

Chapter 7

Using Demographic Sensitivity Testing to Guide Management of Gopher Tortoises at Fort Stewart, Georgia: A Comparison of Individual-Based Modeling and Population Viability Analysis Approaches

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7.1 Background

One of the challenges with conserving rare species is identifying the most effective management targets; that is, the demographic traits most likely to positively influence population persistence through either manipulation of the habitat or the wild-life population. Furthermore, these targets should represent the most efficient use of limited resources, especially given that resource managers need to balance multiple, often complex issues (Reed et al. 2009). Population models can often aid managers in this process, and such models are frequently used to rank relative threats to specific populations, evaluate effects of proposed management actions or regulations, determine which demographic or ecological variables have greatest influence on extinction risk, and identify information gaps and research priorities (Tuberville et al. 2009 and references therein).

Population viability analysis (PVA) models represent a traditional modeling approach that has been used to support management decision-making for both game and nongame species. Unfortunately, robust PVA models require extensive population-level data for accurately estimating demographic parameters. Developing PVAs for rare species can be difficult, therefore, because complete life history

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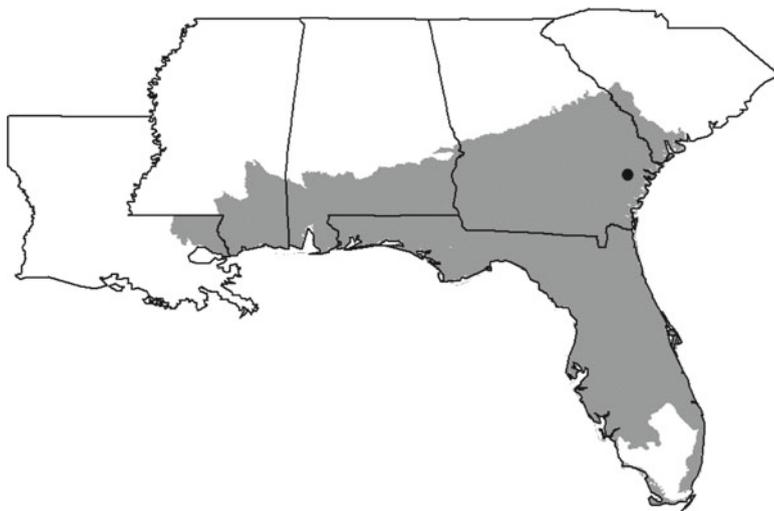


Fig. 7.1 Location of Fort Stewart Army installation (*dot*) within geographic range of the gopher tortoise (*shaded area*)

information and long-term population trend data often are not available. For many rare species, however, detailed information is known about their natural history and the behavior of individuals, including how they interact with each other and the landscape and how they respond to environmental cues. For these species, individual-based models (IBMs) may be more appropriate than PVA models for performing demographic sensitivity analysis; IBMs have the added advantage of imposing a spatially explicit landscape context.

The gopher tortoise (*Gopherus polyphemus*) is an example of a species whose life history data are incomplete, but whose natural history and individual behavior are well characterized. This species is considered to be declining throughout its range (Smith et al. 2006). It is federally listed as threatened in the western portion of its range (USFWS 1987) and is currently under consideration for listing throughout the remainder of its range (USFWS 2009). Gopher tortoise populations occur on many military installations throughout the southeastern USA (Wilson et al. 1997) and the species has been identified for management under the Army's Species at Risk (SAR) program. The SAR program seeks to develop proactive management strategies to ensure long-term viability of imperiled species that currently reside on military installations (NatureServe 2004).

Fort Stewart is the largest Army installation within the range of the gopher tortoise (Fig. 7.1). Given the current and anticipated increase in training demands at Fort Stewart—in terms of both intensity and spatial extent—resource managers are challenged to maintain viable populations of rare species within a limited or even diminishing footprint. One of the most practical ways to address this challenge is by improving demographic conditions for “at-risk” species through improvement of their existing habitat. Population models, used with demographic sensitivity analysis

in particular, can help to determine the extent that habitat management alone can influence demographic parameters of rare species (such as the gopher tortoise) so that their abundance and likelihood of persistence will increase.

7.2 Objectives

As previously stated, IBMs and PVA models are both techniques that have been employed for developing long-term species management strategies. Although the two techniques have similar capabilities, some of the finer details can vary significantly. These variable details include the type of data required to develop the models, how scenarios are simulated, and the format and ways in which output data can be applied. A comparison of these two techniques can provide insight into which method is more sensitive to changes in parameter estimates and how a spatially explicit context may affect model results. Furthermore, as the SAR program and other management initiatives rely increasingly on predictive models, the use of multiple theoretical approaches can buffer the biases that are inherent in any one particular model. Eliminating biases will lend stronger support to management recommendations based on results from such models.

Our research objectives are listed here.

1. Develop a spatially explicit IBM to predict population-level dynamics that reflect the current understanding of the life history of the gopher tortoise. The IBM would simulate the collective behavior of individuals across multiple populations at Fort Stewart.
2. Conduct demographic sensitivity analysis of the developed IBM by comparing model output among simulations with different values for select demographic parameters.
3. Compare demographic sensitivity analysis results from the IBM to sensitivity analysis results from a traditional PVA.
4. Identify gopher tortoise life history parameters that may be amenable to manipulation via habitat management or that need additional research at Fort Stewart.

7.3 Model Description

NetLogo 4.0.4 (Wilensky 1999) was chosen for development of the IBM.¹ Vortex software (version 9.7) was used to generate the PVA and to help validate the IBM. NetLogo provides an accessible programming environment to support spatially explicit IBM simulation modeling (Wilensky 1999). Vortex is a population-based ecological modeling system (Lindenmayer et al. 1995). It captures dynamics of age-specific cohorts with respect to survival and reproduction statistics, and it also generates probabilities of metapopulation survival over time.

¹ An operational copy of this model is available through <http://extras.springer.com>.



Fig. 7.2 Map of Fort Stewart lands, depicting data layers used in individual-based model (IBM). *Grayscale shading* corresponds to estimated carrying capacity (with *darker shading* for higher carrying capacity and *white* for unsuitable patches). Gopher Tortoise Management Areas (GTMA) are shown as *polygons* with *solid boundaries* and indicate the known concentrations of gopher tortoises. Army ranges are delineated with *double dashed lines*

7.3.1 Purpose

Our purpose was to assess the demographic factors most likely to influence persistence and abundance of gopher tortoises across Fort Stewart's range lands. However, the most influential (i.e., "sensitive") parameters were not necessarily the ones most amenable to manipulation, but some demographic traits were known to be influenced by habitat quality and thus could potentially serve as management targets. Ultimately, the purpose of the model was to guide management of gopher tortoises at the installation level by determining whether current habitat conditions and management practices would be likely to ensure the species' continued persistence on the installation, and if not, to evaluate whether increased habitat manipulation would be likely to influence demographic parameters sufficiently to improve overall species viability.

7.3.2 State Variables and Scales

7.3.2.1 Spatial and Temporal Scale

The spatial extent of the model's landscape is Fort Stewart (Fig. 7.2) which is the largest Army installation east of the Mississippi River (113,090 ha or approximately 54 × 30 km). Each patch in our model corresponded to a 150 × 150 m (2.25 ha) area. This size was large enough to allow us to model across the entire Fort Stewart

landscape and for each patch to support more than one tortoise, yet not so large as to preclude movement among patches by individual tortoises during their lifetime. Each time step in the model represented 1 month to allow movement of individual tortoises between patches and to capture seasonal differences in movement probability (active vs. inactive season). Data were output from the model at 20-year intervals over the course of 100-year simulations.

7.3.2.2 Patch Variables

The primary patch variable was carrying capacity which is the number of adult tortoises each patch is predicted to support based on the soils and canopy cover within the patch (see Sect. 7.3.6). In this context, carrying capacity serves as a proxy for habitat quality. Gopher tortoises prefer deep sandy soils in which to burrow, and soil types have been previously classified as to their suitability for gopher tortoises (McDearman 1995; Hermann et al. 2002). In addition, burrow densities (and presumably tortoise densities) have been documented as varying with soil suitability (Jones and Dorr 2004). Canopy cover also has been shown to exert a strong influence on habitat selection by tortoises and thus is an important component of habitat carrying capacity (Aresco and Guyer 1999; Jones and Dorr 2004; Tuberville et al. 2007).

Patches also were characterized by whether a certain percentage of their area was comprised of the following features: (a) wetlands which serve as barriers to movement by tortoises, (b) active firing ranges and tank maneuver areas (hereafter referred to collectively as ranges) many of which are inaccessible and therefore have not been surveyed or do not have the potential for future gopher tortoise management due to this inaccessibility, and (c) Gopher Tortoise Management Areas (GTMA) which correspond to delineated areas on Fort Stewart known to support concentrations of gopher tortoises (see Fig. 7.2 for ranges and GTMA). The number of successful recruits (egg-to-juvenile stage) also was a patch variable which was based on the number of females that occupied each patch, the probability that a particular female reproduced in that year, and clutch size (which was affected by patch quality).

7.3.2.3 Individual (Agent) Variables

Agent-based variables were selected and parameterized to represent demographic traits associated with individual gopher tortoises. Individuals were classified as one of two types of agents (juveniles and adults) that behaved differently in the model. Mortality probability, dispersal probability, and dispersal distance varied between juveniles and adults. Juveniles graduated to adult status at age 15 years. Default parameter values were based on published values for gopher tortoises from Fort Stewart or the southeastern Georgia region when possible, or from data collected elsewhere in the species' range (Table 7.1). When published data were not available

Table 7.1 Individual parameters in the gopher tortoise model, their default values, and additional values tested to evaluate demographic sensitivity

Demographic parameter	Default	Other parameter values tested	References
Longevity	100	60, 70, 80, 90	Miller et al. (2001)
Age of sexual maturity (years)	15	None	
<i>Mortality probability (annual)^a</i>			
Egg stage to age 1 (combined egg and hatchling mortality)	92	90, 91, 93, 94, 95, 96	Alford (1980), Landers et al. (1980), Pike and Seigel (2006), Tuberville et al. (2009)
Juvenile	13.5	9, 18, 22.5, 27	Modified from Tuberville et al. (2009)
Adult	1.5	3, 6, 9, 12	Ashton and Burke (2007), Tuberville et al. (2008), Guyer (unpublished data)
<i>Dispersal probability (annual)^b</i>			
Juvenile	10	None	
Adult	2	None	Eubanks et al. (2003)
<i>Reproduction</i>			
Average clutch size ^c	6	4, 5, 7, 8	Rostal and Jones (2002), Mitchell (2005)
Proportion of females breeding (%)	80	60, 70, 90, 100	Rostal and Jones (2002), Mitchell (2005)
Sex ratio of clutch	0.5	None	

Tested values are based on the references provided

^a Annual mortality rates were converted to monthly mortality rates in NetLogo, assuming mortality could occur with equal probability in any month of the year including when tortoises are relatively inactive

^b Annual dispersal rates were converted to monthly dispersal rates, assuming dispersal occurred with equal probability in any month in which movement by tortoises is likely to occur (April–October in this model)

^c For any given simulation, average clutch size also varies with habitat suitability, as specified in the reproduction submodel

for a particular parameter, default values were chosen based on values used in previous demographic models developed for gopher tortoises (Miller et al. 2001; Tuberville et al. 2009). Additional parameter values were tested to investigate model sensitivity by manipulating a single variable at a time and then comparing model results.

7.3.3 Process Overview and Scheduling

This model proceeded in monthly time steps for the duration of the 100-year simulations. Although 100 years may only represent at most three tortoise generations, our objectives relied on testing a timeframe more realistic to land and wildlife management goals. Based primarily on life history data available for the species in the

literature, our model specified that the following processes (see also Sect. 7.3.7) occur each year during the month(s) indicated. An individual can disperse from or be evicted from its patch and attempt to relocate to another patch (April–October), assess the relative quality of its patch compared to surrounding patches (May) (see Sect. 7.3.7.2), reproduce (June), age (December), and die (January–December). In addition, mortality in the first year of life (egg stage-to-age 1) occurred in September.

7.3.4 Design Concepts

7.3.4.1 Emergence

The life cycle and behaviors of individuals were explicitly modeled through simple empirical rules governing the processes of mortality, reproduction, dispersal, and movement between patches. Population dynamics emerged from the collective behavior of individuals in the landscape. Emergent population dynamics included total population size, change in population size over the course of the simulation, and probability of extinction. In addition, population regulation emerged through the interaction between agents and patches; when the number of adult tortoises within a patch exceeded the patch's carrying capacity, the youngest adult tortoise was forced to move from the patch until the number of adult tortoises inside in patch was at or below carrying capacity.

7.3.4.2 Adaptation and Fitness

In the NetLogo model, each tortoise annually (in May) assessed the carrying capacity of its current patch relative to the eight neighboring patches. It then moved to (or remained in) the patch with the highest carrying capacity as long as the patch had space available (i.e., carrying capacity [number of adults in patch] > 0). Sufficient differences in carrying capacity (a proxy for habitat quality) between patches translated into differences in clutch size (Ashton et al. 2007). Finally, tortoises were allowed to move during any month of the activity season (April–October), but if they were not able to find a suitable patch with space available by the end of the activity season, they were forced to die in November. Thus, adaptation and fitness seeking were not explicitly modeled but resulted from the empirical rules governing individual behavior.

7.3.4.3 Sensing

Individual tortoises were able to sense the quality of their current and neighboring patches, and then behaved according to the movement, mortality, and reproductive rules specified for their individual sex and life stage in the model.

7.3.4.4 Interaction

The only interaction assumed to occur in the model was when carrying capacity was exceeded, the youngest adult was evicted from the patch and forced to search for another suitable patch with space available.

7.3.4.5 Stochasticity

The primary demographic and behavioral parameters including dispersal, mortality, and reproduction were interpreted as probabilistic processes. This approach was chosen because the default parameter values used in the model were based on population-level data from the literature and because we were interested in emergent population-level phenomena. Randomization was incorporated into the model during initialization of tortoises at the start of each simulation with sex, age, and location being assigned randomly according to the criteria described in Sect. 7.3.5. For each parameter combination (scenario), we ran 100 replicate simulations from which we calculated means from the response variables that were output from the model. Temporal environmental stochasticity (biotic or abiotic) was not incorporated into the model due to high levels of uncertainty that would confound assessments of demographic sensitivity.

7.3.4.6 Observation

We were interested in population-level variables such as the change in population size over course of the simulation and the probability of extinction. As part of model verification (*sensu* Rykiel 1996), during simulation runs the user interface plotted the tortoise population (juvenile, adult, total), tortoise density (overall and in suitable habitat only), and age distribution of the population. User-interface plots can be updated at each time step, or as with our models, updated annually in the time step corresponding to the month of reproduction (June) so that we could monitor population trends during simulations.

7.3.5 Initialization

The initial population size (3,000 tortoises) was based on an installation-wide survey for gopher tortoises conducted in 2009 (Macey, unpublished data), using the line transect, distance-sampling protocol described in Smith et al. (2009b). Because survey effort focused on those GTMAs that could be accessed by installation biologists, tortoises in the model were randomly placed among patches that were within GTMAs but outside of Fort Stewart's ranges. Although initial tortoise placement was restricted to outside the ranges, tortoises were allowed to subsequently move through ranges. Placement of tortoises in the landscape also was constrained by the

model such that total number of tortoises populating a given patch was less than or equal to the carrying capacity of the patch. Finally, age and sex were randomly assigned to individuals such that the overall tortoise population had a 1:1 sex ratio and a normal adult age distribution with mean age of 30 years.

7.3.6 Input

The model inputs were raster and vector geographic information system (GIS) maps developed using the GRASS GIS (<http://grass.itc.it>). Raster maps were used to initialize patch variables and vector maps were used for visualization purposes. Raster maps included carrying capacity (generated from soils and canopy cover maps), wetlands, GTMAs, ranges, and study area boundaries. Vector maps included roads, streams, GTMAs, ranges, and study area boundaries. The primary model input was projected carrying capacity which was used as a proxy for habitat quality. To estimate the carrying capacity of each patch for gopher tortoises, we first generated a soils suitability map and a tree basal area map for Fort Stewart. The soils suitability map was created by reclassifying the Fort Stewart soils map previously digitized from 1:20,000 scale county soil survey maps published by the U.S. Department of Agriculture (USDA) Soil Conservation Service (SCS). Soils were reclassified as marginal, suitable, or priority soils based on established criteria (McDearman 1995; Guyer, Johnson, and Herman (unpublished data)).

Basal area was derived from the 2001 Gap Analysis Program (GAP) canopy cover map developed by the Multi-Resolution Land Characteristics (MRLC) Consortium (http://www.mrlc.gov/multizone_download.php?zone=14) using (7.1) reported for Michigan oak and pine stands (Buckley et al. 1999). We used average oak and pine canopy cover estimates from GAP maps for the Fort Stewart area to generate a basal area map for the installation, with resolution of 30 m and basal area output in units of square meters per hectare.

$$\text{Oak stand basal area} = [(\text{canopy cover} + 1.25) / 15.5] \quad (7.1)$$

$$\text{Pine stand basal area} = [(\text{canopy cover} + 2.91) / 12.14]$$

In addition, a carrying capacity map with 30-m resolution was generated from the soils suitability map and the derived basal area map by using the formulas in (7.2), taken from Guyer, Johnson, and Herman (unpublished data).

$$\text{“Priority” soils} = 9.7 \text{ tortoises/ha} * [100 - (1.43 * \text{basal area})] / 100$$

$$\text{“Suitable” soils} = 2.9 \text{ tortoises/ha} * [100 - (1.43 * \text{basal area})] / 100 \quad (7.2)$$

$$\text{“Marginal” soils} = 1.2 \text{ tortoises/ha} * [100 - (1.43 * \text{basal area})] / 100$$

The 30-m resolution carrying capacity map was resampled at 150×150-m resolution to create the final projected carrying capacity used as input in the model. Vector maps of the installation boundary, GTMAs, ranges, and wetlands were converted to 30-m resolution raster maps and similarly resampled to create input maps with a 150×150-m resolution.

Throughout the model, we assumed carrying capacity related only to the number of adult tortoises in a patch. Juvenile tortoises and their burrows routinely are underestimated when using standard survey methods, due to their small size and cryptic appearance (Smith et al. 2009a; Tuberville and Dorcas 2001). In addition, habitat quality and social factors are both likely to influence the carrying capacity of a patch, with the latter factor presumably more likely to affect adults than juveniles. Therefore, the carrying capacity input map was used both in initializing tortoises in patches at the start of each simulation and in dictating eviction of the youngest adult tortoises from patches when carrying capacity was exceeded during the simulation.

Finally, a habitat class map was derived by categorizing individual patches in the carrying capacity map into the following habitat quality classes based on projected tortoise densities per hectare: habitats were classified as unsuitable (<0.5 tortoises/ha), low (0.5–2.9), moderate (3.0–5.0), and high quality (≥ 5). The habitat class map was used to apply reproductive penalties (reduced clutch sizes) to tortoises occupying lower-quality habitat patches (Ashton et al. 2007).

7.3.7 Submodels

7.3.7.1 Eviction from Patch

Adult tortoises were forced to move from their patch when carrying capacity within the patch was exceeded. The model evicted the youngest adult until the patch was again at or below carrying capacity. Once a tortoise was forced to leave a patch, the individual assessed the immediately surrounding eight patches and moved to the patch with the greatest space available (i.e., the greatest difference between carrying capacity and number of adult tortoises currently occupying the patch). If none of the neighboring cells had space available, the evicted tortoises moved to a randomly selected neighboring patch and continued to search for available space. The evicted tortoise could make up to eight attempts to find space available in neighboring patches per monthly time step, corresponding to a maximum cumulative movement distance of 1.2 km/month. The only additional constraint on movement in the eviction submodel was that tortoises, although allowed to move through ranges, could not move through patches that were classified as wetland. Eviction and the resulting search for patches with available space could occur in any month in which tortoise movement occurs (April–October).

7.3.7.2 Search for Better Habitat

Once per year, tortoises had the opportunity to relocate to better habitat. Every May, each individual assessed whether any of the neighboring patches had space available and then compared the habitat quality (i.e., carrying capacity) of those neighboring patches relative to its current patch. If habitat quality was highest in its current

patch, the individual remained in the patch. If habitat quality was higher in one or more neighboring patches with space available, it would relocate to the neighboring patch with the highest habitat quality. Habitat quality (i.e., carrying capacity) was maintained as a static feature in our model based on the presumption that current habitat management efforts for gopher tortoises would continue and because tortoises in our model were ejected from a patch when carrying capacity was exceeded, thereby preventing resource depletion. Thus, as long as an individual did not move from its patch, an individual's associated habitat quality did not change during model simulations. However, other factors in our model elicited movement among patches by tortoises. This submodel provided tortoises the opportunity to respond to a heterogeneous landscape by moving among patches based on habitat quality and resource availability. In reality, gopher tortoises may elect to search for better habitat in any month during the active season. However, to significantly reduce simulation run time, we constrained the model so that this behavior was only allowed to occur in 1 month (May).

7.3.7.3 Dispersal

Gopher tortoises in high-quality habitat have small home ranges generally defined as 1–2 ha for adult males and <0.5 ha for adult females (Diemer 1992; Eubanks et al. 2003; Smith et al. 1997). While gopher tortoises occasionally will make long-distance excursions outside their home range, they will return to their core use areas. However, each year a small percentage of tortoises will disperse from their home range and establish a new home range in another location (Eubanks et al. 2003). We incorporated dispersal behavior into the model, assuming that dispersal could be motivated by factors other than habitat quality or carrying capacity of the current patch. In the dispersal submodel, a certain number of juvenile and adult tortoises were randomly selected to disperse based on previously defined dispersal probabilities. Dispersing tortoises oriented in a random direction and searched for patches with space available and occupied by at least one other tortoise. The maximum dispersal distance varied between adults and juveniles, but if individuals could not find an occupied patch within that distance, they were forced to stop. If tortoises encountered wetland patches while dispersing, they were forced to continue searching and move through patches that were not dominated by wetlands. Dispersal could occur during any month from April–October.

7.3.7.4 Reproduction

In the reproduction submodel, females produced eggs in June, which is the peak nesting month for gopher tortoises in southern Georgia (Landers et al. 1980). Adult females were randomly selected to reproduce according to the reproductive probability specified in the model. Clutch size varied among females, based on the habitat quality of their patch. Females in high and moderate quality patches produced

the average clutch size specified in the model. Females in patches labeled as “low quality” incurred a reproductive penalty by producing two fewer eggs than the average clutch size. Females in unsuitable patches were not allowed to reproduce. Eggs hatched in September.

7.3.7.5 Aging

The age of individuals increased 1 year every December. After that time, individuals of the appropriate age graduated to the next life stage.

7.3.7.6 Mortality

A certain percentage of gopher tortoises died in each monthly time step based on stage-specific mortality probabilities for egg-to-age 1, juveniles, and adults. Monthly mortality probabilities were converted from the annual mortality probabilities specified in Table 7.1, assuming mortality could occur with equal probability in any month of the year including when tortoises were relatively inactive. In addition, any tortoises unable to locate suitable habitat patches by October were not allowed to overwinter there and were forced to die in November. Finally, tortoises were not allowed to live more than 100 years in the model.

7.4 Simulation Experiments

7.4.1 Model Calibration

As part of the model calibration process (*sensu* Rykiel 1996), we adjusted the default value for juvenile survivorship (the parameter that is least well known) until the combination of default parameters resulted in a sustained population. Initially, we set juvenile mortality to 15% based on previous work by Tuberville et al. (2009). However, we found that a 10% reduction was required to produce a stable population in NetLogo (i.e., for a juvenile, a resulting mortality rate of 13.5% was set as the default value). Once we selected the combination of default values for our IBM, we varied parameters individually over a range of biologically realistic values (Table 7.1) to perform demographic sensitivity analysis.

7.4.2 Model Validation

We intended to validate the demographic sensitivity results of our IBM by performing a similar analysis using the more traditional PVA approach. We constructed a

PVA in Vortex 9.7 by using the default and range-of-parameter values identified in Table 7.1 and systematically varying each parameter, one at a time. Each scenario (i.e., parameter combination) was run for 100 years and repeated for a total of 100 simulations. Each simulation was initialized with a starting population of 300 tortoises, characterized by an age structure that mirrored the starting age structure in the IBM simulations. We selected a starting population size of 300 tortoises (10% of the population estimate for Fort Stewart that was used as the initial population size for the IBM simulations), which was based on minimum reserve sizes estimated by McCoy and Mushinsky (2007) and Styrsky et al. (2010), and the number of tortoises predicted to occur on those reserves. Although Vortex will support models with multiple populations linked in a metapopulation structure, we did not have sufficient data for Fort Stewart to estimate dispersal among GTMAs. Thus, our Vortex simulations were not spatially explicit and assumed a single cohesive population rather than several “populations” distributed among habitat patches across the landscape. For each PVA scenario, we reported the average population size at 20-year intervals and the probability of extinction over the 100-year simulation. To scale our demographic sensitivity results from the PVA to results from the IBM, we also reported the percentage change in population size for both sets of results.

7.4.3 *Effects on Population Trends and Probability of Extinction*

Simulations of the baseline scenario (i.e., all parameters set to default values) for our IBM resulted in an average population increase of 7.1% (Table 7.2). Any scenario in which a single parameter was set at a value less favorable than in the baseline scenario predicted a population decline during the 100-year simulations, although rarely did it result in extinction (defined here as when fewer than two individuals remain at end of simulation). In fact for our IBM model, the probability of extinction (P_E) was greater than zero only when annual adult mortality was set to 9 or 12%, which resulted in a P_E of 0.11 and 0.87, respectively.

Compared to IBM simulations, PVA simulations of the same scenario were less likely to predict a population decline than IBM simulations (Table 7.2). However, for those scenarios where the PVA *did* predict a decline, the P_E tended to be higher for PVA than for IBM. When both IBM and PVA simulations projected a positive change in population size (e.g., when longevity was set to 90 years or juvenile mortality to 9%), the PVA predicted a greater percentage increase than did the IBM; the converse was observed when both the model types projected a negative change in population size (e.g., when adult mortality was set to 3% or proportion of females breeding to 60%). When the direction of population change differed between the two model types (i.e., positive or negative), the IBM predicted a population decrease while the PVA predicted a population increase. Finally, the PVA model exhibited a greater magnitude of responses among scenarios than did the IBM.

Table 7.2 Comparison of IBM and PVA model results based on same set of scenarios and parameter combinations

Scenario name	IBM results ($N_0=3000$ tortoises)			PVA results ($N_0=300$ tortoises)		
	Final N	Change (%)	P_E	Final N	Change (%)	P_E
Baseline (all default parameters)	3,215	+7.2	0	544	+81.4	0
Longevity=90 years	3,092	+3.1	0	482	+60.6	0
Longevity=80 years	2,891	-3.6	0	411	+37.1	0
Longevity=70 years	2,674	-10.9	0	311	+3.5	0
Longevity=60 years	2,357	-21.4	0	207	-30.9	0
Adult mortality=3%	899	-70.0	0	189	-36.9	0
Adult mortality=6%	78	-97.4	0	26	-91.3	0.02
Adult mortality=9%	7	-99.8	0.11	8	-97.3	0.62
Adult mortality=12%	<1	-100.0	0.87	<1	-100.0	1.00
Juvenile mortality=9%	10,213	+240.4	0	2,721	+806.9	0
Juvenile mortality=18%	1,497	-50.1	0	134	-55.3	0
Juvenile mortality=22.5%	925	-69.2	0	40	-86.6	0
Juvenile mortality=27%	701	-76.6	0	14	-95.5	0.03
Egg-to-juvenile mortality=90%	4,907	+63.6	0	912	+204.1	0
Egg-to-juvenile mortality=91%	4,003	+33.4	0	705	+135.0	0
Egg-to-juvenile mortality=93%	2,554	-14.9	0	409	+36.4	0
Egg-to-juvenile mortality=94%	2,004	-33.2	0	279	-7.0	0
Egg-to-juvenile mortality=95%	1,551	-48.3	0	198	-33.9	0
Egg-to-juvenile mortality=96%	1,178	-60.7	0	133	-55.8	0
Mean clutch size=8	5,844	+94.8	0	1,070	+256.5	0
Mean clutch size=7	4,374	+45.8	0	796	+165.3	0
Mean clutch size=5	2,321	-22.6	0	362	+20.9	0
Mean clutch size=4	1,645	-45.2	0	225	-25.0	0
Proportion females breeding=100%	4,690	+56.3	0	917	+205.8	0
Proportion females breeding=90%	3,881	+29.4	0	704	+134.6	0
Proportion females breeding=70%	2,625	-12.5	0	398	+32.7	0
Proportion females breeding=60%	2,133	-28.9	0	286	-4.7	0

Scenarios are grouped according to parameter manipulations and are ordered from most favorable to least favorable conditions within each parameter. All IBM simulations start with initial population size of 3,000 tortoises; PVA simulations start with 300 tortoises. For each model type, the following are reported: gopher tortoise population size at end of simulation (Final N), percent change in population size during simulation (% change), and probability of extinction (P_E ; range of possible values 0–1). *Shaded cells* correspond to simulations resulting in population decline and/or $P_E > 0$

7.4.4 Demographic Sensitivity Analysis

For each model type, we evaluated sensitivity to changes in six demographic parameters by individually varying those parameters over a range of biologically realistic values. However, due to expected differences in plasticity of corresponding life history traits, the range of values tested varied among parameters. In order to relate the magnitude of differences in parameter values tested to the magnitude of resulting responses, we calculated the following two ratios.

Parameter ratio = scenario parameter value/baseline parameter value

Response ratio = scenario population size/baseline population size

For example, for the scenario where adult mortality = 3%, the parameter value for the scenario was 3% compared to the baseline scenario's default value of 1.5%, resulting in a parameter ratio of 2. Based on the IBM, the predicted final tortoise population for the scenario of interest was 899, compared to a final population size of 3,215 in the baseline scenario (Table 7.2). This scenario resulted in a response ratio of 899/3,215 or 0.28. Based on these ratios, the IBM predicted that a doubling of the baseline adult mortality rate would result in a 78% smaller ending population when compared to a scenario using default values. For the baseline scenario, the parameter ratio and the response ratio always were equal to 1.

Results of these ratio calculations are shown in Fig. 7.3, where the parameter ratio (independent variable) was plotted on the x axis, and the response ratio (dependent variable) was plotted on the y axis; the steepness of the curve indicates the sensitivity of the model to changes in parameter value. Ratios for each of the six demographic parameters were plotted separately, with ratios for both the IBM and PVA model presented in the same graph. All results were plotted on the same scale to facilitate comparisons among parameters.

Despite differences in population size and percentage change in population size observed between our IBM and PVA model (Table 7.2), the two model types exhibited remarkable congruence in their sensitivities to manipulation of demographic variables. In fact, the results are so similar that it sometimes is difficult to discern that two distinct data sets are plotted (Fig. 7.3). The one notable exception is juvenile survivorship, which predicted similar responses in the IBM and PVA at parameter values greater than or equal to baseline value; although both model types predicted dramatically larger populations when juvenile mortality rates were lower than baseline, the PVA model predicted a greater response than the IBM.

As mentioned previously, we varied values for each demographic parameter over a range of biologically realistic values. Keeping that in mind, several observations can be made from our results.

1. The baseline values for adult mortality and longevity represented the most optimistic scenario (i.e., no scenario has a parameter ratio greater than 1); all other parameter values predicted smaller population sizes (i.e., response ratio less than 1).
2. Scenarios varying juvenile mortality exhibited the greatest magnitude in responses among scenarios over the range of values tested.

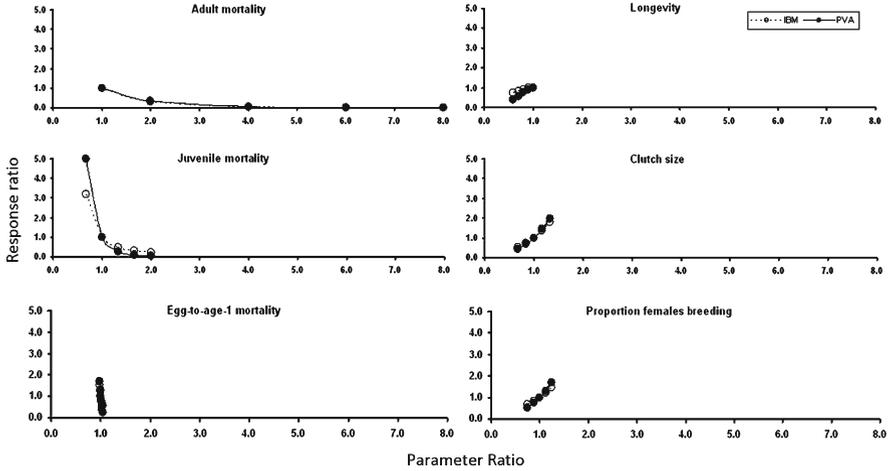


Fig. 7.3 Comparison of demographic sensitivity analysis results between IBM (*dashed lines, open circles*) and population viability model (*solid lines and circles*). For each demographic parameter, the parameter ratio (scenario parameter value/baseline parameter value) is plotted on the *x*-axis and the response ratio (scenario population size/baseline population size) on the *y*-axis. Note that results for all parameters are plotted at the same scale

3. Based on the nearly vertical plots for egg-to-age 1 mortality, this demographic parameter predicted the greatest difference in population size per unit difference (i.e., the models were most sensitive to changes in this parameter).

7.5 Discussion

7.5.1 Population Trends and Probability of Extinction

Although we reported final population sizes and probability of extinction after 100 years for each scenario tested, the primary goal of the IBM and PVA models was to identify parameters to which our simulated populations were most sensitive rather than to predict the specific outcome of any given scenario. Therefore, one must be cautious about interpreting and applying the results of our models to specific management scenarios for gopher tortoises on Fort Stewart. However, our results are useful for identifying patterns and potential factors contributing to those patterns.

One major pattern we observed was that when any demographic parameter (except longevity) was set to a value less optimistic than the baseline scenario, the IBM predicted a population decline. In the case of adult mortality, the default value was the most optimistic value, suggesting that any chronic increase in adult mortality above baseline would result in declines that could potentially compromise long-term

persistence if all other parameters remained the same. The importance of high adult survivorship in the life history of most turtle species and in the management of individual populations is well documented (e.g., Congdon et al. 1993, 1994). We did not run simulations with adult mortality less than 1.5% because we wanted to only test parameters with biologically realistic values. The most optimistic value used in our simulations was based on studies of gopher tortoise populations on protected lands (Ashton and Burke 2007; Tuberville et al. 2008), and we are aware of no published study to date that has documented lower mortality rates.

The other major pattern that emerged was that the PVA was more likely than the IBM to predict a population increase and to predict an increase of greater magnitude. Apparent discrepancies between the two model types are probably best explained by additional challenges imposed by the spatial context of the IBM modeling environment. The PVA we constructed in Vortex assumed a single population that was closed to immigration and emigration, and in which all individuals were exposed to the same habitat conditions. Furthermore, carrying capacity for the entire population was set at ten times the initial population size (i.e., 3,000).

In contrast, carrying capacity was specified for each patch (i.e., pixel) in the IBM. Carrying capacity could have affected overall population in at least two ways. First, the sum of carrying capacity values for individual patches determined the maximum population size possible for the entire installation (at least for adults), although population sizes in our simulations never approached this maximum value. More importantly, however, carrying capacity of individual patches influenced the initial placement of tortoises and also determined whether tortoises were forced to leave a patch to search for suitable habitat elsewhere. NetLogo initiated each simulation by placing tortoises in suitable patches among GTMAs, which were distributed across Fort Stewart and interspersed with unsuitable habitat, effectively fragmenting the installation's tortoise population. In addition, when carrying capacity for an individual patch was exceeded, individual tortoises were ejected from the patch and forced to search for a suitable patch that had not yet reached carrying capacity. In some cases, individuals were not able to find a patch meeting these criteria before activity season ended, at which time they were forced to die. Thus, the landscape context of the IBM (particularly when that landscape is patchy) created a more complex real-world environment for the simulated population. It is likely the landscape context also contributed to the differences in population trends that we observed between the two types of models.

7.5.2 Demographic Sensitivity Analysis

When considering sensitivity to individual parameters, the congruence between model types suggests that IBMs, such as the one we developed for gopher tortoises in NetLogo, can be a valuable approach to conducting demographic sensitivity analysis. Because the overall sensitivity results from the IBM and PVA models were so similar, we will restrict our discussion to the IBM.

Although scenarios in which adult mortality rates were elevated above baseline level were the only scenarios likely to result in population extinction (Table 7.2), adult mortality was not the parameter to which the model was most sensitive (Fig. 7.3). In addition, adult mortality rate in the baseline scenario (1.5%) was the most optimistic value tested. The baseline value corresponded to long-term estimates that have been published about two different translocated populations (Ashton and Burke 2007; Tuberville et al. 2008). We could find no estimates of long-term adult mortality rates for any naturally occurring gopher tortoise populations in the peer-reviewed literature, but the estimate used in our model is among the lowest adult mortality estimates reported for chelonians (Iverson 1991; Wilbur and Morin 1988). From an application perspective, these findings imply that although it may not be feasible to reduce adult mortality below 1.5%, monitoring and management efforts should prevent or mitigate threats that could potentially cause chronic increases in adult mortality.

The parameter associated with the greatest magnitude of change in population size over the values tested was juvenile mortality. The lowest juvenile mortality rate (9%) predicted population sizes that were three times the size predicted by the baseline scenario in which juvenile mortality was set to 13.5%. Juvenile mortality rates could conceivably be reduced through habitat management particularly in areas where canopy cover is excessively high or herbaceous vegetation is limited. Low canopy cover ($\leq 60\%$) and basal area ($30 \text{ m}^2/\text{ha}$) are important for providing necessary thermal conditions for tortoises and for promoting diverse and abundant herbaceous vegetation in the understory (Aresco and Guyer 1999; Tuberville et al. 2007; Wilson et al. 1997). In turn, the herbaceous understory provides forage for growth and camouflaging cover from predators while vulnerable juveniles are active outside their burrows. We are aware of no studies comparing juvenile survivorship rates among different habitat types; indeed, few data at all are available for estimating juvenile survivorship (but see Wilson 1991; Tuberville et al. 2008; and inferred estimates from Pike et al. 2008). Obtaining information on juvenile tortoise mortality rates from Fort Stewart would greatly improve the predictive value of the IBM and its utility for guiding management of gopher tortoise populations on the installation.

The parameter for which the smallest change predicted the greatest effect on population size was egg-to-age 1 mortality. Mortality rates for both eggs and hatchlings are known to be high and are suspected—at least for the egg stage—to be quite variable among sites and years (Landers et al. 1980; Pike and Seigel 2006; Wright 1982). Such high and variable mortality rates highlight the importance of this parameter in the model and the challenge of making broadly applicable management recommendations. Mortality in the egg-to-age 1 stage probably can be influenced by habitat management in the same manner that we suspect juvenile mortality may be influenced. Egg-to-age 1 mortality also probably is influenced to a greater extent by environmental stochasticity and predator population cycles than is juvenile mortality. Thus, although habitat management may improve conditions such that hatchling survivorship increases, other factors more difficult to control may hinder the ability of habitat management to have an appreciable effect on population level.

Finally, our IBM appears sufficiently sensitive to changes in both clutch size and proportion of females breeding to suggest that those two demographic traits merit consideration as management targets. For both parameters, we observed a twofold difference in population size between scenarios with the baseline vs. the maximum parameter values. Data from Fort Stewart and a nearby state park suggest that these demographic traits can vary among sites with differing habitat quality (Rostal and Jones 2002). It is therefore feasible that these demographic traits could be improved through habitat-based management approaches.

7.6 Conclusions and Recommendations

We found IBM to be a useful tool for performing demographic sensitivity analysis, and we observed remarkable agreement between sensitivity results from our IBM and PVA models for gopher tortoises on Fort Stewart. Our analyses identified several demographic traits that appeared to disproportionately influence size of simulated populations, particularly mortality rates in the juvenile stage and egg-to-age 1 stage. Although there are few data comparing these rates among sites with varying habitat quality, we suspect both traits are fairly responsive to changes in habitat quality and thus, habitat manipulation. In addition, it is important to keep in mind our analyses varied by only a single parameter at a time, whereas habitat improvement at poorer quality sites should positively influence a suite of demographic traits simultaneously. Furthermore, our baseline model, which was intended to reflect demographic traits for tortoises under current management conditions at Fort Stewart, predicted a population increase during the 100-year simulations. Based on these factors, we believe current management conditions are conducive to long-term persistence of gopher tortoises in the Fort Stewart landscape, and that habitat management is a practical and effective means to improve population conditions at poorer quality sites.

Should there be a net loss of suitable habitat for gopher tortoises—perhaps as a result of range construction or infrastructure development—resource managers likely will need to improve habitat conditions for tortoises on remaining patches. Most of Fort Stewart is comprised of soils considered to be unsuitable for gopher tortoises (Fig. 7.4a), which limits the ability of resource managers to implement large-scale improvements in habitat quality across the installation. However, approximately 13% of the landscape can be characterized as marginal habitat occurring on suitable soils (Fig. 7.4b). Habitat improvements targeting these patches could increase carrying capacity of individual patches, hopefully offsetting any potential losses in suitable habitat.

There are two important caveats to our conclusions that stem from the following assumptions in our model: (1) parameter values in our IBM are representative of demographic traits for gopher tortoises on Fort Stewart, and (2) current wildlife and land management practices will be maintained so that there is no change in the amount, quality, or distribution of suitable habitat patches across the installation.

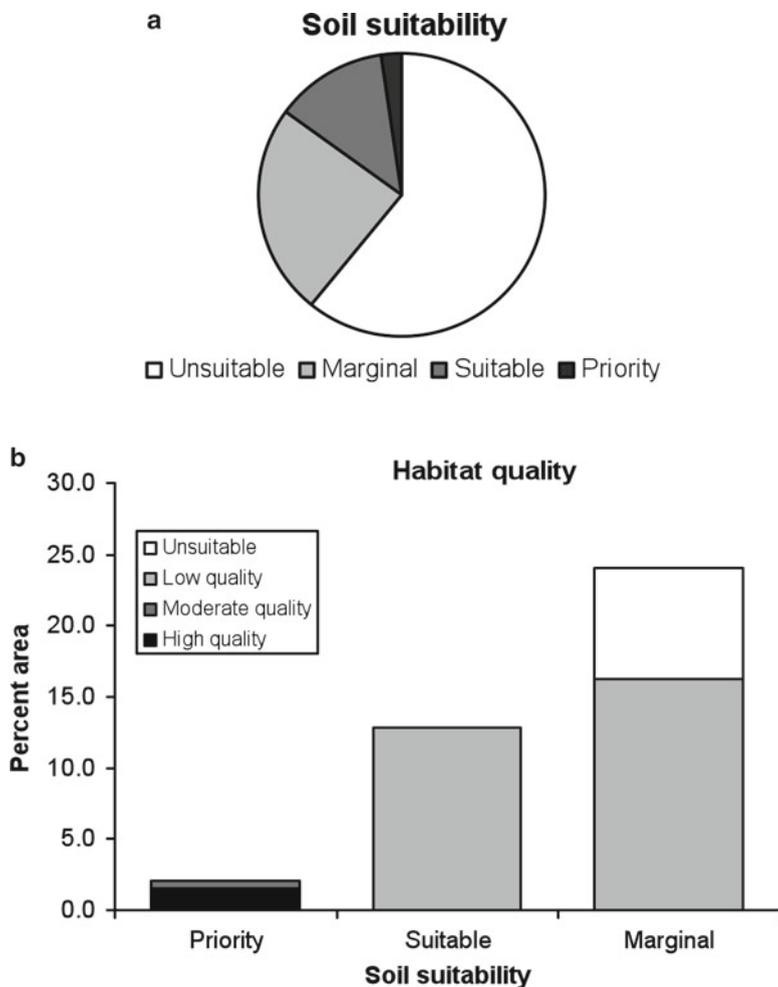


Fig. 7.4 Habitat conditions for gopher tortoises in the Fort Stewart landscape in terms of: **(a)** relative abundance of unsuitable, marginal, suitable, and priority soil types (categories based on information presented in McDearman 1995; Hermann et al. 2002), and **(b)** habitat quality of patches associated with each soil suitability category

We estimated parameters for our IBM from the literature, using data specific to Fort Stewart or the surrounding region whenever possible. However, for some parameters—particularly juvenile mortality and longevity—few data or no data were available. In addition, parameters estimated from data from other portions of the species' range may not reflect demographic traits for gopher tortoises on Fort Stewart. However, as more data become available, parameter estimates can be modified to refine the model and make it more useful to resource managers making

installation-specific management recommendations. Resource managers also can adapt the model to examine gopher tortoise dynamics under changing or altered landscapes, such as conversion of tortoise habitat to training areas or habitat improvement in suitable patches outside of GTMAs. These landscape changes can affect not only the suitability of individual patches for gopher tortoises but also the distribution of suitable patches and the ability of tortoises to move between patches. By considering both demographic traits and behavior of individuals—particularly regarding how they interact with the landscape—IBMs offer a powerful means for resource managers to evaluate the likelihood of long-term persistence of rare species under current or alternative landscape conditions and to identify and implement appropriate management actions.

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