Individual-based modeling to project viability of gopher tortoise populations under alternative management scenarios: A case study with two Alabama Wildlife Management Areas

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Abstract: Population projection models are applied tools for considering the potential effects of land and population management alternatives. Incorporating spatially explicit processes and individual dynamics into these models can be important when assessing viability for relatively small populations in patchy habitats. We developed a spatially explicit, individual-based population simulation model (IBM) for gopher tortoises (*Gopherus polyphemus*) incorporating demographic rates from published studies throughout the range of the species. We then demonstrated this approach's utility for evaluating potential viability under projected forest management with and without tortoise population augmentation on two areas of state-managed property in southern Alabama. Under all scenarios, projected populations declined to local extinction within 100–200 years. The IBM projected sharper declines compared to projections from a non-spatial, stochastic, stage-structured model, potentially indicating the importance of considering spatial dynamics and individual interactions in this context. The IBM approach is especially useful when dealing with actual management units because it identifies projected hotspots of consistent occupancy and important habitat connections on the landscape.

Key words: population modeling, gopher tortoise, population viability

Management of wildlife populations often involves significant uncertainty about the current state and demographic rates of the population as well as the likely consequences of potential management actions. In the face of such uncertainty, population models are important applied tools for conservation planning and decision making (Starfield 1997, Conroy et al. 2008). These tools are highly applicable to conservation of the gopher tortoise (*Gopherus polyphemus*), a keystone species endemic to much of the southeastern Coastal Plain. The species is listed as Threatened under the Endangered Species Act in the western portion of its range and is of high conservation concern range-wide (USFWS and SERPPAS 2013). Multiple factors have likely contributed to long-term population declines, including habitat loss and fragmentation, disease, invasive species, and human harvest (Smith et al. 2006). However, there is high uncertainty about current demographic rates and trends for most gopher tortoise populations and about how to ensure local and range-wide species viability. Therefore, numerous population models have been developed for gopher tortoises to help assess population viability, determine sensitivity of population projections to uncertainty in vital rates, and evaluate habitat and population management options (Cox et al. 1987, Cox 1989,

Seigel and Dodd 2000, Miller 2001, Root and Barnes 2006, Tuberville and Gibbons 2009, Tuberville et al. 2002, Westervelt and MacAllister 2012).

There are many types of applied population models that can be developed for species such as gopher tortoises. Age- or stage-structured matrix models are easy to develop, yet provide powerful insights about key demographic patterns such as the expected long-term finite rate of increase (λ), and sensitivity of λ to changes in each demographic rate (Caswell 2000). However, matrix models treat discrete subpopulations or demographic groups (e.g., sex/age classes) as the basic unit of analysis, with all individuals within this basic unit assumed to share the same distributions of demographic rates (DeAngelis and Gross 1992). Matrix models for discrete subpopulations can be expanded to produce spatially explicit metapopulation models (Caswell 2000). However, they cannot easily incorporate complex spatial structure in populations and effects of landscape heterogeneity on demographic performance of individuals. This can be problematic because landscape composition, configuration of suitable patches, and spatial structure in populations can have important consequences for movement, demographic rates, and persistence of populations (Turner et al. 2001, Law et

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al. 2003). Many non-spatial models and standard metapopulation models treat every organism as having equal influence on every other individual in the same population unit; in reality, individual organisms are primarily affected by nearby organisms (DeAngelis and Gross 1992). Proximity-dependent interactions may be particularly important for small or localized populations of species with limited mobility, such as gopher tortoises.

In a population modeling context, Individual (or Agent) Based Models (IBMs) track simulated individuals as discrete entities with properties such as sex, age, and weight (Grimm 1999) and incorporate variability and mechanisms at the level of individual interactions (Huston et al. 1988). Population-level dynamics emerge from the aggregated behavior of modeled individuals (DeAngelis and Gross 1992, Grimm and Railsback 2005). The IBM approach is well suited to spatially explicit modeling because modeling of individual movements and interactions can directly incorporate factors such as proximity of individuals, patch-level population density, and connectivity among patches (Dunning et al. 1995, Huston et al. 1998, Grimm 1999). Additionally, IBMs can easily be integrated with current and projected spatial data such as forest stand information for a management unit (McRae et al. 2008, Tuberville et al. 2012) or other habitat layers (e.g., Butler et al. 2005, Elderd and Nott 2008, Allen et al. 2016).

Previous studies have developed IBMs for gopher tortoises and applied them to specific management areas in Georgia based on current landscape patterns or simple alternative habitat configurations (Tuberville et al. 2012, Westervelt and MacAllister 2012). We built on these previous studies to further demonstrate the potential utility of this approach. We describe the components of our stochastic IBM and apply it to model gopher tortoise populations in two southern Alabama study areas. Because gopher tortoise habitat consists primarily of upland sandy soils with open-canopy conditions (Auffenberg and Franz 1982), we incorporated effects of soil and forest stand structural states on patch suitability. Stand states in our IBM also changed dynamically and were based on data incorporated from a previous project from our study areas that projected long-term effects of forest management alternatives on wildlife habitat and species occurrence. We compared population projections under scenarios with and without one-time population augmentations, and we assessed the impact of incorporating spatially explicit individual behavior into population projections by comparing results from the IBM with those from a non-spatial matrix model.

Study Areas

We simulated gopher tortoise movements and population viability for two focal areas of state-managed land in southern Al-

abama (Figure 1). One area included two adjacent properties in the Southern Hilly Gulf Coastal Plain ecoregion (Omernik and Griffith 2014), near the northern edge of the species' range in Alabama: Barbour Wildlife Management Area (approximately 11,656 ha) and the Wehle Forever Wild Tract (approximately 630 ha; hereafter "Barbour" and "Wehle"). Collectively these two properties included a diverse array of cover types, with mature open-canopy longleaf pine (*Pinus palustris*) stands being the dominate cover type on Wehle, and those on Barbour consisting of both longleaf and loblolly (*P. taeda*) pine stands of various ages and densities, mixed hardwood stands, and food plots. Sandy soils suitable for gopher tortoises are patchily distributed on low-relief sand ridges separated by drainages and upland clay soils (Figure 1). Tortoises currently present on Wehle resulted from a 2006–2009 reintroduction effort that released 55 tortoises; 13 tortoises remained on Wehle as of summer 2013 whereas other surviving individuals may have moved onto Barbour (E. Soehren, Alabama Department of Conservation and Natural Resources State Lands Division, personal communication). The second focal area, Perdido River Wildlife Management Area (hereafter "Perdido"; approximately 7,327 ha), is further south in the East Gulf Coastal Plain (Southern Pine Plains and Hills ecoregion, Omernik and Griffith 2014), and includes much larger patches of deep sandy soils (Figure 1),
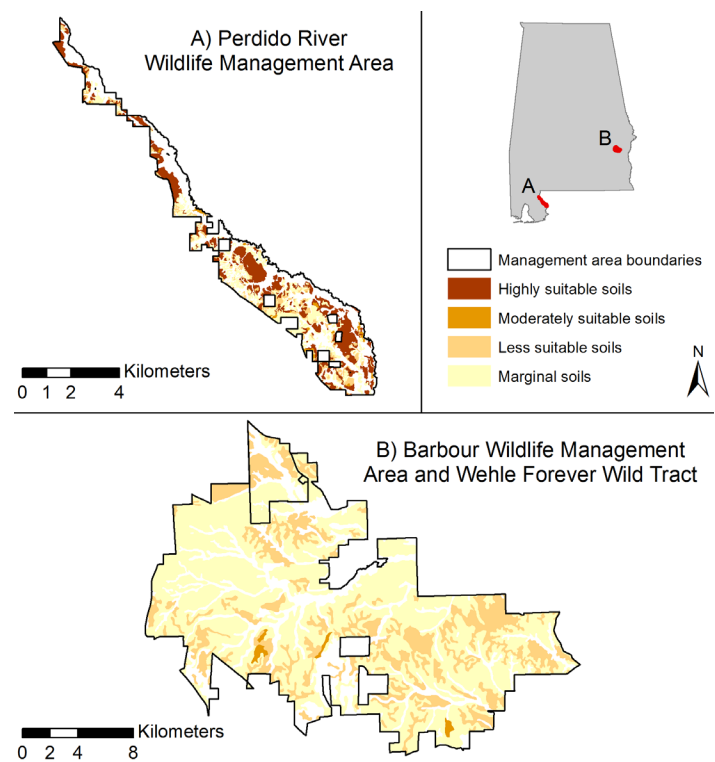
Figure 1. Two Alabama study areas for gopher tortoise individual-based projection modeling and gopher tortoise soil suitability maps for these areas. See Table 2 and text for more information about soil suitability classification.

with dense pine stands, clearcut areas, intermittent bogs, and some areas of longleaf pine restoration. As of 2015 the site supported approximately 300–700 gopher tortoises (S. M. Hermann, Auburn University, unpublished data).

Methods

Projecting Habitat Conditions and Patch Carrying Capacities

Our IBM simulated locations, movements, reproduction, and mortality of individual tortoises in a raster-format landscape of 1-ha cells. The raster layers we used for each study area combined soil type maps and time-specific projected forest stand states (see below) to specify the maximum number of tortoises each cell could support at each time step. In the IBM, simulated tortoises occupied cells, and we allowed them to move to other cells in response to changes in habitat and tortoise density in their current cells. Our simulated tortoises were assigned unique attributes such as age, sex, and locations of patches (cells) each individual had visited in previous time steps. Spatial configuration of habitat in the raster landscape affected probability of successfully moving to another patch, while the proximity of other tortoises affected probability of reproducing. Our projected changes in abundance and distribution of tortoises in each study were the aggregate result of simulated movements and demography of individual tortoises.
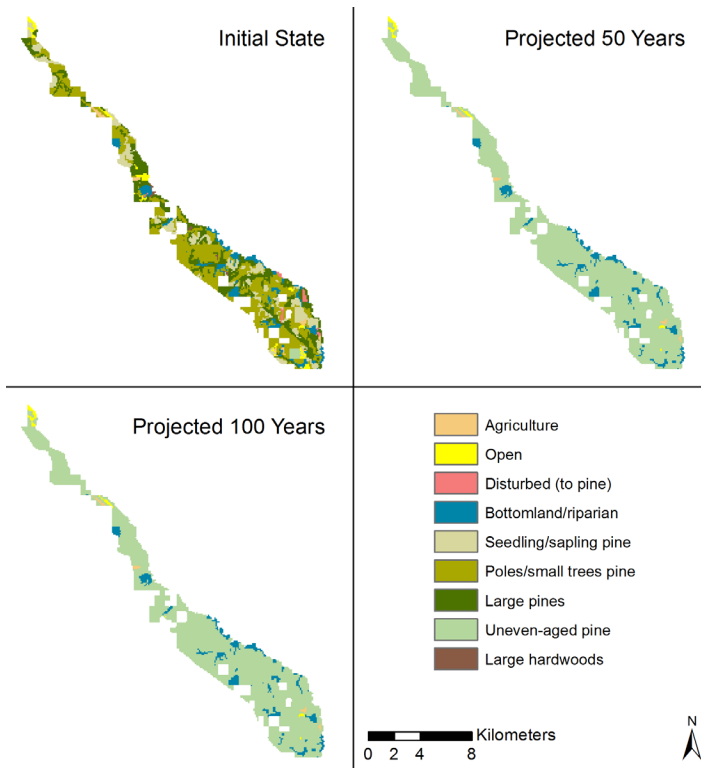
In both focal areas, forest stands and similar management units had been delineated and projected, from a 2011 baseline, in yearly time steps for 100 years as part of a decision analysis evaluating predicted consequences of forest management alternatives for these and other selected properties managed by Alabama Department of Conservation and Natural Resources (Silvano 2013). To project forest conditions, Silvano (2013) developed a state-space model whereby stands on each property were subject to transitions representing both natural and management-caused agents of change (e.g., prescribed burning, succession). Silvano's (2013) model included 25 possible states for each stand in each yearly time step. Herein, we focus on projections from one of 11 alternatives ("Alternative 9"; example in Figure 2) examined by Silvano (2013) in which all upland stands were managed for uneven-aged pine, floodplains were managed for uneven-aged bottomland forest types, and wildlife openings were retained in either agricultural crops or native warm-season grasses. Stochastic projections of Silvano (2013) resulted in a probability distribution for the state of each stand at each time step; in our study, we used the most likely state of each stand at each step. Ignoring state uncertainty likely did not have a strong impact on our results. The most important variation in assumed carrying capacity for tortoises was between pine and open states vs. bottomland and hardwood states (see Methods: "Projecting Habitat Conditions and Patch Carrying Capacities" below). Most of Perdido and most of the portion of Barbour-Wehle that was occupied by tortoises in our simulations were already in pine states initially and projected to be managed for uneven-aged pine as the terminal state. Therefore, state uncertainty would translate into modest uncertainty about time-specific carrying capacities for the pine areas.

For integration with these stand projections, we classified soil types on our study areas into one of five suitability categories for gopher tortoises according the USFWS and NRCS (2012) classification scheme using U.S. Department of Agriculture Natural Resource Conservation Service Soil Survey Geographic (SSURGO) soils data. Highly Suitable soils consist of deep, sandy, well-drained soils that are preferred by gopher tortoises and support the highest densities of tortoise populations. Moderately Suitable and Less Suitable soils have increasing clay content and shallower depths of soils suitable for burrowing. Marginal soils contain features such as high clay content and a higher seasonal water table; gopher tortoises are generally expected to use marginal soils only when other habitat factors (such as extremely dense vegetation) prohibit the use of preferred soil types. Unsuitable soils have properties that prevent the establishment and/or maintenance of tortoise burrows, such as a high water table, frequent flooding, or high gravel content.

For subsequent use in our IBM, we created raster layers of 1-ha cells across each property and categorized each cell based on soil type (assumed permanent) and year-specific projected stand states. For each possible combination of stand state and soil suitability category, we assigned a hypothesized maximum number of tortoises a 1-ha cell could support (i.e., carrying capacity). The carrying capacity values were based on extrapolation from reported densities ranging from <1 to ~3 tortoises/ha, based on studies across much of the gopher tortoise's range (Hermann et al. 2002, Guyer et al. 2012, Ballou 2013, USFWS and SERPPAS 2013, Tuberville et al. 2014). Nonetheless, these densities often were estimated for broader areas (e.g., public land parcels) and do not capture heterogeneity in density at smaller scales. Therefore, similar to Tuberville et al. (2012), we assumed that high-quality habitat patches could have higher carrying capacities at the scale of 1-ha cells.

We assigned maximum carrying capacity values separately for stand states and soil suitability categories. Specified carrying capacities for 1-ha cells were as follows for stand states: seven for uneven-aged pine and openings within pine; five for large pine, two-age pine, and agricultural area (e.g., wildlife food plots) within pine; three for seedling/sapling pine, poles/small pine, and disturbed lands managed to pine; one for open developed areas; and zero for all hardwood state types and other sites managed for hardwoods, bottomlands, and water. A cell's carrying capacity could

Individual-based Population Simulation Model

Following Tuberville et al. (2012) and Westervelt and MacAllister (2012), we developed our IBM in the NetLogo modeling environment (Wilensky 1999) with the R extension for NetLogo (Thiele and Grimm 2010). For each study area and management alternative, 1000 replicate 200-year simulations were performed with monthly time steps for each replicate. We used published information and expert opinions to determine plausible values and ranges of uncertainty for each demographic parameter for each tortoise life stage (Table 1). We incorporated two levels of demographic uncertainty. To reflect parametric uncertainty about long-term average values for demographic parameters, we drew the replicate-specific mean value for each parameter at the start of each replicate from probability distributions with specified parametric ("replicate") standard deviations (Table 1). We incorporated yearly demographic variation by randomly drawing each year's parameter value from a probability distribution described by the replicate-specific mean and corresponding temporal standard deviation (Table 1). While we did not conduct a formal sensitivity analysis on the chosen demographic parameters, drawing a range of values across replicates incorporated uncertainty about the true value of these parameters into our model. We converted yearly demographic rates to corresponding monthly rates. At the beginning of each simulation year, we updated the carrying capacity raster to reflect habitat change as described above. Yearly carrying capacity rasters did not vary among the replicate simulations for each study area.

Tortoise movement was allowed only during the active season for gopher tortoises, from April through October, in our simula-

Figure 2. Initial and projected habitat conditions used in individual-based gopher tortoise projection modeling for the Perdido River Wildlife Management Area. Projections assume forest management focused on developing and maintaining uneven-aged pine over most of the landscape (Alternative 9 in Silvano 2013).

stay constant or change each year because of the yearly time step used in state projections, and did not depend on prior states of the cell. Cell carrying capacities were seven, five, three, one, and zero, respectively, for Highly Suitable, Moderately Suitable, Less Suitable, Marginal, and Unsuitable soils. We then combined the carrying capacity values for a given stand state/soil suitability category and assigned the lower of the two values as the hypothesized maximum carrying capacity for that categorization. Resulting carrying capacity rasters were created for each year of the 100-year stand projection of Silvano (2013) for each of our two focal areas. Although Silvano's (2013) projections had a 100-year window, with our IBM we projected gopher tortoise populations for an additional 100 years because of the long life span and time to maturity of this species. For years 101–200, we kept stand states and thus carrying capacity rasters constant, using the most likely state of each stand in Year 100. This approach was reasonable because the terminal projected stand state with the most relevance to gopher tortoises (uneven-aged pine) had a high (≥75%) probability of being achieved in target stands by Year 100, while by that time seedling/sapling pine and small pine states had a low (<2%) probability of occurring (Silvano 2013; see also Figure 2).

Table 1. Parameter values of probability distributions used for stochastic gopher tortoise population projection modeling for two Alabama study areas. In the Individual-Based Model (IBM), replicate average and within-replicate yearly survival were drawn from beta probability distributions with specified mean and standard deviation (SD). Individual survival at each time step was determined by drawing a random number between 0 and 1; if this value was less than the probability of mortality for that individual, it would die. In the IBM, clutch size for reproducing females was drawn from a Poisson distribution. In the matrix model, all adult females had the same average egg production, with each year's value randomly drawn from a Poisson distribution. Females ≥20 yr and males ≥18 yr could reproduce (Landers et al. 1982, Aresco and Guyer 1999a). An expected sex ratio of 1:1 was assumed for all stages and for augmented tortoises, with individual sex determined by a Bernoulli trial.

Stage	Mean	SD Replicates	SD Years	Key references
Egg survival	0.4	0.05	0.1	Smith et al. (2013)
Hatchling (<1 yr) survival	0.128	0.05	0.1	Perez-Heydrich et al. (2012)
Juvenile (1–4 yrs) survival	0.5	0.07	0.07	Wilson (1991)
Subadult (5–14 yrs) survival	0.9	0.05	0.05	Tuberville et al. (2008)
Adult (≥15 yrs) survival	0.97	0.02	0.01	Tuberville et al. (2014)
Clutch size	5	–	2.24	Epperson and Heise (2003), Perez-Heydrich et al. (2012), Averill-Murray et al. (2014)

tions. Tortoises moved from a cell only if the number of tortoises in the cell exceeded carrying capacity, which could result from other tortoises entering the cell or reduction in carrying capacity due to changing habitat conditions, corresponding to habitat-related burrow abandonment (Aresco and Guyer 1999b, Jones and Dorr 2004). Juvenile and hatchling tortoises are more difficult to detect than adults and thus are often underrepresented during distance sampling surveys (Smith et al. 2009). Our carrying capacity values were based on density estimates from such surveys; therefore, like Tuberville et al. (2012), we limited this movement out of cells to older age classes. If the number of tortoises in a cell exceeded carrying capacity, the youngest tortoise ≥5 years old moved from that cell into one of eight neighboring cells, based on which neighbor had the most space (carrying capacity minus the number of tortoises ≥5 years old in the cell) available. If no neighboring cells had space, the tortoise would randomly move to one of the eight neighboring cells, check again for neighboring cells with available space, and either move to the neighbor with the most space if available or move to a randomly chosen neighboring cell. In the latter case, an individual's choices would be limited to cells it had not occupied within the past year to prevent tortoises from randomly moving back to cells known to be unsuitable. We only allowed juvenile tortoises (1–4 years old) to move if the cell they were on had a carrying capacity of zero, in which case they followed the same procedure described above. We did not allow hatchlings (<1 year old) to move. If a tortoise moved to a cell outside of the study area, we specified that it had a 6% chance of being permanently lost to the population (to simulate leaving the property altogether) and a 94% chance of returning to the property on a neighboring cell. We chose these values because in preliminary simulations they produced rates of permanent off-site dispersal that appeared reasonable relative to actual off-site movements by Barbour-Wehle tortoises (E. Soehren, Alabama Department of Conservation and Natural Resources State Lands Division, personal communication). Barbour-Wehle was bordered by private lands that were frequently in unsuitable cover types (e.g., dense pine) and without known populations of gopher tortoises; Perdido was also bordered by largely unsuitable cover types on the southwest side, and by the Perdido River on the northeast side. We therefore assumed immigration was negligible. Each month, survival of each individual was randomly determined (Table 1). However, if a tortoise was in a cell with carrying capacity of zero in November it would die automatically, as tortoises cannot overwinter in unsuitable habitat.

We modeled reproduction based on the following patterns: Most mating attempts between gopher tortoises occur in late summer and early fall, although mating attempts can occur throughout the active season (Johnson et al. 2007). Female tortoises are known

to store sperm, and likely do so at least over winter (Johnson et al. 2007, Rostal 2014). Whereas most male movements to visit female burrows are believed to be <200 m, males have been known to travel further (Guyer et al. 2012). In our IBM, each June, female tortoises would lay eggs if they had been within 500 m of a reproductive-aged male tortoise during the previous year, thus ensuring that isolated females did not reproduce. Hatching occurred in September, with clutch size and egg survival randomly determined (Table 1). If a hatchling survived to age 1, it would become mobile and have its sex assigned randomly based on an expected 1:1 sex ratio.

We initialized the number and location of tortoises at the beginning of each simulation replicate, with the initial number specified or randomly generated based on recent information about tortoise numbers in each area (see Study Areas). For Barbour-Wehle, our model was initiated with 16 20-year-old tortoises with sex randomly assigned based on a 1:1 sex ratio. We placed tortoises within two areas encompassing known locations of tortoises as of 2013 and the original translocation release sites at Wehle. Within these areas, tortoises were randomly placed in cells that also had a carrying capacity >0. At Perdido, the initial number of tortoises for each replicate was randomly chosen from a normal distribution ($\overline{x} = 434$, SD = 114). Following Tuberville et al. (2012), we randomly chose the ages of initial tortoises at Perdido with younger individuals making up more of the population than older age classes, and with an expected 1:1 sex ratio. Perdido is known to support breeding tortoises; however, the current density of young tortoises (i.e., juveniles and younger age classes) is unknown. Thus, the reproductive processes described above were used at the start of each simulation replicate to produce an initial population of eggs, hatchlings, and juveniles. The initial population of tortoises on Perdido was randomly distributed on contiguous areas of Highly Suitable soils ≥5 ha that had non-zero carrying capacity under initial landscape conditions.

Augmentation Scenarios

Relocation is a commonly employed management strategy for gopher tortoises (Dodd and Seigel 1991). To assess potential impacts of one-time augmentations on population viability, we compared a no-augmentation vs. augmentation scenario at Barbour-Wehle, and a no-augmentation vs. two augmentation scenarios at Perdido. At Barbour-Wehle, our simulated augmentation added 25 tortoises to the two starting areas on the Wehle Tract. For Perdido, our augmentations occurred in two large (223- and 303-ha) areas of highly suitable soils in the central and southern parts of the property. In one Perdido scenario ("north and south augmentation"), 25 tortoises were added to each area in random

locations. In the other scenario, we added 50 tortoises to the more northern area only ("north only"). For augmentation scenarios at both study areas, our tortoises were released in June of Year 10. Because relocated or translocated tortoises are often taken opportunistically from various sources, we randomly assigned age from a uniform distribution between ages 5 and 60. We randomly assigned sex based on an expected 1:1 sex ratio. Once added to the population, we assumed translocated tortoises were equivalent to resident tortoises in movements and demography. Although translocated gopher tortoises often have high dispersal rates that can result in low retention rates, translocated tortoises that become established in the translocation area may have survival and retention rates similar to previously established individuals (Lohoefener and Lohmeier 1986; Burke 1989; Tuberville et al. 2005, 2008; Ashton and Burke 2007). Thus, our augmentations model the number of released tortoises that became established.

For all IBMs, we used R v. 3.2 (R Core Team 2015) for data analysis and summarized spatial output with ArcMap v. 10.3 (Environmental Systems Research Institute, Redlands, California). All analyses of population size included all individuals at least one year of age and older, as population targets for management are typically focused on older age classes (e.g., Gopher Tortoise Council 2013). For each iteration, we compared the population size at 100 and 200 years to the starting population size of that iteration; the mean percent change between these time steps and the initial population size was then calculated by averaging across all iterations for each alternative. We calculated the extinction probability after 100 and 200 years as the number of iterations in which population size reached fewer than two individuals ≥1 year by those time steps, out of the total number of replicates for that scenario. The functional extinction threshold of two individuals was chosen because below this number, breeding cannot occur.

Matrix Model

To examine the degree to which projected population trends from the IBM were a function of baseline demographic rates or assumed relationships of spatially explicit habitat patterns and individual movements, we developed a stage-structured matrix model (Caswell 2000) that used the same demographic stages and demographic parameter distributions as the IBM (Table 1). Our matrix modeling used yearly time steps and did not incorporate study area-specific information, spatial structure, or individual-level dynamics other than stochastic survival and reproduction. The number of eggs produced per female each year was drawn from a Poisson distribution with a mean of 5, multiplied by half the adult population at that time step, thus assuming a 1:1 sex ratio and that all adult females breed in a given year.

Our stochastic transition matrix was multiplied by the population vector at each time step to project the population, with two initial populations examined. The larger starting population consisted of 250 adults, 125 subadults, 125 juveniles, 250 hatchlings, and 500 eggs; we chose these values because the population size was well within the range of uncertainty about the current tortoise population at Perdido (see Study Areas), and because 250 adult gopher tortoises corresponds to one rule-of-thumb for minimum viable population size (Gopher Tortoise Council 2013). Our second starting population consisted of 16 adults, as in the Barbour-Wehle IBM projections. We developed the model in R v. 3.2, with each scenario run for 10,000 replicated simulations of 200 yearly time steps each.

Results

At both study areas under all augmentation scenarios, there was a significant decline in total tortoise abundance overtime, approaching zero tortoises after 200 years (Table 2). The only population increase observed from Year 0 to Year 50 was at Barbour-Wehle under the population augmentation scenario which added tortoises at Year 10; however, the population declined substantially by Year 100. Extinction probability was high for both properties for all augmentation scenarios. At Barbour-Wehle, augmentation lowered extinction probability moderately, particularly within the first 100 years (Year 100: 64% probability of extinction with augmentation vs. 85% probability of extinction without augmentation). The Perdido population had comparatively low extinction probability (<35%) after 100 years under all scenarios. Both Perdido augmentation strategies produced similar extinction probabilities, though both were slightly lower than the no-augmentation scenario.

Because of consistent declines in populations, few cells of the simulated landscapes were occupied by tortoises in Years 100 and 200 (e.g., Figure 3). Cells that were occupied were generally limited to starting area cells and close neighbors. Therefore, at Barbour-Wehle, the simulated populations did not successfully expand from Wehle to non-adjacent portions of Barbour. For both sites, population augmentation appeared to increase the probability of cells being occupied at later time steps.

The matrix population model, similar to the IBM, projected population declines with both starting population sizes tested (Table 2). However, the matrix model consistently projected less extreme declines and lower probability of extinction compared to similar projections with the IBM. With a starting population of 500 tortoises ≥1 years old, extinction probability based on matrix-model projections was lower in Years 100 and 200 than under any scenario projected with the IBM. For the smaller (16 adults) initial population, extinction probability from the matrix projec-

Table 2. Population size (≥1 yr; n), cumulative percentage change, and extinction probability at Years 100 and 200 from gopher tortoise population projections using a matrix model and Individual-Based Models (IBMs) for populations at Barbour Wildlife Management Area/Wehle Forever Wild Tract and Perdido River Wildlife Management Area. Mean (SE) values are across all simulation replicates for that scenario.

Scenario	Year 100			Year 200		
	Mean (SE) n	Mean % change (SE)	Extinction probability	Mean (SE) n	Mean % change (SE)	Extinction probability
Barbour−Wehle IBM						
No augmentation	1.0 (0.1)	−93.7 (0.8)	0.85	0.4 (0.3)	−97.2 (2.1)	0.98
With augmentation	3.0 (0.2)	−81.5 (1.4)	0.64	0.8 (0.2)	−95.3 (1.5)	0.96
Perdido IBM						
No augmentation	23.4 (2.0)	−94.8 (0.4)	0.34	5.7 (2.1)	−98.9 (0.4)	0.89
North only augmentation	25.2 (2.1)	−94.4 (0.5)	0.30	5.6 (2.2)	−98.8 (0.45)	0.87
North / south augmentation	31.2 (2.5)	−93.0 (0.5)	0.29	8.2 (1.8)	−98.3 (0.4)	0.87
Matrix Model						
Large initial population size	88.4 (1.2)	−82.3 (0.2)	0.11	51.1 (1.8)	−89.8 (0.4)	0.43
Small initial population size	4.5 (0.06)	−72.1 (0.4)	0.48	2.7 (0.11)	−83.2 (0.7)	0.76
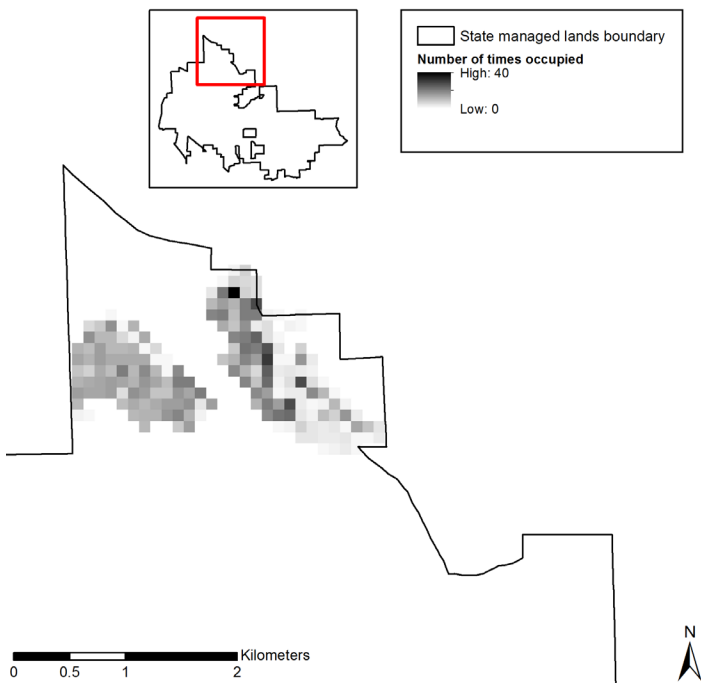
Figure 3. Number of times individual cells of the Barbour Wildlife Management Area/Wehle Forever Wild Tract, Alabama, simulated raster landscapes were occupied by at least one simulated gopher tortoise (≥1 yr) after 100 years of the population augmentation scenario during the 1000 iterations of the individual-based gopher tortoise population projection.

tion was 0.48 at Year 100 and 0.76 at Year 200, compared to 0.64–0.85 at Year 100 and 0.96–0.98 at Year 200 in the Barbour-Wehle IBM projections with the same starting population size.

Discussion

With both the IBM approach and the non-spatial matrix model, we projected pessimistic futures for gopher tortoises on our focal areas. Even with the non-spatial stage-structured matrix model, average demographic rates for all models result in $\lambda < 1.0$. Thus, long-term population declines would be projected regardless of spatial habitat configuration or current population sizes assumed for our two management areas, although those factors affected the projected rate of decline. These results are similar to those of previous population modeling studies of gopher tortoises that have found low growth rates when using demographic parameters based on the available published literature (Tuberville and Gibbons 2009, Tuberville et al. 2012). The results from simulations using the matrix model, which ignored any potential limiting effects of spatial structure and individual-scale dynamics, suggest that the primary pattern in the IBM results (i.e., strong declines) was not sensitive to finer-scale movement assumptions we incorporated in the IBM.

Regardless of whether a local population currently is above any threshold of minimum viable population size, the population will not be self-sustaining unless its demographic rates result in $\lambda \geq 1.0$. A critical question is whether actual demographic rates of our focal populations are accurately represented by the aggregation of available published estimates. For example, clutch size is known to be correlated with body size in gopher tortoises (Landers et al. 1980), which was not accounted for in our model. There is also

significant uncertainty about survival rates of juveniles and sub-adults and variability in survival of eggs and hatchlings (Tuberville et al. 2009, McCoy et al. 2014). It is also unknown how much and how quickly reproductive success and survival may increase in response to broad-scale habitat restoration. Moreover, survival and reproduction likely continues to be affected by broad-scale changes to historical coastal plain landscapes and ecosystems (e.g., habitat degradation, Aresco and Guyer 1999b; habitat restoration, Tuberville et al. 2014; established invasive species, Dziadzio et al. 2016a). As additional research continues to expand our understanding of gopher tortoise demographic rates (e.g., Dziadzio et al. 2016b, Radzio et al. 2017), population projection models should be iteratively refined.

Augmentation slightly increased long-term projected abundance and, at Barbour-Wehle, produced a several decades-long boost to the population. Nonetheless, augmentation could not rescue populations in our scenarios. Augmentation may benefit real populations if translocated individuals become socially and reproductively functional members of a stable or increasing population. However, there remains high uncertainty about the long-term utility of augmentation. Translocated tortoises typically have high rates of dispersal from release sites, particularly if not penned on-site prior to release (Lohoefener and Lohmeier 1986; Burke 1989; Tuberville et al. 2005, 2008; Ashton and Burke 2007). It is also unclear how translocated tortoises integrate into and affect the complex social structure of resident tortoises (Guyer et al. 2014).

It could be argued that our IBM approach goes beyond what is currently known about gopher tortoise movements and other behavior to be more than a modeling exercise. However, the development of explicit rules determining simulated individual movements makes the IBM approach a valuable platform for evaluating current knowledge about movement behavior and for advancing alternative hypotheses for the pattern and causes of movements. A next step with our IBM would be to assess relative sensitivity of projections to alternative hypotheses and other sources of uncertainty. For example, the current model stipulated simplified rules for movements between adjacent cells, whereas actual dispersal movements and patch-abandonment dynamics are poorly understood. Eubanks et al. (2003) recorded two male tortoises emigrating long distances (>1 km) from high-quality habitat (old growth longleaf pine with abundant herbaceous forage) in southwestern Georgia for unknown reasons, indicating that tortoises may rarely move long distances and establish burrows in new areas regardless of habitat quality. Additionally, the social behavior of the species (Guyer et al. 2014) suggests that a tortoise may seek out other tortoises when moving to a new location, a behavior not included in the current model.

Compared to non-spatial models, the IBM approach forces more explicit consideration of the current and potential future spatial characteristics of a specific management landscape. In our applications, the rate of decline was much greater in IBM than stochastic matrix projections. This is to be expected because the IBM explicitly incorporated landscape pattern, patch-level carrying capacity, spatial distribution of individuals, and proximity-dependent breeding. Although we do not argue that the IBM projections are more "correct" because of these complexities, ignoring spatial factors may lead to overestimation of potential population viability (Law et al. 2003, Akçakaya et al. 2004).

Moreover, such spatial constraints are important to on-the-ground management. Local populations of vulnerable species such as gopher tortoises are often highly clustered in relatively small portions of a management area (e.g., Thompson et al. 1990, Smith et al. 2003). Suitable habitat for a species may be patchily distributed, such as the sandy soils and open-canopy vegetation structure that characterize gopher tortoise habitat (Auffenberg and Franz 1982, Aresco and Guyer 1999b, Jones and Dorr 2004) in the Barbour-Wehle landscape (Figure 1). The IBM approach is a useful and flexible tool for site-specific management (Travis et al. 2011), such as prioritizing where prescribed burning or other management actions should occur to maintain occupied patches, increase connections among these patches, and provide potential pathways of expansion to other suitable areas (Allen et al. 2016).

Although the models of this study, like all models, include simplifications and assumptions based on limited information, they nonetheless highlight the potential challenges in conserving small populations in spatially complex and temporally stochastic environments. As ongoing studies across the range of gopher tortoises produce more information about demographic rates (e.g., Dziadzio et al. 2016b, Radzio et al. 2017), population models will be a fundamental tool for assessing how updated estimates affect projected viability. Spatially explicit models, such as IBM's, involve additional technical complexity, but are particularly useful for informing management of patchily distributed, small populations.

Acknowledgments

Literature Cited

Akçakaya, H. R., V. C. Radeloff, D. J. Mladenoff, and H. S. He. 2004. Integrating landscape and metapopulation modeling approaches: Viability of the sharp-tailed grouse in a dynamic landscape. Conservation Biology 18:526–537.

Allen, C. H., L. Parrott, and C. Kyle. 2016. An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (*Ovis canadensis*). PeerJ 4:e2001.

Aresco, M. J. and C. Guyer. 1999a. Growth of the tortoise *Gopherus polyphemus* in slash pine plantations of southcentral Alabama. Herpetologica 55:499–506.

——— and ———. 1999b. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63:26–35.

Ashton, K. G. and R. L. Burke. 2007. Long-term retention of a relocated population of gopher tortoises. Journal of Wildlife Management 71:783–787.

Auffenberg, W. and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). Pages 95–126 in R. B. Bury, editor. North American tortoises: Conservation and ecology. U.S. Fish and Wildlife Service, Wildlife Research Report 12, Washington, D.C.

Averill-Murray, R. C., L. J. Allison, and L. L. Smith. 2014. Nesting and reproductive output among North American tortoises. Pages 110–117 in D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland.

Ballou, A. R. 2013. Aspects of gopher tortoise (*Gopherus polyphemus*) populations in Georgia: Status, landscape predictors, juvenile movements, and burrow use. Master's thesis. University of Georgia, Athens.

Burke, R. L. 1989. Florida gopher tortoise relocation: Overview and case study. Biological Conservation 48:295–309.

Butler, M. J., T. W. Dolan, J. H. Hunt, K. A. Rose, and W. F. Herrnkind. 2005. Recruitment in degraded marine habitats: A spatially explicit, individual-based model for spiny lobster. Ecological Applications 15:902–918.

Caswell, H. 2000. Matrix population models: Construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts.

Conroy, M. J., R. J. Barker, P. W. Dillingham, D. Fletcher, A. M. Gormley, and I. M. Westbrooke. 2008. Application of decision theory to conservation management: Recovery of Hector's dolphin. Wildlife Research 35:93–102.

Cox, J. 1989. Survival characteristics of small gopher tortoise populations and their possible influence on relocation efforts. Pages 7–14 in J. E. Diemer, D. R. Jackson, J. L. Landers, J. N. Layne, and D. A. Wood, editors. Gopher tortoise relocation symposium proceedings. Florida Game and Freshwater Fish Commission Nongame Wildlife Program Technical Report No. 5., Tallahassee.

———, D. Inkley, and R. Kautz. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Office of Environmental Services, Florida Game and Freshwater Fish Commission Nongame Wildlife Program Technical Report No. 4., Tallahassee.

DeAngelis, D. L. and L. J. Gross, editors. 1992. Individual-based models and approaches in ecology: Populations, communities, and ecosystems. Chapman and Hall, New York, New York.

Dodd, C. K. and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336–350.

Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: Current forms and future uses Ecological Applications 5:3–11.

Dziadzio, M. C., R. B. Chandler, L. L. Smith, and S. B. Castleberry. 2016a. Impacts of red imported fire ants (*Solenopsis invicta*) on nestling and hatchling gopher tortoises (*Gopherus polyphemus*) in southwest Georgia, USA. Herpetological Conservation and Biology 11:527–538.

———, L. L. Smith, R. B. Chandler, and S. B. Castleberry. 2016b. Effects of nest location on gopher tortoise nest survival. Journal of Wildlife Management 80:1314–1322.

Elderd, B. D. and M. P. Nott. 2008. Hydrology, habitat change and population demography: An individual-based model for the endangered Cape Sable seaside sparrow *Ammodramus maritimus mirabilis*. Journal of Applied Ecology 45:258–268.

Epperson, D. M. and C. D. Heise. 2003. Nesting and hatchling ecology of gopher tortoises (*Gopherus polyphemus*) in southern Mississippi. Journal of Herpetology 37:315–324.

Eubanks, J. O., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica 59:311–321.

Gopher Tortoise Council. 2013. Gopher tortoise minimum viable population and minimum reserve size working group report.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? Ecological Modelling 115:129–148.

——— and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, New Jersey.

Guyer, C., S. M. Hermann, and V. M. Johnson. 2014. Social behaviors of North American tortoises. Pages 102–109 in D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland.

———, V. M. Johnson, and S. M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (*Gopherus polyphemus*). Herpetological Monographs 26:122–134.

Hermann, S. M., C. Guyer, J. H. Waddle, and M. G. Nelms. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, *Gopherus polyphemus*. Biological Conservation 108:289–298.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. Bioscience 38:682–691.

Johnson, V. M., C. Guyer, and M. D. Boglioli. 2007. Phenology of attempted matings in gopher tortoises. Copeia 2007:490–495.

Jones, J. C. and B. Dorr. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. Wildlife Society Bulletin 32:456–464.

Landers, J. L., J. A. Garner, and W. A. McRae. 1980. Reproduction of gopher tortoises (*Gopherus polyphemus*) in southwestern Georgia. Herpetologica 36:353–361.

———, W. A. McRae, and J. A. Garner. 1982. Growth and maturity of the gopher tortoises in southwestern Georgia. Bulletin of the Florida State Museum, Biological Sciences 27:81–110.

Law, R., D. J. Murrell, and U. Dieckmann. 2003. Population growth in space and time: Spatial logistic equations. Ecology 84:252–262.

Lohoefener, R. and L. Lohmeier. 1986. Experiments with gopher tortoise (*Gopherus polyphemus*) relocation in southern Mississippi. Herpetologica 17:37–40.

McCoy, E. D., G. Aguirre L., R. T. Kazmaier, and C. R. Tracy. 2014. Demography of North American tortoises. Pages 134–142 in D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland.

McRae, B. H., N. H. Schumaker, R. B. McKane, R. T. Busing, A. M. Solomon, and C. A. Burdick. 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. Ecological Modelling 219:77–91.

Miller, P. S. 2001. Preliminary population viability assessment for the gopher tortoise (*Gopherus polyphemus*) in Florida. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota.

Omernik, J. M. and G. E. Griffith. 2014. Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. Environmental Management 54:1249–1266.

Perez-Heydrich, C., K. Jackson, L. D. Wendland, and M. B. Brown. 2012. Gopher tortoise hatchling survival: Field study and meta-analysis. Herpetologica 68:334–344.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radzio, T. A., J. A. Cox, and M. P. O'Conner. 2017. Hatching success and other reproductive attributes of gopher tortoises in southwest Georgia. Chelonian Conservation and Biology 16:103–105.

Root, K. V. and J. Barnes. 2006. Risk assessment for a focal set of rare and imperiled wildlife in Florida. Florida Fish and Wildlife Commission Contract No. 03111 Final Report.

Rostal, D. C. 2014. Reproductive physiology of North American tortoises. Pages 37–45 in D. C. Rostal, E. D. McCoy, and H. R. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland.

Seigel, R. and C. Dodd. 2000. Manipulation of turtle populations for conservation: Halfway technologies or viable options? Pages 218–238 in M. Klemens, editor. Turtle Conservation. Smithsonian Institution Press, Washington, D.C.

Silvano, A. L. 2013. Incorporating long-term spatial and temporal effects in a state space model to evaluate land management alternatives for imperiled species conservation in Alabama. Master's thesis. Auburn University, Auburn, Alabama.

Smith, D. R., R. F. Villella, and D. P. Lemarié. 2003. Application of adaptive cluster sampling to low-density populations of freshwater mussels. Environmental and Ecological Statistics 10:7–15.

Smith, L. L., J. M. Linehan, J. M. Stober, M. J. Elliott, and J. B. Jensen. 2009. An evaluation of distance sampling for large-scale gopher tortoise surveys in Georgia, USA. Applied Herpetology 6:355–368.

———, D. A. Steen, L. M. Conner, and J. C. Rutledge. 2013. Effects of predator exclusion on nest and hatchling survival in the gopher tortoise. Journal of Wildlife Management 77:352–358.

———, T. D. Tuberville, and R. A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise (*Gopherus polyphemus*), Joseph W. Jones Ecological Research Center, 16–17 January 2003: Final results and recommendations. Chelonian Conservation and Biology 5:326–330.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261–270.

Thiele, J. C. and V. Grimm. 2010. NetLogo meets R: Linking agent-based models with a toolbox for their analysis. Environmental Modelling and Software 25:972–974.

Thompson, S. K. Adaptive cluster sampling. Journal of the American Statistical Association 85:1050–1059.

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods in Ecology and Evolution 2:477–488.

Tuberville, T. D., K. M. Andrews, J. D. Westervelt, H. E. Balbach, J. Macey, and L. Carlile. 2012. 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. Pages 109–131 in J. D. Westervelt and G. L. Cohen, editors. Ecologist-Developed Spatially Explicit Dynamic Landscape Models. Springer, Boston, Massachusetts.

———, E. E. Clark, K. A. Buhlmann, and J. W. Gibbons. 2005. Translocation as a conservation tool: Site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8:349–358.

———, J. W. Gibbons, and H. E. Balbach. 2009. Estimating viability of gopher tortoise populations. U.S. Army Corps of Engineers Construction Engineering Research Laboratory, Final Report, Washington, D.C.

———, T. M. Norton, B. D. Todd, and J. S. Spratt. 2008. Long-term apparent survival of translocated gopher tortoises: A comparison of newly released and previously established animals. Biological Conservation 141:2690–2697.

———, B. D. Todd, S. M. Hermann, W. K. Michener, and C. Guyer. 2014. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management 78:1151–1160.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice. Springer, New York, New York.

U.S. Fish and Wildlife Service (USFWS) and Natural Resources Conservation Service (NRCS). 2012. Gopher tortoise (*Gopherus polyphemus*) soil classifications for the federally listed range using the National Soil Information System database, version 1.

U.S. Fish and Wildlife Service (USFWS), and Southeast Regional Partnership for Planning and Sustainability (SERPPAS). 2013. 4th annual report, candidate conservation agreement for the gopher tortoise.

Westervelt, J. D. and B. MacAllister. 2012. Forecasting gopher tortoise (*Gopherus polyphemus*) distribution and long-term viability at Fort Benning, Georgia. Pages 85–107 in J. D. Westervelt and G. L. Cohen, editors. Ecologist-Developed Spatially Explicit Dynamic Landscape Models. Springer, Boston, Massachusetts.

Wilensky, U. 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, Illinois.

Wilson, D. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. Journal of Herpetology 25:376–379.