individuals affects the survival of a relatively large number of animals and, therefore, their entry into subsequent age classes including the productive adult class. Moreover, an adult may reside in this developmental “stage” for a considerable period of time, producing large numbers of offspring almost every year. These two life history aspects alone can explain the model sensitivity shown here.

While it is very instructive to investigate the sensitivity of our model to uncertainty in demographic input, it is also important to recognize that detecting mortality rates to the level of precision discussed here is highly impractical. For example, statistical power analyses conducted on typical types of field demographic and survey data (e.g., Forcada 2000) suggest that either large sample sizes (say, in the hundreds of individuals) or long periods of observation (10 – 15 years) are necessary to detect changes in population numbers in the short term with reasonable levels of precision. Similarly, very large and detailed field studies would be required to successfully differentiate between, for example, a juvenile mortality rate of 93% and 95%. Consequently, the analysis presented here is typically to be used at more of a “strategic” level; when faced with the need for population management in the face of measurement uncertainty and limited institutional resources, research and/or management prioritization can be accomplished through a comparative study of sensitivity analysis data. Having said this, it is also important to note that those parameters to which a demographic model is most sensitive may **not** be the same parameters that are most directly affected by human activities and are therefore

putting the population at risk. Successful conservation requires careful additional study to identify the specific risks the populations face and to develop appropriate remedial actions.

Population Risk Analysis

I. Baseline Population Analysis

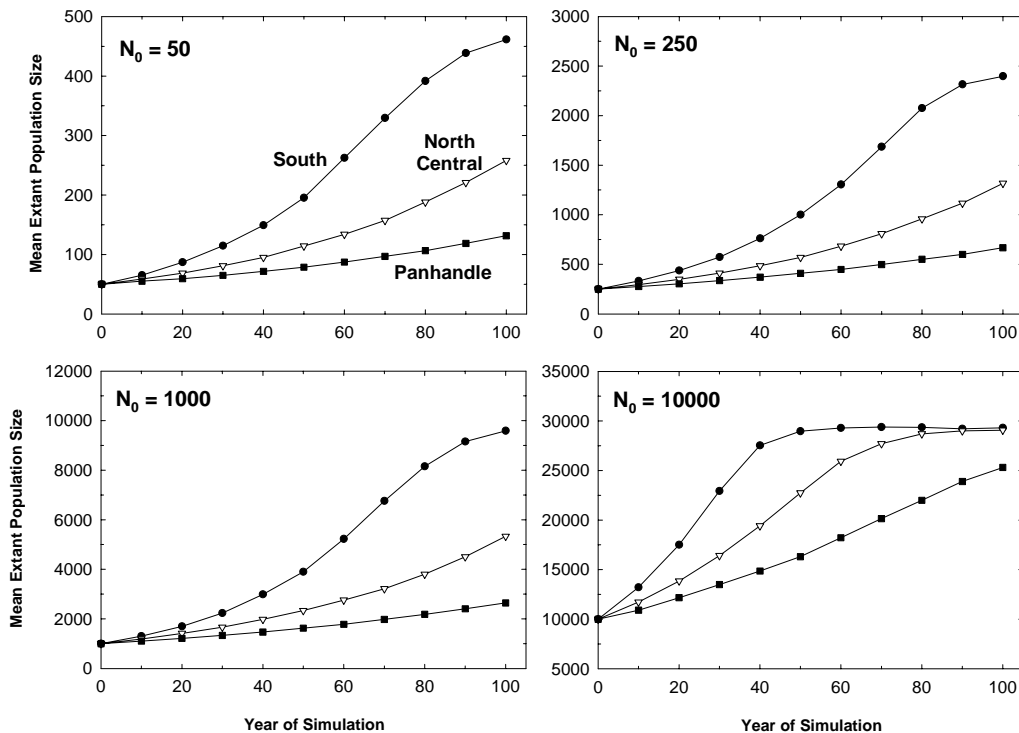
The first set of models presented here represents a population that is free from UR TD infection. Moreover, the populations are assumed to be far from their ecological habitat carrying capacity and, therefore, can grow to as much as 10 times their original number.

Table 4. Florida gopher tortoise population viability analysis: Baseline regional analysis. Results include stochastic growth rate (r_s (SD)), risk of population extinction (P(E)), final mean size of extant populations (N_{100} (SD)), and final population heterozygosity (H_{100}). See text for additional details on model input and output.

Region	N_0	r_s (SD)	P(E)	N_{100} (SD)	H_{100}
South	50	0.026 (0.067)	0.000	461 (61)	0.965
	100	0.027 (0.064)	0.000	958 (80)	0.983
	250	0.027 (0.061)	0.000	2398 (187)	0.993
	500	0.027 (0.060)	0.000	4811 (329)	0.997
	750	0.027 (0.060)	0.000	7210 (434)	0.998
	1000	0.027 (0.060)	0.000	9590 (730)	0.998
	2500	0.027 (0.060)	0.000	24120 (1377)	0.999
	5000	0.027 (0.060)	0.000	29327 (997)	1.000
	10000	0.027 (0.060)	0.000	29304 (995)	1.000
	20000	0.027 (0.059)	0.000	29210 (1156)	1.000
North Central	50	0.016 (0.063)	0.000	258 (97)	0.957
	100	0.016 (0.057)	0.000	522 (186)	0.979
	250	0.016 (0.054)	0.000	1318 (415)	0.992
	500	0.016 (0.052)	0.000	2681 (706)	0.996
	750	0.016 (0.052)	0.000	3936 (1092)	0.997
	1000	0.016 (0.052)	0.000	5329 (1502)	0.998
	2500	0.016 (0.051)	0.000	13276 (3480)	0.999
	5000	0.016 (0.051)	0.000	24568 (4618)	1.000
	10000	0.016 (0.051)	0.000	29069 (1253)	1.000
	20000	0.016 (0.051)	0.000	29053 (1182)	1.000
Panhandle	50	0.009 (0.061)	0.000	131 (61)	0.947
	100	0.009 (0.054)	0.000	261 (93)	0.975
	250	0.009 (0.049)	0.000	667 (187)	0.990
	500	0.010 (0.047)	0.000	1344 (346)	0.995
	750	0.009 (0.047)	0.000	1954 (507)	0.997
	1000	0.009 (0.047)	0.000	2644 (722)	0.998
	2500	0.010 (0.047)	0.000	6924 (1732)	0.999
	5000	0.009 (0.046)	0.000	13223 (3458)	1.000
	10000	0.010 (0.046)	0.000	25312 (4098)	1.000
	20000	0.010 (0.046)	0.000	28694 (1433)	1.000

The results of the baseline regional analysis are shown in Table 4. Within a given region, note that the stochastic population growth rate is very consistent. However, of greater importance is the observation that the mean stochastic growth rate changes markedly with geographic region (and, more specifically with respect to the structure of the *VORTEX* model, age of first breeding). In the South region, where females begin breeding at 11 years of age, a population can grow at a rate of approximately 2.7% per year. But this rate decreases to just 1.6% in the North Central region and about 1.0% in the Panhandle, where females on average begin breeding at ages 16 and 20, respectively. In other words, we see a decrease in the stochastic population growth rate of more than 60% as we move north across the state of Florida. These depressed growth rates result in substantially smaller final population sizes in the North Central and Panhandle populations relative to those in the South.

Figure 2. Size trajectories for simulated gopher tortoise populations over a range of initial population sizes. Different plots within each graph show trajectories for populations within specific regions. See text for additional details.



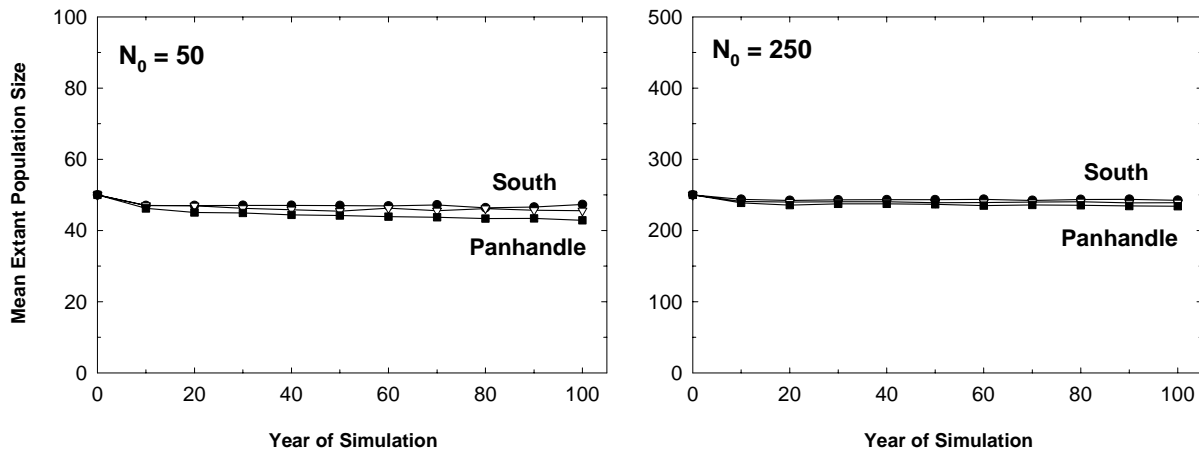
Despite the lower growth rates in the northern part of the state, all populations are able to increase in size with no risk of decline to extinction (Figure 2). (Note that the reduced growth capability for the largest populations are not biologically real but are merely a consequence of an upper limit to population size imposed by the *VORTEX* modeling package.) In addition, all simulated populations are able to retain nearly all of their original genetic variation; only the smallest population in the Panhandle loses more than 5% of the original heterozygosity in place at the beginning of the simulation. With this level of retention of genetic variation, the frequency of inbreeding is low and, therefore, any impacts such a process may have on population fitness (inbreeding depression) is also slight.

From this analysis, based on our best estimates of parameters that describe the demography and ecology of gopher tortoise populations in Florida, we can conclude that when ecological conditions are favorable and external threats are reduced, simulated gopher tortoise populations can exhibit marked population growth, most notably in the southern reaches of the state. As a result, even the smallest populations – composed of as few as 15 adult females – are largely immune from extinction over the time span analyzed here. However, the regional specificity of growth rate makes populations in the North Central region, and particularly the Panhandle, more vulnerable to demographic perturbations brought about by human activity.

II. Restricted Population Carrying Capacity

While it is possible that gopher tortoise populations across Florida may be at relatively low density and are therefore capable of considerable growth beyond current numbers, there may also be many populations that are presently at or near their maximum sustainable numbers. Could this limit on future growth result in an additional risk of future decline, particularly among smaller populations? To investigate this scenario, we developed a set of models identical to the baseline set presented above with the exception that the initial population size was equivalent to the habitat carrying capacity, K .

Figure 3. Size trajectories for regional gopher tortoise populations under conditions of restricted population carrying capacity ($N_0 = K$). See text for additional details.



The results of this analysis are shown in Table 5 and Figure 3. Because of the consistency across initial population sizes in model results previously described, the graphical presentation of results will be limited to those smaller populations initiated with 50 or 250 individuals as these are expected to show the greatest stochastic instability in the face of human threat.

As in the baseline models presented above, all tortoise populations have nearly identical stochastic growth rates even when carrying capacity is reduced. This is to be expected since the life table information – basic data on age-specific survivorship and fecundity – is unchanged from the baseline models. However, because of the restriction imposed through the reduction of carrying capacity, the regional specificity seen earlier is no longer evident. Despite the reduced opportunity for population expansion, it is important to note that even the smallest population is able to maintain a stable size with no risk of extinction.

Table 5. Florida gopher tortoise population viability analysis: Baseline regional analysis with restricted population carrying capacity ($K = N_0$). Results include stochastic growth rate (r_s (SD)), risk of population extinction ($P(E)$), final mean size of extant populations (N_{100} (SD)), and final population heterozygosity (H_{100}). See text for additional details on model input and output.

Region	N_0	r_s (SD)	$P(E)$	N_{100} (SD)	H_{100}
South	50	0.025 (0.080)	0.000	47 (4)	0.898
	100	0.027 (0.070)	0.000	96 (5)	0.948
	250	0.027 (0.064)	0.000	242 (11)	0.979
	500	0.027 (0.061)	0.000	489 (18)	0.990
	750	0.027 (0.061)	0.000	734 (27)	0.993
	1000	0.027 (0.060)	0.000	979 (33)	0.995
	2500	0.027 (0.060)	0.000	2445 (84)	0.998
	5000	0.027 (0.060)	0.000	4882 (180)	0.999
	10000	0.027 (0.060)	0.000	9744 (341)	1.000
	20000	0.027 (0.059)	0.000	19438 (777)	1.000
North Central	50	0.015 (0.072)	0.000	46 (5)	0.909
	100	0.016 (0.062)	0.000	95 (6)	0.954
	250	0.016 (0.056)	0.000	239 (13)	0.981
	500	0.016 (0.053)	0.000	483 (22)	0.991
	750	0.016 (0.053)	0.000	723 (31)	0.994
	1000	0.016 (0.052)	0.000	966 (46)	0.995
	2500	0.016 (0.052)	0.000	2413 (98)	0.998
	5000	0.016 (0.052)	0.000	4845 (188)	0.999
	10000	0.017 (0.051)	0.000	9705 (381)	1.000
	20000	0.016 (0.051)	0.000	19414 (793)	1.000
Panhandle	50	0.009 (0.069)	0.000	43 (7)	0.911
	100	0.009 (0.058)	0.000	91 (9)	0.958
	250	0.009 (0.051)	0.000	234 (16)	0.984
	500	0.009 (0.048)	0.000	473 (27)	0.992
	750	0.010 (0.048)	0.000	716 (38)	0.995
	1000	0.010 (0.047)	0.000	954 (47)	0.996
	2500	0.010 (0.046)	0.000	2397 (114)	0.998
	5000	0.010 (0.046)	0.000	4782 (234)	0.999
	10000	0.010 (0.047)	0.000	9541 (473)	1.000
	20000	0.009 (0.046)	0.000	19138 (892)	1.000

These results, in conjunction with those of the baseline models presented earlier, point out the impact on population performance of low levels of environmental variability (EV) in demographic rates. When these rates display little random variation over time, a stochastic population dynamics model begins to behave more like its deterministic cousin. As a result, a smaller population is less likely to show the demographic or genetic instability that is characteristic of populations inhabiting highly variable environments that can lead to wide swings in rates of reproduction and / or survival. Field study of gopher tortoises in Florida indeed appears to show low levels of variability in vital rates from year to year. Nevertheless,

knowledge gained from this modeling process suggests that additional insight into the nature of variability in vital rates would be extremely valuable.

III. Demographic Impacts of Upper Respiratory Tract Disease (URTD)

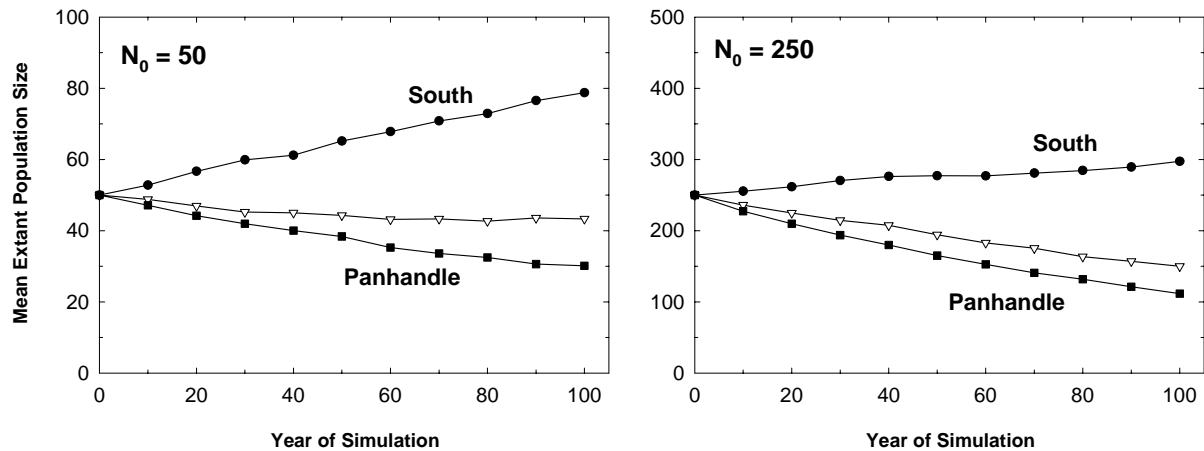
The recent discovery of URTD in Florida gopher tortoise populations has caused a great deal of concern among some conservation managers in the state. In order to evaluate the potential impact that the disease may have on gopher tortoise populations, we developed another set of models that incorporated a suite of demographic impacts that are thought to be largely consistent with observations made on selected tortoise populations across Florida. The results of these analyses are shown in Table 6 and Figure 4.

Table 6. Florida gopher tortoise population viability analysis: Baseline regional analysis with inclusion of Upper Respiratory Tract Disease (URTD). Results include stochastic growth rate (r_s (SD)), risk of population extinction (P(E)), final mean size of extant populations (N_{100} (SD)), and final population heterozygosity (H_{100}). See text for additional details on model input and output.

Region	N_0	r_s (SD)	P(E)	N_{100} (SD)	H_{100}
South	50	0.002 (0.082)	0.000	79 (48)	0.899
	100	0.002 (0.072)	0.000	136 (61)	0.950
	250	0.001 (0.065)	0.000	297 (138)	0.978
	500	0.001 (0.063)	0.000	636 (271)	0.989
	750	0.002 (0.062)	0.000	984 (381)	0.993
	1000	0.001 (0.061)	0.000	1259 (542)	0.994
	2500	0.003 (0.061)	0.000	3493 (1401)	0.997
	5000	0.003 (0.062)	0.000	7180 (2765)	0.998
	10000	0.003 (0.063)	0.000	14756 (5501)	0.998
	20000	0.004 (0.063)	0.000	24078 (4912)	0.998
North Central	50	-0.004 (0.083)	0.032	43 (24)	0.881
	100	-0.004 (0.069)	0.000	77 (37)	0.937
	250	-0.006 (0.060)	0.000	150 (55)	0.972
	500	-0.006 (0.057)	0.000	285 (114)	0.986
	750	-0.005 (0.055)	0.000	474 (185)	0.991
	1000	-0.006 (0.055)	0.000	609 (209)	0.993
	2500	-0.005 (0.054)	0.000	1523 (501)	0.997
	5000	-0.005 (0.054)	0.000	3382 (1245)	0.998
	10000	-0.004 (0.054)	0.000	7069 (2335)	0.999
	20000	-0.004 (0.055)	0.000	14435 (4384)	0.999
Panhandle	50	-0.008 (0.079)	0.044	30 (17)	0.873
	100	-0.008 (0.065)	0.004	52 (25)	0.930
	250	-0.009 (0.055)	0.000	111 (42)	0.970
	500	-0.010 (0.050)	0.000	198 (59)	0.984
	750	-0.010 (0.049)	0.000	299 (112)	0.990
	1000	-0.010 (0.048)	0.000	400 (132)	0.992
	2500	-0.009 (0.047)	0.000	1025 (288)	0.997
	5000	-0.008 (0.047)	0.000	2247 (626)	0.998
	10000	-0.009 (0.047)	0.000	4446 (1264)	0.999
	20000	-0.008 (0.047)	0.000	9211 (2742)	0.999

The effects of this disease on gopher tortoise population dynamics is clearly evident from the model results. All stochastic growth rates are considerably reduced from their baseline values, population trajectories are therefore severely attenuated, and population heterozygosity is reduced among the smallest populations to a level at or below what is considered to be minimally viable. Most importantly, we see that the specific response of a population to this disease has strong regional specificity: Stochastic population growth rates in the South region remain (only slightly) positive, but the North Central and Panhandle regions now show negative growth rates as low as -1.0% annually. As a result, the final population size is reduced by as much as 60% of the original number. More detailed simulations (not presented here) indicate that the primary agent responsible for the population decline is the chronic increase in annual mortality and not the periodic catastrophic changes in survivorship and reproductive success.

Figure 4. Size trajectories for regional gopher tortoise populations with the inclusion of Upper Respiratory Tract Disease (URTD). See text for additional details.



As can be seen from Table 6, this dramatic reduction in growth rate now carries with it a risk that the smallest populations among those distributed across Florida may become demographically and/or genetically unstable and decline to extinction. Moreover, this risk will likely be even greater than that listed here for the smallest populations in the state, since the smallest simulated population here consisted of 50 individuals. Data in Appendix II suggest that about 35 populations may contain less than fifty tortoises.

Based on our analysis, we may conclude that URTD is a significant threat to gopher tortoise populations across Florida, with those populations inhabiting the North Central and Panhandle regions at greatest risk for significant detrimental effects. While certainly possible, it is important to remember that the field data linking individual tortoise mortality to URTD infection is scanty or indirect at best. Our parameterization of the disease and its demographic consequences is essentially very conservative; in other words, we are aiming to develop scenarios that may describe what could happen in the event of widespread URTD infection of tortoise populations across Florida. The results presented here should raise a red flag to those involved in gopher tortoise management; priority should be given to a more systematic and detailed analysis of the prevalence of the disease and, more importantly, the detailed impacts on tortoise survival.

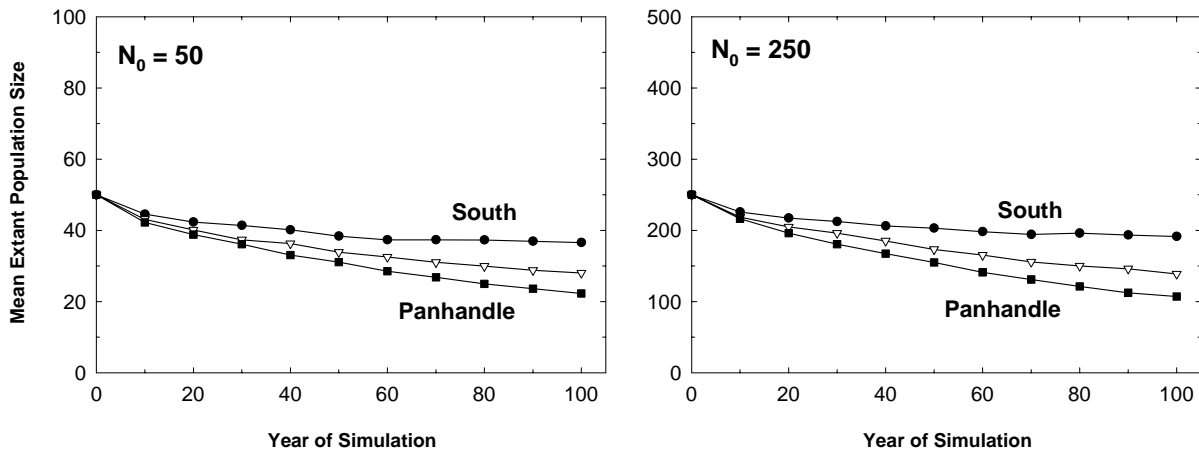
IV: URTD and Restricted Population Carrying Capacity

We then combined the two scenarios described above – restricted population carrying capacity and the introduction of Upper Respiratory Tract Disease – into a single set of region-specific modifications to the baseline data set. The results from these models are presented in Table 7 and Figure 5.

Table 7. Florida gopher tortoise population viability analysis: Baseline regional analysis with restricted population carrying capacity ($K = N_0$) and inclusion of Upper Respiratory Tract Disease (URTD). Results include stochastic growth rate (r_s (SD)), risk of population extinction ($P(E)$), final mean size of extant populations (N_{100} (SD)), and final population heterozygosity (H_{100}). See text for additional details on model input and output.

Region	N_0	r_s (SD)	$P(E)$	N_{100} (SD)	H_{100}
South	50	0.004 (0.089)	0.008	37 (12)	0.862
	100	0.002 (0.076)	0.000	74 (19)	0.931
	250	0.001 (0.066)	0.000	191 (43)	0.973
	500	0.001 (0.063)	0.000	390 (84)	0.986
	750	0.002 (0.062)	0.000	595 (113)	0.991
	1000	0.001 (0.062)	0.000	780 (156)	0.993
	2500	0.002 (0.061)	0.000	2078 (350)	0.997
	5000	0.003 (0.062)	0.000	4153 (707)	0.998
	10000	0.003 (0.063)	0.000	8493 (1259)	0.998
	20000	0.003 (0.063)	0.000	16946 (2605)	0.998
North Central	50	-0.004 (0.087)	0.032	28 (13)	0.850
	100	-0.004 (0.071)	0.000	57 (22)	0.923
	250	-0.005 (0.061)	0.000	139 (48)	0.970
	500	-0.006 (0.057)	0.000	245 (73)	0.984
	750	-0.006 (0.056)	0.000	401 (129)	0.990
	1000	-0.006 (0.055)	0.000	537 (170)	0.992
	2500	-0.005 (0.054)	0.000	1426 (410)	0.997
	5000	-0.005 (0.054)	0.000	2919 (771)	0.998
	10000	-0.004 (0.054)	0.000	6150 (1580)	0.999
	20000	-0.004 (0.055)	0.000	12676 (3119)	0.999
Panhandle	50	-0.009 (0.084)	0.036	22 (12)	0.844
	100	-0.008 (0.067)	0.000	45 (20)	0.922
	250	-0.009 (0.055)	0.000	107 (41)	0.969
	500	-0.010 (0.051)	0.000	187 (59)	0.983
	750	-0.010 (0.049)	0.000	268 (81)	0.989
	1000	-0.010 (0.048)	0.000	379 (118)	0.992
	2500	-0.009 (0.046)	0.000	995 (291)	0.997
	5000	-0.009 (0.047)	0.000	2031 (539)	0.998
	10000	-0.008 (0.047)	0.000	4336 (1229)	0.999
	20000	-0.008 (0.047)	0.000	8665 (2431)	0.999

Figure 5. Size trajectories for regional gopher tortoise populations with restricted population carrying capacity and the inclusion of Upper Respiratory Tract Disease (URTD). See text for additional details.



As expected, the results of these models closely follow those in which URTD is included but the carrying capacity is not altered. The most notable difference is the observation that populations in the South region are no longer capable of growing at a 0.1 – 0.2% annual rate as before when carrying capacity was not restricted (see Figure 4). Despite the general similarity, the increased rate of loss of heterozygosity in the smaller populations (Table 7) suggests that a reduced habitat carrying capacity can put smaller populations (i.e., less than 250) at an increased risk for stochastic destabilization from both demographic and genetic processes.

V. Baseline Regional Analysis – Increased Juvenile Mortality

The demographic sensitivity analysis presented earlier indicates that our model of gopher tortoise population dynamics is very sensitive to measurement uncertainty in the mortality rate of juveniles (age class 0 – 1). Based on this observation, it is instructive to investigate the behavior of our risk assessment models when some aspect of this measurement uncertainty is incorporated. Towards that end, we have repeated the entire suite of 120 models presented in subsections I – IV of this risk assessment discussion, and we have now increased juvenile mortality from its baseline value of 94.89% to 96.89%. This higher value is clearly within the biologically realistic range although, for reasons discussed previously, functionally indistinguishable from the original value in the field. Our purpose here is to assess a portion of the range of plausible outcomes for gopher tortoise populations across the state of Florida in the face of different vectors of human activity, uncertainty in our estimates of tortoise population biology and ecology, and the vagaries of stochastic population processes.

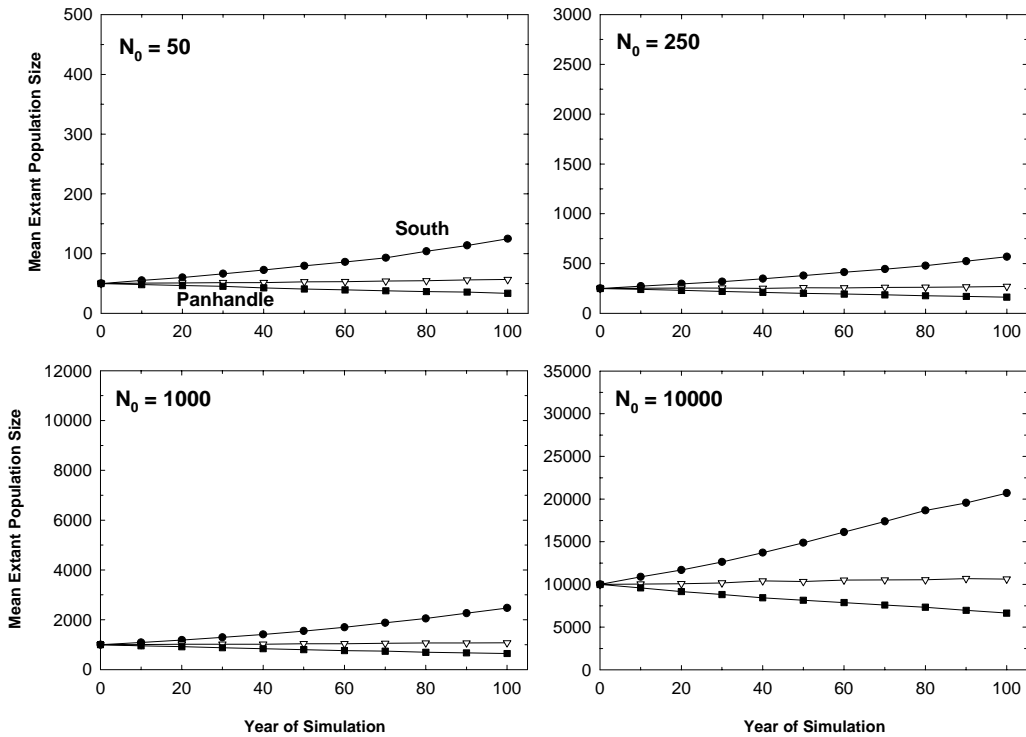
Increased juvenile mortality acts to markedly reduce population growth rates and, in Panhandle populations, leads to population decline over time (Table 8 and Figure 6). The magnitude of the effect is less than that seen in our URTD simulations, but it is substantial nevertheless. It is worth noting here that this reduction in growth rate – from about 2.6% to just 0.7% among South region populations – is the result of what, at first glance, seems like a rather small change in the rate at which newly-laid eggs survive to one year of age. More specifically, an increase in juvenile mortality from 94.89% to 96.89% means a decrease in the number of eggs that survive their first year from 0.35 to 0.21 individuals per successfully breeding adult female (given a

mean clutch size of 6.77 eggs per adult female). While these number may sound small, we are in effect reducing the reproductive output of each successful adult female by about 40%. The resultant effect on population performance is not so small. These additional models only serve to reinforce the results of our earlier sensitivity analysis, graphically illustrating the impact that small changes in a single demographic parameter can have on overall population dynamics.

Table 8. Florida gopher tortoise population viability analysis: Baseline regional analysis with elevated juvenile (age 0–1) mortality. Results defined as in Tables 4 – 7. See text for additional details.

Region	N_0	r_s (SD)	P(E)	N_{100} (SD)	H_{100}
South	50	0.007 (0.086)	0.000	125 (80)	0.938
	100	0.007 (0.081)	0.000	234 (131)	0.969
	250	0.007 (0.077)	0.000	568 (284)	0.988
	500	0.007 (0.075)	0.000	1158 (510)	0.994
	750	0.008 (0.075)	0.000	1774 (863)	0.996
	1000	0.008 (0.076)	0.000	2473 (1281)	0.997
	2500	0.007 (0.075)	0.000	5768 (2679)	0.999
	5000	0.008 (0.075)	0.000	11686 (4888)	0.999
	10000	0.007 (0.075)	0.000	20699 (6282)	1.000
	20000	0.007 (0.074)	0.000	25963 (3675)	1.000
North Central	50	-0.001 (0.081)	0.000	57 (34)	0.920
	100	0.000 (0.074)	0.000	108 (50)	0.960
	250	0.000 (0.069)	0.000	270 (121)	0.984
	500	0.001 (0.068)	0.000	577 (242)	0.993
	750	0.000 (0.067)	0.000	848 (345)	0.995
	1000	0.000 (0.066)	0.000	1072 (435)	0.996
	2500	0.000 (0.066)	0.000	2664 (958)	0.998
	5000	0.000 (0.065)	0.000	5264 (2018)	0.999
	10000	0.000 (0.066)	0.000	10643 (4275)	1.000
	20000	0.000 (0.065)	0.000	19560 (5842)	1.000
Panhandle	50	-0.006 (0.080)	0.008	34 (19)	0.902
	100	-0.005 (0.069)	0.000	67 (31)	0.953
	250	-0.005 (0.064)	0.000	162 (71)	0.981
	500	-0.005 (0.062)	0.000	336 (134)	0.991
	750	-0.005 (0.061)	0.000	476 (170)	0.994
	1000	-0.005 (0.061)	0.000	642 (261)	0.995
	2500	-0.005 (0.060)	0.000	1572 (540)	0.998
	5000	-0.005 (0.060)	0.000	3305 (1261)	0.999
	10000	-0.005 (0.060)	0.000	6647 (2379)	1.000
	20000	-0.005 (0.059)	0.000	13403 (4918)	1.000

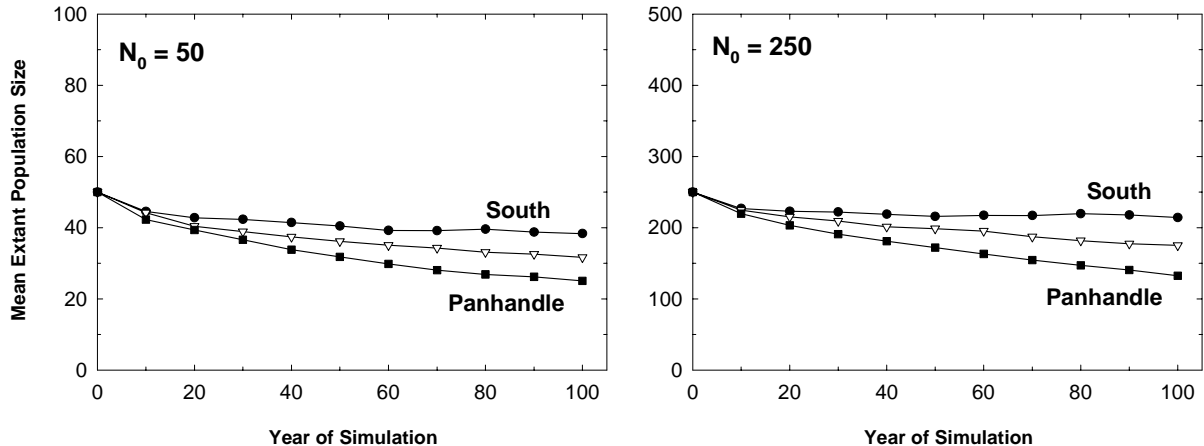
Figure 6. Size trajectories for simulated gopher tortoise populations over a range of initial population sizes and with increased juvenile mortality. Different plots within each graph show trajectories for populations within specific regions. See text for additional details.



VI. Restricted Population Carrying Capacity – Increased Juvenile Mortality

The impacts of increased juvenile mortality are very similar when carrying capacity is reduced to a level equivalent with initial population size (Table 9 and Figure 7).

Figure 7. Size trajectories for regional gopher tortoise populations with increased juvenile mortality and restricted population carrying capacity. See text for additional details.



Under these conditions, the smallest populations lose at least 10% of their original heterozygosity, thereby dipping below the minimum level of retention (90%) considered by many population managers to define long-term genetic viability. In addition, the North Central population in this and the immediately preceding set of models shows an average stochastic population growth rate very close to 0.000. In this case, these populations would not be able to tolerate any additional pressure from human activities that would compromise survival to any additional extent.

Table 9. Florida gopher tortoise population viability analysis: Baseline regional analysis with elevated juvenile (age 0–1) mortality and restricted population carrying capacity ($K = N_0$). Results defined as in Tables 4 – 7. See text for additional details.

Region	N_0	r_s (SD)	P(E)	N_{100} (SD)	H_{100}	
South	50	0.006 (0.091)	0.000	38 (10)	0.898	
	100	0.007 (0.083)	0.000	83 (15)	0.952	
	250	0.007 (0.078)	0.000	214 (29)	0.981	
	500	0.007 (0.076)	0.000	430 (63)	0.990	
	750	0.008 (0.076)	0.000	655 (84)	0.994	
	1000	0.008 (0.075)	0.000	874 (120)	0.995	
	2500	0.007 (0.075)	0.000	2173 (287)	0.998	
	5000	0.007 (0.075)	0.000	4330 (546)	0.999	
	10000	0.007 (0.075)	0.000	8784 (1131)	1.000	
	20000	0.007 (0.075)	0.000	17523 (2080)	1.000	
	North Central	50	-0.001 (0.086)	0.012	32 (12)	0.892
		100	-0.001 (0.075)	0.000	66 (21)	0.947
		250	0.000 (0.069)	0.000	175 (47)	0.980
		500	0.000 (0.068)	0.000	365 (80)	0.991
		750	0.000 (0.067)	0.000	572 (121)	0.994
1000		0.000 (0.066)	0.000	757 (169)	0.995	
2500		0.001 (0.066)	0.000	1917 (389)	0.998	
5000		0.000 (0.066)	0.000	3794 (829)	0.999	
10000		0.000 (0.066)	0.000	7523 (1638)	1.000	
20000		0.000 (0.066)	0.000	14907 (3262)	1.000	
Panhandle		50	-0.007 (0.085)	0.032	25 (12)	0.881
		100	-0.005 (0.071)	0.000	55 (21)	0.947
		250	-0.006 (0.064)	0.000	132 (47)	0.979
		500	-0.005 (0.063)	0.000	281 (85)	0.990
		750	-0.005 (0.061)	0.000	420 (134)	0.993
	1000	-0.005 (0.061)	0.000	578 (175)	0.995	
	2500	-0.005 (0.060)	0.000	1398 (435)	0.998	
	5000	-0.005 (0.060)	0.000	2876 (866)	0.999	
	10000	-0.004 (0.060)	0.000	5816 (1771)	1.000	
	20000	-0.005 (0.060)	0.000	11283 (3209)	1.000	

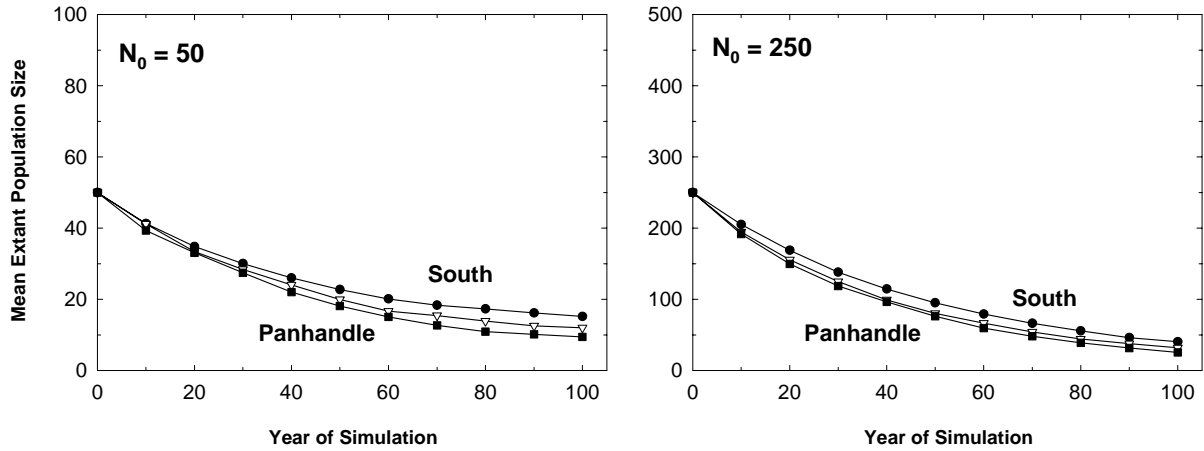
VII. Upper Respiratory Tract Disease – Increased Juvenile Mortality

The combined effect of increased baseline juvenile mortality and the introduction of still greater mortality brought on by URTD is indeed severe (Table 10 and Figure 8). Under this scenario all population growth rates are negative, final populations are correspondingly reduced to just 15 – 30% of their original size, and the smallest populations incur a significant risk of extinction within the 100-year timeframe. Levels of retention of genetic variation drop below acceptable in the two smallest population size classes, and populations as large as 250 individuals are now at risk of extinction.

Table 10. Florida gopher tortoise population viability analysis: Baseline regional analysis with elevated juvenile (age 0–1) mortality and inclusion of Upper Respiratory Tract Disease (URTD). Results defined as in Tables 4 – 7. See text for additional details.

Region	N_0	r_s (SD)	P(E)	N_{100} (SD)	H_{100}
South	50	-0.019 (0.115)	0.284	15 (10)	0.763
	100	-0.020 (0.102)	0.084	21 (14)	0.845
	250	-0.021 (0.089)	0.016	40 (26)	0.923
	500	-0.021 (0.083)	0.000	71 (40)	0.960
	750	-0.022 (0.080)	0.000	102 (61)	0.973
	1000	-0.022 (0.079)	0.000	135 (75)	0.980
	2500	-0.021 (0.077)	0.000	342 (207)	0.992
	5000	-0.020 (0.077)	0.000	824 (488)	0.996
	10000	-0.020 (0.077)	0.000	1522 (854)	0.997
	20000	-0.020 (0.077)	0.000	3114 (1605)	0.997
North Central	50	-0.021 (0.113)	0.324	12 (10)	0.768
	100	-0.022 (0.098)	0.112	17 (12)	0.850
	250	-0.022 (0.083)	0.008	32 (16)	0.921
	500	-0.023 (0.076)	0.000	55 (30)	0.957
	750	-0.023 (0.073)	0.000	81 (39)	0.972
	1000	-0.024 (0.072)	0.000	100 (50)	0.977
	2500	-0.024 (0.070)	0.000	255 (142)	0.991
	5000	-0.024 (0.069)	0.000	536 (299)	0.995
	10000	-0.023 (0.069)	0.000	1118 (512)	0.997
	20000	-0.023 (0.069)	0.000	2286 (1138)	0.998
Panhandle	50	-0.025 (0.106)	0.444	9 (6)	0.779
	100	-0.024 (0.093)	0.172	14 (10)	0.847
	250	-0.025 (0.076)	0.008	25 (13)	0.919
	500	-0.025 (0.068)	0.000	47 (24)	0.958
	750	-0.025 (0.066)	0.000	66 (31)	0.970
	1000	-0.026 (0.064)	0.000	85 (42)	0.977
	2500	-0.026 (0.061)	0.000	214 (96)	0.991
	5000	-0.025 (0.060)	0.000	450 (170)	0.996
	10000	-0.025 (0.060)	0.000	878 (395)	0.997
	20000	-0.025 (0.061)	0.000	1792 (783)	0.998

Figure 8. Size trajectories for regional gopher tortoise populations with increased juvenile mortality and inclusion of Upper Respiratory Tract Disease (URTD). See text for additional details.



It is important to observe in Table 10 and especially in Figure 8 that a negligible risk of population extinction does not in any way imply population security. The long generation time in this species helps to mask the impact of a steady population decline, at least from the perspective of detecting a significant risk of population extinction. Among all population size classes, the extent of population reduction is significant and approaches 90% in some cases. Clearly, these populations are highly unstable and subject to near certain extinction just a short time beyond the window of this simulation.

VIII. Restricted Population Carrying Capacity and URTD – Increased Juvenile Mortality

The worst-case scenario combines a higher baseline mortality rate with a restriction in habitat carrying capacity and the introduction of URTD. The results of this final set of simulations is presented in Table 11 and Figure 9.

Figure 9. Size trajectories for regional gopher tortoise populations with increased juvenile mortality, restricted population carrying capacity and inclusion of Upper Respiratory Tract Disease (URTD). See text for additional details.

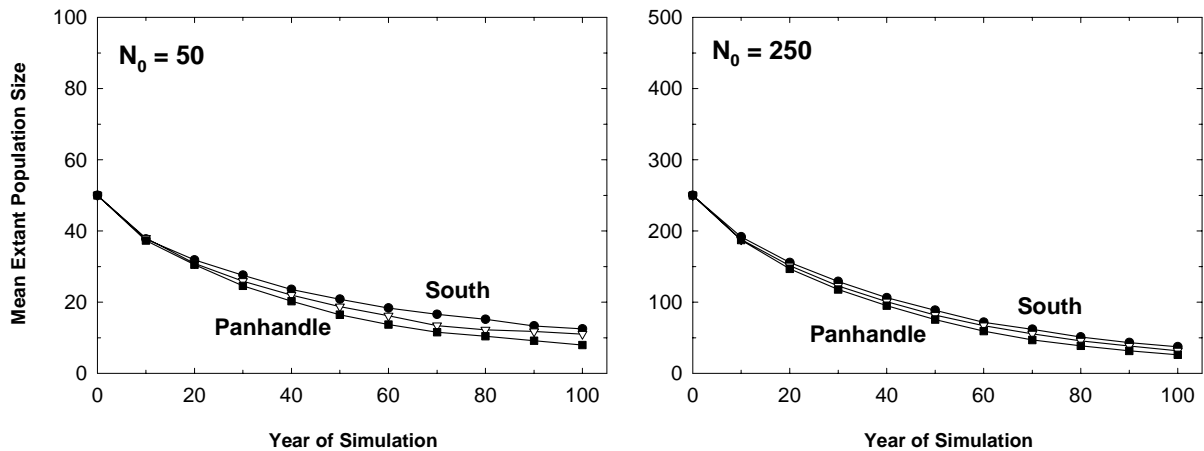


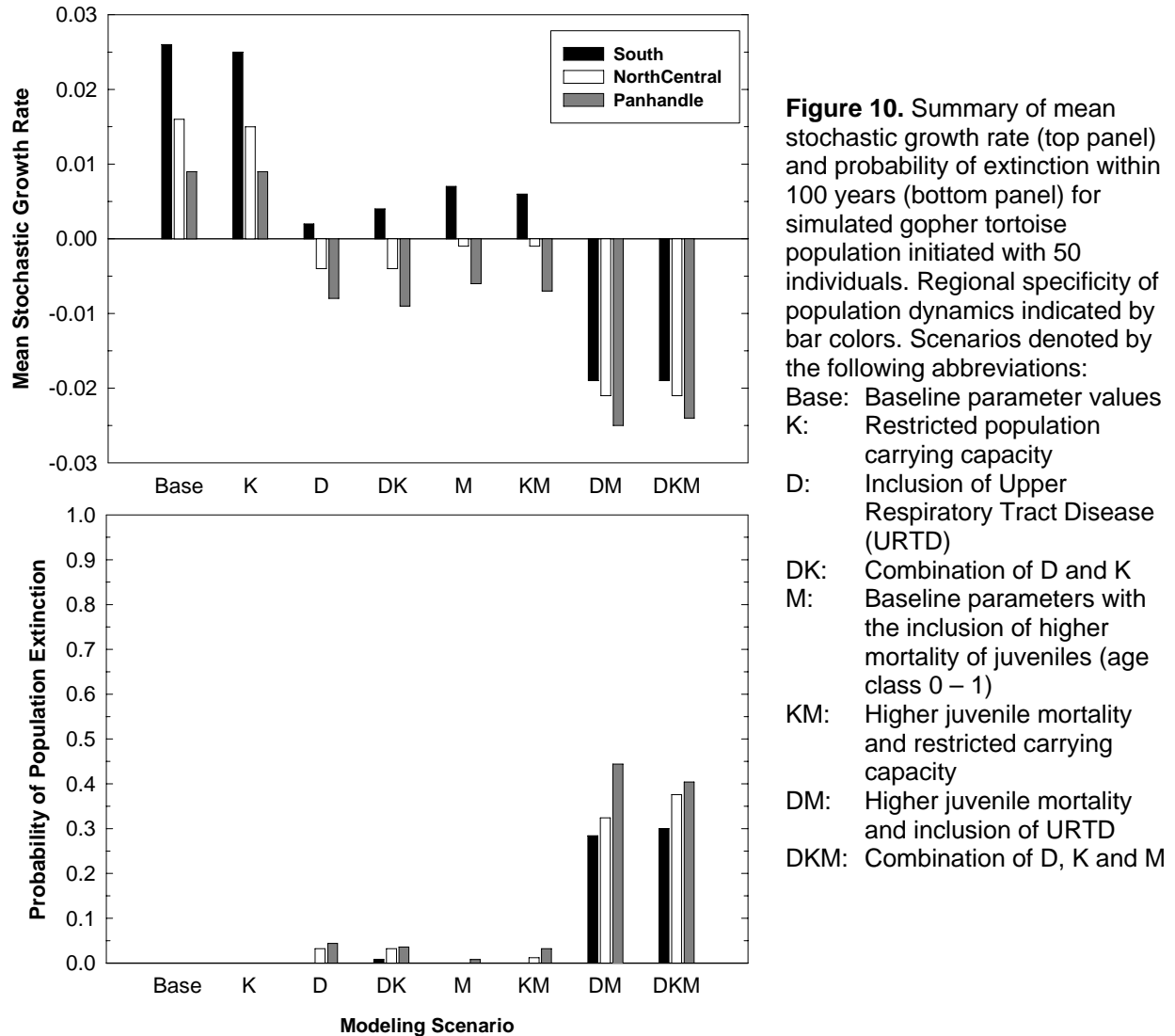
Table 11. Florida gopher tortoise population viability analysis: Baseline regional analysis with elevated juvenile (age 0–1) mortality, restricted population carrying capacity ($K = N_0$) and inclusion of Upper Respiratory Tract Disease (URTD). Results defined as in Tables 4 – 7. See text for additional details.

Region	N_0	r_s (SD)	P(E)	N_{100} (SD)	H_{100}
South	50	-0.019 (0.119)	0.300	12 (9)	0.760
	100	-0.020 (0.104)	0.132	19 (13)	0.842
	250	-0.021 (0.089)	0.000	37 (24)	0.914
	500	-0.021 (0.082)	0.000	67 (37)	0.957
	750	-0.020 (0.080)	0.000	109 (65)	0.974
	1000	-0.022 (0.079)	0.000	127 (73)	0.979
	2500	-0.021 (0.077)	0.000	329 (169)	0.991
	5000	-0.020 (0.077)	0.000	748 (404)	0.995
	10000	-0.020 (0.077)	0.000	1421 (817)	0.997
	20000	-0.019 (0.078)	0.000	3096 (1615)	0.998
North Central	50	-0.021 (0.113)	0.376	11 (7)	0.766
	100	-0.022 (0.098)	0.156	16 (11)	0.837
	250	-0.022 (0.083)	0.004	31 (18)	0.923
	500	-0.024 (0.077)	0.000	51 (25)	0.955
	750	-0.023 (0.074)	0.000	78 (38)	0.969
	1000	-0.024 (0.072)	0.000	96 (45)	0.977
	2500	-0.024 (0.069)	0.000	246 (112)	0.991
	5000	-0.024 (0.069)	0.000	502 (241)	0.995
	10000	-0.023 (0.069)	0.000	1076 (574)	0.997
	20000	-0.023 (0.069)	0.000	2206 (1032)	0.998
Panhandle	50	-0.024 (0.108)	0.404	8 (5)	0.758
	100	-0.024 (0.092)	0.164	13 (8)	0.841
	250	-0.024 (0.076)	0.016	26 (16)	0.916
	500	-0.026 (0.069)	0.004	43 (22)	0.954
	750	-0.026 (0.067)	0.000	62 (31)	0.967
	1000	-0.025 (0.064)	0.000	83 (32)	0.978
	2500	-0.026 (0.061)	0.000	195 (87)	0.991
	5000	-0.026 (0.060)	0.000	406 (175)	0.995
	10000	-0.025 (0.060)	0.000	885 (384)	0.997
	20000	-0.025 (0.061)	0.000	1767 (744)	0.998

Under this unfavorable set of circumstances, we see the familiar pattern: negative population growth rates centered around -0.021 , significant risk of extinction among populations smaller than about 100 individuals, dramatic population declines over the 100-year simulation timeframe, and significant loss of genetic variation in populations of less than 100 individuals. An examination of this entire second set of risk assessment models that included a slight increase in juvenile mortality shows that all gopher tortoise populations – regardless of their current size – are not sustainable and would continue to decline in the absence of specific management actions designed to reduce the pressure on individual survivorship.

Summary

The final results of the 240 risk assessment models that were developed for this gopher tortoise population viability analysis can be summarized by presenting the encapsulated results for the smallest population class in the analysis – initiated with just 50 individuals (Figure 10).



The regional specificity of population growth rates is clearly evident, resulting from delayed onset of breeding in northern populations due to shortened growing season, as is the relatively negligible impact of a restricted population carrying capacity on a species showing very low levels of environmental variability in vital rates. The incorporation of additional mortality – either in the form of URTD affecting adults or through a demonstration of measurement uncertainty in juvenile mortality – leads to a more complicated pattern of regionally-specific responses. While southern populations remain capable of increasing in size, central and northern populations do not have the capacity to buffer themselves against the additional mortality and

show average rates of decline. When additional juvenile mortality is combined with the additional adult mortality inherent to URTD infection, all regional populations are greatly destabilized, growth rates decline dramatically, and the smallest populations are at a substantial risk of extinction within the 100 year window that makes up this analysis.

We can utilize additional information from the demographic sensitivity analysis to develop a simple table of stochastic growth rates under the suite of conditions that are relevant for the Biological Status Report to be drafted for this species in Florida:

Region	Modeling Scenario*							
	A	B	C	D	E	F	G	H
South	0.026	0.007	0.016	-0.006	0.002	-0.019	-0.006	-0.030
North-Central	0.016	-0.001	0.007	-0.010	-0.004	-0.021	-0.012	-0.032
Panhandle	0.009	-0.006	0.001	-0.014	-0.008	-0.025	-0.016	-0.032

* A: Baseline

B: Increased juvenile mortality (96.89%)

C: Increased adult mortality (5.3%)

D: Increased juvenile and adult mortality

E: Baseline with URTD

F: Increased juvenile mortality with URTD

G: Increased adult mortality with URTD

H: Increased juvenile and adult mortality with URTD

This condensed set of information can be used to project future population sizes under a variety of scenarios for populations inhabiting any one of the three regions across the state. The regional specificity in growth rate, the enhanced sensitivity of our *VORTEX* model to uncertainty in both juvenile and adult mortality, and the marked impact of URTD are all apparent in this table.

Conclusions

We may conclude our analysis of Florida gopher tortoise population viability by returning to the original set of questions that provided the foundation for our study.

- *Does the gopher tortoise have a $\geq 20\%$ probability of extinction in Florida over the next 100 years (3 generations)?*

No. While individual small populations may be at risk under specific scenarios, the statewide population is not at risk of extinction. It is important to remember, however, that certain threat scenarios could result in populations across the state to begin a long-term decline that would put the populations at significant risk over longer time periods.

- *Does the gopher tortoise have a $\geq 10\%$ probability of extinction in Florida over the next 100 years (3 generations)?*

No. While individual small populations may be at risk under specific scenarios, the statewide population is not at risk of extinction. It is important to remember, however, that certain

threat scenarios could result in populations across the state to begin a long-term decline that would put the populations at significant risk over longer time periods.

- *Does the gopher tortoise have a $\geq 20\%$ probability of extinction in Florida over the next 100 years (3 generations) considering only populations on public lands? On lands where FWC is the lead manager?*

No in both cases. Extinction risk to any population that exceeds approximately 500 individuals is minimal, even in the most pessimistic scenario created here. It is important to remember, however, that certain threat scenarios could result in populations across the state to begin a long-term decline that would put the populations at significant risk over longer time periods.

- *Does the gopher tortoise have a $\geq 10\%$ probability of extinction in Florida over the next 100 years (3 generations) considering only populations on public lands? On lands where FWC is the lead manager?*

No in both cases. Extinction risk to any population that exceeds approximately 500 individuals is minimal, even in the most pessimistic scenario created here. It is important to remember, however, that certain threat scenarios could result in populations across the state to begin a long-term decline that would put the populations at significant risk over longer time periods.

- *What is the smallest-sized population of long-term (ca. 100+ yrs) conservation value by habitat/geographic strata (acreage and number of mature individuals)?*

Based on the analyses presented here, populations as small as 50 individuals can have significant conservation value under favorable conditions. The low levels of environmentally-induced variability in population demographic rates appear to have a significant buffering effect on the growth dynamics of gopher tortoise populations. This leads to a dampening of the variability in population size from year to year, thereby minimizing the risk of stochastic extinction even among populations that would be considered to be very small in other species of wildlife. Less favorable conditions, such as the introduction of severe forms of Upper Respiratory Tract Disease or an increase in mortality of either adults or juveniles, could render these smaller populations extremely vulnerable to extinction. Populations larger than about 250 individuals would be necessary to provide significant protection against stochastic extinction under these circumstances.

- *Is the current relocation / restocking program an effective component of the statewide tortoise conservation program?*

The analyses presented here are not designed to address this particular management option. Additional analyses specifically designed to simulate the characteristics of the restocking program would be necessary to provide insight into the issue.

- *What are the characteristics and consequences of the upper respiratory tract disease (URTD) now infecting gopher tortoise populations across Florida?*

The URTD analyses developed here show that the disease can have a significant effect on the likelihood of gopher tortoise population persistence. However, because these models are based on very little quantitative field data, substantial refinement of the models with

additional data on URTD epidemiology and ecology would be required before detailed management recommendations could be developed from them.

References

- Diemer Berish, J.E., L.D. Wendland, and C.A. Gates. 2000. Distribution and prevalence of upper respiratory tract disease in gopher tortoises in Florida. *Journal of Herpetology* 34:5-12.
- Forcada, J. 2000. Can population surveys show if the Mediterranean monk seal colony at Cap Blanc is declining in abundance? *Journal of Applied Ecology* 37:171-181.
- Lacy, R.C. 2000. Structure of the *VORTEX* simulation model for population viability analysis. *Ecological Bulletins* 48:191-203.
- Landers, J.L. 1980. Recent research on the gopher tortoise and its implications. Pages 8 – 14 in Franz, R. and R.J. Bryant (eds.). *The Dilemma of the Gopher Tortoise – Is There a Solution? Proceedings of the First Annual Meeting, Gopher Tortoise Council.*
- Landers, J.L., J.A. Garner, and W.A. McRae. 1980. Reproduction of the gopher tortoise (*Gopherus polyphemus*) in southwestern Georgia. *Herpetologica* 36:353-361.
- Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and maturity of the gopher tortoise in southwestern Georgia. *Bulletin of the Florida State Museum of Biological Science* 27:81-110.
- McCoy, E.D., and H.R. Mushinsky. 1992. Studying a species in decline: Gopher tortoises and the dilemma of “correction factors”. *Herpetologica* 48:402-407.
- Miller, P.S., and R.C. Lacy. 1999. *VORTEX: A Stochastic Simulation of the Extinction Process. Version 8 User’s Manual.* Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).

Appendix I

Simulation Modeling and Population Viability Analysis

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

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

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

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

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

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

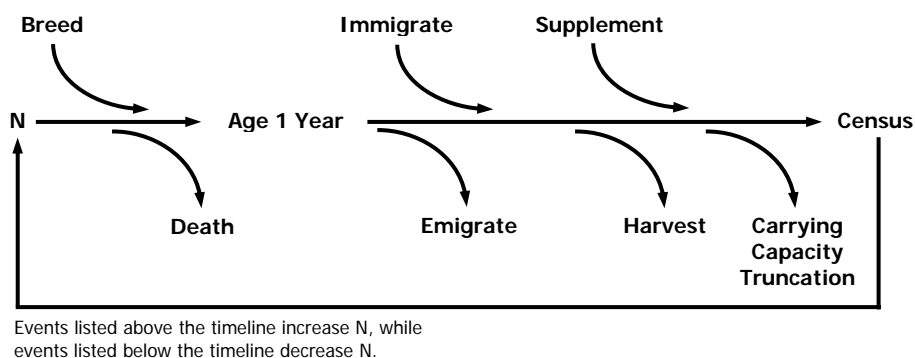
Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon,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

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

The *VORTEX* Population Viability Analysis Model

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

VORTEX Simulation Model Timeline



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

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

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

VORTEX 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 Miller and Lacy (1999) and Lacy (2000).

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.

Literature Cited

- Gilpin, M.E., and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19 – 34 in: Soulé, M.E. (ed.). *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer Associates.
- Jiménez, J.A., K.A. Hughes, G. Alaks, L. Graham, and R.C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266:271-273.
- Lacy, R.C. 1993b. Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biology and Medicine* 36:480-496.
- Lacy, R.C. 1993/1994. What is Population (and Habitat) Viability Analysis? *Primate Conservation* 14/15:27-33.
- Lacy, R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins* 48:191-203.
- Miller, P.S., and R.C. Lacy. 1999. *VORTEX: A Stochastic Simulation of the Extinction Process. Version 8 User's Manual*. Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).
- Ralls, K., J.D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* 2:185-193.
- Shaffer, M.L. 1981. Minimum population sizes for species conservation. *BioScience* 1:131-134.
- Soulé, M., M. Gilpin, W. Conway, and T. Foose. 1986. The millennium ark: How long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101-113.

Appendix III

Sample *VORTEX* Output File

VORTEX 8.41 -- simulation of genetic and demographic stochasticity

GT101D.OUT

Tue Oct 23 17:34:09 2001

1 population(s) simulated for 100 years, 250 iterations

Extinction is defined as no animals of one or both sexes.

No inbreeding depression

First age of reproduction for females: 11 for males: 11

Maximum breeding age (senescence): 60

Sex ratio at birth (percent males): 50.000000

Population: Pop1

Polygynous mating; all adult males in the breeding pool.

% adult females breeding = 95-(9.5*(SRAND(Y+(R*100))<0.02))

EV in % adult females breeding = 1.50 SD

Of those females producing litters, ...

0.00 percent of females produce litters of size 1

0.00 percent of females produce litters of size 2

0.00 percent of females produce litters of size 3

3.20 percent of females produce litters of size 4

12.00 percent of females produce litters of size 5

30.40 percent of females produce litters of size 6

28.80 percent of females produce litters of size 7

14.40 percent of females produce litters of size 8

7.20 percent of females produce litters of size 9

4.00 percent of females produce litters of size 10

94.86 percent mortality of females between ages 0 and 1

EV in % mortality = 3.500000 SD

27.10 percent mortality of females between ages 1 and 2

EV in % mortality = 3.000000 SD

8.40 percent mortality of females between ages 2 and 3

EV in % mortality = 1.000000 SD

3.30 percent mortality of females between ages 3 and 4

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 4 and 5

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 5 and 6

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 6 and 7

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 7 and 8

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 8 and 9

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 9 and 10

EV in % mortality = 0.500000 SD

3.30 percent mortality of females between ages 10 and 11

9 December, 2001

```

EV in % mortality = 0.500000 SD
% mortality of adult females (11<=age<=60) = 6.3+(21.2*(SRAND(Y+(R*100))<0.02))
EV in % mortality = 0.500000 SD
94.86 percent mortality of males between ages 0 and 1
EV in % mortality = 3.500000 SD
27.10 percent mortality of males between ages 1 and 2
EV in % mortality = 3.000000 SD
8.40 percent mortality of males between ages 2 and 3
EV in % mortality = 1.000000 SD
3.30 percent mortality of males between ages 3 and 4
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 4 and 5
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 5 and 6
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 6 and 7
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 7 and 8
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 8 and 9
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 9 and 10
EV in % mortality = 0.500000 SD
3.30 percent mortality of males between ages 10 and 11
EV in % mortality = 0.500000 SD
% mortality of adult males (11<=age<=60) = 6.3+(21.2*(SRAND(Y+(R*100))<0.02))
EV in % mortality = 0.500000 SD

```

EVs may be adjusted to closest values possible for binomial distribution.
 EV in mortality will be concordant among age-sex classes
 but independent from EV in reproduction.

Initial size of Pop1: 50
 (set to reflect stable age distribution)

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14
15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
60	Total													
	2	1	2	1	1	1	2	1	1	1	1	0	1	1
1	0	1	0	1	0	1	0	1	0	0	1	0	0	0
1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	25 Males													
	2	1	2	1	1	1	2	1	1	1	1	0	1	1
1	0	1	0	1	0	1	0	1	0	0	1	0	0	0
1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	25 Females													

Carrying capacity = 500
 EV in Carrying capacity = 0.00 SD

Deterministic population growth rate
 (based on females, with assumptions of
 no limitation of mates, no density dependence, no functional dependencies, and no
 inbreeding depression)

r = 0.011 lambda = 1.011 R0 = 1.287
 Generation time for: females = 23.18 males = 23.18

9 December, 2001

Stable age distribution:	Age class	females	males
	0	0.307	0.307
	1	0.016	0.016
	2	0.011	0.011
	3	0.010	0.010
	4	0.010	0.010
	5	0.009	0.009
	6	0.009	0.009
	7	0.009	0.009
	8	0.008	0.008
	9	0.008	0.008
	10	0.007	0.007
	11	0.007	0.007
	12	0.007	0.007
	13	0.006	0.006
	14	0.006	0.006
	15	0.005	0.005
	16	0.005	0.005
	17	0.005	0.005
	18	0.004	0.004
	19	0.004	0.004
	20	0.004	0.004
	21	0.003	0.003
	22	0.003	0.003
	23	0.003	0.003
	24	0.003	0.003
	25	0.002	0.002
	26	0.002	0.002
	27	0.002	0.002
	28	0.002	0.002
	29	0.002	0.002
	30	0.002	0.002
	31	0.002	0.002
	32	0.001	0.001
	33	0.001	0.001
	34	0.001	0.001
	35	0.001	0.001
	36	0.001	0.001
	37	0.001	0.001
	38	0.001	0.001
	39	0.001	0.001
	40	0.001	0.001
	41	0.001	0.001
	42	0.001	0.001
	43	0.001	0.001
	44	0.001	0.001
	45	0.001	0.001
	46	0.001	0.001
	47	0.000	0.000
	48	0.000	0.000
	49	0.000	0.000
	50	0.000	0.000
	51	0.000	0.000
	52	0.000	0.000
	53	0.000	0.000
	54	0.000	0.000
	55	0.000	0.000
	56	0.000	0.000
	57	0.000	0.000
	58	0.000	0.000
	59	0.000	0.000
	60	0.000	0.000

Population 1: Pop1

Year 10

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 250, P[S] = 1.000
 Mean size (all populations) = 52.76 (0.67 SE, 10.53 SD)
 Means across extant populations only:
 Population size = 52.76 (0.67 SE, 10.53 SD)
 Expected heterozygosity = 0.979 (0.000 SE, 0.003 SD)
 Observed heterozygosity = 1.000 (0.000 SE, 0.000 SD)
 Number of extant alleles = 63.34 (0.49 SE, 7.77 SD)

Year 20

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 250, P[S] = 1.000
 Mean size (all populations) = 56.68 (1.04 SE, 16.40 SD)
 Means across extant populations only:
 Population size = 56.68 (1.04 SE, 16.40 SD)
 Expected heterozygosity = 0.971 (0.000 SE, 0.005 SD)
 Observed heterozygosity = 0.997 (0.000 SE, 0.007 SD)
 Number of extant alleles = 48.05 (0.52 SE, 8.26 SD)

Year 30

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 250, P[S] = 1.000
 Mean size (all populations) = 59.87 (1.50 SE, 23.68 SD)
 Means across extant populations only:
 Population size = 59.87 (1.50 SE, 23.68 SD)
 Expected heterozygosity = 0.962 (0.001 SE, 0.009 SD)
 Observed heterozygosity = 0.989 (0.001 SE, 0.015 SD)
 Number of extant alleles = 39.55 (0.51 SE, 8.14 SD)

Year 40

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 250, P[S] = 1.000
 Mean size (all populations) = 61.16 (1.61 SE, 25.52 SD)
 Means across extant populations only:
 Population size = 61.16 (1.61 SE, 25.52 SD)
 Expected heterozygosity = 0.953 (0.001 SE, 0.014 SD)
 Observed heterozygosity = 0.980 (0.001 SE, 0.022 SD)
 Number of extant alleles = 33.59 (0.53 SE, 8.32 SD)

Year 50

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 250, P[S] = 1.000
 Mean size (all populations) = 65.18 (1.96 SE, 30.93 SD)
 Means across extant populations only:
 Population size = 65.18 (1.96 SE, 30.93 SD)
 Expected heterozygosity = 0.944 (0.001 SE, 0.019 SD)
 Observed heterozygosity = 0.972 (0.002 SE, 0.029 SD)
 Number of extant alleles = 29.50 (0.50 SE, 7.94 SD)

Year 60

N[Extinct] = 0, P[E] = 0.000
 N[Surviving] = 250, P[S] = 1.000
 Mean size (all populations) = 67.79 (2.15 SE, 33.92 SD)
 Means across extant populations only:
 Population size = 67.79 (2.15 SE, 33.92 SD)
 Expected heterozygosity = 0.934 (0.002 SE, 0.026 SD)
 Observed heterozygosity = 0.964 (0.002 SE, 0.032 SD)
 Number of extant alleles = 26.29 (0.49 SE, 7.77 SD)

9 December, 2001

Year 70

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 250, P[S] = 1.000
Mean size (all populations) = 70.82 (2.36 SE, 37.31 SD)
Means across extant populations only:
Population size = 70.82 (2.36 SE, 37.31 SD)
Expected heterozygosity = 0.925 (0.002 SE, 0.034 SD)
Observed heterozygosity = 0.958 (0.002 SE, 0.034 SD)
Number of extant alleles = 23.93 (0.49 SE, 7.68 SD)

Year 80

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 250, P[S] = 1.000
Mean size (all populations) = 72.86 (2.56 SE, 40.49 SD)
Means across extant populations only:
Population size = 72.86 (2.56 SE, 40.49 SD)
Expected heterozygosity = 0.916 (0.002 SE, 0.037 SD)
Observed heterozygosity = 0.947 (0.003 SE, 0.040 SD)
Number of extant alleles = 22.01 (0.48 SE, 7.52 SD)

Year 90

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 250, P[S] = 1.000
Mean size (all populations) = 76.48 (2.92 SE, 46.21 SD)
Means across extant populations only:
Population size = 76.48 (2.92 SE, 46.21 SD)
Expected heterozygosity = 0.908 (0.003 SE, 0.042 SD)
Observed heterozygosity = 0.937 (0.003 SE, 0.043 SD)
Number of extant alleles = 20.44 (0.47 SE, 7.39 SD)

Year 100

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 250, P[S] = 1.000
Mean size (all populations) = 78.71 (3.01 SE, 47.67 SD)
Means across extant populations only:
Population size = 78.71 (3.01 SE, 47.67 SD)
Expected heterozygosity = 0.899 (0.003 SE, 0.054 SD)
Observed heterozygosity = 0.923 (0.004 SE, 0.064 SD)
Number of extant alleles = 19.07 (0.46 SE, 7.28 SD)

In 250 simulations of Pop1 for 100 years:
0 went extinct and 250 survived.

This gives a probability of extinction of 0.0000 (0.0000 SE),
or a probability of success of 1.0000 (0.0000 SE).

Means across all populations (extant and extinct) ...
Mean final population was 78.71 (3.01 SE, 47.67 SD)

Age	1	2	3	4	5	6	7	8	9	10	Adults	Total	
	3.07	2.32	2.08	2.01	1.96	1.81	1.76	1.58	1.67	1.49	19.90	39.64	Males
	3.14	2.26	2.04	2.15	1.76	1.88	1.92	1.59	1.49	1.46	19.38	39.07	Females

Across all years, prior to carrying capacity truncation,
mean growth rate (r) was 0.0024 (0.0005 SE, 0.0825 SD)

Final expected heterozygosity was 0.8990 (0.0034 SE, 0.0536 SD)
Final observed heterozygosity was 0.9230 (0.0041 SE, 0.0645 SD)
Final number of alleles was 19.07 (0.46 SE, 7.28 SD)
