Population Viability Without Population Data: Creating a Virtual Population Profile

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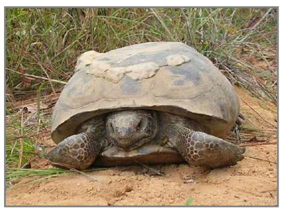


Abstract: Population models can be a powerful tool for management of declining species, but a limiting factor is often the lack of complete life-history data. Such comprehensive data are generally not available for most species, and existing models have generally used data from multiple populations over a shorter time span per population, compiled information from the literature, or have accepted (or even incorporated) uncertainty into the model. We illustrate this situation using as a case study the gopher tortoise (*Gopherus polyphemus*), which is considered to be declining throughout its southeastern U.S. range. Despite extensive study, there is little long-term data on individual populations from which life history parameters can be estimated. We developed a basic population model for the tortoise in VORTEX® based on >20 published studies, unpublished data, and expert opinion. We then manipulated the population model to reflect a range of initial population conditions and management scenarios (location within the range, habitat quality, population size) and to test parameter sensitivity. The overall goals of our effort were to: 1) evaluate the viability of individual populations, 2) estimate the capacity for habitat-based management approaches to improve population viability, and 3) determine whether non-viable populations require more intensive management or are more likely to contribute to conservation of the species through augmentation or translocation. We think this model represents the current understanding of gopher tortoise life history based on the best available estimates for parameter values. Bioinformatics can assist this by making more available the many small pieces of data necessary to develop a full picture, especially for declining species.

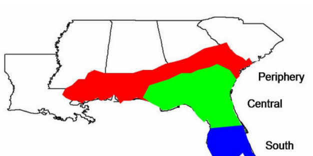
Our Plan…and Our Dilemma

VORTEX

We used the Vortex® PVA application to develop the viability analysis for the gopher tortoise (*Gopherus polyphemus*). The model inputs include standard life history parameters such as Breeding system, Age at first reproduction (Female/Male), Longevity, Annual % adult females reproducing, Maximum clutch size, Mean clutch size, Offspring sex ratio, Percent of adult males in breeding pool, and % annual mortality (by life stage). The problem was…we did not know most of these! So far as we could determine, no full data set had ever been recorded for a single population, and many of these parameters had never been firmly determined. Where to start? Fortunately, the Gopher tortoise has a fairly close-knit research community. We were able to assemble our data, or reasonable estimates, by delving into the literature and consulting with experts regarding their unpublished data. This is not always possible…or successful. One cannot help but feel that, in situations like this, bioinformatics databases such as the Encyclopedia of Life could fill a very useful role to bridge gaps in life history information for a species. The needs are not just for DNA catalogs, but also for more simplistic data such as we needed for the PVA.

Creating the Virtual Population

Thus, we developed baseline PVA models for the gopher tortoise using our personal knowledge, published data from throughout the species' range, and a large set of inputs from colleagues. Our models simulate single, closed populations based on the presumption that most remaining populations are functionally isolated from one another by habitat fragmentation and that populations under different management jurisdiction are generally managed as separate entities. We categorized simulated populations broadly in terms of intrinsic (e.g., initial population size) and extrinsic characteristics (e.g., location within the range, habitat quality) that land managers can apply to focal populations based on readily available information or easily collected data. The map shows our division into the Central, South and Peripheral areas, among which evidence suggests that tortoises have different potential for growth and sustainment. Within each of these geographic areas, we elected to define marginal and optimal habitats, related to soils and vegetation regimes. Thus, we had six combinations of region and habitat which we believed could affect one or more of the defined life history parameters. The table below shows the results of our search for Vortex® model data input parameters for our "baseline" model:



Vortex® input parameter	Values we used	Source(s) for Estimated Values
Breeding system	polygynous	Sources: Moon *et al.* 2006; Johnson *et al.* 2007
Age at first reproduction (Female/Male)		Site-specific factors (such as location within geographic range and habitat quality) presumably have systematic effects on tortoise growth and, as a result, age at maturity. Although length of the activity season (and opportunity for growth) varies with latitude, there is also evidence growth rates among tortoises can vary significantly among local populations as a result of habitat quality. Sources: Landers *et al.* 1982; Mushinsky *et al.* 1994; Aresco and Guyer 1999a;
Southern periphery - optimal habitat	13 / 12	
South periphery - marginal habitat	15 / 13	
Central range- optimal habitat	15 / 11	
Central range - marginal habitat	17 / 15	
Northern/western periphery - optimal habitat	20 / 17	
Northern/western periphery - marginal habitat	23 / 20	
Longevity	60	*Per* Miller et al. (2001)
Annual % adult females reproducing (S.D.)		Annual proportion of females in a population reproducing will presumably be greater and less variable from year to year in optimal habitat than marginal or unmanaged habitat. We chose less optimistic values (even under "optimal" habitat) than the values used in Miller *et al.* 2001. Sources: Smith *et al.* 1997; Rostal and Jones 2002;
optimal habitat	95 (5)	
marginal habitat	80 (10)	
Maximum clutch size	12	Sources: Landers *et al.* 1980; Diemer and Moore 1994; Mushinsky *et al.* 1994; Butler and Hull 1996; Smith *et al.* 1997; Rostal and Jones 2002; Epperson and Heise 2003; Pike and Seigel 2006;
Mean clutch size (S.D.)		Mean clutch sizes are categorized according to location within geographic range. Model constraints assume that clutch sizes do not vary with age of female. Sources: Iverson 1980; Wright 1982; Diemer and Moore 1994; Mushinsky *et al.* 1994; Butler and Hull 1996; Smith *et al.* 1997; Rostal and Jones 2002; Epperson and Heise 2003; Pike and Seigel 2006; we note that raw clutch size here ignores losses prior to hatching, which may be significant
Southern periphery	7.0 (2.5)	
Central range	6.25 (2.0)	
Northern/western periphery	5 (1.5)	
Overall offspring sex ratio	0.5	Assumption based on typical conditions. Some temperature effects possible, but not verifiable
Percent of adult males in breeding pool	100	Assumption, but not based on significant number of studies
% annual mortality		Annual mortalities are based on information from the literature. There are very few data available in the literature on which to base survivorship/mortality estimates. Sources: *hatchlings* – Butler and Sowell 1996; Epperson and Heise 2003; Pike and Seigel 2006; juveniles – Wilson 1991; *translocated juveniles* – Tuberville *et al.* 2008b; *translocated adults* – Ashton and Burke 2007; Tuberville *et al.* 2008b; We note that several studies of hatchling survival failed to see any survival past year 2, thus the actual rate must be very low, though not zero. Episodic survival success is a known phenomenon and was modeled separately
hatchlings	96	
yearlings	55	
juveniles (age 2-4)	25	
subadult (age 5 – maturity)	3	
adult	1.5	

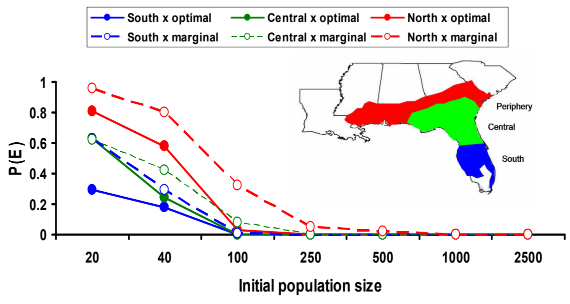
Baseline Model: These parameters were used to develop viability trends for gopher tortoise populations across the range. They were then used in a sensitivity analysis.

Results

Population Growth Rate

- All scenarios showed population declines
- Larger initial populations persisted longer
- Within a geographic region, population declines were less severe in optimal habitat than in marginal habitat
- We felt that the model adequately presented realistic responses to varying environmental conditions.

Probability of Extinction within 100 Years



Sensitivity Analysis

Such an analysis can be a useful tool for identifying which parameters exert the strongest influence on model outcome by varying individual parameters one at a time within a realistic range. We focused on those parameters we considered poorly understood, amenable to manipulation by resource managers, and/or likely to influence population dynamics of gopher tortoises.

If a high degree of uncertainty is associated with either the parameter estimates themselves or how they are used to construct the model, those parameters should become research or monitoring priorities so that better data can be obtained. If a parameter with strong influence on model outcome is already well understood, it may be an effective management target.

For the sensitivity analysis conducted here, we start with a population of 100 tortoises located in the central geographic range and occupying optimal habitat (hereafter referred to as the baseline model). We chose this baseline model because we wanted to simulate conditions likely to be encountered on public conservation lands within the core of the species' range. Many public conservation lands are likely to be large enough to support a population of 100 tortoises if habitat is managed appropriately. Also, based on simulation durations of 100 years, initial population sizes of 100 were the smallest populations resilient to variation in geographic locations and habitat quality and, therefore, "viable" over the long term. The values highlighted in red in the table at the right were the only parameters whose manipulation (within realistic ranges) might potentially result in stable or positive long term growth rates.

Sensitivity Analysis from Grouped Data

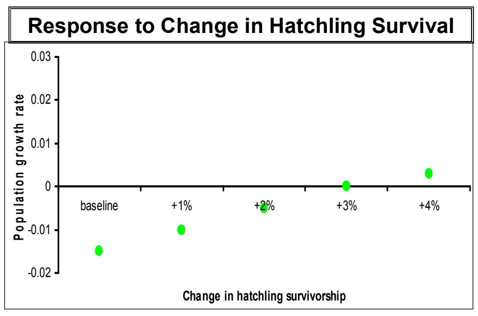
Parameter modified	Relationship to baseline (B)	Parameter value	Lambda (λ)	Population persistence (yrs)
Longevity	B – 20 yrs	40	-0.036	94.6
	B – 10 yrs	50	-0.023	135.1
	B	60	-0.015	165.2
	B + 10 yrs	70	-0.011	172.6
	B + 20 yrs	80	-0.008	196.5
	B + 40 yrs	100	-0.004	>200
Clutch size	B – 2	4.25	-0.025	122.5
	B – 1	5.25	-0.020	144.7
	B	6.25	-0.015	165.2
	B + 1	7.25	-0.011	173.6
	B + 2	8.25	-0.008	177.8
% F breeding	B – 15%	80	-0.021	143.5
	B – 10%	85	-0.018	150.3
	B – 5%	90	-0.017	151.4
	B	95	-0.015	165.2
	B + 5%	100	-0.014	167.1
Sex ratio (% M)	B – 10%	40	-0.010	178.2
	B – 5%	45	-0.013	172.8
	B	50	-0.015	165.2
	B + 5%	55	-0.018	151.4
	B + 10%	60	-0.021	143.1
Hatchling mortality	B	96%	-0.015	165.2
	B – 1%	95%	-0.010	171.7
	B – 2%	94%	-0.005	193
	B – 3%	93%	0.000	>200
	B – 4%	92%	0.003	>200
	B – 5%	91%	0.007	>200
Yearling mortality	B + 10%	65%	-0.022	135.4
	B + 5%	60%	-0.019	150.9
	B	55%	-0.015	165.2
	B – 5%	50%	-0.012	173.6
	B – 10%	45%	-0.009	177.4
	B – 30%	25%	-0.001	>200
Juvenile mortality	B + 10%	35%	-0.027	120.8
	B + 5%	30%	-0.021	147.2
	B	25%	-0.015	165.2
	B – 5%	20%	-0.010	169.2
	B – 10%	15%	-0.005	177.7

Management Implications

The primary value of this sensitivity analysis for us was its potential application to management actions that might feasibly be taken to improve the viability of gopher tortoise populations. The table at the right shows those parameters which showed, in the sensitivity analysis, at least some potential for decreasing the pattern of decline.

Parameter	Is it well quantified?	Can it be managed via habitat?	Can it be feasibly managed by other means?	Effect on viability
Longevity	no	no	no	moderate
% females breeding	no	yes	no	small
Clutch size	yes	yes	no	moderate
Juvenile mortality	no	yes	yes	moderate
Yearling mortality	no	yes	yes	moderate
Hatchling mortality	no	yes	yes	large

Response to Change in Hatchling Survival



Hatchling Mortality

One reason why all population scenarios predicted declines may be that some parameters are not well-established. Hatchling and juvenile survivorship are certainly two of these. Episodic hatchling survival…the occasional "good" year…may also play a role here. This may be extremely variable and "good years" are probably infrequent, but may serve an important supporting role in a very long lived species such as the tortoise.

Potential Contribution from Bioinformatics Development

In our opinion, the role that bioinformatics initiatives, such as the ***Encyclopedia of Life*** could play to support even these relatively simplistic information needs has been underemphasized. The application of population viability analyses to the practical needs of land managers has, we believe, been demonstrated clearly here and elsewhere. While efforts to map and record genomes is surely important to a better understanding of taxonomic and evolutionary relationships, we found that often even simple, "everyday" life history facts were not known…or never recorded…and assembled only with great difficulty. This study focused on a declining but still relatively widespread species. When the management goal is to identify aspects of the life history which have the greatest potential for positive intervention, every scrap of information which may shape an input variable is vital. This is a sort of "forgotten" niche where the bioinformatics efforts can be utilized – to fill simple knowledge gaps.