

EVALUATING THE UTILITY OF TRANSLOCATION FOR TURTLE CONSERVATION:  
A CASE STUDY BASED ON THE BEHAVIORAL AND DEMOGRAPHIC RESPONSES OF  
GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*)

by

TRACEY D. TUBERVILLE

(Under the direction of direction of J. Whitfield Gibbons)

ABSTRACT

Two-thirds of the world's turtle species are considered threatened. As exploitation and habitat alteration continue to cause population declines and extirpations, translocations play an increasingly important role in turtle conservation. However, few translocation efforts have been thoroughly evaluated to determine their success. I present a framework for evaluating translocation success, using the gopher tortoise (*Gopherus polyphemus*) as a case study. This framework includes monitoring three processes that influence population stability – emigration, survivorship and reproduction. Experimental releases and two years of subsequent monitoring via radiotelemetry were conducted on the Savannah River Site, SC, to test the relative effectiveness of no penning, 9-month and 12-month penning treatments. Penning significantly increased site fidelity both in terms of reducing activity areas and reducing the proportion of animals dispersing. Long-term survivorship was investigated in a population of gopher tortoises established through multiple releases on St. Catherines Island (SCI), GA. Based on 12 years of mark-recapture data analyzed in program MARK, apparent survival of newly released tortoises was temporarily reduced, most likely as a result of permanent dispersal of some tortoises from the release area. However, apparent survival of translocated tortoises was consistently high once

they became established as residents. Mating system was also investigated in the SCI translocated population by genetic sampling of 27 adult males, 34 adult females, and 121 offspring collected from 19 clutches. Paternity (and maternity, if not already known) was assigned based on genotypes at five microsatellite loci. Reproductive success varied among males, with larger males siring more offspring. Among successful sires, previously established resident males sired a disproportionate number of the offspring sampled, despite being significantly smaller than subsequently released males. Finally, population models based on current literature suggest that gopher tortoise populations are either declining or the species' life history is inadequately characterized. Simulation of different translocation scenarios indicate that translocation can be used to establish viable populations but that release protocols can have important long-term demographic consequences. These studies demonstrate that translocation can be a useful tool for managing gopher tortoise populations and also provide a comprehensive framework for evaluating translocation success in other species.

INDEX WORDS: translocation, reintroduction, conservation, turtle, tortoise, gopher tortoise, *Gopherus polyphemus*, dispersal, apparent survival, mating system, reproductive success, population viability analysis

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TRACEY D. TUBERVILLE

B.S. Furman University, 1993

M.S. University of Georgia, 1998

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by

TRACEY D. TUBERVILLE

Major Professor: J. Whitfield Gibbons

Committee: Justin D. Congdon  
Travis C. Glenn  
Craig Guyer  
Patricia A. Gowaty

Electronic Version Approved:

Maureen Grasso  
Dean of the Graduate School  
The University of Georgia  
May 2008

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CHAPTER 1  
INTRODUCTION AND LITERATURE REVIEW

## POPULATION MANIPULATIONS AS TOOLS FOR TURTLE CONSERVATION

As ecosystems become more and more impacted by human activities, natural processes become increasingly disrupted and the ability of species to compensate for these perturbations diminishes. As a result, species become more vulnerable to local extirpations and even range-wide extinction. Although non-intrusive management approaches such as habitat protection, restoration, and management are critical to maintaining biodiversity and ecosystem function, some species will require more intensive management measures, including population manipulations.

### Types of manipulations

A broad array of population manipulations have been used to manage turtle species, including head-starting, repatriation, and augmentation (Seigel & Dodd 2000). Below I describe some of the most common population manipulations that are used in species management. Because these terms have not always been used with consistent meanings in the literature, the specific definitions as used here are provided below. The categories below are not mutually exclusive. Depending on the history of a project and the types of manipulations employed, a particular project can fall under more than one category.

*Head-starting* – the rearing of hatchlings (either from natural nests or eggs incubated in the lab) in captivity until they have ‘outgrown their period of greatest vulnerability to predators’ (Spinks et al. 2003) in order to increase survivorship.

*Relocation* – displacement of wild-caught animals from their habitat to avoid immediate threats such as development (Dodd & Seigel 1991); relocation is not motivated by conservation goals but is focused on the welfare of individual animals in response to human-animal conflicts.

*Translocation* – the intentional release of individuals of a species at a *within-range* location different from their capture location in order to ‘establish, reestablish, or augment a population’ (Griffith et al. 1989); translocations typically use wild-caught individuals, although head-started animals may also be used.

*Repatriation* – a type of translocation in which individuals of a species are released at a location where the species formerly occurred but from which it has been extirpated; typically there is direct evidence of historical occupation by the species, although animals may also be released into appropriate within-range habitat where species were only suspected to have occurred; release animals can be wild-caught or head-started animals and the purpose is to re-establish a viable population of the species.

*Population augmentation* – release of individuals of a species at a location already occupied by the species but where the resident population is too small to be viable on its own; release animals may be wild-caught or captive-reared.

*Introduction* – release of individuals of a species outside their historical range either by accident (e.g., fire ants in the southeastern U.S.) or in order to establish a population for conservation research (e.g., ringtailed lemur colony on a Georgia barrier island).

*Re-introduction* – although this term is often used interchangeably or in place of “repatriation,” we will avoid the use of “re-introduction” because of its close affinity to the way “introductions” are defined here.

### Concerns about manipulating populations

There is understandable reluctance or hesitation to employ manipulative techniques to manage species or individual populations. Much of the criticisms of manipulations such as translocation and head-starting stem from misguided attempts to portray such techniques as silver bullets—without considering alternative approaches or a combination of approaches (Seigel and Dodd 2000). In addition, these techniques are still largely viewed as experimental due to the lack of subsequent monitoring in individual projects to evaluate the techniques’ effectiveness (Frazer 1992, Seigel and Dodd 2000).

Most importantly, when such techniques simply mask the symptoms of the problem (e.g., increasing the number of animals in a declining population) rather than solve the root problem itself (e.g., increased adult mortality on roads), they constitute half-way technologies that are unlikely to succeed (Frazer 1992). Without addressing the causes of the decline, released animals would be subjected to the same threats and no more likely to survive in the natural environment. However, population manipulations could be appropriate under circumstances when the threats and causes of decline have been removed but the populations are so small or so

vulnerable that they are likely to disappear without temporary intervention (Frazer 1992; Heppell et al. 1996).

In short, population manipulation requires careful consideration and planning (IUCN 1998, Seigel and Dodd 2000) and should not be undertaken without:

- 1) understanding of the species' and system's ecology
- 2) considering the associated ecological, financial, or logistical constraints
- 3) considering other alternative management techniques in terms of their relative benefits and risks
- 4) verifying that the threats or causes of the original decline have been abated
- 5) developing detailed protocols
- 6) planning subsequent monitoring of affected populations
- 7) ensuring long-term security & management of habitat / site
- 8) coordinating with all stake holders

## REVIEW OF TRANSLOCATION LITERATURE FOR TURTLES

Translocations are commonly used in the management of native birds and mammals, although success rates have differed between game (86%) and non-game species (46%).

Variation in success rate has been attributed to number of animals released, habitat quality at the release site, location of the release site within the species' range, and the species' life history (Griffith et al. 1989, Wolf et al. 1996). The documented success rate for amphibian and reptile projects is lower (19%; Dodd & Seigel 1991) although little research and post-translocation monitoring have been conducted.

However, with reptiles and amphibians experiencing world-wide population declines (Alford and Richards 1999, Gibbons et al. 2000) and at least two-thirds of the world's turtle species considered threatened with extinction by the IUCN, translocations are considered critical conservation components for repatriation of the most threatened species (Turtle Conservation Fund 2002). Despite the controversy surrounding translocations and the dearth of post-translocation monitoring data available to evaluate its effectiveness for management of turtle populations, translocation may sometimes be the only option for re-establishing extirpated populations and reconnecting fragmented ones.

Most turtle translocation projects have been conducted with terrestrial turtles, particularly desert and gopher tortoises in the U.S. There have been a few studies on box turtles in the U.S. and with tortoise species elsewhere. Most post-monitoring has focused on movement patterns and site fidelity and has typically been only short term (lasting 1-2 yrs). The major findings of select published studies are provided below.

## Terrestrial turtles

### Gopher tortoises

Gopher tortoises have been the subject of several translocation studies, which have varied in their conclusions regarding the successfulness of the technique. Post-translocation site fidelity and home ranges have varied among studies, sites, and individuals depending on release protocols, distance between capture and release site, and life stage and sex of the individual. Based on studies with adult animals, fidelity to the release site can be dramatically increased with long-term penning (9-12 months, Tuberville et al. 2005) and tortoises that do not disperse from the release site during the first several months generally tend to settle in the release area for

the duration of the study (2-17 years; Tuberville et al. 2005, Heise and Epperson 2005, Ashton and Burke 2007). Tortoises translocated on-site tend to exhibit greater fidelity than tortoises translocated off-site (Heise and Epperson 2005), especially if the release site is within homing range of the capture location. Contrary to expectations based on natural movement patterns, adult females exhibited lower site fidelity than did adult males and required longer penning durations (Tuberville et al. 2005). One study found that individuals that interacted with conspecifics during penning were more likely to remain in the release area than those that did not (C. Guyer, pers. comm.).

Home range sizes of translocated gopher tortoises can be dramatically larger than those of undisturbed tortoises, although home range sizes tend to decrease over time as the tortoises settle in to the release area (Tuberville et al. 2005). Home ranges are generally smaller in subadult than adult tortoises and in animals that were subjected to penning compared to those that weren't. However, some individuals show consistently larger home range sizes or repeatedly attempt to disperse (Tuberville et al. 2005). These behaviors may be due to differential response of individuals to the disturbance of translocation or may be due to natural variation among individuals in their propensity for long-distance movements, a phenomenon that has been observed in undisturbed gopher tortoises (S. Bennett, SCDNR, pers. comm.).

Survivorship of both juveniles and adult translocated gopher tortoises is high (T. Tuberville & K. Buhlmann, unpublished data; T. Norton, unpublished data), except when individuals are unsuccessful in their attempts to cross high-traffic roads. Reproduction initially declined in females following translocation, but the effects appear to be temporary (MacDonald 1996, Small and MacDonald 2001).



## Box turtles

In the Piedmont of North Carolina, eastern box turtles that were translocated to a site already occupied by resident box turtles had larger home range sizes (18 vs. 6.5 ha) and moved greater daily distances (18 vs. 8.6 m). Translocated box turtles also had a 40% mortality rate and 10% disappearance rate during the first year compared to resident box turtles, which had 0% mortality and no disappearances (Hester et al., *in press*). In Missouri, translocated three-toed box turtles also had larger home ranges than residents (Rittenhouse et al. 2007). Resource selection of three-toed box turtles following translocation was influenced by habitat of the turtles' source site, suggesting that habitat at both source and recipient sites need to be considered during the planning phase of translocations (Rittenhouse et al. 2008).

A seven year study of adult eastern box turtles translocated to a previously unoccupied site in New York found that approximately 25% of animals dispersed from the release site (Cook 2004). Of the 47% of animals that settled in the release area, most established home ranges within the first year. However, 28% of translocated box turtles died within the first year (due to road mortality & pneumonia), but subsequent survivorship was high (71% overall for first 5 years post-release). The study reported that individual growth, home range size, activity season, habitat use, annual reproductive output, and hatchling recruitment were comparable to natural populations of *T. carolina* (Cook 2004).

## Aquatic turtles

Although none of the introductions were intentional, nor have they been monitored, red-eared sliders (*Trachemys scripta elegans*) have become successfully established in many areas outside of their native range, including Europe and Asia. The only published study on the

translocation of wild-caught aquatic turtles found high site fidelity for adult translocated European pond turtles (*Emys orbicularis*) that were first acclimated in an enclosed temporary holding pond prior to release (Cadi and Miquet 2004).

### General conclusions

Movement patterns of translocated adult turtles can be quite different from undisturbed turtles in their native home range – they generally have larger home ranges and decreased site fidelity. However, these differences in most cases are short-lived, with turtles typically settling into the release area within the first few weeks or months following release. In addition, these differences in movement can be mitigated in some species by the release technique or by selecting juveniles for release programs.

Reproduction and survivorship also do not appear to be negatively affected in the long-term. At least some species may experience high mortality rates in the first year following translocation; wild-caught animals of these species should not be used in translocations.

## REVIEW OF HEAD-STARTING LITERATURE FOR TURTLES

Headstarting is a means of rearing hatchling turtles in captivity to a particular size or age before releasing them into the natural environment. Mortality rates of turtles are typically highest in the first year of life, and decrease with age as turtles grow larger. Head-starting increases growth rates during captivity and presumably survivorship upon release, relative to wild-reared turtles of the same age. Hatchlings used in headstarting programs can be obtained from either field-incubated nests or eggs incubated in the lab.

In order to evaluate the success of head-starting, it must be documented that survivorship of head-started turtles is greater than that of wild-reared turtles and that the time in captivity does not result in significant alterations to the behavior and fitness of released turtles (e.g., foraging ability, predator avoidance; Heppell et al. 1996, McDougall et al. 2006). In addition, to be deemed successful, head-starting must eventually result in recruitment to adult age classes, reproduction, and population growth. Unfortunately, generally few data are available to evaluate the success of specific head-starting projects, often because monitoring does not continue long enough to document maturation and reproduction by head-started individuals.

Head-start programs can garner much public support and participation, but they can also be very expensive, depending on the facilities and length of captivity required. And as with translocation, head-starting efforts are doomed to fail if the root causes of the initial population decline are not addressed (Frazer 1992, Seigel and Dodd 2000). Although head-starting can dramatically increase survivorship during early life stages, these increases cannot compensate for unnaturally high adult mortality (Congdon et al. 1993, Heppell et al. 1996). Management efforts for declining populations are much more likely to succeed if focused on minimizing adult mortality, rather than supplementation with hatchlings and juveniles alone. Head-starting is recommended only as a temporary measure to be used in conjunction with other management methods to stimulate population recovery.

When used in augmentation programs, head-starting is most likely to be successful when the resident population is extremely small, the threats to adults have been minimized, large portions of the eggs laid are used in the head-starting program, and head-started turtles have higher survivorship than their wild counterparts (Heppell et al. 1996). Of potentially even greater benefit than increased first year survivorship of juveniles is the potential for increased

growth rates in head-started turtles to reduce the age at maturity, since maturity in some turtles is size-dependent rather than age-dependent (Frazer et al. 1990).

### Marine turtles

Most head-starting programs for turtles have been conducted with marine species, but none have proven successful. Undoubtedly some of the challenges unique to marine species are the extreme difficulty in sampling released turtles as a result of their incredibly long-distance movements, long generation time, and differential behavior between the sexes and between adults and juveniles. Current sampling focuses almost exclusively on nesting females, thus only survivorship of reproductive females returning to their natal beaches can be estimated. Additionally, early head-starting efforts incubated eggs at temperatures that were later determined to be male-producing temperatures.

### Aquatic turtles

Head-started European pond turtle (*Emys orbicularis*) hatchlings in Poland experienced five times the first year survivorship of their wild counterparts, and once released in the wild, capture rates of head-started turtles were equal to those of wild-reared hatchlings, suggesting that they fared equally well in the natural environment (Mitrus 2005). However, as predicted by previous models (Heppell et al. 1996), increased survivorship of head-started European pond turtles cannot compensate for adult mortality, although both studies predict that increasing the proportion of hatchlings that are head-started will eventually increase the number of adult females in the population under normal adult survival conditions.

In Massachusetts, survivorship of multiple cohorts of head-started northern red-bellied cooter (*Pseudemys rubriventris*) hatchlings was monitored following their release. Head starting significantly increased first-year survivorship. Survivorship varied among same-aged head-started turtles released at different sizes – 36% for turtles with CL of 65mm or less, 66% for 66-95mm CL turtles, and 92% for turtles at least 96mm CL (Haskell et al. 1996). Differences in post-release survivorship decreased in subsequent years as surviving turtles grew larger. The study concluded that head-starting for one over-winter period was the most cost-effective. Survivorship was similar between head-started and wild-reared juveniles of similar sizes.

A study of western pond turtles (*Clemmys marmorata*) in California found that head-started turtles were no more likely to be captured than wild-reared turtles and concluded that captivity did not significantly alter the behavior of turtles towards humans (Spinks et al. 2003). Overall survivorship of head-started turtles was 63%.

Blanding's turtle head-start programs have been initiated in New York, Illinois, Massachusetts, and Ohio. New York reported 44% survivorship in the wild over two years of head-started hatchlings reared to the size of 4-yr-olds (A. Breisch, pers. comm. in Compton 2006). Head-started hatchlings grown to size of 3 yr olds and released at the Concord unit of the Great Meadows NWR had 100% survivorship during their first activity season (Windmiller 2004). The Concord head-started juveniles stayed within 125m of their release site during the first year and survived drawdown of the wetland by burrowing under mud among cattail root masses. There are no published data available to evaluate the success of the Ohio and Illinois head-starting programs.

## General findings

Head-starting is only likely to be beneficial when populations are small, adult survivorship is high, and a large portion of the hatchlings are head-started. Head-starting may be most appropriate as a stop-gap measure to prevent imminent extirpation of a population, when used in combination with efforts to reduce adult mortality (Frazer 1992, Heppell et al. 1996, Mitrus 2005). In addition to shepherding juveniles through the period they are most vulnerable to predation, head-starting may decrease age at first reproduction.

### GENERAL DECISION-MAKING TREE FOR POPULATION MANIPULATIONS

This “decision tree” is a series of questions that should be addressed when deciding whether or not translocation or other population manipulations are necessary and appropriate for a particular site. They are presented in roughly the order that they should be considered during the decision making process. At any point in the process, it may be decided that population manipulations should not be pursued, at least under the current conditions. The series of questions can be applied and modified to suit any number of species and scenarios.

Decision 1: Is the species secure in the region?

- Yes: No manipulation necessary
- No: Proceed to Decision 2

Decision 2: Is the proposed site within the natural geographic range of the species?

- Yes: Proceed to decision 3
- No: Population manipulations are not appropriate

Decision 3: Does the proposed target site have a viable, resident population?

- Yes: No manipulation necessary
- No: Proceed to Decision 4

Decision 4: Does the target site have appropriate habitat of sufficient extent to support a resident population?

- Yes: Proceed to Decision 5
- No: Population manipulations are not appropriate at this time. If habitat can be improved through management, population manipulations could be reconsidered once restoration is complete.

Decision 5: Is the site secure and have potential or historical threats to the species been removed or mitigated?

- Yes: Proceed to Decision 6
- No: Population manipulations are not appropriate at this time and should not be reconsidered until threats have been abated.

Decision 6: What life stage is most appropriate for population manipulations? This decision will be influenced by the life history and ecology of the species, feasibility of working with particular life stages, and potential effects on source population(s).

- Hatchlings: If the proposed source population can donate individuals without jeopardizing its own viability, then population manipulations are appropriate.
- Juveniles: If the proposed source population can donate individuals without jeopardizing its own viability, then population manipulations are appropriate.
- Adults: If the proposed source population can donate individuals without jeopardizing its own viability, then population manipulations are appropriate.

The decision to proceed with population manipulations is only the first step. It is crucial that managers and researchers develop protocols detailing the goals of the project, the anticipated duration, number of animals to be used, and the exact methodology for conducting the manipulation, including the collection, handling, care, and release of animals. Most importantly, a commitment must be made to monitor the project to determine its success. In order to evaluate success, particularly for long-lived species, it will be necessary to have both short-term (e.g., site fidelity to release site) and long-term measures of success (e.g., successful reproduction by offspring born or hatched on-site). The indicators selected to measure success will determine the length of monitoring required and the specific type of data that should be collected.

#### CONCEPTUAL FRAMEWORK FOR MEASURING SUCCESS

One of the main hindrances to evaluating the utility of translocation as a management tool is the lack of explicit criteria for defining success. For many projects, success is never clearly defined, even for translocations proclaimed as “successful.” The standard definition for success is that the translocation results in a self-sustaining population (Griffith et al. 1989), but this definition falls short of elaborating how populations can be determined to be self-sustaining. A basic tenet of population ecology is that in order for populations to be stable or “self-sustaining”, four basic population processes have to be in equilibrium, such that:

$$\text{Births} + \text{Immigrations} = \text{Deaths} + \text{Emigrations}$$

Most post-translocation monitoring focuses on a single population process (e.g., site fidelity to the release area or evidence of successful reproduction) evaluating project success.



However, when determining whether or not translocated populations are self-sustaining, all four population processes are important. Because translocations are basically managed immigrations, the remaining three processes (births, deaths, and emigrations) are of primary interest.

Therefore, a conceptual framework for evaluating population viability—and hence the success of individual translocation projects—should consider post-release site fidelity, survivorship and reproduction (Fig. 1.1).

## OBJECTIVES & OUTLINE OF DISSERTATION RESEARCH

The objective of my dissertation research was to illustrate how this conceptual framework can be used to evaluate translocation success for an individual species, using the gopher tortoise (*Gopherus polyphemus*) as a case study. Each chapter focuses on a different component of the framework (Fig. 1.2) and is placed in the context of other relevant studies of both translocated and naturally occurring populations. Chapter 2 reports on the short-term site fidelity and home range of gopher tortoises translocated to the Savannah River Site, SC, and compares the relative effectiveness of three different release protocols in promoting site fidelity. Chapter 3 summarizes results from a 12-yr mark-recapture study of a gopher tortoise population established through multiple releases on St. Catherines Island, GA. The data are used to compare the apparent survival patterns of newly released tortoises to previously established residents. In Chapter 4, I present a preliminary characterization of the mating system of the St. Catherines' Island population based on genetic analysis of clutches collected during two field season after more than a decade following translocation.

Because gopher tortoises, like most turtle species, are long lived, even the 10+ years of post-release monitoring at St. Catherines Island represents less than half a generation time for the

species. Population viability models can be constructed to reflect the population dynamics of translocated populations and attempt to predict their long-term persistence. In Chapter 5, I use information from the literature and data collected as part of my dissertation to develop population models for both translocated and naturally occurring populations of gopher tortoises. I use the models to determine the conditions under which naturally occurring populations are likely to require population manipulations in order to ensure their persistence and to evaluate which release strategies are most likely to result in establishment of viable populations.

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## A conceptual framework for evaluating translocation success

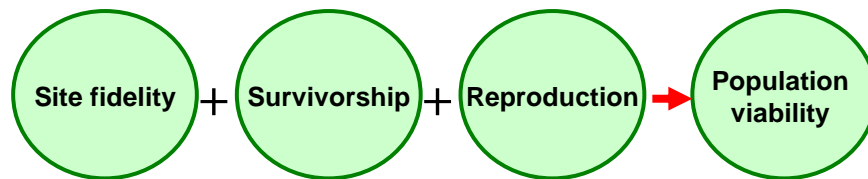


Figure 1.1. Conceptual framework for measuring success of translocation as a conservation tool for individual species.

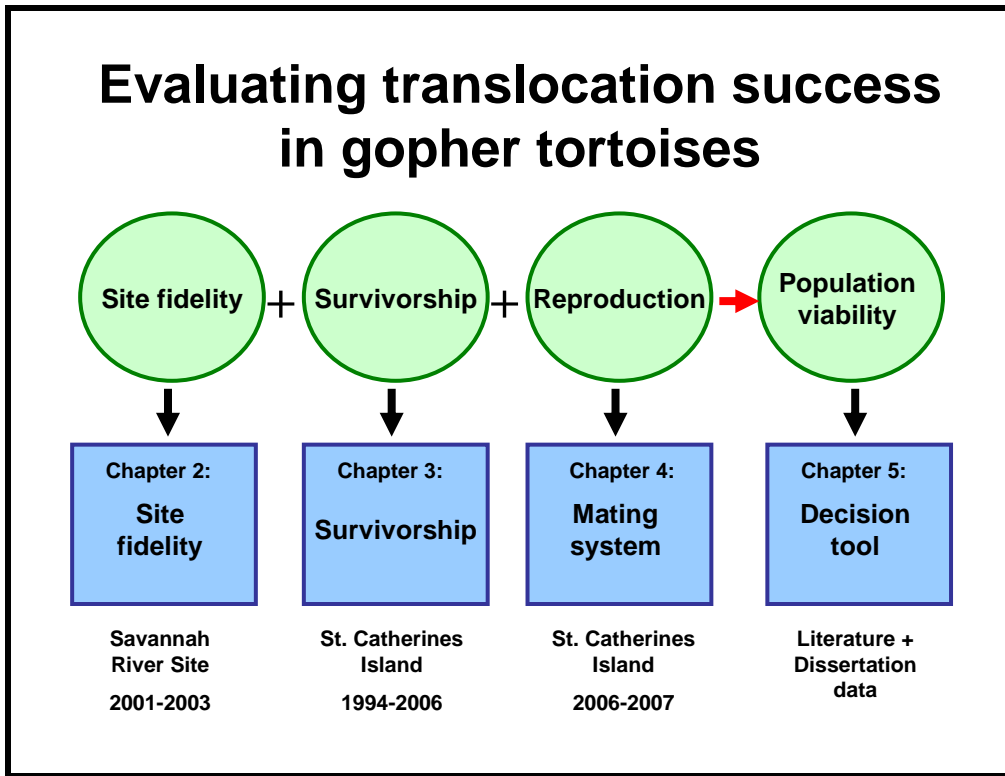


Figure 1.2. Application of conceptual framework to the study of translocation success in gopher tortoises.

## CHAPTER 2

### TRANSLOCATION AS A CONSERVATION TOOL: SITE FIDELITY AND MOVEMENT OF REPATRIATED GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*)<sup>1</sup>

<sup>1</sup>Tuberville, T.D., E.E. Clark, K.A. Buhlmann, and J.W. Gibbons. 2005. *Animal Conservation* 8:349-358. Reprinted here with permission of publisher.

## ABSTRACT

Efforts to evaluate the efficacy of translocation as a conservation tool have mostly been inadequate, particularly for reptiles and amphibians, leading many biologists to discount translocation as a viable management option. Nonetheless, with two-thirds of the world's tortoise and freshwater turtle species at risk, translocation may be one of the few remaining options for re-establishing extirpated populations and reconnecting fragmented ones. We translocated 106 gopher tortoises (*Gopherus polyphemus*) to a protected area within the historical range but with no resident tortoises, and tested the effects of penning on site fidelity and activity area size. We assigned 38 adults and subadults to one of three penning treatments (9-mo., 12-mo., and no penning) and radio-tracked them for two years. Penning significantly increased site fidelity and resulted in smaller activity areas. Our data suggest that translocation coupled with penning will improve the likelihood of establishing self-sustaining tortoise populations.

## INTRODUCTION

Translocation—the intentional release of individuals of a species at a within-range location different from their capture location in order to “establish, reestablish, or augment a population” (Griffith et al. 1989)—is commonly used in the management of native mammals and birds. However, success rates have differed between game (86%) and non-game species (46%) and varied depending on factors such as number of animals released, habitat quality at the release site, and location of the release site within the species' range (Griffith et al. 1989, Wolf et al. 1996). Many valid biological and political concerns are associated with the intentional movement of wildlife (Berry 1986, Dodd and Seigel 1991, Seigel and Dodd 2000, Zug et al. 2001), although some can be avoided or minimized by releasing animals at sites without resident



populations (Berry 1986). Careful planning prior to translocation is critical for achieving effective conservation and minimizing the risk of unintended consequences (Conant 1988, Kleiman 1989, IUCN 1998).

Compared to birds and mammals, very little research has been conducted on translocation of reptiles and amphibians, and the success rate for known projects (19%) is much lower (Dodd and Seigel 1991). However, reptiles and amphibians around the world are experiencing declines (Alford and Richards 1999, Gibbons et al. 2000, Stokstad 2004, Stuart et al. 2004). Two-thirds of the world's turtle species are considered threatened by the IUCN, and many of the remaining third have not been evaluated (Turtle Conservation Fund 2002). Human exploitation of turtles has resulted in population declines, local extirpations, and even extinction of some species (Thorbjarnarson et al. 2000). As exploitation and habitat alteration continue, translocations and repatriations will play an increasingly important role in turtle conservation. A recent global action plan for tortoises and freshwater turtles lists translocation and repatriation as critical conservation components for the most threatened species (Turtle Conservation Fund 2002).

Of all the amphibian and reptile species of the southeastern United States, the gopher tortoise (*Gopherus polyphemus*) has been the target of the most numerous and extensive relocations (i.e., displacement of animals from their habitat to avoid immediate threats such as development; Dodd and Seigel 1991). Because the primary goal of most relocations is the welfare of individual animals rather than conservation of populations or species, very little subsequent monitoring has been conducted to evaluate the overall success of projects. Despite the controversy associated with the deliberate movement of wildlife and the paucity of data available to evaluate its effectiveness as a management tool for reptiles and amphibians,

translocation may sometimes be the only option for reestablishing extirpated populations and reconnecting fragmented ones.

The goals of this project were to: (1) re-establish a protected, viable population of gopher tortoises within the species' natural range, and (2) test whether use of temporary outdoor enclosures (hereafter, "penning") and penning duration affects site fidelity and activity area size during the first two years following release. One of the primary concerns associated with translocation projects is post-release site fidelity. Techniques that encourage acclimation of translocated animals to the release area have been recommended as ways to increase translocation success in mammals (e.g., bobcats *Felis rufus*, Diefenbach et al. 1993; swift foxes *Vulpes velox*, Moehrensclager and MacDonald 2003), and may enhance translocation success in tortoises. Although the effectiveness of short-term penning (i.e., <25 days) in promoting site fidelity by gopher tortoises has been disputed (Doonan 1986, Burke 1989), we predicted that long-term penning would facilitate acclimation of tortoises to the release site and result in increased site fidelity and smaller activity areas. If long-term penning can be demonstrated to be effective, it is relatively inexpensive and easy to implement, making it a prime candidate technique for future conservation efforts.

## METHODS

### Study animal

The gopher tortoise is a large (max carapace length [CL] 381 mm), herbivorous, long-lived terrestrial turtle, attaining reproductive maturity at 230-255 mm CL and 10-21 yrs (Iverson 1980, Landers et al. 1980, Ernst et al. 1994). They construct large underground burrows (up to 6 m long and 3 m deep; Hansen 1963, Tuberville and Dorcas 2001), and individual tortoises will

use multiple burrows throughout their lifetime, often even within a single year (Diemer 1992, Smith et al. 1997, Eubanks et al. 2003). Gopher tortoises are social animals—they occur in local “colonies” and frequently visit each other at their respective burrows (Waddle 2000, Boglioli et al. 2003). Although they tend to occupy burrows singly (McRae et al. 1981, Diemer 1992, Smith et al. 1997), several tortoises may sequentially occupy a given burrow throughout the active season. In addition, because the burrows themselves are also long-lived (Guyer and Hermann 1997), they may be used by many different individuals over multiple years.

Gopher tortoises are diurnal, but even during the day spend a large proportion of the time underground in their burrows. They also have discrete seasonal activity patterns, with a winter dormancy period during which they may bask at the burrow entrance on warm days but rarely travel away from or between burrows (McRae et al. 1981, Diemer 1992). Although the duration of the dormancy period varies throughout the species’ range (with longer periods of inactivity in the northern populations), gopher tortoises in all regions are active from at least April – October (Douglass and Layne 1978, Eubanks et al. 2003)

The gopher tortoise is the only tortoise species inhabiting the southeastern USA, where it occurs in the Coastal Plain and Sandhills physiographic provinces (Fig. 2.1). It is associated with deep sandy soils and a wide variety of xeric habitats. Its historical habitat was the longleaf pine (*Pinus palustris*) forest, of which only about 2% remains (Noss et al. 1995). Due primarily to habitat loss, the gopher tortoise is federally-threatened in the western portion of its range (i.e., western Alabama, Mississippi, Louisiana; USFWS 1987) and is considered declining throughout its range (Auffenberg and Franz 1982, Smith et al. 2006).

### Founder population

The donor site was a 40-ha industrial development site in southeast Georgia, USA (Fig. 2.1). Primary habitats at this disturbed site included recent clearcuts and densely-planted young pine forests on sandy soils (Lakeland, Kleg, and Ona series; USDA 1961). During August – October 2001 (Fall), we located and trapped as many intact tortoise burrows as we could find (144 of 173 burrows were intact) at the donor site. We captured 74 tortoises (including adults, subadults, and juveniles) by hand, with pitfall traps at burrow entrances, or by manual excavation of burrows. In addition, 32 were hatched in the lab from 7 nests encountered in the field, for a total founder population size of 106 tortoises.

### Study site

The recipient site was the Savannah River Site (SRS; Aiken County, South Carolina, USA), a 800 sq km government reserve approximately 217 km north of the donor site (Fig. 2.1). The SRS is owned by the U.S. Department of Energy and managed by the U.S. Forest Service (White and Gaines 2000). Although Holbrook (1842) noted that tortoises were historically “numerous in Edgefield and Barnwell districts,” which border the recipient site, no resident population of gopher tortoises was present on the SRS at the time this study was initiated, probably as a result of historical intensive agriculture in the region (White and Gaines 2000). A small, isolated population of gopher tortoises was discovered in 1992 approximately 17 km to the northeast of the SRS (Clark et al. 2001).

The release site was located in the northeast corner of the SRS, in an 882 ha timber management compartment with sandy soils (Lakeland and Troup series). The forest type is primarily open-canopy longleaf pine (52% of compartment area), flanked by floodplain

sweetgum (*Liquidambar styraciflua*) forests (13%), and interspersed with small patches of other upland forest types. The estimated age of the timber stand is approximately 50-60 yrs (P. Johnston, pers. comm.). The understory comprises mixed-oak (*Quercus* spp.) shrub and a diverse herbaceous layer. Management is directed towards improving site conditions for the federally-endangered red-cockaded woodpecker (*Picoides borealis*; USFWS 1970) and re-establishing wiregrass (*Aristida stricta*), a dominant understory species of the longleaf pine ecosystem eliminated prior to establishment of the SRS due to intensive agriculture (White and Gaines 2000). The release site is treated with prescribed fire approximately every 3 years and was burned during spring/summer 2001.

#### Experimental release pens

Three separate arrays of starter burrows were constructed in the core release area (Fig. 2.2) at the center of the timber compartment. Arrays were 50-105 m apart and positioned so that approximately 50% of each array contained wiregrass, an important food item for gopher tortoises (Garner and Landers 1981, MacDonald and Mushinsky 1988). Two of the 3 arrays were enclosed by 92-cm tall aluminum flashing buried approximately 30 cm in the ground and reinforced with wooden stakes; the third was not enclosed. The arrays were 1 ha in size.

Each array consisted of 24 starter burrows (Fig. 2.2). Burrows were created using a gas-powered auger with a 46 cm bit placed at a 30 degree angle to excavate burrows to approximately 1 m in length. Burrow entrances were manually shaped to more closely resemble tortoise-constructed burrows, and the excavated sand was used to form a mound to imitate the “apron” typically found outside burrow entrances. Each burrow was permanently marked and its location recorded using GPS technology.

### Experimental subjects and penning treatments

All tortoises were measured (only mid-line CL to nearest mm reported here) and permanently marked by drilling or filing notches in unique combinations of marginal scutes (Gibbons 1990). Tortoises >235 mm CL were considered adults and identified as male or female based on degree of plastral concavity (Iverson 1980, Landers et al. 1980). Tortoises 181-235 mm CL were classified as subadults. Although the founder population included many juveniles ( $\leq 180$  mm CL), only adults and subadults were intensively monitored in this study (Fig. 2.3). Data on juveniles will be presented elsewhere. All adults and subadults were assigned to one of three penning treatments, each treatment consisting of 12-13 animals, with similar sex ratios and size distributions among treatments. Tortoises from all three treatments were temporarily held offsite until transport to the release site (approx. 25 km away). Each tortoise was fitted with two radio-transmitters (#LF-2-2/3A-CTM-RS-T, LL Electronics, Mahomet, IL; wt 40 g with epoxy) mounted on the anterior-most costals—one on each side of the carapace.

Individuals in the “no-penning” treatment remained at the offsite holding area until 29 March – 3 April 2002 (Spring 2002; approx. 190 days offsite), when they were transported to the core release area and placed into starter burrows in the “no pen” burrow array. Individuals in the 9-mo. penning and 12-mo. penning treatments were transported from the offsite holding area in October 2001 (Fall; approx. 60 days offsite) and placed into starter burrows in their respective burrow arrays, where they spent the first winter. The 9-mo. penning group was “released” on 8 July 2002 by removing the aluminum flashing encircling their burrow array. The 12-mo. penning group was “released” on 23 September 2002.

### Post-release monitoring

Following release, animals were located daily through October 2002, then approximately once per week thru 30 November 2002 (Year 1 post-release). From March – October 2003 (Year 2), tortoises were located approximately 2-3 times per week. Burrows constructed by tortoises were assigned a unique number and permanently marked. All tortoise and new burrow locations were recorded using GPS technology (Trimble Pro-XR, Sunnyvale, CA, with sub-meter accuracy).

Tortoises that traveled more than 1 km from the core release area (i.e., the burrow arrays) without establishing a burrow were considered to have dispersed from the release site. Dispersers were retrieved and re-released in the core release area. Although we continued to monitor these animals, they were considered translocation “failures.”

### Data processing and statistical analyses

Site fidelity was evaluated by comparing the proportions of dispersers and non-dispersers among the release groups using tests for goodness of fit. Separate analyses were conducted for Year 1 and Year 2 (both including and excluding animals that attempted to disperse in Year 1 but were returned to the core release area). Because each animal had two radio-transmitters, individuals lost from the study were presumed to have dispersed great distances.

Activity areas were minimum convex polygons (MCP) calculated for each individual for Year 1 and Year 2 using ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) and the MOVEMENT extension (Hooge and Eichenlaub 1997). Activity areas include all points where animals were located, including all dispersal attempts by an individual. Because the release date—and therefore, the number of days individuals were

tracked—in Year 1 varied with penning treatment, Year 1 activity areas were calculated using only the first 50 tracking locations. Previous analyses of home range data for gopher tortoises by Eubanks et al. (2003) suggest that samples of at least 50 consecutive locations are sufficient to eliminate the potential effects of serial autocorrelation on activity area (i.e., home range) estimates. All 2003 tracking dates were used for calculating Year 2 activity areas. Four individuals were lost during the first 15 days following initial release and were eliminated from analyses of activity areas. Activity areas for both Year 1 and Year 2 could be calculated for the remaining individuals.

Activity area values were  $\log_{10}$ -transformed to reduce variance among groups. Activity areas were compared among penning treatments and among sexes (adult males [M], adult females [F], subadults [S]) using separate two-way ANOVAs (Statistical Analysis System V8e, Cary, NC, USA) for each year. Post-hoc comparisons of means were conducted for main effects and interactions found to be statistically significant. Because we suspected that activity area sizes for individuals would change between years, we performed separate paired t-tests (Year 1 vs. Year 2) for each release group. All means are reported  $\pm 1$  S.E. and alpha was set at 0.05 for all statistical procedures. Additional Year 1 data and analyses are presented in Clark (2003).

## RESULTS

### Site fidelity

Site fidelity varied significantly among penning treatments during Year 1 ( $\chi^2=12.15$ ,  $df=2$ ,  $p=.0023$ ). Only 23.1% (3 of 13) of no-penning animals stayed in the release site (i.e., timber management compartment) without attempting to disperse, whereas 61.5% (8 of 13) of 9-mo. penning and 91.7% (11 of 12) of 12-mo. penning animals remained during the first year



after release (Fig. 2.4). Four tortoises (no pen: 1F, 1S; 9-mo. pen: 1F; 12-mo. pen: 1F) were lost from the study within 15 days of release during their initial dispersal attempt, presumably because they traveled out of signal range between daily tracking periods. Tortoises that dispersed during Year 1, on average, made the initial attempt 25 days post-release (range: 6-94 days; n=16; Clark 2003). After excluding those lost from the study, length of penning treatment also resulted in differences in the number of dispersal attempts made by tortoises during Year 1. Half of the no-penning dispersers attempted to disperse 2-4 times before settling in the release site. In contrast, the four 9-mo. penning dispersers (2F, 1M, 1S) attempted to disperse only once. The single 12-mo. penning disperser was lost from the study.

The proportion of individuals dispersing during Year 2 was not significantly different among penning treatments regardless of whether we considered all animals (i.e., including Year 1 dispersers that were retrieved and returned to the core release area;  $\chi^2=.4979$ ,  $df=2$ ,  $p=.7796$ ) or included only animals not attempting to disperse in Year 1 ( $\chi^2=1.0476$ ,  $df=2$ ,  $p=.5923$ ). During Year 2, only 4 of the 34 remaining animals (some of which attempted to disperse in Year 1) attempted to disperse (11.7% overall; no pen: 1M [dispersed twice], 1F; 9-mo. pen: 1F; 12-mo. pen: 1M). Except for the male from the 12-mo. penning treatment, all Year 2 dispersers had also attempted to disperse during Year 1. Although we cannot say how far animals would have dispersed if we had not retrieved them, male #7 (no-penning treatment) traveled 5.1 km N and established a burrow on private property before we located and retrieved him.

### Activity areas

Year 1 activity areas varied significantly among penning treatments ( $F_{2,25}=19.19$ ,  $p<.0001$ ) and among sexes ( $F_{2,25}=6.66$ ,  $p=.0048$ ; Fig. 2.5a, 2.6a). Year 1 activity areas were

significantly smaller for 12-mo. penning treatment ( $1.96 \pm 1.07$  ha) than either no-penning ( $93.54 \pm 33.43$  ha) or 9-mo. penning treatments ( $37.06 \pm 14.08$  ha); no-penning and 9-mo. penning treatments were not significantly different. Activity areas of both males ( $45.23 \pm 23.67$  ha) and females ( $64.12 \pm 18.45$  ha) were significantly larger than activity areas of subadults ( $12.16 \pm 6.90$  ha) but were not significantly different from each other. The group\*sex interaction was nearly significant ( $F_{4,25}=2.54$ ,  $p=.0653$ ), with females exhibiting a weaker response to penning than males or subadults. When animals that attempted to disperse during Year 1 were excluded from analyses, the main effects of penning treatment ( $F_{2,14}=5.24$ ,  $p=.02$ ) and sex ( $F_{2,14}=5.99$ ,  $p=.0132$ ) were still significant.

Year 2 activity areas were not significantly different among penning treatments (Fig. 2.5b, 2.6b), regardless of whether animals that attempted to disperse in Year 1 were included in ( $F_{2,25}=.73$ ,  $p=.4910$ ) or excluded from ( $F_{2,21}=.69$ ,  $p=.5155$ ) the analyses. Similar to the results of Year 1, activity areas in Year 2 varied among sexes ( $F_{2,25}=12.04$ ,  $p=.0002$ ), with adult male ( $22.19 \pm 12.33$  ha) and adult female ( $12.13 \pm 6.69$  ha) activity areas significantly larger than activity areas of subadults ( $0.52 \pm 0.44$  ha) but not different from each other.

Overall, activity areas were smaller in Year 2 than in Year 1 (Fig. 2.5-2.6), even though Year 1 activity areas only included the first 50 daily tracking locations, whereas Year 2 activity areas were based on 48-72 tracking locations per individual collected over the entire activity season (230 days). The difference among years was significant for the no-penning treatment ( $t=-2.30$ ;  $n=11$ ,  $p=.0440$ ), nearly significant for 9-mo. penning ( $t=-1.95$ ;  $n=12$ ,  $p=.0776$ ), but not for 12-mo. penning treatment ( $t=1.14$ ;  $n=11$ ;  $p=.2791$ ). Year 2 activity areas were more similar to home ranges reported for naturally occurring populations, particularly when dispersers are excluded from analyses (Table 2.1).

## DISCUSSION

### Site fidelity

Penning and penning duration dramatically increased site fidelity of translocated gopher tortoises by reducing the proportion of animals attempting to disperse and the number of times an individual attempted to disperse. Most dispersal occurred during the first year following release, and most initial attempts occurred within the first 25 days of release. An argument could be made that the low dispersal rate of the 12-mo. penning treatment (September release) was influenced by the onset of the winter inactivity period. However, based on dispersal behavior of animals from the previous releases, we believe the six weeks remaining in the activity season allowed adequate time for tortoises from the 12-mo. penning treatment to attempt to disperse. Dispersal rates in Year 2 were lower than in Year 1 and were not affected by penning treatment, and animals remaining in the release site at the end of Year 1 (whether voluntarily or "by force") tended to eventually settle there.

As predicted, an unnaturally high proportion of translocated animals attempted to disperse shortly after their release. During Year 1, we observed dispersal rates of 76.9% (no-penning), 38.5% (9-mo. penning), and 8.3% (12-mo. penning), compared to only 2% reported for a naturally-occurring population (Eubanks et al. 2003). Most animals that attempted to disperse in Year 2 had also attempted to disperse the previous year, suggesting that certain individuals have a greater propensity to disperse. However, most Year 1 dispersers that were re-released in the core release area did not attempt to disperse in Year 2. Both penning and retrieval of dispersing animals proved to be effective in curbing the initial flight response of tortoises released into their new, unfamiliar environment.

### Activity areas: comparison among penning treatments

Twelve-month penning was significantly more effective than either 9-mo. penning or no penning in reducing the area over which animals roamed during Year 1. Lack of a significant difference in activity area size between 9-mo. penning and no-penning was surprising. However, during Year 1, activity areas for adult males and subadults were an order of magnitude smaller for the 9-mo. penning compared to the no-penning treatment, whereas activity areas for females from the 9-mo. penning treatment were nearly as large for females from the no-penning treatment (Fig. 2.6a). These results suggest that effectiveness of penning varies with sex, with adult females requiring longer term penning.

The variation observed among penning treatments in Year 1 is presumably a result of different penning durations rather than time of year, and did not affirm an expectation that “translocations may be less successful during late summer-early fall, when tortoises are more likely to disperse” (Berish 2001). For example, adult males in naturally occurring populations exhibit peak movement during July-September (Diemer 1992, Eubanks et al. 2003). Instead, we found that male activity area size decreased for each successive release from spring to fall (March to September). Likewise, peak activity of adult females from natural populations occurs in September as well as during the May-June nesting season (Diemer 1992, Eubanks et al. 2003). Hence, the largest Year 1 activity areas for females would have been expected for the 12-mo. penning treatment in which activity area, as determined by the first 50 daily locations after release, was based on Sept-Oct movement (the nesting period was not represented by Year 1 activity areas for any release group). In Year 1 of our study, greatest activity sizes were observed for females from the 9-mo. penning (July-Aug) and no-penning treatments (late March-early May).

### Activity areas: Year 1 vs. Year 2

Compared to Year 1, Year 2 activity areas were smaller, more similar among penning treatments, and more similar to home range sizes reported for residents in naturally occurring populations. The greatest reductions were exhibited by individuals from the no-penning treatment. These results are even more striking considering that the Year 1 activity areas were calculated based on only the first 50 tracking locations compared to the full activity season (Apr-Oct) for Year 2. Some individuals still roamed over relatively large areas (55 – 173 ha) during Year 2, but these large activity areas were associated with animals (from all penning treatments) that attempted to disperse during that year.

### Site fidelity and activity areas: differences among sexes

Subadults may be more likely than adults to establish home ranges near the release area following translocation. In each penning treatment, adult males and females were more likely than subadults to disperse from the core release area and had larger activity areas. In natural populations of turtles, males tend to travel greater distances and more often than females (Morreale et al. 1984, Gibbons 1986, Eubanks et al. 2003). However, in this study, female tortoises were more likely than males to disperse immediately following translocation. Three of four animals lost from the study were females, and half of the remaining females were forced to stay in the release site. Based on these findings, in combination with weaker response of females to penning, we conclude that adult female gopher tortoises may be more sensitive to disturbance associated with translocation than adult males or subadults. Burke (1989) also reported lower site fidelity by relocated females compared to the overall population average, although sample sizes were small.

### Comparison with previous penning experiments in gopher tortoises

Previous studies have implemented different penning protocols for gopher tortoises, with mixed conclusions regarding the technique's effectiveness in promoting site fidelity of translocated animals. However, these studies penned animals individually or in small groups, confined animals for much shorter time periods (<30 days for adults), included captive animals or animals from multiple localities, inferred site fidelity from burrow surveys rather than mark-recapture or radio-telemetry methods, or had extremely small sample sizes (Doonan 1986, Lohoefener and Lohmeier 1986, Burke 1989). The effectiveness of our translocation can be attributed to: 1) using longer penning durations more appropriate for long-lived species; 2) translocating an entire, intact population of tortoises that included all size classes; and 3) providing opportunity for tortoises within a penning treatment to associate with familiar individuals, thus facilitating social interactions. Our study design did not allow us to make conclusions regarding the importance of penning during the dormancy period (versus activity season only) on post-release site fidelity, but this issue should be explored. Further research is needed to evaluate how other factors such as time of year of release, size of founder population, and habitat conditions affect site fidelity, movement patterns, and ultimate population demography.

### CONCLUSIONS

Although we observed considerable among-individual variation in the dispersal and movement behavior of translocated tortoises, several patterns emerged: 1) Penning and penning duration were important in reducing dispersal rates and activity area size during the first year; 2) During the second year, activity areas were smaller and more similar to those reported for

naturally occurring populations; 3) Some individuals had a greater propensity to disperse than others, regardless of penning treatment; 4) Subadult tortoises had smaller activity areas and may be more likely to settle in the core release area; and 5) Adult females may require longer penning durations relative to adult male and subadults tortoises. Our data suggest that translocation can be implemented to successfully repatriate gopher tortoises, and that relatively inexpensive, easy-to-implement techniques (e.g., penning) may improve the likelihood of establishing self-sustaining, resident populations. Long-term monitoring of the site fidelity, survivorship, and reproduction of this population will be required to determine its viability.

Penning was an effective release technique for the species we investigated and has potential application to other tortoise species with similar space use patterns. However, release techniques and protocols should be tailored to the target species, their habitat, and the conservation goals of the project, and must be based on a thorough understanding of the species' biology and behavior. The development of translocation protocols is recognized as a critical components for safeguarding the world's most endangered tortoise and freshwater turtle species. Although it is not a panacea for all species or all situations, translocation should be considered one of the many tools in the conservation toolbox.

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Table 2.1. Summary of home range estimates for gopher tortoises from naturally occurring populations compared to this study of translocated tortoises. Reported values are mean values (range; number of individuals) to nearest .1 ha. Means for this study are reported both including and excluding animals that dispersed from the study site; animals lost from study are not included because there were too few data to calculate home ranges for those individuals. Means are provided for each penning treatment separately for Year 1 but are combined for Year 2.

<u>Mean home ranges (ha)</u>					
Location	Study duration	Adult females	Adult males	Landuse	Source
<b>Natural populations</b>					
Southwest GA	13 mo.	0.4 (0-3.4; n=53)	1.1 (0-4.8; n=70)	Ecological preserve	Eubanks et al. 2003
East-central FL coast	20 mo.	0.6 (0.3-1.1; n=4)	1.9 (0.3-5.3; n=10)	Military/wildlife refuge	Smith et al. 1997
North-central FL	24 mo.	0.3 (0-1.2; n=5)	0.9 (0.2-2.9; n=6)	Wildlife management area	Diemer 1992
Southwest GA	8 mo.	0.1 (0.04-0.14; n=5)	0.45 (0.1-1.4; n=8)	Industrial forest	McRae et al. 1981
Northeast FL	17 mo.	0.4 (0-1.4; n=14)	---	Ecological preserve	Smith 1995
<b>Translocated population</b>					
West-central SC		<b>Year 1*</b>		Defense facility	This study
No pen		84.2 (5.0-145.3; n=3)	116.5 (0.7-373.7; n=6)	"	"
No pen (no dispersers)		5.0 (n=1)	17.5 (0.7-34.2; n=2)	"	"
9-mo. pen		93.9 (38.9-134.1; n=4)	12.3 (0.4-50.2; n=5)	"	"
9-mo. pen (no dispersers)		72.2 (38.9-105.5; n=2)	14.9 (0.4-50.2; n=4)	"	"
12-mo. pen		4.4 (0.1-11.6; n=3)	1.4 (0.1-5.3; n=6)	"	"
12-mo. pen (no dispersers)		"	"	"	"

	<b>Year 2</b>			
All treatments	12.1 (0.0-55.0; n=10)	23.5 (0.2-173.3; n=17)	"	"
All treatments (no dispersers)	2.2 (0-6.1; n=8)	4.4 (0.2-15.8; n=15)	"	"

\*Year 1 home ranges based on movement during first 50 daily locations following release.

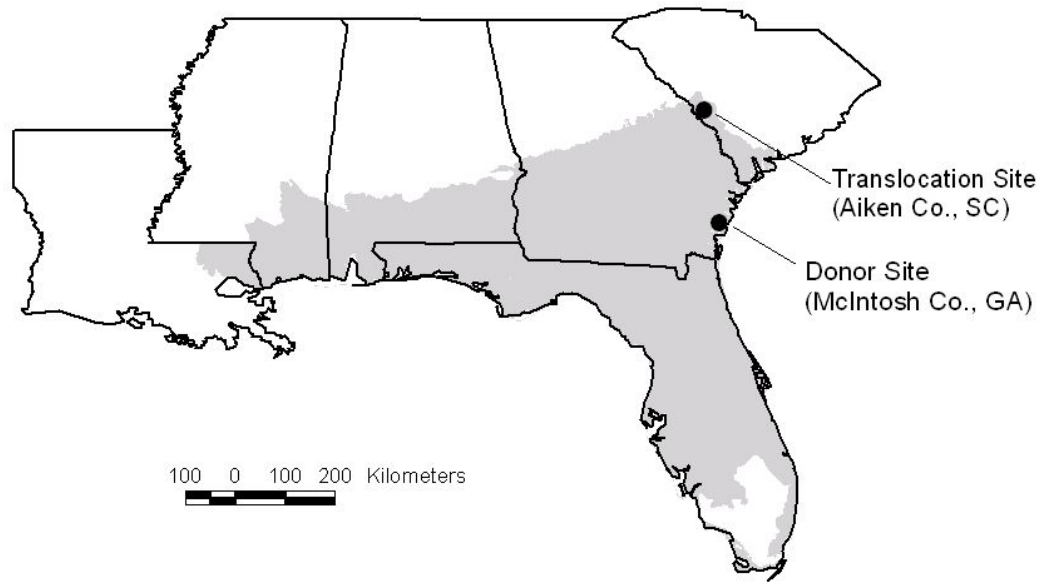


Figure 2.1. Distribution of gopher tortoises (shaded) with locations of donor site and translocation site indicated. Range map is adapted from Iverson (1992).

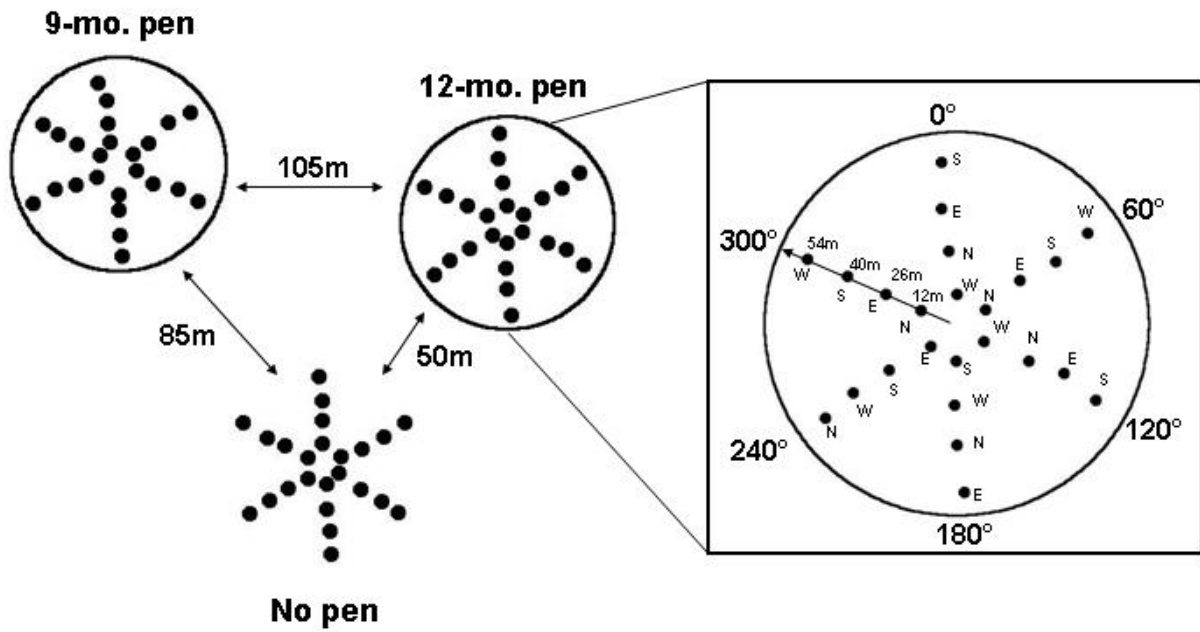


Figure 2.2. Relative locations of 9-mo., 12-mo., and no-penning arrays used for experimental releases. Inset illustrates one of the burrow arrays. Dots represent starter burrows with the position and orientation of burrow entrances indicated.



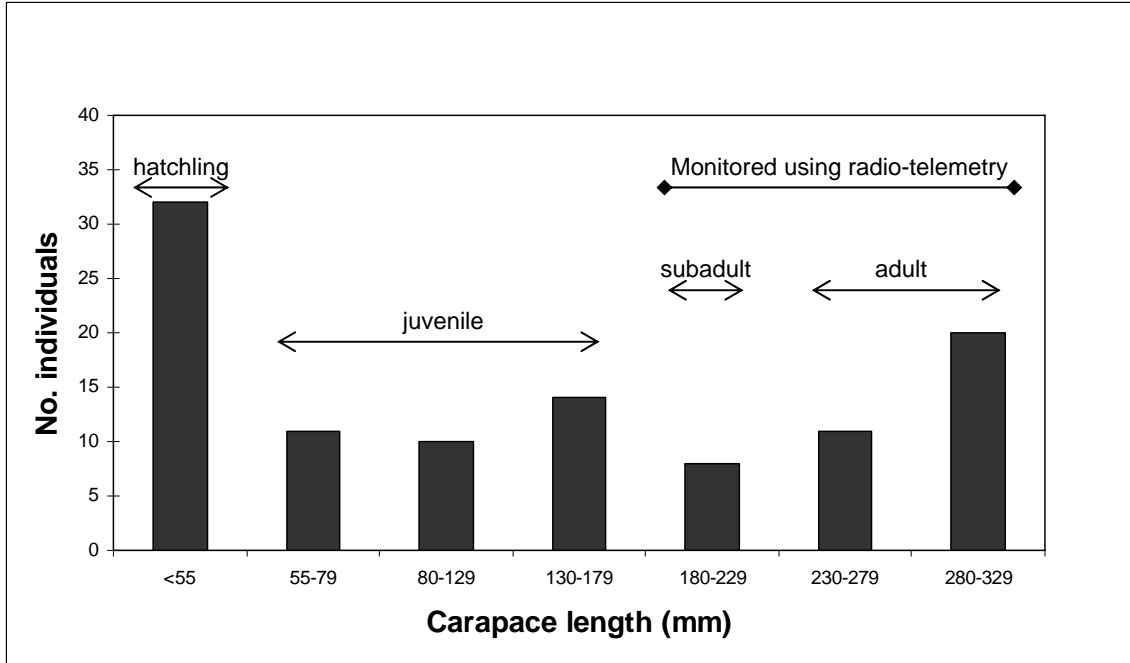


Figure 2.3. Size (mm CL) frequency distribution of founder population (n=106) indicating the size classes for different life stages (as defined in this study). Only subadults and adults were monitored using radio-telemetry.

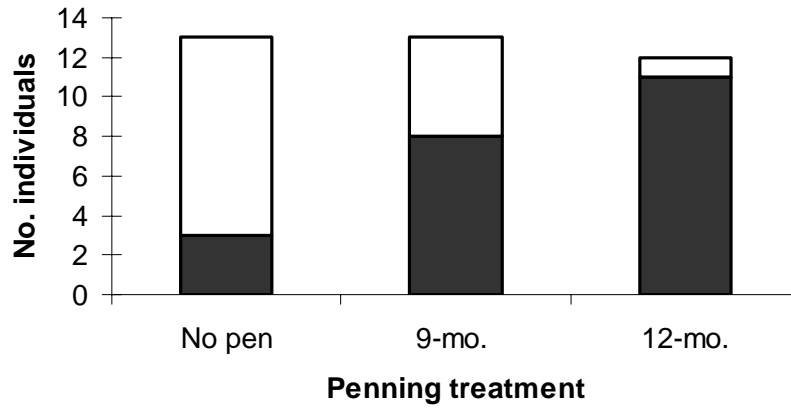


Figure 2.4. Site fidelity by penning treatment during Year 1. Dispersers (unshaded) are animals that traveled more than 1 km from the core release area without establishing a burrow.

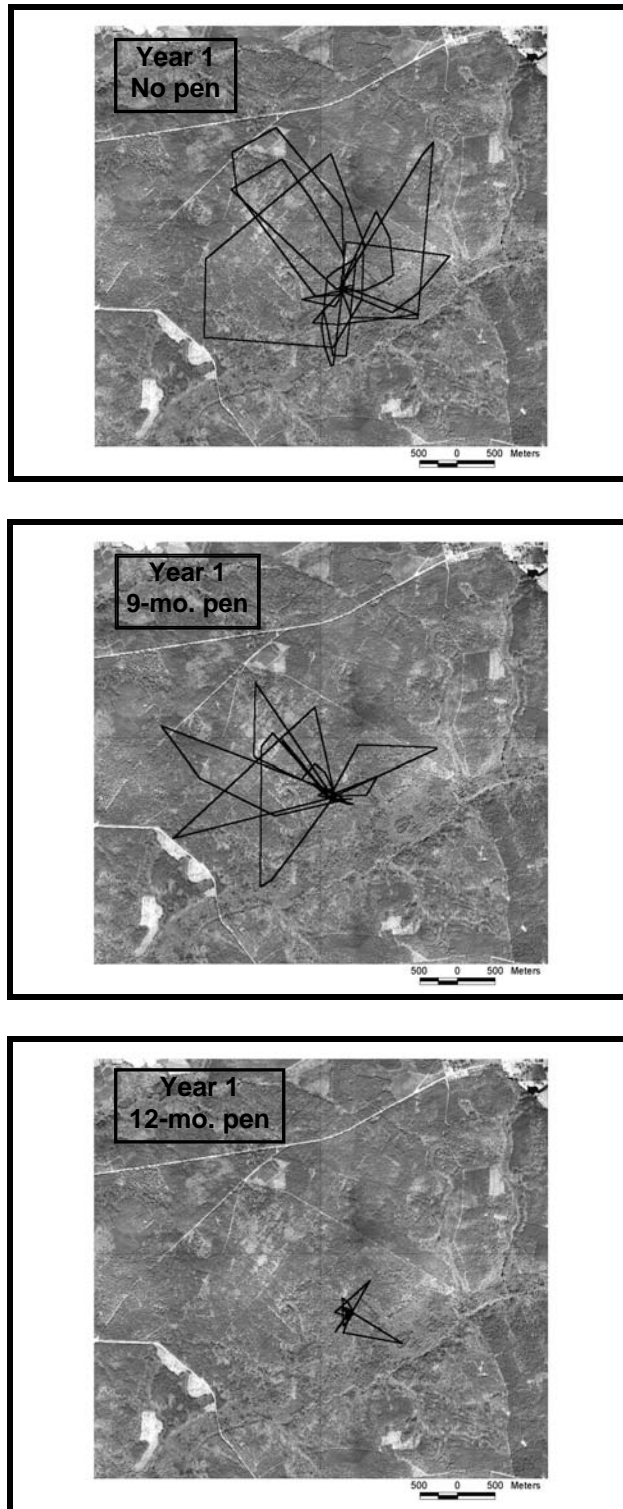


Figure 2.5a. Minimum convex polygons depicting Year 1 activity areas for tortoises from the no pen, 9-mo. pen, and 12-mo. pen treatments. Year 1 activity areas are based on first 50 daily locations only.

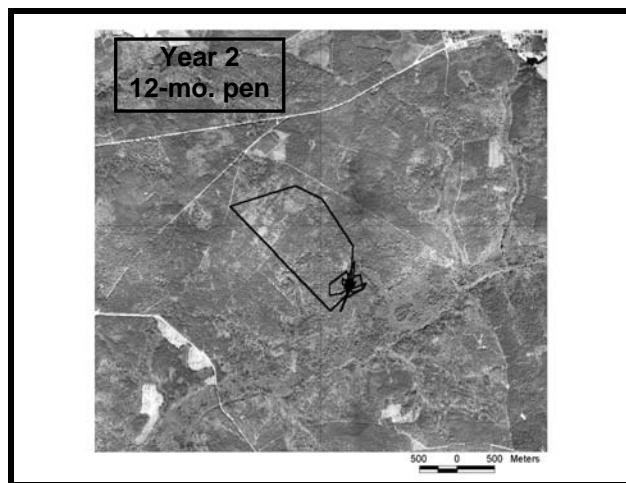
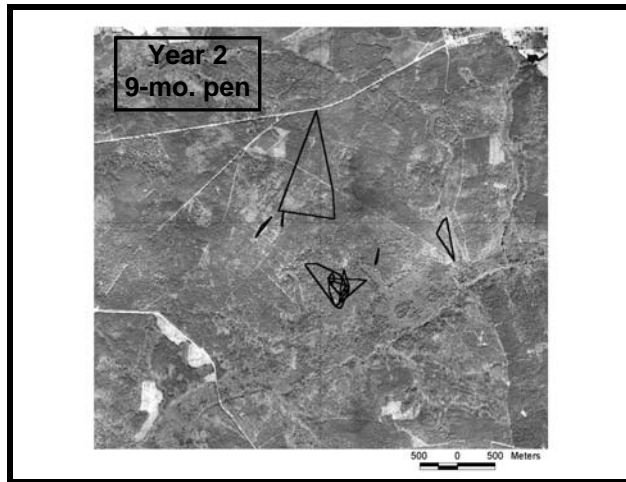
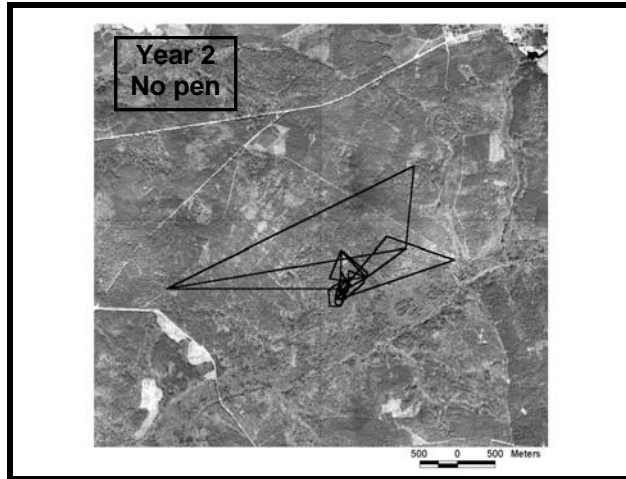


Figure 2.5b. Minimum convex polygons depicting Year 2 activity areas for tortoises from the no pen, 9-mo. pen, and 12-mo. pen treatments.

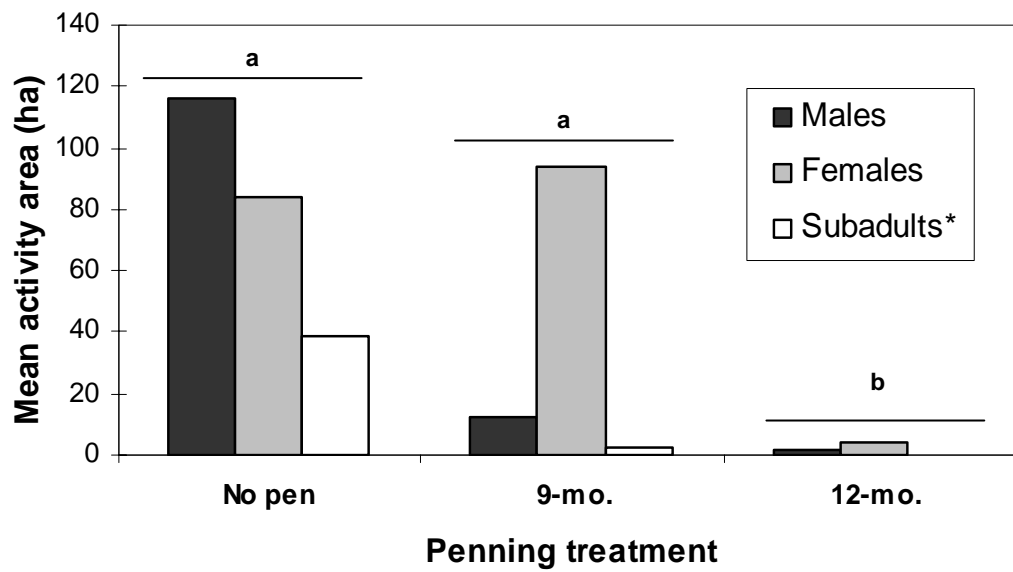


Figure 2.6a. Comparison of mean activity areas for adult males, adult females, and subadults in each penning treatment during Year 1. Significant comparisons among penning treatments are indicated with different letters; significant differences between sexes are indicated with an (\*).

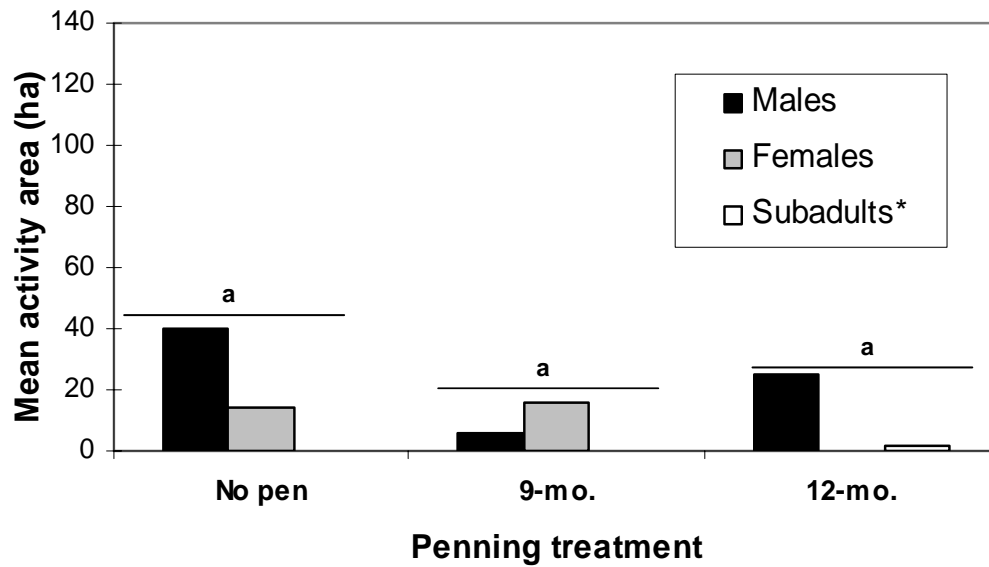


Figure 2.6b. Comparison of mean activity areas for adult males, adult females, and subadults in each penning treatment during Year 2. Significant comparisons among penning treatments are indicated with different letters; significant differences between sexes are indicated with an (\*).

## CHAPTER 3

# LONG-TERM APPARENT SURVIVAL OF TRANSLOCATED GOPHER TORTOISES: A COMPARISON OF NEWLY RELEASED ANIMALS AND PREVIOUSLY ESTABLISHED RESIDENTS<sup>1</sup>

<sup>1</sup>Tuberville, T.D., T.M. Norton, B.D. Todd, and J.S. Spratt. Submitted to *Biological Conservation*, 30 January 2008.

## ABSTRACT

Most turtle species require high adult survivorship to maintain stable populations. Translocations are often implemented to manage turtle populations but may cause demographic disturbances as a result of increased mortality or dispersal of released animals. The gopher tortoise (*Gopherus polyphemus*) is one of the most frequently translocated turtle species. Short-term monitoring indicates that dispersal by released tortoises is common, but few long-term data are available to determine if losses are sustained for multiple years. We investigated long-term apparent survival of gopher tortoises translocated to St. Catherines Island, Georgia, USA, based on 12 years of mark-recapture data. We analyzed capture histories in program MARK to compare apparent survival of newly released tortoises and previously established residents and to determine if apparent survival varied as a result of sex or initial size at release. Apparent survival did not vary between adult males and females (0.98 per six-month interval), but was lower in sexually immature animals (0.83 per six-month interval) and varied as a function of initial size (carapace length) at release. We documented a temporary reduction in apparent survival of newly released tortoises (0.67 during first six months) that we attribute to permanent dispersal, but consistently high survival of translocated tortoises once they became established as residents (0.98 per six-month interval). Comparable data from naturally-occurring populations are currently unavailable. Long-term studies of both translocated and naturally-occurring populations are needed to improve management of remaining tortoise populations.

## INTRODUCTION

Turtles, as a taxonomic group, have life histories characterized by delayed sexual maturity, relatively low annual fecundity, high egg and hatchling mortality, long reproductive



life span, and high adult survivorship (Moll 1979, Wilbur and Morin 1988, Iverson 1991; but see Buhlmann 1998). Although values for each trait may vary among species of turtles and among populations of the same species, individual populations appear to be constrained in their ability to withstand demographic disturbances (Congdon et al. 1993). In addition, turtle populations can be more sensitive to changes in some life history traits (e.g., adult survivorship, age at maturity) than others (e.g., nest success, hatchling survivorship; Frazer 1992, Heppell et al. 1996, Heppell 1998). For terrestrial and freshwater turtles, maintenance of stable populations appears to depend on high adult survival, with reported annual survival rates typically >80% but as high as 90-98% in many species (see summary table in Iverson 1991). Chronic disturbances that increase adult mortality – such as intentional harvest (Congdon et al. 1993, Congdon et al. 1994, Reed et al. 2005), incidental by-catch (Hoyle and Gibbons 2000, Dorcas et al. 2007), or fragmentation by roads (Gibbs and Shriver 2002) – cannot be sustained by long-lived turtle species.

Even short-term increases in adult mortality can potentially affect population stability. For example, a population of flattened musk turtles (*Sternotherus depressus*) in Alabama experienced a brief disease outbreak during which bi-weekly survival briefly dropped from 98-99% to 82-88% for a single month, before returning to 96-99% (Fonnesbeck and Dodd 2003). The population had declined by 50% within a year (Dodd 1988) and still had not recovered to pre-disease abundance a decade later (Bailey and Guyer 1998). Other sources of short-term adult mortality reported for turtle populations include drought (*Gopherus agassizii*, Longshore et al. 2003), habitat disturbance (*Terrapene carolina*, Dodd et al. 2006; *Testudo hermanni*, Stubbs et al. 1985) and changes in predator abundance or behavior (*Chelydra serpentina*; Brooks et al. 1991).

Not all short-term losses of adults result in long-term population declines. High drought-related mortality has been documented for adult desert tortoises at sites with low forage abundance or unpredictable availability (Longshore et al. 2003). Longshore et al. (2003) concluded that the desert tortoise population at the poor quality site was able to persist due to immigration of tortoises from surrounding source populations in more productive habitats. Germano and Joyner (1988) attribute recovery of another population of desert tortoises from a short period of high adult mortality to immigration of new animals into the population and high juvenile growth and survival. Dodd et al. (2006) reported higher than normal mortality of box turtles (*T. carolina*) immediately following habitat disturbance, but determined that disturbance effects on the population were short-lived and did not result in long-term demographic consequences. Whether disturbances that cause increased losses of adults will affect long-term population stability appears to be influenced by the length and severity of the disturbance, how long survival is affected once the source of the disturbance is removed, the abundance of juveniles for recruitment into the adult stage, and whether affected populations are isolated from surrounding populations.

Translocations, although they may be implemented in order to achieve conservation objectives (e.g., establishing or augmenting populations), can be considered perturbations to focal populations (Sarrazin and Barbault 1996). If large numbers of released animals are lost through mortality or dispersal, or if even small losses are sustained for many years, translocations could even be considered catastrophic events from which turtle populations must recover (Dodd et al. 2006). Tortoises, particularly gopher tortoises (*G. polyphemus*) and desert tortoises (*G. agassizii*), have been the subjects of numerous translocation projects. Short-term monitoring (usually 1-2 yrs) of translocated populations indicates that some adults are usually

lost from the founder population as a result of dispersal (Doonan 1986, Burke 1989, Heise and Epperson 2005, Tuberville et al. 2005). Ultimately, loss of newly translocated individuals—whether from dispersal or mortality—causes reductions in apparent survival, a term used to describe the proportion of animals remaining in a population. Few long-term data are available to determine whether tortoise losses are restricted to the period immediately following translocation or whether losses are sustained for multiple years (Seigel and Dodd 2000, but see Ashton and Burke 2007). We used data from a 12-year mark-recapture study of translocated gopher tortoises to answer the following questions: 1) Does apparent survival vary between newly released and previously established tortoises? 2) Does apparent survival of newly released animals change over time? 3) Does apparent survival vary among adult males, adult females, and sexually immature tortoises? 4) Does initial size of released animals affect probability of apparent survival?

## MATERIALS AND METHODS

### Study site and study population

Our study was conducted on St. Catherines Island, a privately owned barrier island 6.4 km off the coast of Liberty County, Georgia, USA. The 5670 ha island is approximately 16 km long and 3.2 – 4.8 km wide. The main study area is a 162 ha pasture at the north end of the island that was created for cattle grazing in 1950 and planted with Bermuda grass (*Cynodon* sp.), spangle grass (*Chasmanthium latifolium*), and broomsedge (*Andropogon* sp.). Although grazing by cattle has been discontinued since 1982, the open habitat is maintained by mowing, resulting in a savanna-like grassland with a scarce overstory of longleaf (*Pinus palustris*), slash (*P. elliotii*), and loblolly (*P. taeda*) pines (Thomas et al. 1978). The pasture was burned in 1989.

A population of 74 gopher tortoises (*G. polyphemus*; 23 males [235-345 mm CL], 32 females [217-335 mm CL], and 19 immature tortoises [53-205 mm CL]) was translocated from a development site in Bulloch County, Georgia to St. Catherines Island in 1994. These tortoises, hereafter referred to as founders, were permanently marked prior to release and provided with manually dug starter burrows. Based on health screening for Upper Respiratory Tract Disease (URTD; Brown et al. 2002), 80% of founders tested positive for exposure to *Mycoplasma agassizii* when released in 1994. All founders recaptured in 2004 (n=21) tested positive for exposure to and, in 50% of founders, *Mycoplasma* was directly cultured from nasal wash samples using polymerase chain reaction (Norton and Spratt, unpublished data). However, no tortoise exhibited clinical symptoms of URTD during the study and the population appears very healthy based on long-term health evaluations.

Approximately 25-30 free-ranging tortoises (referred to as residents) had been previously released on the island between 1987 and 1993 and, consequently, were already present when founders from Bulloch Co., Georgia, were released on the island. For many of the residents, the wild population from which they originated was unknown. Residents had not been permanently marked before their release. In Spring 1994, trapping was conducted to catalogue the resident population.

Following translocation of the founders in Spring 1994, bi-annual trapping was conducted each fall and spring from Fall 1994 – Spring 1998. No sampling occurred in 1999 or 2000; annual spring sampling resumed in 2001 – 2006. Spring sampling occurred primarily during May – June, and Fall sampling in September – October, although exact timing, duration and trapping effort varied among the 15 sampling periods. Trapping was conducted using 5-gallon plastic buckets buried at the entrance of tortoise burrows and covered with heavy duty

paper (Burke and Cox 1988), except during Fall 1994 when tortoises were manually extracted from their burrows with a pulling hook (Taylor 1982) and during Spring 2006, when wire live traps (Burke and Cox 1988) were used in addition to bucket traps. Sampling effort focused on recapturing tortoises released on the island with less emphasis placed on capturing tortoises recruited into the population as a result of on-island reproduction.

On initial capture (or first recapture for residents), tortoises were permanently marked by filing notches in unique combinations of marginal scutes (Cagle 1939) and most were also injected in the inguinal region or intramuscularly in an anterior leg with an electronic transponder chip (Trovan Electronic Identification Devices Ltd.). Mass to the nearest 0.01 kg and mid-line carapace length (CL) to the nearest mm were also recorded. Mature tortoises with concave plastrons and elongated gular scutes were classified as males. Tortoises that lacked secondary sexual characteristics were classified as females if CL was at least 220 mm CL; smaller tortoises were classified as immatures. Because most tortoises were initially captured as reproductively mature adults, annuli counts could not be used to accurately age individuals.

### Demographic analysis

We used capture history data collected from Spring 1994 to Spring 2006 to estimate apparent survival rates ( $\Phi$ ) and recapture probabilities ( $p$ ) of tortoises. We grouped animals into one of the following three sex/maturity classes based on the aforementioned criteria: (1) mature males, (2) mature females, or (3) immature tortoises, including non-reproductive subadults and juveniles whose sex could not be determined. Hatchling gopher tortoises are infrequently encountered in field studies (Morafka 1994) and we excluded the five hatchlings captured during the 12 years of data collection because four of them were never recaptured and the fifth was only

recaptured once. We also classified animals into two categories based on their origin/timing of release: (1) resident animals, including those that had been released on the island prior to 1994 or which were recruited via on-island reproduction, and (2) newly released animals, including the founders translocated to the island as a single group in Spring 1994 and one additional animal (“waif”) released onto the island during Fall 1994 – Spring 1995. Thus, we had six comprehensive groups of animals based on their origin and demographic status: resident males, resident females, resident immature tortoises, new males, new females, and new immature tortoises.

We used a standard Cormack-Jolly-Seber (CJS) open population model to generate parameter estimates from the capture-recapture data and to test hypotheses about the data. We assumed equal recapture probabilities among the six tortoise groups in all models. However, because trapping effort and duration varied among sampling periods, we allowed recapture probability to vary over time in all models. We used program MARK (White and Burnham 1999) to fit the following six models to the tortoise capture histories (Table 3.1):

Models 1 and 2.— Time-varying recapture probability ( $p_t$ ) with constant ( $\Phi$ ) or time-varying ( $\Phi_t$ ) apparent survival across intervals, but differing between resident and newly released animals.

Models 3 and 4.— Time-varying recapture probability ( $p_t$ ) with constant ( $\Phi$ ) or time-varying ( $\Phi_t$ ) apparent survival across intervals, but differing among males, females, and immature tortoises.

Model 5.— Time-varying recapture probability ( $p_t$ ) with apparent survival differing between resident and newly released animals in the first year, but constant over time ( $\Phi$ ) and equal between residents and newly released animals thereafter.

Model 6.— Time varying recapture probability ( $p_t$ ) with apparent survival differing between resident and newly released animals for the first two years, but constant over time ( $\Phi$ .) and equal between residents and newly released animals thereafter.

We used goodness-of-fit tests in program RELEASE embedded in program MARK to test the overall fit of the global model to the data. The global model included effects for both time and group variation in apparent survival and recapture probability and allowed all parameters to vary across capture intervals.

Our models provide differing interpretations of the underlying processes responsible for the observed demographic parameters. Thus, we chose the most parsimonious model of the six possible models based on minimization of Akaike's Information Criterion using an information theoretic approach (Akaike 1973, Burnham and Anderson 2002). The model selection procedure allowed us to choose the best model given the limitations and constraints imposed by the underlying data but we caution that even the "best model" will always be an approximation of biological reality. To account for uncertainty given model selection weights, we present model averaged parameter estimates with unconditional standard errors using all of our candidate models to generate weighted averages. Lastly, we modified the most parsimonious model to determine whether carapace length at first capture (or upon initial release in founders and waifs) had a significant effect on apparent survival.

## RESULTS

### Mark-recapture summary

Capture success per sampling period varied from 4 tortoises captured in Fall 1997 to 50 captured in Spring 1998 (mean = 25 tortoises per sampling period). The 75 newly released animals were recaptured 0 - 12 times (mean = 5.4 for animals recaptured at least once) with a total of 260 recaptures made throughout the study. Twenty-seven newly released tortoises (10 adults, 17 immature) were never recaptured following release (Fig. 3.1). Adults were recaptured more frequently than were immature tortoises. Eighty percent of newly released adults were recaptured an average of 6.0 times per tortoise for a total of 233 recaptures. Only 37% of newly-released immature tortoises were recaptured, for an average of 2.7 times and a total of 27 recaptures. The maximum interval between release and first recapture for any newly released tortoise was four years.

During the 1994-2006 study, twenty of the previously-released residents were recaptured 1-10 times (mean = 4.0) for a total of 79 recaptures. Because detailed records of tortoise releases and sightings were not kept prior to 1994, we do not know exactly how many tortoises released prior to 1994 were never sighted again. However, 12 previously-released residents were recaptured during the first year of the mark-recapture study. The maximum interval between initiation of the mark-recapture study and first recapture of a resident was 12 years. In addition, 15 residents resulting from on-island recruitment were captured 1-5 times (mean = 1.3) for a total of 20 captures. Recruited residents ranged from 49-173mm CL at time of first capture.



## Demographic analysis

Goodness-of-fit tests using program RELEASE embedded in program MARK revealed that the global model adequately fit the data (combined TESTS 2 and 3:  $\chi^2 = 44.7$ , 46 df,  $P = 0.53$ ). Model selection procedures to evaluate various CJS models revealed little support for the models where origin/timing of release (Models 1 and 2) or sex/maturity (Models 3 and 4) were the only factors allowed to affect apparent survival (Table 3.1). In contrast, the top two models (Models 5 and 6) both had constant survival across time and among all 6 tortoise groups except during the initial two years of the study, when survival during recapture intervals was allowed to differ between newly released tortoises and resident tortoises already present at the study site. The most parsimonious model, Model 5, allowed apparent survival of newly released tortoises to differ from residents for the first 2 six-month intervals. However, support for this model was equivocal when compared to a similar model (Model 6) where survival of newly released tortoises was allowed to differ from residents for the first 4 six-month intervals ( $\Delta AIC < 2.0$ ). Nevertheless, both Models 5 and 6 were superior to Model 1, which similarly constrained survival as constant across time, but further constrained survival to differ between residents and newly released tortoises for the entire duration of the study.

Model-averaged estimates of apparent survival and recapture probabilities with unconditional standard errors were calculated based on model weights of all candidate models. Average recapture probability was  $0.41 \pm 0.06$  SE but varied among sampling periods depending on year, season, or sampling effort. Recapture probability during the course of the study ranged from a low of  $0.07 \pm 0.03$  in Fall 1997 to a high of  $0.87 \pm 0.05$  in Spring 1998 (Fig. 3.2). Apparent survival for six-month intervals averaged  $0.97 \pm 0.01$  SE across all intervals and groups. However, apparent survival was initially low for newly released animals ( $0.67 \pm 0.07$ ) compared

to resident animals ( $0.98 \pm 0.01$ ), but increased over subsequent intervals to match survival of resident animals (Fig. 3.2).

Although there was very little support for Models 1–4 ( $\Delta AIC$  weights  $>10$ , Table 3.1), a closer look at parameter estimates from Model 3 revealed overlapping confidence intervals for estimates of apparent survival between males and females, providing additional evidence for a lack of sex effect on survival. In contrast, immature tortoises had lower estimates of apparent survival and non-overlapping confidence intervals compared to mature males and mature females (immature tortoises:  $0.83 \pm 0.03$ ; mature males:  $0.98 \pm 0.07$ ; mature females:  $0.98 \pm 0.06$ ), implicating possible size/age effects on survivorship. Subsequently, the addition of carapace length, which is somewhat founded with tortoise age, to the top model as a factor in survivorship greatly improved the fit of the model (Model 5: 1,091 AIC; Model 5 with carapace length: 1,063 AIC); survival was higher for tortoises of greater initial length.

## DISCUSSION

Although more than 25,000 gopher tortoises were legally displaced as a result of habitat destruction during the 1990s in Florida alone (Enge et al. 2002), data from long-term monitoring of displaced populations are virtually lacking (but see Ashton and Burke 2007). Empirical data are crucial for evaluating whether translocation can be used effectively to manage gopher tortoise populations. Cox (1989) recognized that evaluations of the viability of translocated tortoise populations would need to consider any behavioral or demographic responses (such as dispersal) of tortoises to translocation. Seigel and Dodd (2000) were the first to develop a population viability model explicitly for translocated tortoises. They varied adult survivorship to reflect the anticipated loss of adults due to post-translocation dispersal and concluded that annual

retention rates of at least 90% would be necessary to maintain a viable population. However, their model assumed that retention rates would remain constant following translocation rather than increase over time.

Several studies have used radio-telemetry to monitor the short-term fate of adult translocated gopher tortoises (Doonan 1986, Heise and Epperson 2005, Tuberville et al. 2005). Altogether, these studies indicate that individuals are lost from the population primarily through dispersal from the release site rather than direct mortality, with site fidelity during the first year ranging from 31% without prior penning (i.e., hard release) to 69 - 92% with prior penning (soft release). A consistent observation among studies is that dispersal is typically confined to the first few weeks following release, demonstrating that the effects of translocation on tortoise behavior are apparently short-lived. Presumably, movement patterns eventually stabilize such that translocated tortoises subsequently exhibit site fidelity comparable to native, undisturbed tortoises.

Based on long-term mark-recapture data, we report an apparent survival of 0.67 for newly released tortoises on St. Catherines Island during the first six months, which is identical to six-month site fidelity reported by Doonan (1986) using radio-telemetry. However, six-month apparent survival of newly released tortoises at St. Catherines Island increased dramatically to 0.96 during the subsequent six-month interval, resulting in an overall apparent survival of 0.64 in the first year. Annual survival of newly released animals was 0.96 (0.98 per six-month interval) throughout the remainder of the 12-year study. Our findings mirror results from Ashton and Burke (2007), the only other published study of long-term site fidelity of translocated gopher tortoises. They reported post-translocation retention rates of 73% in year one, 92% in year two, and an annual average of 98.5% over the subsequent 15 years leading up to the resurvey.

Apparent survival of previously established resident gopher tortoises at St. Catherines Island was consistently high throughout the study, averaging 0.96 annually (six-month survival = 0.98)—the same apparent survival we report for new tortoises after the first year following their release. Although the “resident” tortoises were not native to the island, our findings that resident survival was relatively unchanged throughout the study period and that survival of new releases quickly matched resident survival, indicate that residents had become established in the survey area prior to our mark-recapture study. Contrary to findings by Bertolero et al. (2007) for reintroduced Hermann’s tortoises (*T. hermanni hermanni*), augmentation of the St. Catherines gopher tortoise population did not appear to result in any negative demographic consequences for either previously established residents or subsequently released tortoises.

How our reported values for long-term survival of St. Catherines Island residents compare to survival of gopher tortoises from naturally-occurring populations is unknown. Unfortunately, there are no published estimates of long-term mortality or dispersal rates for natural populations. Mortality events due to disease have been reported (Gates et al. 2002, Seigel et al. 2003), but reference values for healthy populations are not available. Dispersal appears to be a rare event, is difficult to document in short-term studies, and is not well-quantified for naturally-occurring populations. Based on a one year telemetry study of 123 tortoises, Eubanks et al. (2003) documented dispersal of 2% of adults in unfragmented, high-quality habitat. Despite the paucity of available survival and dispersal data, it seems unlikely that tortoises in naturally-occurring populations could maintain much higher long-term apparent survival than the 96-98.5% per year reported here and by Ashton and Burke (2007). We suspect that when data become available, survival rates for naturally-occurring populations will be similar to long-term rates observed for translocated gopher tortoises.

We did not observe a difference in apparent survival between adult male and adult female tortoises, but annual survival differed significantly between immature (0.69) and adult tortoises (0.96), with tortoises of smaller initial size (i.e., carapace length at time of release) exhibiting lower survival than larger tortoises. Although immature tortoises may have smaller home ranges or exhibit higher site fidelity than adults following release (Berry 1986, Tuberville et al. 2005), because of their smaller size and sometimes softer shells they are vulnerable to a wider array of predators. Immature tortoises are also difficult to effectively sample because their small, cryptic burrows are difficult to find. Few comparative data on survivorship of immature gopher tortoises (other than hatchlings, which were excluded from our analysis) are available, but range from 45% (Wilson, 1991) to >80% (Tuberville and Buhlmann, unpublished data). Both estimates are based on short-term studies, so the wide range in values may reflect year-to-year variation in survival. Although sample size is small, our 12-year study at St. Catherines provides a long-term estimate of apparent survival in immature gopher tortoises that was previously lacking for this species.

Our findings document an immediate short-term reduction in apparent survival of newly released tortoises relative to previously established residents, which we attribute mostly to permanent dispersal of newly released tortoises from the study area. By the end of the first year, annual apparent survival of newly released tortoises corresponds with apparent survival of residents, is consistently high through the remainder of the study, and is similar to values reported for another translocated population (Ashton and Burke 2007). Long-term apparent survival of both newly released tortoises and previously established residents exceeds the minimum estimate required to maintain viable populations of gopher tortoises (90%; Seigel and Dodd 2000) and closely related desert tortoises (95%; USFWS 1994), suggesting that, at least in

some circumstances, translocation can be used as a management tool for maintaining or establishing viable populations of tortoises.

One of the primary impediments to effectively managing populations of gopher tortoises and other rare turtle species is the lack of complete life history data. Our study provides estimates of long-term survivorship of immature and adult gopher tortoises, which have not been well-documented in the literature. Although our results also indicate that survivorship varies as a function of life stage (immature vs. adult) and initial size, we were not able to estimate age- or size-specific survivorship. Long-term studies of both translocated and naturally-occurring populations are needed to better understand tortoise survivorship and how it may vary among life stages, among years in response to fluctuating environmental conditions, and among sites as a result of local habitat conditions. A better understanding of the life history of gopher tortoises is necessary to provide effective long-term management of remaining populations, particularly when manipulations such as translocation or augmentation are implemented.

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Table 3.1. Analysis of group-specific effects (as a function of either group origin or sex/maturity, or both) and temporal variation in survival of translocated gopher tortoises. The six competing models were evaluated using the Cormack-Jolly-Seber open population model in program MARK.

Model	Time effect on survival	Group effect on survival	Recapture probability	Number of Parameters	AIC	$\Delta$ AIC
1	constant	varied by origin group	time varying	16	1140.3	49.3
2	time varying	varied by origin group	time varying	41	1118.9	27.9
3	constant	varied by sex/maturity group	time varying	17	1101.9	10.9
4	time varying	varied by sex/maturity group	time varying	56	1139.7	48.7
5	constant	varies first year between origin groups	time varying	17	1091.0	0.0
6	constant	varies first two years between origin groups	time varying	18	1092.7	1.7

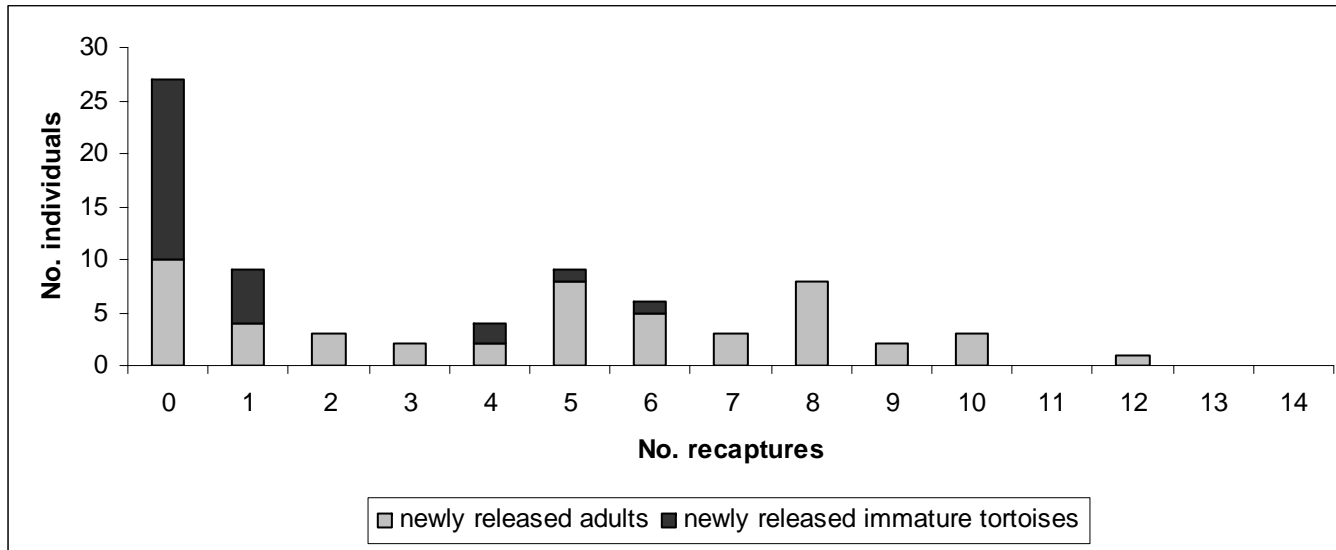


Figure 3.1. Recapture history of newly released adult (gray bars) and immature (black bars) gopher tortoises at St. Catherines Island, Liberty Co., Georgia, USA, over 14 sampling periods from Fall 1994-Spring 2006. Only the first capture of an individual per sampling period is included.

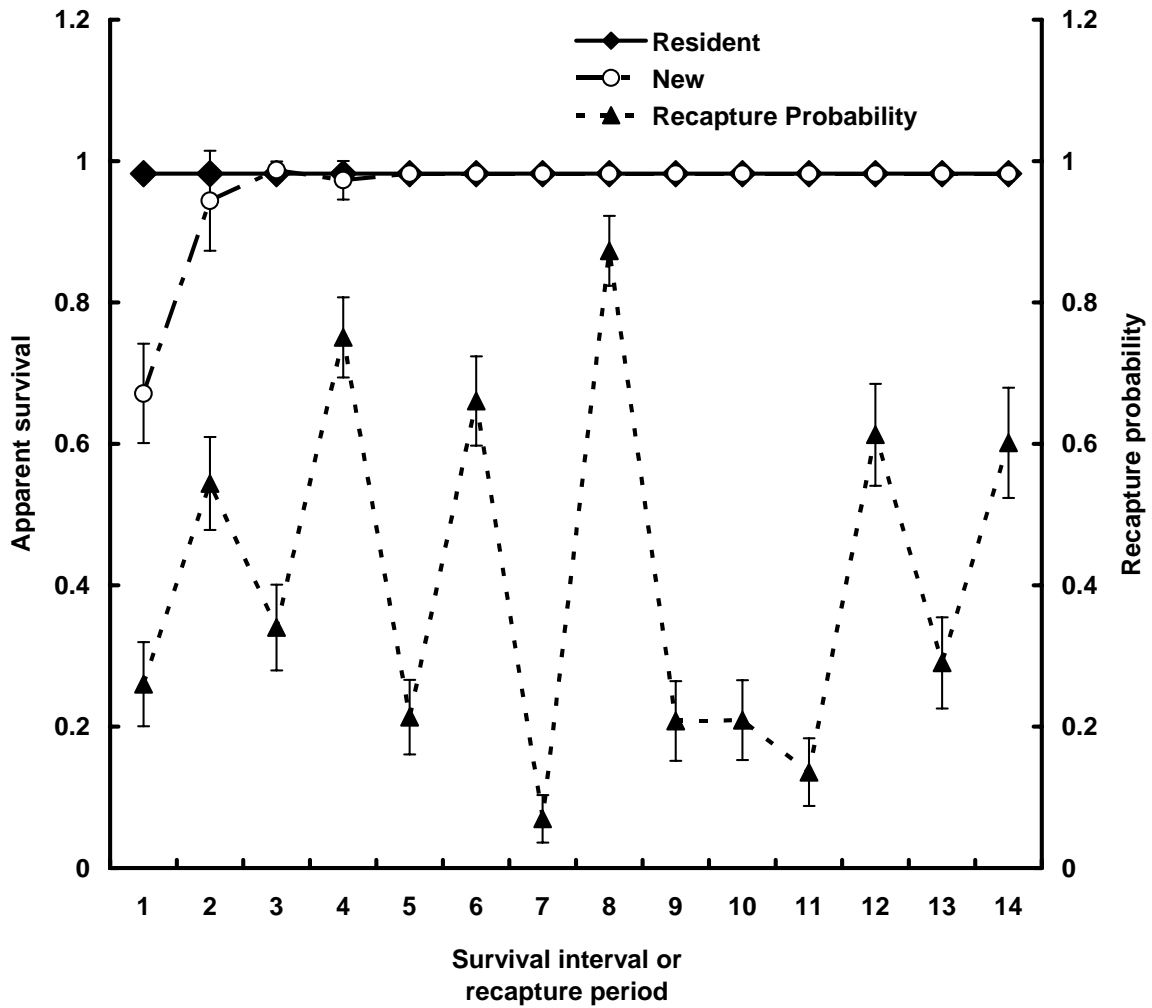


Figure 3.2. Apparent six-month survival of previously established resident (filled diamonds) and newly released (open circles) gopher tortoises at St. Catherines Island during 1994-2006. Apparent survival of residents and newly released tortoises are equivalent during and subsequent to the third survival interval. Recapture probability (filled triangles) varies throughout the study, as did sampling effort.

CHAPTER 4  
MATING SYSTEM IN A GOPHER TORTOISE POPULATION ESTABLISHED THROUGH  
MULTIPLE RELEASES:  
APPARENT ADVANTAGE OF PRIOR RESIDENCE<sup>1</sup>

<sup>1</sup>Tuberville, T.D., T.M. Norton, T.C. Glenn, and B.J. Waffa. To be submitted as part of manuscripts to *Molecular Ecology Notes* and *Animal Conservation*

## ABSTRACT

Population manipulations such as translocation are becoming increasingly important tools in the management of rare and declining species. Evaluating the effectiveness of such manipulations requires comprehensive monitoring of population processes, including dispersal, survivorship, and reproduction. We investigated the mating system of a translocated population of gopher tortoises (*Gopherus polyphemus*) established through multiple releases, which occurred primarily during 1987-1994. During 2006-2007, we sampled and genotyped 27 candidate males, 34 candidate females, and 121 offspring from 19 clutches at 5 polymorphic microsatellite loci to determine the relative frequency of multiple paternity and to estimate individual reproductive success. Multiple paternity was detected in 57% of clutches genotyped, and females of single-sire clutches and females of multiple-sire clutches were of similar size. Reproductive success varied among male tortoises, and successful sires were significantly larger than males to which no offspring were attributed. Among successful sires, previously established resident males sired a disproportionate number of the offspring sampled, despite being significantly smaller than subsequently released males. The high variance in individual reproductive success and the apparent reproductive advantage associated with prior residence observed in this gopher tortoise population has important implications for the design of future translocation projects.

## INTRODUCTION

Conservation genetics has become ubiquitous in the management of wildlife populations, particularly for rare or declining species. The wide range of available genetic markers provides biologists with the necessary tools for investigating questions at multiple scales, from resolving



taxonomic issues at the species level, characterizing genetic exchange or divergence among populations, detecting inbreeding or bottlenecks within small populations, to identifying individual animals (Parker et al. 1998). Molecular markers can play an important role in assessing the need for management interventions such as captive breeding or translocations, as well aid as in the planning and monitoring of those interventions.

Post-release genetic monitoring can be a useful means of evaluating success of individual projects, determining the need for additional intervention, and identifying ways to improve future translocation efforts. Few studies, however, have employed molecular tools to investigate mating system parameters in translocated populations, including reproductive success of individual animals. Milinkovich et al. (2004) sampled free-ranging captive-reared Galapagos tortoise offspring (*Geochelone hoodensis*) and assigned maternity and paternity to calculate the relative contribution of each captive breeder. Knapp and Malone (2003) sampled a translocated population of iguanas (*Cyclura cyclura inornata*) 10 yrs post-release to characterize relative reproductive success of the adult founders, but their molecular markers were not sufficiently informative to assign parents to individual offspring. Castro et al. (2004) investigated variance in reproductive success and the effects of extra-pair copulations on effective population sizes in a reintroduced population of a New Zealand bird, the hihi (*Notiomystis cincta*). In a translocated population of an Australian mammal, the bridled nailtail wallaby (*Onychogalea graenata*), Sigg et al. (2005) estimated reproductive success of individual males and identified characteristics correlated with male success.

There are several reasons why mating systems might be expected to differ in translocated populations relative to naturally-occurring populations. First, the stress associated with translocation could potentially suppress or interfere with reproduction, at least temporarily

(Teixeira et al. 2007, Wingfield and Sapolsky 2003). In addition, the increased movement behavior often observed during the “settling” phase immediately following release (Cook 2004, Reinert and Rupert 1999, Tuberville et al. 2005) could be so energetically costly that insufficient stores remain to devote to reproduction. Animals released in an unfamiliar environment may not be able to locate important resources related to reproduction, including nest sites or even potential mates, particularly if the release animals are solitary or occur at low densities (Courchamp et al. 1999, Stephens and Sutherland 1999). Finally, augmentation of an existing population could result in competitive interactions that affect the relative reproductive success of newly released animals compared to previously established residents (Berry 1986).

Among reptiles, tortoises are the taxonomic group that has most frequently been managed through translocations (Seigel and Dodd 2000). To evaluate the potential effects of translocation on the mating system of tortoises, we investigated multiple paternity and individual reproductive success in a translocated population of gopher tortoises (*Gopherus polyphemus*). The population was established through multiple releases over a 20-yr period (1987-2007). Although several studies have described the behavioral mating system and the genetic mating system of gopher tortoises in naturally-occurring populations (Moon et al. 2006, Johnson et al. 2007, Boglioli et al. 2003), none have characterized the mating system in translocated populations. Our study addressed the following questions: What is the relative occurrence of single versus multiple paternity within individual clutches? Does reproductive success vary among males? What proportion of translocated males sire offspring? Does order of establishment at the release site influence reproductive success?

## METHODS

### Study species

Gopher tortoises (*Gopherus polyphemus*) are long-lived terrestrial turtles, attaining sexually maturity at 220-255 mm carapace length (CL) and 10-21 years of age (Iverson 1980, Landers et al. 1980), with individuals from populations at higher latitudes or in lower quality habitats taking longer to reach maturity. Gopher tortoises are restricted to the Coastal Plain of the southeastern United States, where they occur in local ‘colonies’ and construct large burrows in deep sandy soils. Individuals will use multiple burrows throughout the activity season, and several tortoises may sequentially occupy a given burrow (Eubanks et al. 2003). Although they tend to occupy burrows singly, gopher tortoises frequently visit each other at their respective burrows, with most social interactions occurring on the mound of sand (‘apron’) outside the burrow entrance (Boglioli et al. 2003).

Behavioral observations indicate that both sexes mate with multiple mates (Boglioli et al. 2003), with individual females experiencing an average of 26 mating attempts by 6-14 individual males in a single year (Johnson et al. 2007). Hormonal, morphological, and behavioral data suggest that female gopher tortoises can store sperm from the fall peak mating season to fertilize eggs laid the following spring (Johnson et al. 2007, Ott et al. 2000, Gist and Congdon 1998). Sperm storage from multiple matings also provides the opportunity for multiple males to sire a single clutch, a phenomenon that has been corroborated with genetic analysis of clutches collected from known females (Moon et al. 2006). An adult female produces only a single small clutch of eggs (typically 3-9) during the reproductive season, often depositing them in the burrow apron, but may not reproduce every year (Diemer and Moore 1994, Rostal and Jones 2002).

### Study population

We conducted our study on St. Catherines Island, a privately owned barrier island 6.4 km off the coast of Liberty Co., Georgia, USA. Gopher tortoises are not native to the island but approximately 105-115 tortoises from multiple source populations have been released. The largest release of tortoises occurred in Spring 1994, when a population of 74 wild-captured tortoises (“founders”) was translocated to the island from a development site in Bulloch Co., GA. Prior to 1994, approximately 25-30 tortoises (“residents”) had been introduced but the wild populations from which they originated are not known. Since 1994, at least 13 formerly captive or rehabilitated tortoises (“waifs”) have been released. All tortoises except residents were permanently marked prior to release. Residents were marked upon first recapture. Mark-recapture with variable sampling effort was conducted during 1994-2007 to monitor survivorship, reproduction and recruitment in the study population. Mark-recapture histories of individual tortoises allow us to estimate the current size of the breeding pool.

### Sample collection

We intensively trapped burrows during 2004, 2006 and 2007 to capture sexually mature adults. We weighed (to nearest 0.01 kg) and measured (mid-line carapace length [CL] to the nearest mm) each individual and classified tortoises at least 220 mm CL in size as adults. We classified adults with concave plastrons and elongated gular scutes as males and adults lacking these secondary sexual characteristics as females.

During the nesting seasons (May-early July) of 2006 and 2007, we radiographed adult females to detect the presence and number of shelled eggs (Gibbons and Greene 1979). We injected females having fully calcified eggs with oxytocin to induce oviposition prior to their

release (Ewert and Legler 1978). We incubated eggs collected directly from females at 28-30°C until hatching, approximately 85-100 days later (Burke et al. 1996, Demuth 2001). Gopher tortoises exhibit temperature-dependent sex determination. Therefore, we selected incubation temperatures to encompass the pivotal temperature for sex determination so as to produce clutches with approximately a 1:1 sex ratio. We collected additional clutches by searching burrow aprons for natural nests during May – September. In 2006, we completely excavated nests and placed them in incubators until hatching. In 2007, we protected nests from predators with wire cages and allowed nests to incubate in the field until 21 August, shortly before hatching.

We collected blood from the brachial vein of adults and large juveniles and from the subcarapacial vein of hatchlings and small juveniles (Hernandez-Divers et al. 2002). We stored blood samples in lysis buffer (100mM Tris pH 8.0, 100mM EDTA, 150mM NaCl, 1% SDS) until extracting DNA using a protocol modified from Carter and Milton (1993; see modified protocol at [http://www.uga.edu/srel/DNA\\_Lab/MUD\\_DNA'00.rtf\\_.rtf](http://www.uga.edu/srel/DNA_Lab/MUD_DNA'00.rtf_.rtf)). We dissected eggs that were damaged during nest excavation or that failed to hatch and collected tissue from partially developed embryos. We did not dissect unhatched eggs until after the normal hatchling emergence period (mid-October) and due to tissue deterioration, were not always able to obtain high quality DNA.

### Microsatellite genotyping

We developed five polymorphic microsatellite loci for *G. polyphemus* using the protocol by Glenn and Schable (2005). We optimized polymerase chain reaction (PCR) conditions for each locus using genomic DNA from 24 individuals originating from McIntosh Co., GA

(Tuberville, unpublished data). The basic properties and PCR conditions for each locus, based on samples collected from St. Catherines, are presented in Table 4.1. We modified one primer in each pair at the 5' end with an engineered sequence (CAG tag 5'-CAGTCGGGCGTCATCA-3'; see [http://www.uga.edu/srel/DNA\\_Lab/protocols.htm](http://www.uga.edu/srel/DNA_Lab/protocols.htm)) to allow use in the PCR of a third primer that is fluorescently labeled for detection on the ABI 3130xl sequencer.

We performed single-locus PCR amplifications in a 11.5  $\mu$ L volume (10 mM Tris pH 8.4, 50 mM KCl, 25.0  $\mu$ g/ml BSA, 0.4  $\mu$ M unlabeled primer, 0.04 $\mu$ M tag labeled primer, 0.36 $\mu$ M universal dye-labeled primer, 3-4.5 mM MgCl<sub>2</sub>, 0.15 mM dNTPs, 0.5 units JumpStart Taq DNA Polymerase (Sigma), and 5-50ng DNA template) using an Applied Biosystems (GeneAmp PCR System 9700) or Eppendorf Mastercycler Gradient thermal cycler. For amplification, we used touchdown thermal cycling programs (Don et al. 1991) encompassing a 10° span of annealing temperatures ranging between 65-55°C (TD65) or 60-50°C (TD60). Our cycling parameters were 95°C for 3 min, 21 cycles of 96°C for 20 s, highest annealing temperature (decreased 0.5°C per cycle) for 20 s, and 72 °C for 30 s; and 15 cycles of 94 °C for 20 s, lowest annealing temperature for 20 s, and 72 °C for 30 s.

We pooled PCR products from Gopo-2, Gopo-5, and Gopo-14 in a single well that also contained a Naurox size standard prepared as described in DeWoody et al. (2004). We similarly pooled PCR products from Gopo-1 and Gopo-12. We ran the pooled PCR products and internal size standard on an ABI-3130x automated DNA sequencer and analyzed results using GENEMAPPER version 4.0 (Applied Biosystems).

## Statistical analyses

Using CERVUS 3.0 (Kalinowski et al. 2007), we calculated allele frequencies for the study population based on genotypes of sexually mature adults. We used GenAlEx version 6 (Peakall and Smouse 2006) to detect deviations from Hardy-Weinburg equilibrium. We used CERVUS estimate the frequency of null alleles and to calculate single- and multi-locus probabilities of identity (probability that two unrelated individuals share the same genotype) and probabilities of exclusion when neither parent is known and when one parent is known (Table 4.2). We tested for linkage disequilibrium between loci using Genepop 1.2 (Raymond and Rousset 1995, <http://genepop.curtin.edu.au/>).

We performed parentage analysis on each clutch using both categorical allocation and parental reconstruction. Parental reconstruction uses genotypes of full-sib or half-sib progeny arrays (in this case, clutches collected directly from females or from natural nests) to reconstruct all possible combinations of paternal and maternal genotypes that could explain the observed offspring genotypes (Jones and Ardren 2003). When more than one combination of maternal and paternal genotypes is possible, the solutions are ranked based on allele frequencies in the population and the rules of Mendelian inheritance. GERUD 2.0 (Jones 2005) allows reconstruction of parental genotypes from progeny arrays, whether or not the maternal genotypes are known. Parental reconstruction is possible even when candidates of one or both sexes are unsampled in the population, provided that allele frequencies have been estimated. If candidate parents have been sampled, the reconstructed genotypes can be compared to genotypes from the pool of candidate parents (Jones and Ardren 2003). Although the program will not always generate a multi-locus genotype that *exactly* matches the genotypes of one of the candidate fathers, GERUD is useful for detecting multiple paternity within progeny arrays, determining the

minimum number of fathers necessary to explain the offspring genotypes, and estimating reproductive skew among males contributing to multiply-sired clutches.

Categorical allocation is a likelihood based approach to assigning parentage from a pool of candidate parents when the identity of one or both parents is unknown (Jones and Ardren 2003). For each offspring, the genotypes of candidate parents are searched to identify all parents with compatible genotypes. For each offspring and candidate parent (if one parent known) or parent-pair (if neither parent known) combination, the  $\log_e$  likelihood ratio (LOD score) is calculated comparing the likelihood that a candidate parent (or parent-pair) is the true parent (or parent-pair) of the offspring to the likelihood that they are unrelated (Jones and Ardren 2003). Offspring are assigned to the parent or parent-pair with the highest LOD score. CERVUS 3.0 (Kalinowski et al. 2007) can be used to identify the most likely parent or parent-pair for individual offspring, even when parent-offspring mismatches occur due to mutations, null alleles or genotyping error. However, CERVUS requires at least partial sampling of candidate parents and an estimate of the proportion of breeders sampled to calculate meaningful LOD scores. Offspring whose true parent was unsampled may be assigned to an unrelated candidate parent with the most compatible genotype, resulting in a false positive, or remain unassigned, but LOD scores will be low for these offspring-parent pairs. CERVUS is useful for calculating reproductive success of candidate males.

For clutches from known females (i.e., hatched from eggs collected directly from females), we visually inspected offspring genotypes to verify their compatibility with the maternal genotype. We analyzed the hatchling and maternal genotypes of each clutch in GERUD 2.0 to calculate the minimum number of sires necessary to explain the observed offspring genotypes. Next, we performed paternity analysis in CERVUS with all sampled males



included in the list of candidate fathers. We then determined the number of sires contributing to the clutch by compiling the list of fathers assigned in CERVUS to individual offspring comprising the clutch. Finally, we compared the minimum number of sires calculated by CERVUS and GERUD for each clutch. When CERVUS and GERUD differed in the number of sires assigned to individual clutches, we visually inspected the genotypes of the offspring, mother, and putative fathers assigned to the clutch. We chose the more conservative estimate of number of fathers when the additional sire was assigned to a single offspring but was not needed to explain that offspring's genotype (i.e., the offspring was compatible with the other father(s) assigned to the clutch).

For field-collected nests for which identity of the mother was unknown, we analyzed hatchling genotypes in GERUD 2.0 to calculate the minimum number of sires. Next, we performed parentage analysis in CERVUS to identify the most likely parent-pair for each offspring. We included all sampled males in the list of candidate fathers. However, we created a separate list of candidate mothers for each clutch by excluded any female that was hormonally-induced to lay eggs in captivity or whose clutch size determined from radiographs did not match clutch size of the field-collected nest. We calculated the number of sires contributing to each clutch by comparing fathers assigned by CERVUS to individual offspring comprising the clutch. We compared the number of sires estimated by GERUD and CERVUS as previously described. Similarly, we compared the female assigned to individual offspring comprising the clutch. For those clutches in which a single female was consistently assigned as the most likely mother of all offspring, we reanalyzed offspring genotypes in both GERUD and CERVUS with that female designated as the known mother.

## RESULTS

We captured 27 candidate males (248-350 mm CL, mean = 309 mm CL) and 34 candidate females (255-244 mm CL, mean = 316 mm CL), each representing 57% of the estimated total number of each sex released on St. Catherines Island. However, after excluding animals not captured in the past 10 years (i.e., since 1996), we estimate that we sampled at least 84% of the adult males and 75% of the adult females still resident at the release site.

The five microsatellite loci had 6-18 alleles per locus with observed heterozygosity ranging from 0.65 – 0.90 (Table 4.2) in the mixed breeding pool, which consisted of adult founders, residents, and waifs (i.e., tortoises from multiple source populations). None of the markers conformed to expectations of Hardy-Weinberg Equilibrium, particularly Gopo-12 and Gopo-14, which had estimated null allele frequencies of 0.050 and 0.066, respectively (Table 4.1). We did not detect any linkage disequilibrium among the 10 paired loci comparisons.

The probability of two unrelated tortoises sharing the same genotype (probability of identity) was  $3.06 \times 10^{-8}$  (Table 4.2). Single-locus probabilities of detecting multiple paternity ranged from 0.3533-0.7067 when the mother's genotype was unknown and 0.5342 – 0.8281 when the mother's genotype was known. The multi-locus probability of detecting multiple paternity was 0.9818 when the mother's genotype was unknown and 0.9979 when the mother's genotype was known.

We collected a total of 192 eggs from 24 clutches – 71 eggs from 8 clutches in 2006 and 121 eggs from 16 clutches in 2007. Thirty-three eggs from 5 clutches in 2006 and 83 eggs from 14 clutches in 2007 successfully hatched. In addition, we were able to extract DNA from four partially developed embryos in 2006 and one embryo in 2007, for a total of 121 offspring from 19 clutches genotyped during the study (Table 4.3). Some eggs failed to hatch due to damage

during oviposition or nest excavation, incubator overheating, early embryonic death, or unknown causes. Five clutches (totaling 42 eggs), including both lab- and field-incubated nests, experienced complete hatching failure.

We classified clutches represented by at least four genotyped offspring as having either single or multiple sires and calculated the proportion of offspring within a clutch assigned to each male (Table 4.3). Females with multiply-sired clutches were not significantly different in size (mm in CL) than females of singly-sired clutches ( $t_{df=7}=-1.233$ ,  $P=0.257$ ). Even though multiple paternity was detected in clutches with as few as three offspring (clutch 2006-03), clutches with fewer than four offspring ( $n=5$ ) were excluded from calculations because only a small proportion of the original clutch was genotyped (<40%). Of the remaining 14 clutches, six (42.9%) were sired by a single male. In one of the six clutches, CERVUS assigned a second sire, but both GERUD analysis and visual inspection indicated that all offspring genotypes could be explained by a single candidate male. Eight clutches (57.1%) were fathered by multiple sires. CERVUS assigned a third sire to a single offspring in three of the eight multiply-sired clutches. However, GERUD analysis and visual inspection revealed that the third sire was not necessary to explain the offspring genotypes, leading us to conclude that the eight multiply-sired clutches were each likely fathered by only two males. An average of 74.5% (range 57.1-87.5%) of offspring from multiply-sired clutches were assigned to the primary male (i.e., the male siring the most offspring; Fig. 4.1). For each multiply-sired clutch, the primary male tended to be larger in CL than the other male assigned to the clutch, but the trend was not significant ( $t_{df=8}=1.872$ ,  $P=0.098$ ).

The 19 clutches producing offspring for analyses (including those with fewer than 4 offspring genotyped) were attributed to 18 females, with only female 152 having clutches

represented in both years of sampling. Male 221 was assigned as the sole sire to both of female 152's clutches. The 18 assigned females included 10 founder (55.6%), 6 resident (33.3%), 1 waif (5.5%), and one unsampled female (5.5%). Fifty percent of the candidate females were represented by clutches we sampled during 2006-2007.

Eleven males (40.7% of the candidate males we sampled) were attributed to the 19 clutches with genotyped offspring. Successful sires were larger in CL than non-sires, and this trend was nearly significant ( $t_{df=23}=2.059$ ,  $P=0.051$ ). All of the 11 successful males were represented in the 14 clutches from 2007, but only four of those males were also represented in the five clutches from 2006, probably due in part to the reduced sampling effort in 2006. Among the 11 successful males were four resident (36.4%) and seven founder (63.6%) males. One or more unsampled males were also assigned to nine offspring from six clutches. Two (7.4%) candidate males accounted for 46.3% of all offspring sampled – male 221 (a resident) sired 35 offspring from five clutches and male 305 (also a resident) sired 21 offspring from three clutches. In contrast, only a single offspring (0.8%) was assigned to male 103 (Fig. 4.2). Of the total male candidate breeding pool, resident males represented 18.5% of the breeders but sired 60.3% of all offspring while founder males represented 66.7% of breeders but sired 32.2% of offspring (Fig. 4.3). Founder males comprising the pool of candidate breeders were significantly larger (mm CL) than resident males ( $t_{df=7}=2.501$ ,  $P=0.041$ ).

We documented successful matings between founders and residents of both sexes (Table 4.3). Only a single waif (female 502) was known to have successfully reproduced, but only 6 of the 13 released waifs were sexually mature and all were released during our 2006-2007 study. Female 502 was released during May 2006 and was not gravid at the time of her release. The

following year, she successfully nested and the resulting offspring were assigned to male 118 (a founder).

## DISCUSSION

Multiple paternity occurred in at least 8 of 14 clutches (57.1%) and potentially occurred in as many as nine clutches (64.3%) from the population of translocated gopher tortoises established on St. Catherines Island, Georgia. Moon et al. (2006) observed multiple paternity in only 28.6% of clutches from a naturally-occurring population in Florida. The lower incidence of multiple paternity reported by Moon and colleagues may be an artifact of a smaller sample size (n=7 clutches) and the reduced power of their markers to detect multiple paternity (0.876 when the mother's genotype was known vs. 0.998 in our study). Both studies, however, demonstrate that multiply-sired clutches are a common occurrence in gopher tortoise populations, a finding consistent with behavioral observations that females experience as many as 26 mating attempts by 6-14 individual males in a single year (Johnson et al. 2007). Multiple paternity appears to be a common phenomenon among turtles and is facilitated by the ability of females to store sperm within and between mating seasons (Galbraith 1993, Pearse and Avise 2001).

For each clutch we classified as multiply-sired, two sires were sufficient to explain the observed offspring genotypes, although a third male potentially sired a single offspring in three of the eight clutches. Assuming that multiply-sired clutches were each sired by only two males, the contribution of the primary male (i.e., the male siring more offspring) ranged from 57.1-87.5% of genotyped offspring within the clutch. The primary male tended to be larger (~20 mm CL) than the secondary male. Overall, successful sires—whether of singly- or multiply-sired clutches—also tended to be larger than males to which no offspring were attributed. Although

these size trends did not quite reach statistically significant levels, we nonetheless consider them biologically meaningful. In addition, more than 60% of successful sires fertilized eggs produced by more than one female, demonstrating that males also mate with multiple females. Without taking order of establishment into account (i.e., whether sire was a founder or resident), greater reproductive success by larger male tortoises suggests that larger males have a competitive over smaller males. Size has been documented as an important determinant of male social rank in snapping turtles (Galbraith et al. 1987). In wood turtles rank was positively correlated with weight and age, and higher ranking males obtained more copulations with females (Kaufmann 1992) and successfully sired more offspring than lower ranking males (Galbraith 1991).

As had been observed in a naturally-occurring population of gopher tortoises (Moon et al. 2006), reproductive success was highly skewed among candidate translocated male tortoises, with the two most successful males siring 46.3% of all genotyped offspring. Interestingly, the three most successful males, in terms of number of offspring sired, were all resident tortoises that were established on the island prior to the release of any founders or waifs. In fact, resident males, even though significantly *smaller* (~30mm CL) than founder males, were three times more likely to sire offspring than expected based solely on their relative abundance in the population (resident males were assigned to 60.3% of all offspring but only represented 18.5% of the candidate males sampled). “Incumbent advantage” in terms of increased survivorship of previously established animals over newly released animals has been documented for common lizards (*Lacerta vivipera*; Massot et al. 1994) and Hermann’s tortoises (*Testudo hermanni*; Bertolero et al. 2007). Our findings suggest that order of establishment may also be an important factor influencing reproductive success of male translocated gopher tortoises, even after more than a decade following release. Despite a possible reproductive advantage of resident over

founder males, founders and residents of both sexes have been incorporated into the pool of breeders. In addition, one waif female (#502) successfully mated with a previously established founder male within the first year of her release. An apparent lack of dominance hierarchy in females may allow newly released female tortoises to be integrated into an existing breeding population more quickly than newly released males.

Our study investigated the mating system of translocated gopher tortoises more than a decade following their initial release, presumably long after most tortoises had become established in the release area. However, male-female and same-sex social interactions and how they shape mating success may differ markedly during the “settling phase” immediately following release. In contrast to tortoises from naturally-occurring populations or to previously-established translocated tortoises, recently released tortoises are unfamiliar with their surrounding environment and the location of important resources, including potential mates. In addition, burrow fidelity may be lower in female gopher tortoises from translocated populations than in females from naturally-occurring populations (Tuberville et al. 2007), perhaps further hindering the ability of recently released males to locate females. Consequently, mating opportunities may be temporarily disrupted in translocated populations. Parentage analysis of offspring from recently translocated gopher tortoises would provide valuable insight into the factors affecting mating success during the “settling phase” of reintroductions.

Paternity data reported by Moon et al. (2006) for a naturally-occurring population provide a basis of comparison for our results from the translocated population on St. Catherines, but additional parentage studies of both naturally-occurring and translocated tortoise populations are needed to fully characterize the potential effects of translocation on the genetic mating system. Additionally, multi-year studies could reveal how mating system dynamics and

individual reproductive success vary from year to year, by addressing the following questions: Do individual females consistently produce either singly- or multiply-sired clutches? Are successive clutches sired by the same male or set of males? Do males that sire a large proportion of offspring in one year do so every year or does relative reproductive success of individual males change from year to year?

Nonetheless, even with limited sampling, we observed several patterns that are important to consider when designing future translocations of gopher tortoises or other turtle species with dominance hierarchies. First, reproductive success was highly skewed among candidate males, with only a few males contributing to a large proportion of the offspring sampled. Such pronounced reproductive skew, if sustained, could significantly reduce effective population size of the translocated population (Milinkovich et al. 2004). To maximize genetic diversity in a reintroduced population, decisions regarding the number of animals targeted for release and the individuals selected for release should consider the likelihood of large variance among males in their genetic contribution to the next generation. At least some representative translocated populations should be genetically monitored for loss of heterozygosity or other signs of inbreeding.

Second, many of the offspring resulted from successful matings between founders and residents, demonstrating the integration of adult gopher tortoises from multiple source populations into the St. Catherines breeding pool. However, males with prior residence appeared to have a reproductive advantage over subsequently released males, even though both groups had been established on the island for more than a decade. This apparent trend has important implications for translocation projects designed to augment existing populations or to establish new populations through multiple releases. When only a few animals are introduced into small,



fragmented population to increase genetic diversity or simulate metapopulation structure, releasing females may be more effective than releasing males, both in terms of increasing offspring production and in quickly incorporating newly released animals into an existing breeding pool. Behavioral studies of social interactions between previously established and recently-released tortoises would help clarify the role of social structure in population dynamics in these manipulated populations.

Finally, translocated populations provide an excellent opportunity to investigate mating systems and conservation genetics of free-ranging turtle populations. Prior to release, animals can be permanently and uniquely marked for future identification, and tissue or blood samples can be collected for genetic analysis. Populations established in previously unoccupied habitat can be completely catalogued, with the identity, size, and life stage of each animal known. Post-release monitoring can provide detailed histories on health, survivorship and breeding status of individual animals—information useful for interpreting results of genetic analyses.

Translocations can also be designed to experimentally test specific hypotheses regarding mating systems, by manipulating release conditions such as number of animals released, sex ratios, or use of captive-reared vs. wild-born stock. As translocations and other population manipulations play an increasingly important role in turtle conservation, such studies will help guide development of effective strategies for the establishment and management of translocated populations.

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Table 4.1. Characterization of 5 polymorphic microsatellite loci for *Gopherus polyphemus*. The portion of the primer sequence corresponding to the engineered CAG tag is indicated in italics. TD is the initial annealing temperature for amplifications. Size indicates the range of allele sizes in bp observed among adult breeders in the St. Catherines Island population. Polymorphic information content (PIC) and the frequency of null alleles were estimated using CERVUS 3.0. Deviations from Hardy-Weinburg equilibrium (HWE) were calculated in GenAlEx 6.0.

Primer	Sequence 5'-3'	Dye	TD	Repeat motif	Size (bp)	PIC	HWE	F(null)
Gopo-01 F	<i>CAGTCGGGCGTCATC</i> AGGTCTC TTTCAACCCTAATCTT	FAM	65	(AAAG) <sub>21</sub>	250-326	0.893	p<.0001	-0.0002
Gopo-01 R	GCAGCCAATTCTTATTA ACTAA							
Gopo-02 F	<i>CAGTCGGGCGTCATC</i> AGGCAGC AGAGAATAGAT	VIC	60	(AGAT) <sub>23</sub>	244-340	0.909	0.004	0.0156
Gopo-02 R	TATCAGCTATCCC GTGTA							
Gopo-05 F	<i>CAGTCGGGCGTCATC</i> ATCTGTA ATGCCTAGAATCAA	FAM	60	(AAAG) <sub>10</sub> (ACTC) <sub>6</sub>	331-383	0.834	0.006	0.0296
Gopo-05 R	TGCCATTTCTGTTAA AGTTC							
Gopo-12 F	<i>CAGTCGGGCGTCATC</i> ACTTTGG AAGCCATTGTAATA	NED	65	(AAAC) <sub>13</sub>	348-368	0.714	0.040	0.0501
Gopo-12 R	CATTTGCACCAGTTTAA ACTA							
Gopo-14 F	GTCCTGGGATTACAAT CAAT	NED	60	(ATCC) <sub>13</sub>	161-211	0.715	p<.0001	0.0662
Gopo-14 R	<i>CAGTCGGGCGTCATC</i> ACCAATC TTTTTCGTAATGTAT							

Table 4.2. Basic properties of five microsatellite loci for *G. polyphemus*, as observed in the St. Catherines Island mixed population. The number of alleles ( $k$ ), observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosities, probability of identity and probabilities of exclusion were calculated in CERVUS 3.0 for each individual locus and for all loci combined.

Locus	k	$H_O$	$H_E$	Probability of identity	<u>Exclusion probabilities</u>		
					First parent (when neither parent known)	Second parent (when first parent known)	Parent pair
Gopo-01	16	0.900	0.909	0.018216663	0.6680	0.8015	0.9374
Gopo-02	18	0.883	0.922	0.005164358	0.7067	0.8281	0.9520
Gopo-05	14	0.800	0.857	0.035555298	0.5430	0.7054	0.8750
Gopo-12	6	0.678	0.755	0.100322442	0.3533	0.5342	0.7240
Gopo-14	11	0.650	0.741	0.091321642	0.3680	0.5567	0.7693
Multi-locus				$3.06 \times 10^{-8}$	0.98181152	0.99792498	0.99997607



Table 4.3. Characteristics of clutch, mother, and father for single and multiple-sired clutches. Number of offspring genotyped includes both live hatchlings and embryos salvaged from unhatched eggs. Clutches with fewer than four genotyped offspring were excluded from calculations of number of sires and reproductive skew among males within multiply-sired clutches.

Clutch ID	No. eggs	No. hatchlings	Hatching success (%)	No. offspring genotyped (%)	Mother ID	Mother's origin	Mother CL (mm)	Min. # sires	Father ID	No. assigned offspring (%)	Father's origin	Father CL (mm)
<b>Single sire</b>												
2006-01	8	8	100.0	8 (100.0)	423 <sup>a</sup>	resident	282	1	213	8 (100.0)	resident	314
2006-08	11	9	81.8	10 (90.9)	152 <sup>c</sup>	founder	334	1	221	10 (100.0)	resident	304
2007-03	12	12	100.0	12 (100.0)	152 <sup>c</sup>	founder	334	1	221	12 (100.0)	resident	304
2007-10	8	6	75.0	6 (75.0)	214 <sup>b</sup>	resident	300	1	213	6 (100.0)	resident	314
2007-14	9	9	100.0	9 (100.0)	410 <sup>b</sup>	resident	284	1	305	9 (100.0)	resident	322
2007-16	7	6	85.7	6 (85.7)	129 <sup>a</sup>	founder	328	1*	127	6 (100.0)	founder	311
<b>Multiple sires</b>												
2006-02	9	8	88.9	9 (100.0)	154 <sup>c</sup>	founder	344	2*	118 221	6 (66.6) 3 (33.3)	founder resident	324 304
2006-04	8	6	75.0	7 (87.5)	119 <sup>c</sup>	founder	329	2	221 unsampled	6 (85.7) 1 (14.3)	resident	304
2007-04	6	3	50.0	4 (66.7)	159 <sup>a</sup>	founder	329	2	156 unsampled	3 (75.0) 1 (25.0)	founder	328
2007-06	7	7	100.0	7 (100.0)	174 <sup>b</sup>	founder	298	2*	143 157	4 (57.1) 3 (42.9)	founder founder	332 350
2007-08	10	10	100.0	10 (100.0)	145 <sup>b</sup>	founder	334	2	151 221	6 (60.0) 4 (40.0)	founder resident	344 304
2007-09	6	6	100.0	6 (100.0)	142 <sup>b</sup>	founder	323	2*	156 103	5 (83.3) 1 (16.7)	founder founder	328 293
2007-12	8	7	87.5	8 (100.0)	unsampled			2	305 unsampled	7 (87.5) 1 (12.5)	resident	322
2007-15	6	6	100.0	6 (100.0)	414 <sup>a</sup>	resident	294	2	305 203	5 (83.3) 1 (16.7)	resident resident	322 294

<b>Excluded</b>												
2006-03	8	2	25.0	3 (37.5)	116 <sup>c</sup>	founder	332	2	203	2	resident	294
									unsampled	1		
2007-13	8	3	37.5	3 (37.5)	212 <sup>b</sup>	resident	NR	1	unsampled	3		
2007-11	? <sup>1</sup>	3		3	215 <sup>a</sup>	resident	329	1	157	3	founder	350
2007-17	7	2	28.6	2 (28.6)	168 <sup>a</sup>	founder	312	1	unsampled	2		
2007-02	9	2	22.2	2 (22.2)	502 <sup>c</sup>	waif <sup>2</sup>	320	1	118	2	founder	324

<sup>a</sup>Maternity was known because eggs were collected directly from female

<sup>b</sup>Maternity was assigned by CERVUS

<sup>c</sup>Maternity was assigned by CERVUS and corroborated by field observations

\*CERVUS assigned an additional sire to a single offspring but the additional sire was not necessary to explain observed offspring genotypes

<sup>1</sup>Complete clutch size not known because female laid some eggs in trap and eggs were too damaged to count

<sup>2</sup>First released on island in May 2006

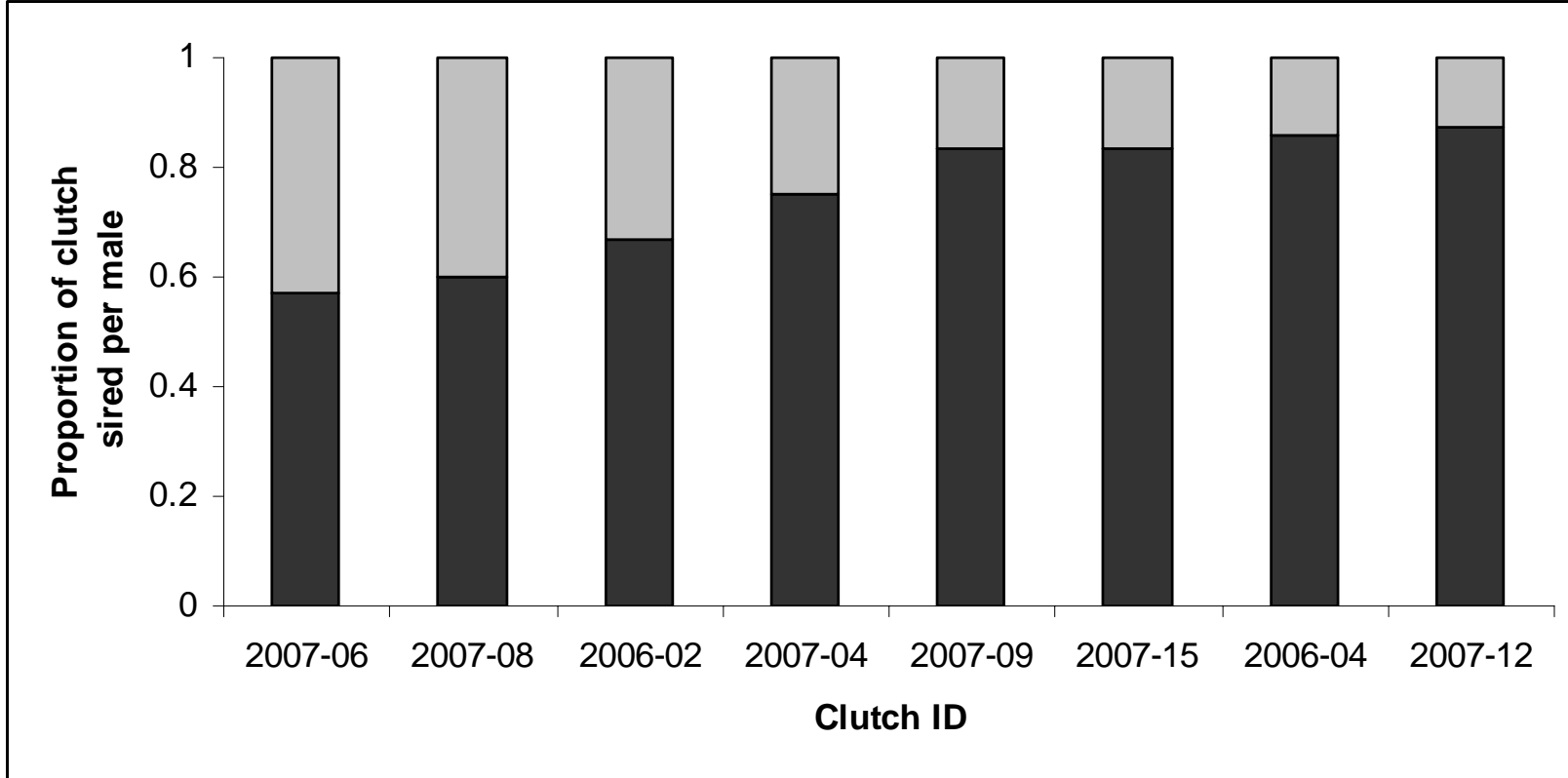


Figure 4.1. Reproductive skew among males of multiply-sired clutches collected from a translocated gopher tortoise population at St. Catherines Island, GA during 2006-2007.



Figure 4.2. Distribution of reproductive success (i.e., number of offspring sired) among candidate male gopher tortoises based on 121 offspring from 19 clutches collected from St. Catherines Island, GA during 2006-2007, including offspring attributed to one or more unsampled males.

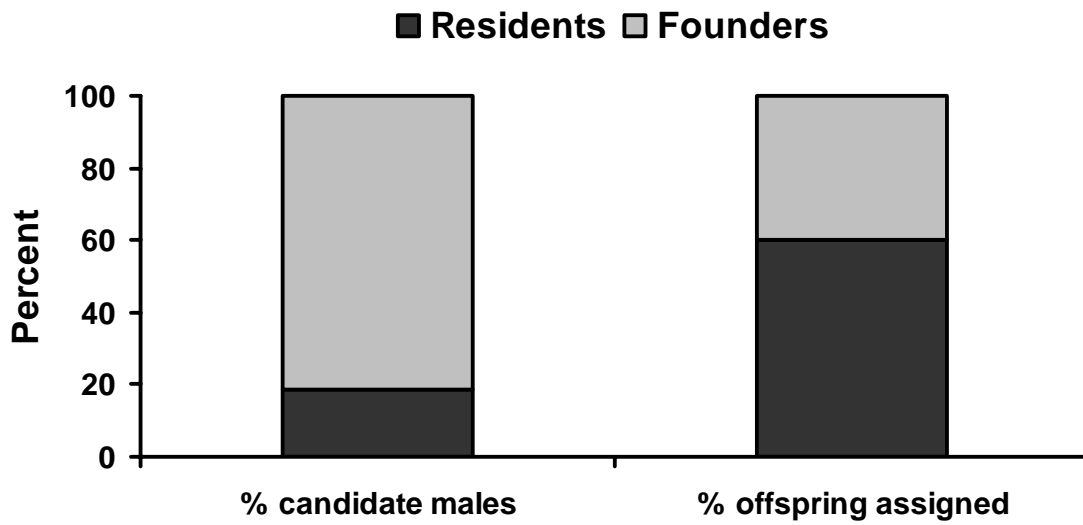


Figure 4.3. A comparison of the relative abundance of previously established male gopher tortoises to founder males subsequently released on St. Catherines Island and the proportion of 2006-2007 offspring they sired. Candidate males sampled during our study (n=27) represented approximately 84% of estimated males comprising the resident breeding pool. Offspring (n=121) were assigned to candidate males using CERVUS.

## CHAPTER 5

# MODELING EXTINCTION RISK OF NATIVE AND TRANSLOCATED GOPHER TORTOISE POPULATIONS: DEVELOPING A DECISION TREE FOR MANAGING “AT-RISK” POPULATIONS<sup>1</sup>

<sup>1</sup>Tuberville, T.D., J.W. Gibbons, and H.E. Balbach. To be submitted to *Ecological Applications*.

## ABSTRACT

The gopher tortoise (*Gopherus polyphemus*) is still widespread across the southeastern U.S. where soil conditions and forest cover are favorable. It was listed as “threatened” in its far western range in 1987, and a listing petition for the eastern populations was filed in 2006. It is thus clear that the species is believed to be in serious decline. How, though, are biologists and land managers to make the many decisions about how best to manage any particular population? There are a variety of in-site and ex-site management options (e.g., on-site relocation, off-site translocation, augmentation, etc.) that might be considered when determining how best to conserve individual populations. However, there are no good decision tools for evaluating or predicting whether the existing population is viable in the long term. WE have developed demographic models for both native and translocated gopher tortoise populations and propose to use those models to predict outcomes (i.e., population persistence times and extinction probabilities) for a variety of population conditions and management scenarios. The major limiting factor in the development of models was the availability of complete life-history data. Feedback from fellow tortoise biologists has helped to guide development of population models believed to be realistic for this species in the absence of sufficient long-term demographic data.

## INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is considered to be declining throughout its range (Smith et al. 2006) and is federally listed in the western portion. The U.S. Fish and Wildlife Service has also been petitioned to list the Florida populations. In addition, a primary goal identified at recent regional workshops (e.g., Fall-Line Sandhills Workshop, SREL, March 2005; Interagency Gopher Tortoise Habitat (Eastern population) Workshop, Fort Gordon, June

2005) is to avoid further federal listing of the gopher tortoise in the eastern portion of its range through more effective management of tortoises and their habitats.

The Florida Fish and Game Commission estimates that—in that state alone— 74,000 gopher tortoises have been impacted by incidental take permits issued to developers in the past 14 years (J. Berish, pers. comm.). Although the estimate does not necessarily represent number of tortoises actually killed (because some were relocated), the extent of the loss is alarming and is not sustainable in a long-lived species such as the gopher tortoise in which population stability is contingent on high adult survivorship (Congdon et al. 1993). Ironically, many sites that *are* permanently protected and have appropriate or restorable habitat, no longer support “viable” tortoise populations.

In-situ habitat management and protection are the preferred conservation tools for promoting viable tortoise populations. However, habitat-based approaches may not always be the most effective strategy or even be possible in some circumstances (e.g., severely-degraded habitats, small habitat patches, or sites with remnant tortoise populations, etc). There are a variety of other in-situ and ex-situ management options (e.g., on-site translocation, off-site translocation, augmentation, etc.) that should be considered when determining how to most effectively conserve individual populations.

Translocations have become an accepted management tool for game species and have been successfully implemented in the recovery of deer, turkey, bison, and otter in the U.S. (Barick 1951, Larter et al. 2000, Serfass et al. 1993). In contrast, translocations of rare, non-game species have generally been viewed with skepticism, especially for reptiles and amphibians (Dodd and Seigel 1991, Seigel and Dodd 2000). Two of the major concerns that have been raised regarding translocations of gopher tortoises are that translocations: 1) are not a proven



conservation tool for the species, and 2) will undermine land conservation efforts by offering developers an “easy way out.”

Despite the frequent use of displacement of tortoises as a mitigation tool for development (“relocation” in this context), there has been little subsequent monitoring. However, initial results of efforts to re-establish gopher tortoises on the Savannah River Site (Aiken Co., South Carolina) suggest that certain release techniques can encourage translocated tortoises to settle in the release area, a critical first step in establishing a viable population (Tuberville et al. 2005). Additional research and monitoring on the SRS population (T. Tuberville & collaborators, unpublished data), a translocated population on St. Catherine’s Island, GA (Tuberville et al., Chapter 2; Norton, Spratt, unpublished data), and from other translocation projects (Ashton and Burke 2007, Heise and Epperson 2005) provide valuable data for evaluating the effectiveness of translocation as a conservation measure. Data from the literature and unpublished data from the SRS population indicate that translocated populations *may*, at least temporarily, exhibit reduced reproduction (e.g., Small and MacDonald 2001) and unusually high rates of dispersal (Doonan 1986, Ashton and Burke 2007). Therefore, in order to critically evaluate this management technique, it will be necessary to compare demographic patterns and population processes in both native and translocated populations.

Currently, there are no good decision tools for evaluating or predicting when translocation would be an effective management option for a specific population or management scenario. The appropriate and judicious use of translocation as a conservation tool should *support* land management efforts rather than compete with them, by determining the most efficient and effective use of limited conservation resources—including appropriate habitat and remaining tortoise populations.

## Project objectives

1. Develop separate demographic models for native and translocated gopher tortoise populations derived from the literature, unpublished data of the principal investigators and collaborators, data generously provided by colleagues, and expert opinion.
2. Use the models to predict outcomes (i.e., population persistence times and extinction probabilities) for different initial population conditions and management scenarios.
3. Develop a decision tool for evaluating the best options for managing declining or other “at-risk” populations.

The following project background provides a more comprehensive discussion of how population models have been used to address conservation issues facing turtles. We also summarize the findings of other models developed for tortoise species and how our model differs from previous applications. Next, we detail how we constructed the models for both naturally-occurring and translocated populations using the software program VORTEX. The results are presented as a series of three parts: Part 1 - baseline model for naturally-occurring populations, Part 2 - demographic sensitivity testing, and Part 3 – translocation models comparing alternative release protocols. Finally, we provide an overall summary of our findings and our recommendations for their application to the conservation and management of individual populations of gopher tortoises.

## Utility of population modeling for managing turtle populations

Population models can be a powerful tool for management of turtle populations and have been used to: 1) rank relative threats to specific populations, 2) evaluate effects of proposed

management actions or regulations, 3) determine which demographic or ecological variables have greatest influence on extinction risk, and 4) identify information gaps and research priorities. The major limiting factor in the development of realistic population models is the availability of complete life-history data. Congdon and colleagues developed some of the first and most complete life tables for individual turtle species, based on over 30 years of intensive data collection on *Emydoidea blandingii* and *Chelydra serpentina* (Congdon et al. 1993, 1994). However, given that such comprehensive data is generally not available for most species, most existing models have used data from multiple populations over a shorter time span per population, compiled information from the literature, or have accepted (or even incorporated) uncertainty in their model.

For those species lacking complete life history data, population models can still be useful for managing populations. For example, Rivera and Fernandez (2004) and Horne et al. (2003) conducted threat analysis for specific populations of *Emys orbicularis* and *Graptemys flavimaculata*, respectively, in order to develop management plans for those populations. Pedrona et al. (2004) evaluated the likely effectiveness of exchanging individuals between captive and wild populations of *Geochelone yniphora* to simulate a metapopulation. Heppell et al. (2005) used population models to evaluate the potential effects of turtle excluder devices on reducing by-catch of sea turtles; Heppell et al. (1996) used models to explore the potential utility of head-starting as a management tool. Heppell (1998) used life table data from populations of several different species and conducted an elasticity analysis to look for similarities across species in those demographic variables most likely to determine whether populations continue to decline.

### Previous population models for *Gopherus*

Several population models have specifically modeled population dynamics of the gopher tortoise or its western counterpart, the desert tortoise. Although their life histories are not identical, the two species have many ecological similarities, face many of the same management issues, and are often subjected to translocation efforts. We discuss each population model, highlighting the major findings that are relevant to our modeling effort.

#### *Gopherus agassizii* - PVA for western Mojave Desert (Doak et al. 1994)

Doak et al. (1994) developed a population model to determine the potential impact of the proposed expansion of Ft. Irwin on *Gopherus agassizii* populations. The model is stage-based (meaning that demographic characteristics are a function of developmental stage rather than age). It is a regional model for the western Mojave Desert (rather than for a single population) and is based on periodic census data collected from eight Bureau of Land Management sites, with 2 – 4 census periods per site during the period of 1979-1989. The model is based on data from females only and demographic rates are assumed to be constant over the time interval between censuses. The model was designed to specifically investigate temporal variability in demographic rates and the correlation among demographic rate responses to environmental variables.

Doak et al. (1994) concluded that the models were most sensitive to changes in survival rates, particularly of subadult females just entering reproduction, and that better survival estimates were needed. They also determined that both the temporal variability in demographic rates and the correlated responses among demographic rates resulted in greater variability of

population growth rates, dramatically increasing uncertainty about how accurately the predicted short-term population trends reflect long-term fate of desert tortoise populations.

*Gopherus polyphemus* – Survival characteristics of small populations (Cox 1989)

Cox (1989) conducted a population viability analysis in order to determine the importance of small populations of gopher tortoises and their relative vulnerability to extinction under harsh, moderate and favorable conditions. Both deterministic and stochastic models (that is, without and with demographic and environmental variation incorporated) were constructed for initial population sizes of 6, 10, 14, 20, 30 and 40 individuals. Both adult-only and mixed (50% adults, 50% subadult) populations were simulated. For each scenario, 40 simulations were conducted and simulation duration was 200 yrs. The potential effects of competition, density-dependence and immigration were not modeled, but effects of inbreeding depression were incorporated into the model. The selected demographic parameters were based on data from Florida and south Georgia.

Based on the persistence of populations of 20 or more individuals for more than 100 years, Cox concluded that 20 individuals was a pivotal number under the conditions modeled and that even small populations can contribute to the species' long-term persistence. The model was most sensitive to changes in adult and subadult survivorship, then secondarily by additionally increasing either survivorship of other classes or fecundity. As might be predicted, model outcomes were particularly sensitive to stochasticity when population sizes were small.

Although the model is based on data from naturally-occurring populations, Cox notes the potential application of the model results to relocation and emphasizes that the model would need to be modified to reflect changes in tortoise behavior (e.g., dispersal) and demography

resulting from relocation. For example, mixed-stage populations performed slightly better than adult-only populations, suggesting the value in relocating individuals from all stages in the population. Also, populations of relocated tortoises may exhibit higher mortality and/or dispersal rates than those reported for naturally occurring populations, and would likely dramatically affect model outcome.

*Gopherus polyphemus* – Estimating population viability (Cox et al. 1987)

The Cox et al. (1987) model is similar to the model presented in Cox 1989 but models populations over a wider set of initial population sizes (10–150 tortoises) and with greater demographic structure (10% juveniles, 30% subadults, and 60% adults). Minimum viable population sizes (defined by Cox as minimum initial population size with at least 90% probability of surviving for at least 200 years) were calculated under harsh (little or no management), moderate, and favorable conditions in order to simulate the effects of management. The different management conditions were modeled by varying survival of all age classes and fecundity among the scenarios.

Even large populations had difficulty persisting under harsh conditions and an estimated minimum of 310 tortoises was needed for the population to have at least 50% chance of surviving for 200 years. Under moderate conditions, even relatively large populations persisted for longer periods than under harsh conditions but still did not meet desired management goals. At least 130-150 tortoises were needed to persist under moderate conditions. Under favorable conditions, even small populations of at least 40-50 animals performed well.

*Gopherus polyphemus* – PVA of relocated populations (Seigel and Dodd 2000)

The purpose of the Seigel and Dodd (2000) model was to examine how retention rates of translocated adult gopher tortoises could influence short-term population viability. Because gopher tortoises are long-lived animals, the authors note that the species is vulnerable to changes in survivorship (or site fidelity) of adults and older juveniles, which might be expected to occur following translocation.

Seigel and Dodd modeled populations initially composed of 50 adult animals for a 30 year period, with age at maturity, first year survivorship, and all reproductive parameters based primarily on data collected from Mississippi and Louisiana at the western limit of the species' range. Adult survivorship was varied among scenarios to reflect post-translocation annual retention rates of 80, 85, 90, and 95%, which were held constant for the duration of the simulation. For each scenario, they ran 10 simulations and calculated the average number of turtles remaining after 30 years and the probability that the modeled population would go extinct during the simulation period.

The resulting model predicted rapid population decline except when retention rates of adult relocated tortoises were very high (at least 90%). The authors note that their model is based on the assumption that retention rates remain low over the simulation period rather than increasing over time to levels more representative of naturally-occurring populations. They assert that the short-term nature of post-relocation monitoring, when conducted at all, precludes altering that assumption. However, as noted by Ashton and Burke (2007), data from more extensive post-translocation monitoring are now available.

*Gopherus polyphemus* – PVA for Florida (Miller et al. 2001)

Miller et al. (2001) investigate the probability that gopher tortoises are likely to become extirpated from the state of Florida over the next 100 years, whether considering all known populations within the state or considering only populations on public lands. The model also incorporates regional variation of life-history parameters within Florida and the potential impacts of Upper Respiratory Tract Disease (URTD) on population fate. Parameters used in the model are based on data collected in Florida and southern Georgia, and the initial population sizes in the model were chosen to encompass population estimates from 294 sites in Florida. Construction of the model within VORTEX was guided by expert opinion of workshop participants.

As has been observed with other models for gopher tortoises and other turtle species, model outcomes were most sensitive to survivorship of adult females and juveniles. Effects of regional variation in age at maturity indicate that more northerly populations are less buffered against uncertainty in model parameters and are less able to withstand additional sources of mortality (e.g., Upper Respiratory Tract Disease). So, while the statewide “population” was deemed not at risk of extinction, Miller et al. (2001) note individual populations may be at risk under certain conditions, especially where anthropogenic factors are combined with the unpredictability associated with normal demographic or stochastic variability. However, under favorable conditions, the models indicate that even populations as small as 50 individuals can contribute to the conservation of the species.



### How is the current model different?

Cox (1989) was the first to link the application of Population Viability Analysis (PVA) to relocation / translocation. Although his model did not specifically incorporate relocation / translocation into the model, he acknowledged that the behavior and demography of displaced tortoises might be sufficiently different to warrant changing the basic model parameters. The only model to specifically incorporate translocation (Seigel and Dodd 2000), relied on data from short-term monitoring projects. More extensive monitoring data from translocated populations are now available (Ashton and Burke 2007; Tuberville et al., Chapter 2; and unpublished data by colleagues) and have been incorporated into the current model.

The premise of the current model is that translocated populations may exhibit, at least temporarily, different vital rates (e.g., survivorship, emigration, reproduction) than naturally occurring populations. Under certain combinations of initial population conditions and management scenarios, these altered vital rates could negatively influence population growth rates, persistence times, or extinction probabilities of translocated populations.

However, gopher tortoises will likely continue to be displaced by habitat loss, and permitting agencies are becoming increasingly reluctant to issue incidental take permits. Meanwhile, populations on some protected lands have experienced declines and are unlikely to recover without manipulative management. Therefore, there is a need to be able to evaluate the viability of individual populations, rank the populations most appropriate for in-situ protection, and determine if non-viable populations are likely to contribute to conservation of the species through translocations.

The target audience and end user for the current model is the individual land manager who is charged with evaluating and managing for viability of discrete tortoise populations.

Therefore, the focus is on individual populations, rather than a regional or state-wide collection of populations. We have attempted to broadly categorize populations in terms of intrinsic and extrinsic characteristics that land managers should be able to apply to their population of interest based on data or information that either is likely already available for the population, could be relatively easily collected, or would be part of a tortoise monitoring program. For sites without pre-existing information, the models should help prioritize which data need be collected in order to effectively manage the population of interest.

In addition, the current model draws on data from throughout the range of the gopher tortoise rather than just the core of the species' range, which has been the focus of most previous models. Finally, we place greater emphasis on population growth rates (*lambda*) predicted under different model scenarios. We report final mean population sizes, population persistence times, and probabilities of extinctions, which are all important model output and also make it possible to compare our results to previous models. However, we think focusing on extinction without considering *lambda* values can mask negative population trends that signal a need for management intervention. *Lambda* is also a tangible variable that can be: 1) calculated over specific monitoring intervals from field-collected data, 2) used to measure effectiveness of management activities, and 3) compared to *lambda* estimated by the model in order to evaluate model validity.

### Limitations of the model

Like all other population-based models for the species, our model is based on incomplete knowledge of certain aspects of gopher tortoise life history and must be qualified accordingly. Comprehensive empirical data are completely lacking for some parameters, such as longevity.

In addition, for those parameters for which data are available, estimated values are an amalgamation of values reported from multiple sites across a wide geographic area and that may vary in habitat quality. Because life history trait values are likely to vary among populations and different trait values were available from different study populations, the combination of parameters we use are not necessarily representative of any single population. In addition, many of the published data are based on relatively short-term studies, providing only a snapshot view of tortoise population dynamics. We urge readers to recognize the limitations of currently available data and use care in applying the results of our model, which will necessarily require updating and re-interpretation as more complete data become available.

However, we believe our model adequately represents the current understanding of gopher tortoise life history based on the best available, if not precise, estimates for parameter values. Where appropriate, we drew on the broader literature on turtle life histories to assist in predicting how life history trait values might vary under different model scenarios.

## METHODS: PARAMETER SELECTION AND MODEL DEVELOPMENT

### Baseline model parameters for naturally-occurring populations

The models described here were constructed using VORTEX (version 9.50, Lacy et al. 2005), an individual-based model in which the fate of individual animals is monitored as they experience demographic and stochastic events that follow user-specified probabilities and distributions. VORTEX is an age-based model in which survivorship and fecundity values vary with (and are specified according to) age rather than size or life stages. VORTEX is able to model species with polygynous breeding systems and can easily simulate specific management

scenarios such as catastrophic stochastic events, managed harvests, and translocation (Miller and Lacy 2005). VORTEX was also used in the gopher tortoise models constructed by Miller et al. (2001) and Seigel and Dodd (2000), facilitating comparison of results among the various models.

Listed below are the parameters and their values as we specified them in VORTEX for the current model. For each scenario, 100 simulations were run for 200 years, the maximum duration possible in VORTEX.

### Reproductive System

#### *Breeding system* – Polygynous

Attempted matings with multiple mates within a breeding season has been noted for both male and female gopher tortoises (Boglioli et al. 2003, Johnson et al. 2007). Multiple paternity of single clutches has also been documented (Moon et al. 2006; Tuberville et al., Chapter 3).

#### *Age at first reproduction*

Site-specific factors (such as location within geographic range and habitat quality) presumably have systematic effects on tortoise growth and, as a result, age at maturity (Landers et al. 1982, Mushinsky et al. 1994). Although length of the activity season (and opportunity for growth) varies with latitude, there is also evidence that growth rates among tortoises can vary significantly among local populations as a result of habitat quality (Aresco and Guyer 1999a, Mushinsky et al. 1994). Habitat quality can be manipulated through management; however, it is predicted that viability of populations in the more northerly portions of the species' range will be less resilient to marginal habitat conditions.

Ages at first reproduction specified for the different combinations of geographic location (see Figure 5.1) and habitat quality (Table 5.1). They are intended to reflect the *average* age at first reproduction, not the minimum age at which first reproduction has been reported. Under each scenario, we assumed males matured at a younger age than females.

*Maximum age at reproduction – 60 years*

There is no evidence to suggest that tortoises do not reproduce throughout their adult life. However, there are also no data available for life span of gopher tortoises. Maximum age at reproduction was set at 60 years, as in Miller et al. 2001. How well this estimate reflects either historical or current conditions is unknown.

*Max number of progeny per year – 12*

Although set at 10 in Miller et al. 2001, maximum number of progeny was set at 12 in our model. Clutch sizes of 11 or 12, while not common, do not appear to be an anomaly (Tuberville et al., Chapter 3; Epperson and Heise 2003, Landers et al. 1980, Pike and Seigel 2006, Rostal and Jones 2002). Due to nest failures (e.g., from predation) and less than 100% hatching success (e.g., from infertile eggs, early embryonic death), not all eggs will result in progeny. However, because nest and hatching success tend to vary stochastically as a result of extrinsic factors, it is more appropriate to incorporate them into the model elsewhere rather than here under maximum number of progeny (which we consider a constant intrinsic variable).

*Sex ratio at birth (in % males) – 50%*

Although this ratio can vary from clutch to clutch as a function of nest temperature, it is assumed to be 50:50 for the population as a whole. In general, warmer nest temperatures produce females and cooler temperatures produce males, with temperatures at either extreme limiting hatching success (Burke et al. 1996, Demuth 2001). Theoretically, global warming could produce more female-biased clutches; however, the potential effects of global warming on sex ratios of gopher tortoise cohorts has not been incorporated into our model.

*Density-dependent reproduction*

This option was not activated for the model. However, density-dependent factors such as allee effects, which may occur in gopher tortoise populations (Boglioli et al. 2003, Guyer et al. 2006), could be incorporated in future models.

## Reproductive Rates

*Proportion of females breeding*

The annual proportion of females breeding in a population may be greater (Rostal and Jones 2002) and presumably less variable in optimal, well-managed habitat than in marginal or unmanaged habitat. The parameter values specified in our model (Table 5.2) are significantly less optimistic than the values presented in Miller et al. 2001, but are based on data by Rostal and Jones (2002) and Smith et al. (1997).

### *Distribution of number of offspring per female per year – Normal distribution*

The user can elect to specify the exact distribution of clutch sizes or to have the computer generate an approximation of the normal distribution based on a user-specified mean and standard deviation. Land managers are unlikely to have sufficient data to specify an exact distribution for clutch sizes from their population but are likely to know the average clutch size of their population or a similar one. Therefore, we opted to have the computer generate a normal distribution based on specified means and standard deviations in clutch sizes, which we varied among location within the geographic range (Table 5.3). Model constraints assume that clutch sizes do not vary with age of female. Although this assumption may be violated, there are no data to estimate age-specific fecundity.

### Mortality rates

VORTEX models survivorship as age-specific mortality rates that remain constant once individuals reach maturity. Mortality rates reported for gopher tortoises in the literature are generally reported in relation to life stage rather than age of individuals. In our model, we specified different mortality rates for hatchlings, yearlings, juveniles, subadults and adults. Because age at onset of maturity varies in our model between males and females and as a function of geographic range & habitat quality, the ages corresponding to those life stages varies among model scenarios. The annual mortality rates were specified according to Table 5.4. Age-specific mortality schedules for males and females under different site-specific conditions can be determined by referring to the table of age at first reproduction (see Table 5.1).

Annual mortality rates and their variability are poorly known for gopher tortoises due to the scarcity of long-term mark-recapture studies in the literature. In addition, tortoises are

difficult to accurately age once they reach reproductive maturity and most studies have focused on adults, further limiting the information on age-specific survivorship of gopher tortoises.

Hatchling survivorship rates were based on radio-telemetry studies of hatchlings (Butler and Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006). Juvenile survivorship rates were based on a radio-telemetry study by Wilson (1991). Adult survivorship data are not available for naturally occurring populations but are presumably at least as high as long-term survival rates reported for translocated populations by Ashton & Burke (2007; 98.5%) and Tuberville et al. (Chapter 2; 92%). In the absence of other data, we used long-term adult survivorship data from translocated populations.

#### Mate monopolization

*% of males in breeding pool – 100%*

Although some males may be excluded from the breeding pool as a result of female choice or male-male competition, there are no data to quantify this parameter. We therefore assumed that all males were potential breeders. However, should behavioral or genetic data be available for specific populations, mate monopolization could be incorporated into the model. Data suggesting that mating opportunities are limiting for males under low density conditions could be incorporated into the model as a density-dependent effect (see p. 14).

#### Initial population size

Each combination of parameters was performed on simulated populations with initial sizes of 20, 40, 100, 250, 500, 1000, and 2500 tortoises in order to capture the range of



population sizes likely to occur on discrete management units. Selected population sizes are also based on categories used in Cox 1989, Miller et al. 2001, and Smith et al. 2006.

VORTEX allows the user to specify an exact distribution or to have the software generate a stable age distribution. For the basic model for naturally occurring populations, we used a software-generated stable age distribution for the initial population (see Appendix 5.1).

### Carrying capacity

In our opinion, growth of “at-risk” tortoise populations is less likely to be limited by site carrying capacity than by other factors, such as habitat destruction, road mortality, and previous collection or predation by humans. We have attempted to incorporate the potential effects of habitat quality on population dynamics elsewhere in the model (e.g., reproduction, age at first reproduction) rather than in the carrying capacity module. We follow Miller et al. (2001) in setting carrying capacity (K) at 10 times the initial population size to reflect our assertion that most “at-risk” populations are not currently at carrying capacity. However, there is an option to predict future changes in K as a result of habitat management, which might be useful for modeling some scenarios in the future. In addition, we note that carrying capacity of recipient sites should be determined prior to conducting any translocations to determine target population size and number of animals to be released.

### Baseline model for translocated populations

All parameters and combinations of parameters for translocated populations were the same as those used in the basic model for a naturally-occurring population with an initial

population size of 100 individuals and occurring in optimal habitat in the central portion of the geographic range, except as noted below. Simulations were run for 100 years.

#### Translocations modeled as supplementations

The supplementation model in VORTEX allows the user to specify what year in the simulation the first and last supplementations occur, the interval between supplementations, and the number, sex ratio, and age distribution of animals comprising each release. One potential problem with using the supplementation module is that VORTEX assumes that the supplemented animals behave according to the parameters specified in the basic model – i.e., that translocated animals behave similarly to resident animals. Studies of translocated populations have reported negative effects on reproduction and site fidelity immediately following translocation (MacDonald 1996, Small and MacDonald 2001, Tuberville et al. 2005). However, these effects are apparently short-lived (Ashton and Burke 2007, MacDonald 1996, Small and MacDonald 2001; Tuberville et al., Chapter 2), generally abating by the end of the first year.

We were able to incorporate dispersal response into the model by assuming that dispersal occurred *prior to* release. That is, we only included in the supplementation model the number of animals predicted to remain in the population at the end of the first year following release. We also varied the strength of the response as a function of age of translocated animals to reflect the differential response of translocated juveniles and adults. Reduced reproductive rates were more difficult to incorporate and, thus, have not been specifically modeled here. However, we do not think that ignoring this short-lived factor will substantially alter model outcome.

We developed a series of translocation scenarios to evaluate several alternative release protocols. Each scenario assumes that a total of 100 animals were released into optimal habitat

in the central geographic range. The release group was assumed to have a 1:1 sex ratio. Except in the models examining effects of penning treatment, all scenarios also assumed that tortoises were subjected to long-term penning prior to release.

#### Effects of penning treatment

We examined the effects of penning treatment on long-term population viability by simulating populations subjected to long-term (1 year) penning, short-term (<3 months) penning, or no penning prior to release. All scenarios simulated a single release of 100 adult tortoises, with adult dispersal rates varying among penning scenarios as follows: long-term penning (10%), short-term penning (35%), and no penning (70%).

#### Effects of resident population size

We simulated the single release of 100 adults at unoccupied sites (0 residents) and at sites occupied by small populations of 10, 20, and 50 residents. The resident population, if present, was assumed to have a stable age distribution.

#### Effects of release interval

We simulated the release of 100 adults as either a single release, or as series of 5 releases of 20 individuals per release, with releases occurring every year for five years, every other year for 10 years, or every 5 years over a 25 year period.

## Effects of initial founder demography

The effects of initial demography was explored by specifying the exact age distribution of the translocated population. We simulated the release of “mixed” (10% juv, 30% subadults, and 60% adults), “adult only”, “subadult only”, and “yearling only” populations. For simplicity, animals within a life stage were assumed to be a single-age cohort rather than constructing a more complex age distribution. Head-started yearlings were entered as 2 year olds because presumably they would be of larger sizes than wild-reared yearlings.

The mortality / dispersal rates (Table 5.5) are intended to represent the loss of individuals through death or dispersal as a direct result of translocation. These rates were applied to the number of release animals in each life stage such that “culled” animals were removed from the release population prior to being entered into the supplementation module. Based on the literature, loss of adults and subadults is primarily through dispersal from the release site (Ashton and Burke 2007, Tuberville et al. 2005), whereas juveniles appear to be susceptible to mortality prior to and during the first year following release (Doonan 1986; Tuberville and Buhlmann, unpublished data) but are less likely than adults to disperse from the release site.

## BASELINE MODEL RESULTS FOR NATURALLY-OCCURRING POPULATIONS: EFFECTS OF GEOGRAPHIC LOCATION, HABITAT QUALITY, AND INITIAL POPULATION SIZE

Too few data are available to separate out the individual effects of geographic location and habitat quality on population rates; therefore, the model was constructed to enable us to simulate several conditions as affecting population parameters simultaneously. We discuss

model results under the different combinations (i.e., scenarios) of geographic location, habitat quality, and initial population size.

#### Deterministic population growth rate

All model scenarios resulted in a population decline of 1-3% per year and varied as a function of both habitat quality and location within the range (Fig. 5.2). Populations in optimal habitat at the southern extent were the most stable whereas populations at the periphery exhibited the greatest potential declines, particularly under marginal habitat conditions. From a management perspective, improving habitat conditions should affect population growth rates positively, and hence, the long-term viability of individual populations.

#### Probability of extinction

Simulations were run for 200 years, the maximum duration possible within the VORTEX program, in order to capture as many generation times for gopher tortoises as possible (Fig. 5.3). However, because it is difficult to predict the magnitude of actual changes in extrinsic factors (e.g., climate, habitat fragmentation) and their effects on tortoise populations over such a long time frame, we also show results of simulations after 100 years (Fig. 5.4).

The probability of population extinction (defined here as when only one sex remains) increases with decreasing habitat quality and as a function of location within the range. Populations at the periphery are the most vulnerable, with populations of 500 tortoises in optimal habitat having 60% probability of extinction within 200 years (Fig. 5.3). Under more favorable combinations of geographic location and habitat quality, populations of 250 tortoises are much

less likely (0-20% probability, except for central populations in marginal habitat) to become extinct within 200 years.

Over the first 100 years of simulations, populations of at least 100 tortoises are resilient to variation in habitat quality and location within the geographic range (Fig. 5.4). Only populations at the periphery in marginal habitat have a significant chance of extinction (30%) at that size; populations of 250 tortoises, however, have only a 5% chance of extinction under those same conditions.

#### Population persistence

Extinction under most scenario combinations of geographic range, habitat quality, and initial population size occurred (if at all) between 100-200 years of the simulations (Fig. 5.5), as already demonstrated by Figures 5.3 and 5.4. Within a geographic location, populations in optimal habitat persisted longer than populations of the same size in marginal habitat.

#### Size of extant populations

Under most scenarios, extant populations have fewer than 100 tortoises after 200 years, even when initial population sizes were as large as 1000 tortoises (Fig. 5.5). Populations starting with 500 or more tortoises retain at least 100 tortoises at the end of the first 100 years, except at the periphery of the species' range (Fig. 5.6).

#### Summary of baseline model results

Only initial populations of at least 250 tortoises were able to persist for 200 years. Within a 100-year time frame, initial populations of at least 100 animals were relatively robust,

regardless of location within range and habitat quality (except marginal conditions at edge of range). Populations at the periphery of the species' range were more vulnerable to extinction than populations in the central and south portion of the range, even under optimal habitat conditions and relatively large (>500 tortoises) initial population sizes. Not surprisingly, populations occurring in optimal habitat performed better than populations in marginal habitat. Due to longevity of individual animals, tortoise populations can persist for long periods of time in marginal habitat, making it difficult to detect subtle population declines. If gopher tortoises exhibit low site fidelity due to poor habitat conditions (Aresco and Guyer 1999b, Guyer and Hermann 1997), then our model may underestimate population extinction in those habitats. However, our models demonstrate that the likelihood of long-term persistence of populations occurring in marginal habitat can be increased through effective habitat management.

Under all scenarios modeled, regardless of geographic location and habitat quality, gopher tortoise populations exhibited gradual declines. There are several possible explanations as to why our models predicted universal declines, including—but not limited to—the following:

1) *Some assumptions of the VORTEX software program may make the program inappropriate for modeling the gopher tortoise's life history.* There are two potentially important assumptions of the VORTEX software program that may be violated in gopher tortoises. The first is that the species modeled has age-dependent vs. size-dependent survivorship. Although survivorship may in fact be more closely correlated with size or stage than with age, too few survivorship data are currently available to make this distinction meaningful in terms of model construction. In addition, size and age are correlated, although individual growth rates vary both regionally and

locally. We attempted to capture the relationship between size, age and stage by varying age at maturity as a function of geographic range and habitat quality.

The second important assumption of the VORTEX software is that survivorship and reproductive parameters do not increase with age after individuals reach maturity. Although this assumption may be violated in some turtle species, no data are available to determine whether these parameters change with age (independent of size) in adult gopher tortoises or to model (using other programs) such age-related changes.

2) *The parameter estimates were derived from data collected on declining populations.* If the parameter estimates in our model do adequately represent the population dynamics of currently extant gopher tortoise populations, then the species may be experiencing a range-wide decline even under the most favorable conditions. Results of a demographic sensitivity analysis (see following section, p.29) should provide guidance on the relative likelihood that the declines exhibited in simulated populations are due to parameter uncertainty or that they parallel declines experienced by real populations.

3) *The life history of the species was not sufficiently represented by the parameter values specified in the models.* Although numerous studies have been conducted on gopher tortoises throughout their range, few published data from long-term population studies are available for estimating certain model parameters, particularly longevity and survivorship – both of which are identified as critical research needs for effective conservation of the species (Smith et al. 2006). Demographic sensitivity analysis (see following section, p. 29) can be used to identify the parameters that have the most influence on model outcome. These “sensitive” parameters can



become the focus of research and/or management efforts, depending on the level of uncertainty associated with their estimates.

### Feasible Demography

Because all our modeled scenarios resulted in declining populations in VORTEX, we wanted to evaluate whether the combination of demographic parameters currently available in the literature (and used in our model) represent a feasible demography for gopher tortoises. We define feasible demography (per Dunham and Overall 1994) as “any combination of average...survivorship and fecundity values which allows long-term population persistence.” Following methods by Dunham and Overall (1994) and Congdon et al. (1993, 1994), we conducted standard demographic analyses, manipulating only a single variable at a time, to identify the combination of values that produced the most stable population. The model is not intended to describe any single population of tortoises or any particular scenario we modeled in VORTEX, but rather a “typical” or “average” tortoise population.

The following variables were fixed at constant values, based on literature specifically for gopher tortoises or from life history data from other turtle species, as indicated below:

*Annual fecundity* ( $m_x$ ), the number of female eggs produced annually, based on the assumptions of an equal primary sex ratio, a mean clutch size of 7 eggs (Landers et al. 1980, Mushinsky et al. 1994), and that 95% of adult females reproduce annually (Miller et al. 2001) and lay no more than one clutch annually.

*Adult survivorship* ( $S_{x \text{ Adult}}$ ), the proportion of adult females surviving each year, assuming consistently high survivorship (97%) among all adult age classes. High adult survivorship is supported by long-term mark-recapture studies of translocated gopher tortoise populations in Florida (Ashton and Burke 2007) and Georgia (Tuberville et al., Chapter 2). High adult survivorship has also been documented in long-term studies of other turtle species (Gibbons 1987, Mitchell 1988, Frazer and Gibbons 1990; Congdon et al. 1993, 1994, 2003).

*Nest survivorship* ( $S_{x \text{ Nest}}$ ), the proportion of embryos surviving the period between oviposition and emergence from nests. There are few data available for estimating survivorship of unprotected gopher tortoise nests; survivorship for protected nests varies from 40-86% (Pike and Seigel 2006, Butler and Hull 1996, Epperson and Heise 2003, Smith 1995). We selected nest survivorship values (50%) based on values reported for *Chrysemys picta* (Tinkle et al. 1981, Congdon et al. 2003), whose nesting ecology is well-described and which, like the gopher tortoise, is a species that nests cryptically.

The following variable, for which the fewest data are available, was manipulated:

*Juvenile survivorship* ( $S_{x \text{ Juvenile}}$ ), the average annual survivorship of juvenile females between ages one and age at maturity. Based on comparison of results from studies of gopher tortoise hatchlings (Pike and Seigel 2006, Butler and Sowell 1996, Epperson and Heise 2003) and older juveniles (Wilson 1991, Tuberville et al., Chapter 2), survivorship of juveniles varies over the juvenile period, increasing with size and/or age. For

simplicity, however, we assumed that annual survivorship was consistent throughout the juvenile period and lower than in adults. Because juvenile survivorship is poorly known in tortoises, we input different juvenile survivorship values to determine which value resulted in the most stable population.

The life-table model calculates the following measures of population change for each combination of juvenile survivorship and the other (fixed) demographic variables:

*Reproductive rate ( $R_o$ )*, the mean number of female offspring produced per original female by the end of the cohort (i.e., death of the oldest female in the cohort; a value that indicates both average number of female offspring produced by a female over her lifespan, and the population multiplication factor that will indicate the size of the population in the next generation). Population sizes will decrease when  $R_o < 1.0$ .

*Intrinsic rate of natural increase ( $r$ )*, the change in population size per individual per unit time. Population sizes will decrease when  $r < 1.0$ .

*Population doubling time ( $D_{\text{Time}}$ )*, the number of years required to double (positive value) or halve (negative value) the population size as a consequence of changes in survivorship.

Rather than focusing on the values of  $R_o$  or  $r$ , we chose population doubling-time as a more intuitive measure of population change. The combination of demographic variables that

resulted in the most stable population (i.e., the largest population doubling time) is provided in Table 5.6.

When detailed demographic data are available for a stable population of interest, both the population modeling approach in VORTEX and the feasible demography approach can be used to predict the population's response to specific demographic perturbations. However, when data are limited, the feasible demography approach can be used to develop estimates for poorly known demographic traits (e.g., juvenile survivorship) based on values of other demographic variables for which better estimates are available. In our model, we estimated that annual juvenile survivorship must average approximately 75% over the juvenile period in order to produce a stable population – a value much higher than reported in the literature for the early juvenile years (ages 0 – 4; Butler and Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006, Wilson 1991). The feasible demography approach reveals that our combination of parameters used in VORTEX are unlikely to produce a stable population under any of the scenarios we modeled. We therefore conclude that one or a combination of the following are true: 1) short-term studies do not always allow adequate estimation of long-term demographic rates, 2) juvenile survivorship increases dramatically over the juvenile period, 3) the demographic estimates reported in the literature were based on studies of declining populations.

## DEMOGRAPHIC SENSITIVITY ANALYSIS RESULTS

Sensitivity analysis can be a useful tool for identifying which parameters exert the strongest influence on model outcomes by varying individual parameters one at a time. If a high degree of uncertainty is associated with either parameter estimates themselves or how they are used to construct the model, those parameters should become research or monitoring priorities so

that better data can be obtained. If a particular parameter is already well understood, it may be an effective management target.

For the sensitivity analysis conducted here, we used a baseline model for a population of 100 tortoises located in the central geographic range and occupying optimal habitat. We chose this baseline model because we wanted to simulate conditions likely to be encountered on public conservation lands within the core of the species' range. Based on the results presented in the previous section, initial population sizes of 100 were the smallest populations resilient to variation in geographic locations and habitat quality and, therefore, "viable" over the long term. Many public conservation lands are large enough to support a population of 100 tortoises.

For each parameter we manipulated individually, we present below the corresponding changes in deterministic population growth rate, probability of extinction within 200 years, and mean time to extinction.

#### Maximum age of reproduction (Longevity)

Adult gopher tortoises presumably continue to reproduce throughout their lives, so maximum age at reproduction is essentially equivalent to longevity for the purposes of this model. However, maximum or even average longevity of this species is not known with any certainty but was set at 60 years in our baseline model. For every 10 yr change in expected maximum reproductive age there was a corresponding difference of 10-30% in the probability of extinction and a 10-40 year change in estimated population persistence (Fig. 5.8). Population growth rates were still slightly negative when maximum reproductive age was set at 100 years, but populations were not likely to decline to extinction within 200 years.

## Clutch size

Clutch sizes are fairly well-documented throughout the species' range (e.g., Butler and Hull 1996 [north FL], Diemer and Moore 1994 [north-central FL], Epperson and Heise 2003 [MS], Landers et al. 1980, Mushinsky et al. 1994 [central FL], Rostal and Jones 2002 [southeast GA], Smith 1995 [FL], Smith et al. 1997 [LA, MS], Wright 1982 [SC]) and we think the mean clutch sizes used in our model scenarios are reasonable estimates, suggesting that uncertainty in this parameter is unlikely to play an important role in model predictions. However, management actions have the potential to influence mean clutch size of a population. Habitat management (or an absence thereof) can influence growth rates (Aresco and Guyer 1999a) and, therefore, the age at which females are recruited into the breeding pool and the mean body sizes of those females. In addition, females living in habitat with abundant, high quality forage are likely to have more resources to devote to reproduction than females of the same size living in poor quality habitat. Therefore, we have included clutch size in our demographic sensitivity analysis.

An increase or decrease in mean population clutch size by 2 eggs resulted in no more than a 1% corresponding change in the population growth rate (Fig. 5.9). Although a clutch size increase was not sufficient to result in a stable population growth rate (i.e., equal to 0), it did result in a predicted 40% decrease in the probability of population extinction within 200 years and a 25 year increase in population persistence time. Although we do not know how large a change in population mean clutch size could be produced as a result of habitat manipulations, these results do suggest that management efforts that influence clutch size could have important consequences for long-term population viability.

## Sex ratio

We examined the effect of sex ratio bias on model outcome by varying the proportion of females in the initial population from 40-60%. Although sex ratio among clutches may vary as a result of different thermal conditions among nests, the overall sex ratio of hatchlings within a population is presumably 1:1. And while sex-biased mortality has been documented in adult aquatic turtles (e.g., nesting females are more susceptible to road mortality than males in some species), no data have been presented to confirm or refute whether mortality rates vary between male and female gopher tortoises after hatching. Theoretically, dramatic climate change could eventually influence nest temperatures and sex ratios, with higher nest temperatures producing a higher proportion of females. Nest temperatures could also be manipulated through artificial incubation in the lab, although this is a manually intensive endeavor. Adult sex ratios could be manipulated in translocated populations during the selection of release animals.

For every 5% increase in the proportion of adult females comprising the population, population growth rate increased by <0.3%, probability of extinction decreased by 10-20%, and mean time to extinction increased by 5-10 years (Fig. 5.10). Given the relative resilience of the model to variation in sex ratio, the lack of evidence that sex ratios are likely to be skewed in natural populations of gopher tortoises, and the difficulty in artificially manipulating sex ratios, sex ratios are not an efficient management target.

## Proportion of females breeding

The proportion of female gopher tortoises breeding in a population is not well-documented in the literature. Although short-term studies have reported the percent of females encountered with eggs, it is difficult to determine to what extent these values reflect actual

reproduction rates in the population versus methodology of the study (i.e., how likely were females captured without eggs to have already nested or to nest later in the season?). In addition, few data are available on annual variation and site-specific variation in this parameter. In addition to the high degree of uncertainty regarding the range of values for this parameter in natural populations, the proportion of females breeding is also not likely to be easily manipulated unless it is shown to vary as a function of habitat quality.

We examined the effect of variation in proportion of females breeding on population dynamics by varying the percentage of females breeding from 80-100%, which encompasses the primary values reported in the literature (Rostal and Jones 2002, Diemer and Moore 1994) and the range in values we considered likely to occur in natural populations. For every 10% increase in the proportion of females breeding, the population growth rate increase by 0.3%, probability of extinction decreased by approximately 15%, and mean time to extinction increased by <5 years (Fig. 5.11). This parameter, therefore, is not an efficient management target, and although poorly understood for natural populations, does not appear to be a significant driver of model outcome.

#### Comparative survivorship of immature stages

Adult mortality is widely recognized as being the primary force driving population dynamics for most turtle species (Congdon et al. 1993, 1994). However, because our models already assume a naturally low annual adult mortality rate (1.5%) and still predict population declines under all scenarios simulated, we focus here on the immature classes. Not only are mortality rates uncertain for these age classes, but because mortality rates are likely to be higher



for these age classes than for adults, these mortality rates could prove to be effective management targets.

In the baseline model, the population growth rate was -1.5%, resulting in a population with a 60% probability of extinction within 200 years, and a mean time to extinction of 160 years. The model was more responsive to changes in juvenile mortality rates than to yearling mortality rates, probably due to the longer duration of the juvenile stage (age 2 – 4) compared to the yearling stage. The model was most responsive to changes in hatchling mortality. A 5% decrease (from 96% in the baseline model to 91%) in hatchling mortality was sufficient to shift the population growth rate from slowly declining (-1.5%) to slowly increasing (+1.1%) and to eliminate the probability of extinction within the next 200 years (Fig. 5.12). The hatchling mortality rate used in the baseline model represents a severe bottleneck to recruitment and long-term population viability, highlighting the need for a better understanding of hatchling mortality rates in natural populations.

Hatchling mortality rates have been reported in three published radio-telemetry studies from Florida and Mississippi (Butler and Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006). The naturally high mortality rates combined with the intensive nature of radio-telemetry studies make it difficult, however, to obtain sample sizes large enough to estimate hatchling survivorship and its variability accurately (Pike and Seigel 2006). The changes in hatchling mortality rates necessary to produce significant changes in population dynamics (Fig. 5.13) are small enough to fall within the range of both measurement error/parameter uncertainty and natural variation among years and/or among sites. Further research on hatchling mortality is warranted, and effective management of individual populations may require some basic understanding of site-specific hatchling mortality rates. At the very least, should managers

suspect that hatchling survivorship is low or non-existent, then management actions to increase hatchling survivorship – such as predator control, habitat enhancement, or perhaps even head-starting – should be considered.

## TRANSLOCATION MODEL RESULTS:

### COMPARISON OF ALTERNATIVE RELEASE PROTOCOLS

Based on results of recent translocation studies, we developed a series of models for a simulated translocated population of 100 founders occurring within the central range in optimal habitat and assuming 90% annual hatchling mortality (note: this is lower than the 96% used in the baseline model). We created different model scenarios to evaluate the relative effectiveness of several translocation alternatives. Except for the scenarios comparing penning treatment, all scenarios assumed that animals were subjected to long-term penning prior to release.

#### Effects of penning treatment

In each scenario, 100 tortoises were introduced to a site without resident tortoises. Mortality rates varied among penning treatments (to reflect different dispersal rates) but only during the first year following release. Subsequently, dispersal was removed from the model so that mortality was set to the same value used in modeling native populations.

Penning, by dramatically reducing the number of animals lost to dispersal following release, exerts strong influence on subsequent population trajectories (Fig. 5.14) even though elevated dispersal is only observed during the first year. Without penning, populations starting with 100 founders experience heavy losses and even 20 years following translocation only include an average of 50 animals. These populations do not rebound to the baseline population

of 100 animals until 70 yrs following translocation and only support an average of 125 animals by the end of the 100 year simulation.

Founder populations subjected to short-term penning, however, rebound to 100 animals within first 10 years, increase to approximately 125 animals in first 20 yrs, and grow to include 310 tortoises within 100 years. With long-term penning, founder populations rebound to 100 animals during the first 5 years and increase to approx 160 animals in the first 20 years. After 100 years, populations have increased to 400 animals.

Our model suggests that short-term effects of release techniques on dispersal behavior in released tortoises can have long-term consequences for founder populations. These findings provide strong justification for at least short-term penning of translocated gopher tortoises, with longer-term penning preferred if feasible.

#### Effects of resident population size

To evaluate the effect of population size of resident tortoises, we simulated the release of 100 adult gopher tortoises following 1 yr penning at sites with 0, 10, 20 or 50 resident tortoises. The presence of 20 or fewer resident tortoises only slightly increased final population size at the end of the simulation (Fig. 5.15). The presence of a small resident tortoise population could theoretically shorten the time it takes for a founder population reached a minimum target size. However, this model ignores any potentially negative social or competitive interactions between resident and translocated tortoises, for which there is little information.

### Effects of release interval

We simulated the effects of introducing a total of 100 adult tortoises into unoccupied habitat both as a single release and as a series of five releases of 20 individuals each over 1-yr, 2-yr and 5-yr intervals. Based on the model, release interval has little or no effect on population trajectory, with only slightly more tortoises at the end of the simulation under 2-yr and 5-yr intervals when compared to 1-yr intervals and a single release (Fig. 5.16). Therefore, it seems that the question of whether to conduct single or multiple releases and over what interval is primarily a question of what is feasible or practical to implement in a given situation.

However, at least two arguments could be made for conducting multiple releases:

- 1) Our model ignores any influence of short-term variation in environmental or other extrinsic factors (e.g., predator population levels, drought, etc) in determining release outcome. Implementing a series of releases would presumably avoid releasing all tortoises in a “bad” year, thereby spreading the risk across years. This practice may be more important when releasing young tortoises rather than only adults.
- 2) Conducting multiple small releases rather than a single large release also allows managers or biologists to monitor results in the early phase of the project and make any necessary changes in habitat management or release protocols.

### Effects of founder demography

We examined the effects of founder demography by simulating the release of adults only, head-started yearlings only, and a mixed population of adults, subadults and juveniles. All

scenarios were based on the release of 100 animals in a single release following 1 yr of penning, but mortality (i.e, mortality + dispersal) varied among life-stages.

Under the conditions model, best results are achieved when releasing adults only or a mixed population (Fig. 5.17). Establishing a viable population solely through the release of head-started yearlings is the least effective management alternative due to high mortality of young age classes and the long time to reproductive maturity. However, the release of head-started yearlings could be used in addition to other techniques to manage an “at-risk” population, at least until the population recovers sufficiently to maintain itself.

These model results are based on the assumption that animals are penned for 1 yr prior to release. In the absence of penning, release of younger age classes (either exclusively or in addition to adults) likely becomes more important in promoting site fidelity and population establishment. However, release of tortoises without at least some period of penning is not recommended.

## SUMMARY AND RECOMMENDATIONS

Baseline models for naturally occurring populations were constructed in VORTEX from demographic values currently available in the literature. All model scenarios resulted in declining populations, with populations of at least 100 animals unlikely to experience extinction over the first 100 years of the simulations and populations of at least 250 animals persisting for 200 years. The most likely causes for the predicted decline include: 1) demographic values reported in the literature are based on studies of declining populations, and 2) sufficient data for estimating some demographic parameters are currently lacking.

Gopher tortoises are currently recognized as threatened or endangered by every state in which they occur and are federally listed in the western portion of their range (USFWS 1987). Habitat destruction, fragmentation, and degradation as a result of development, intensive silviculture, and fire suppression have undoubtedly reduced the availability of suitable habitat throughout their range (Aresco and Guyer 1999b, Hermann et al. 2002, Jones and Dorr 2004). However, few long-term mark-recapture data sets are available for documenting trends of individual populations. Based on indirect survey methods (i.e., surveys of burrows rather than direct observation of tortoises), McCoy et al. (2006) concluded that gopher tortoise populations experienced declines over a 10-year period at eight of 10 protected sites in Florida. A burrow survey conducted at a state preserve in South Carolina managed specifically for gopher tortoises estimated that over a 20-year period, the population experienced an annual decline of 2.33% (Tuberville and Dorcas 2001) - which is very similar to the 2.6% annual decline predicted by our model for a population in optimal habitat at the periphery of the range. So, while there is some evidence for localized and even regional declines of gopher tortoises, it remains unclear the extent to which the declines predicted by our models were a result of demographic estimates obtained from declining populations.

Regardless, our demographic feasibility analysis indicated that the combination of parameters used in our model was unlikely to result in a stable population. Specifically, juvenile survivorship rates would need to be much higher than reported in the literature or to increase dramatically over the juvenile period. Demographic sensitivity analysis demonstrated that our models were very sensitive to changes in survivorship of the immature stages. More comprehensive data on juvenile survivorship and its variability are essential to developing more realistic population models and to effectively manage tortoise populations.

Populations that are not likely to be viable will require some level of management intervention, including habitat and/or population manipulations. In-situ protection and management are preferred, where possible. Our models suggest that improved habitat conditions can improve long-term population viability and that populations at the northern periphery are more vulnerable to poor habitat conditions. When habitat management alone is unlikely to ensure population viability, manipulations of the population itself may be necessary.

Results of all translocations of gopher tortoises reported to date identify a translocation cost in the form of permanent loss of adult animals from the population. The effect of these losses on population viability will depend on the number of animals initially released, proportion lost during the settling phase, and how long the settling period lasts. We incorporated this anticipated loss of animals during the first year following release into our translocation models and modeled various release strategies (i.e., penning duration, number and timing of releases, etc.) to predict their relative effectiveness. All scenarios predicted that translocated populations would recover to at least the original founder population size during the 200 year simulation, suggesting that translocation can be used to establish viable populations under the conditions assumed in our models.

However, we consider relative efficiency to be an important consideration in designing translocation strategies. Availability of release animals is limited and any planned manipulations should strive to minimize loss of those animals. Although evaluating population viability of a long-lived species is inherently a long-term undertaking, the more quickly translocated populations can grow to their target population size, the more likely that managers and policymakers will continue to invest resources in maintaining those populations. Longer time

frames also make it more difficult to anticipate the threats that individual populations may be subjected to.

The specific goals and release strategies for individual projects will necessarily be dictated by biological, financial, political, and logistic constraints, including local site conditions (e.g., site carrying capacity), availability of release animals, budgets, and goals of the managing agencies. However, we think translocation *can* be an effective management tool for gopher tortoises (and potentially other turtle species) when less intrusive manipulations are not practical or sufficient. We stress however, that the models and interpretations presented here are limited by the current understanding of gopher tortoise life history and how individuals respond to translocation. As more comprehensive data become available, these models can be refined to more accurately depict tortoise life history and hopefully provide helpful guidance for future translocation efforts.

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Table 5.1. Ages at first reproduction for males and female gopher tortoises under different combinations of geographic location and habitat quality.

Location within geographic range	Habitat quality	<u>Age at first reproduction</u>	
		Females	Males
South	optimal	13	12
	marginal	15	13
Central	optimal	15	11
	marginal	17	15
Periphery	optimal	20	17
	marginal	23	20

Table 5.2. Proportion of females breeding, as specified in our model, based on habitat quality.

<u>Habitat quality</u>	<u>% adult females breeding</u>	<u>E.V.* in % breeding</u>
Optimal	95	5
Marginal	80	10

\*E.V. = environmental variation (S.D.)

Table 5.3. Mean clutch size, as specified in our model, as a function of location within geographic range.

<u>Location within geographic range</u>	<u>Mean clutch size</u>	<u>S.D.</u>
South	7.00	2.5
Central	6.25	2.0
Periphery	5.00	1.5



Table 5.4. Stage-specific mortality rates as specified in our model.

Life stage	Ages	Annual % mortality
Hatchling	age 0 to 1	96
Yearling	age 1 to 2	55
Juvenile	age 2 to 4	25
Subadult	age 4 to (age at maturity* – 1)	3
Adults	age at maturity to 60	1.5

*\*See table of age at first reproduction on p.12*

Table 5.5. Stage-specific mortality / dispersal rates as specified in our model.

Life stage	Cohort age	Mortality / dispersal rate*
Adult	30	10%
Subadult	10	10%
Juveniles	3	12%
Head-started yearling	2	15%

Table 5.6. A summary of demographic values that produced the most stable population of gopher tortoises in our demographic analysis, and the resulting measures of population change.

Reproduction	
Annual fecundity	3.3
Survivorship ( $l_x$ )	
Nest (age 0)	0.5000
Juvenile (ages 1-14)	0.7475
Adult females (ages 15+)	0.9700
Stable population parameters	
Basic reproductive rate ( $R_0$ )	1.0076
Intrinsic rate of population increase ( $r$ )	$1.8820 \times 10^{-4}$
Population doubling time ( $D_{\text{time}}$ )	3682.93

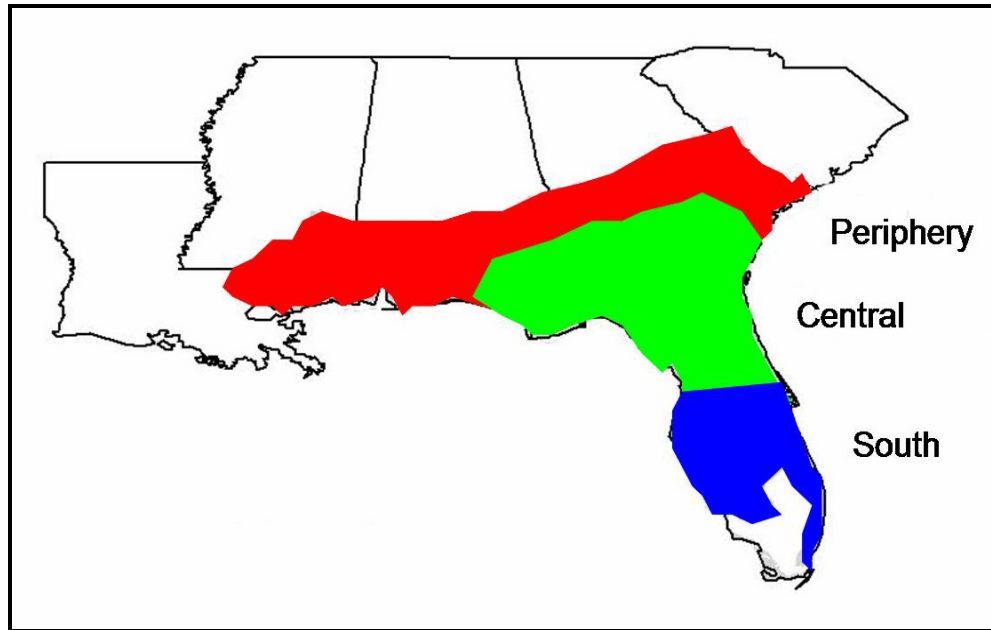


Figure 5.1. Geographic extent of the gopher tortoise, with the south, central, and peripheral portions of the range indicated.

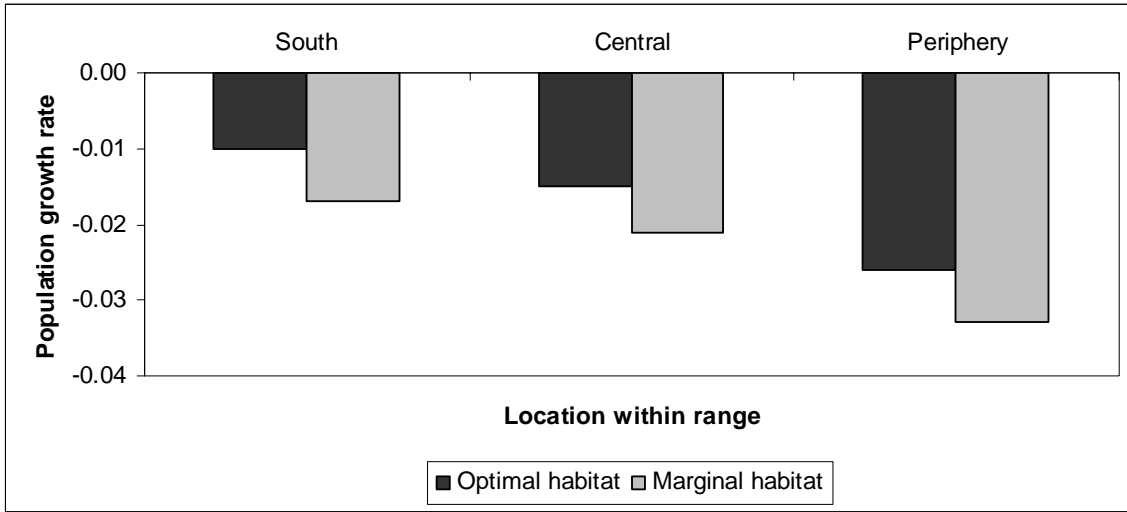


Figure 5.2. Deterministic population growth rate of simulated gopher tortoise populations in optimal (black bars) and marginal (gray bars) habitat conditions in different regions within the geographic range.

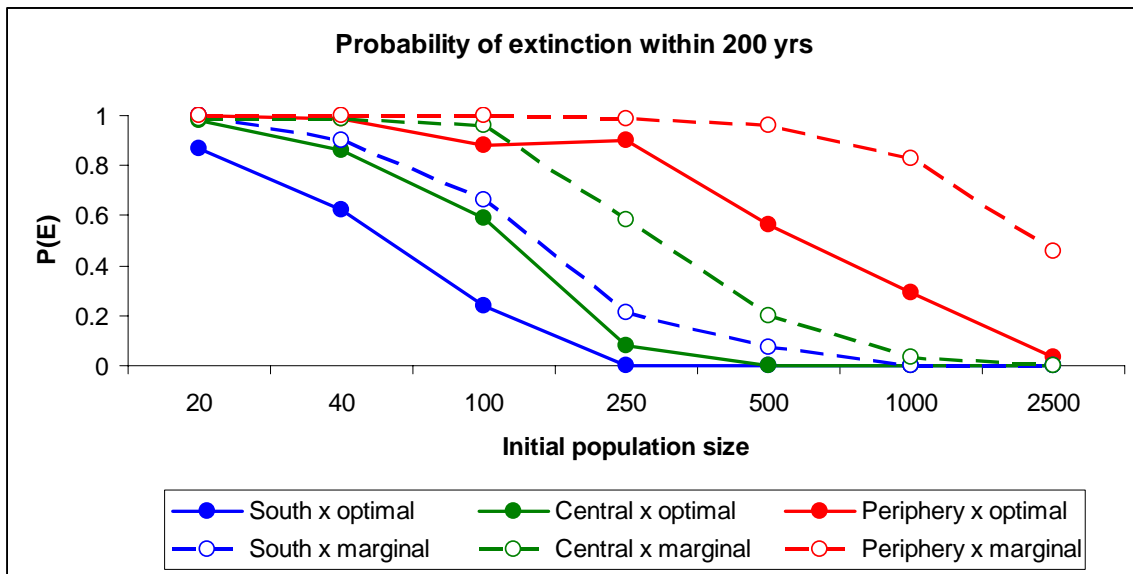


Figure 5.3. Probability of extinction within 200 years for simulated gopher tortoise populations of different initial population sizes based on the population's location within the range and habitat conditions. Note: x-axis scale is not linear

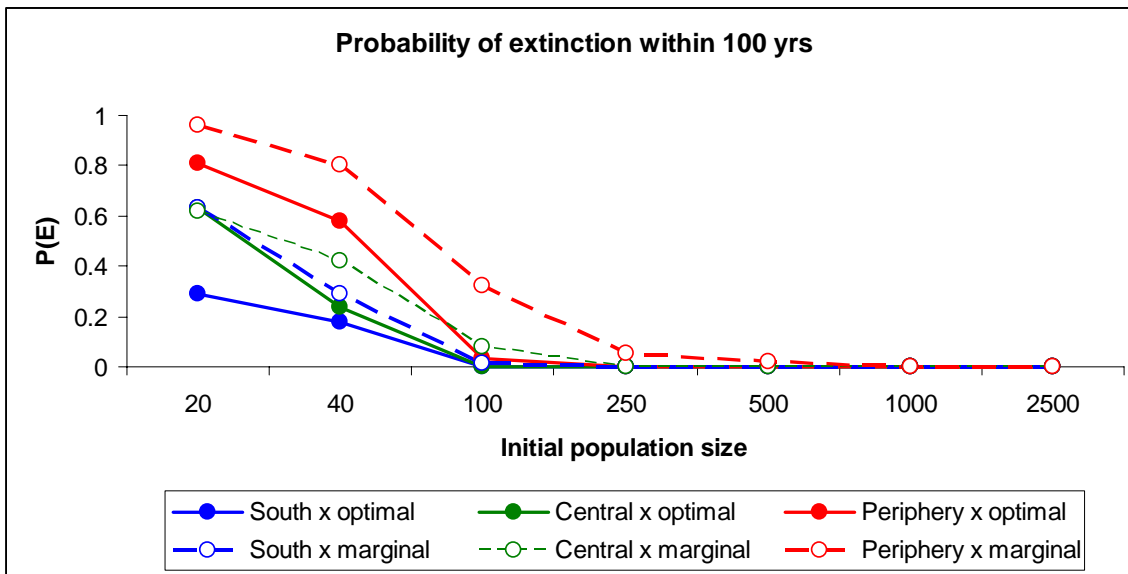


Figure 5.4. Probability of extinction within 100 years for simulated gopher tortoise populations of different initial population sizes based on the population's location within the range and habitat conditions. Note: x-axis scale is not linear

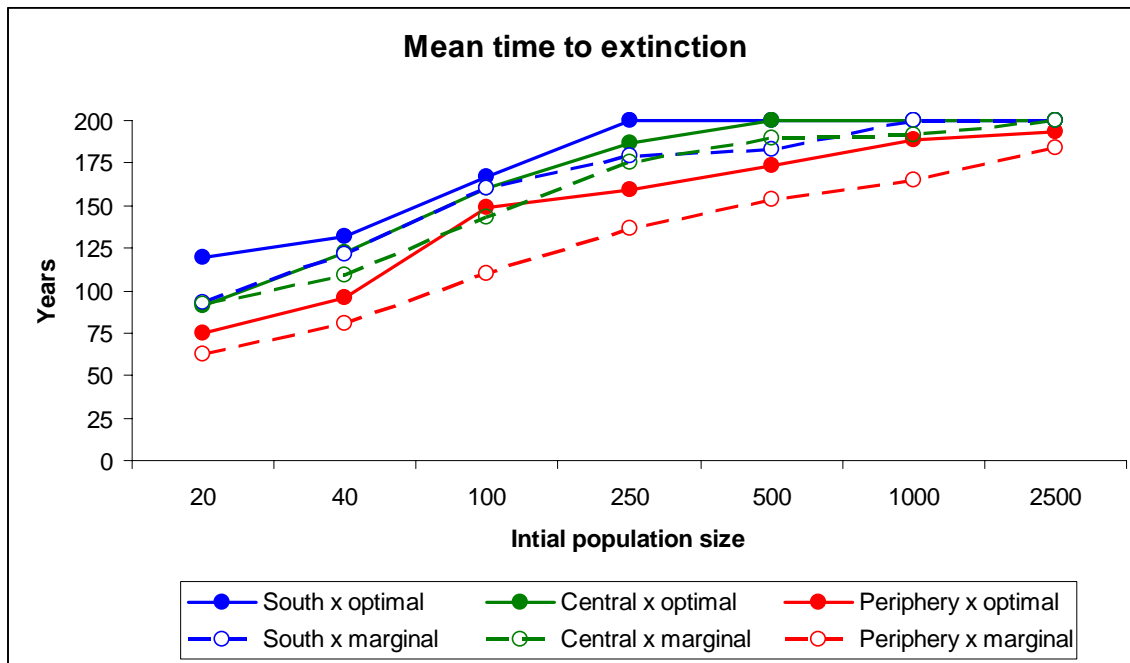


Figure 5.5. Population persistence (or mean time to extinction) for simulated gopher tortoise populations of different initial population sizes based on the population's location within the range and habitat conditions. Graphs plateau at 200 years, the maximum simulation duration possible. Note: x-axis scale is not linear.



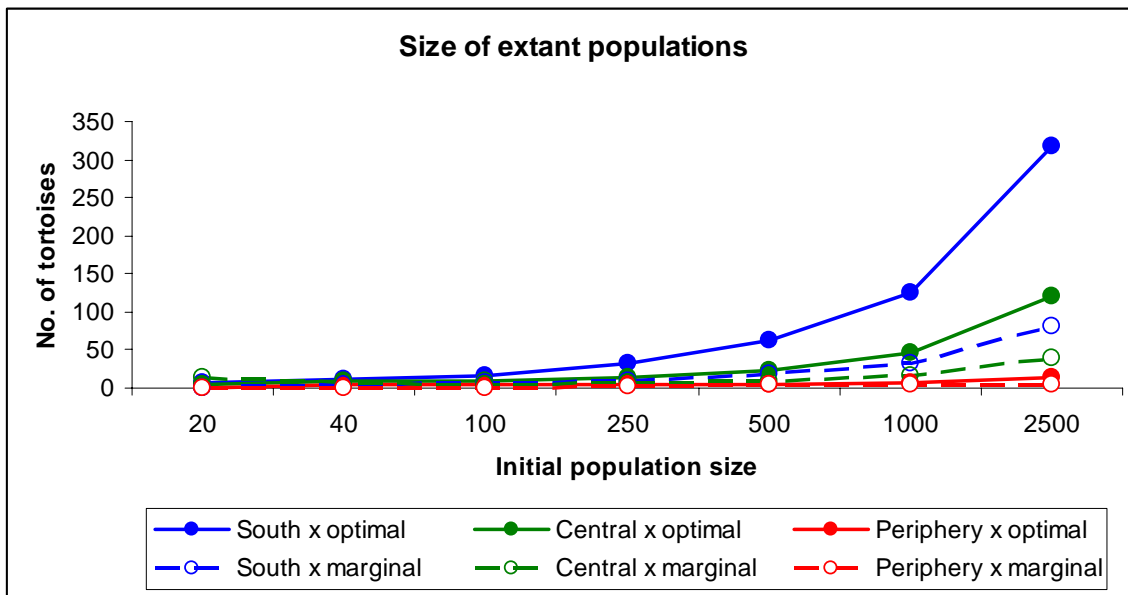


Figure 5.6. Size of populations extant after 200 years based on their initial population size, location with the geographic range (south, central, periphery) and habitat quality (optimal, marginal). Note: x-axis scale is not linear.

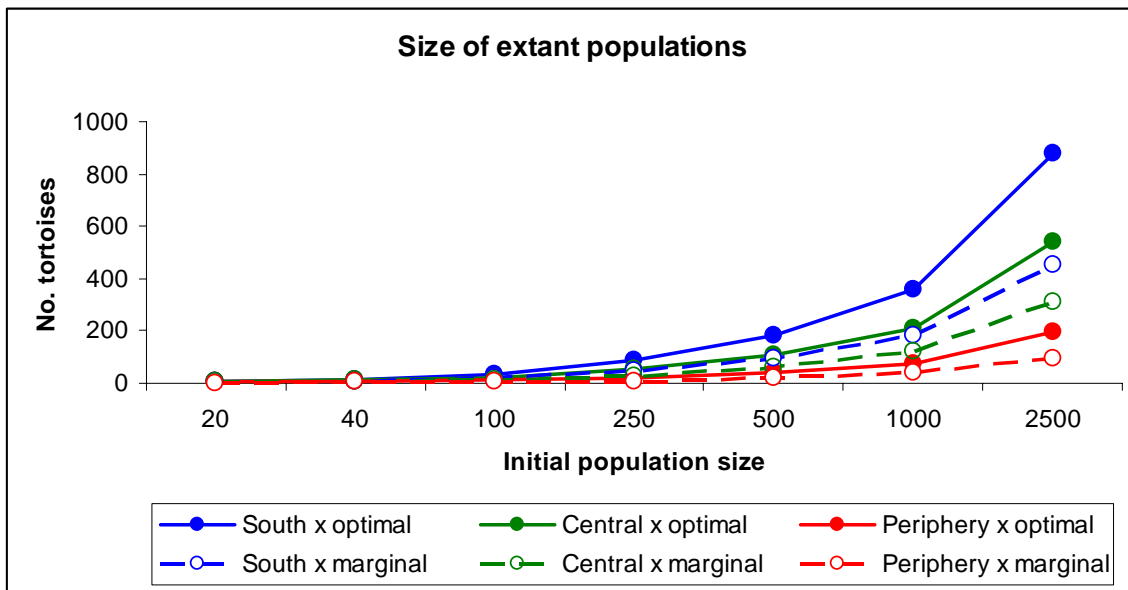


Figure 5.7. Size of populations extant after 100 years based on their initial population size, location with the geographic range (south, central, periphery) and habitat quality (optimal, marginal). Note: x-axis scale is not linear.

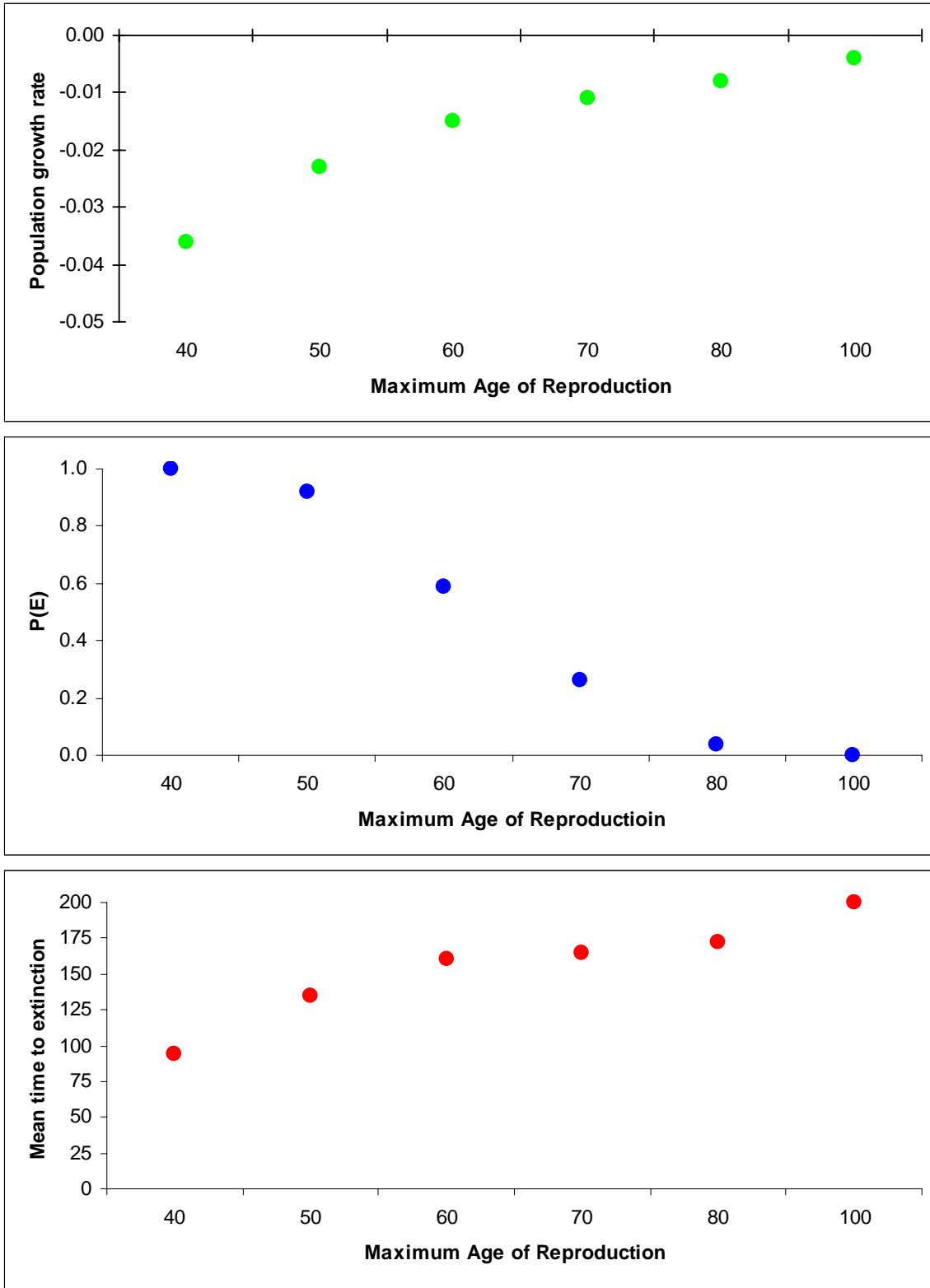


Figure 5.8. Population growth rates (top), probability of extinction within 200 years (center), and mean time to extinction (bottom) as a function of maximum age of reproduction.

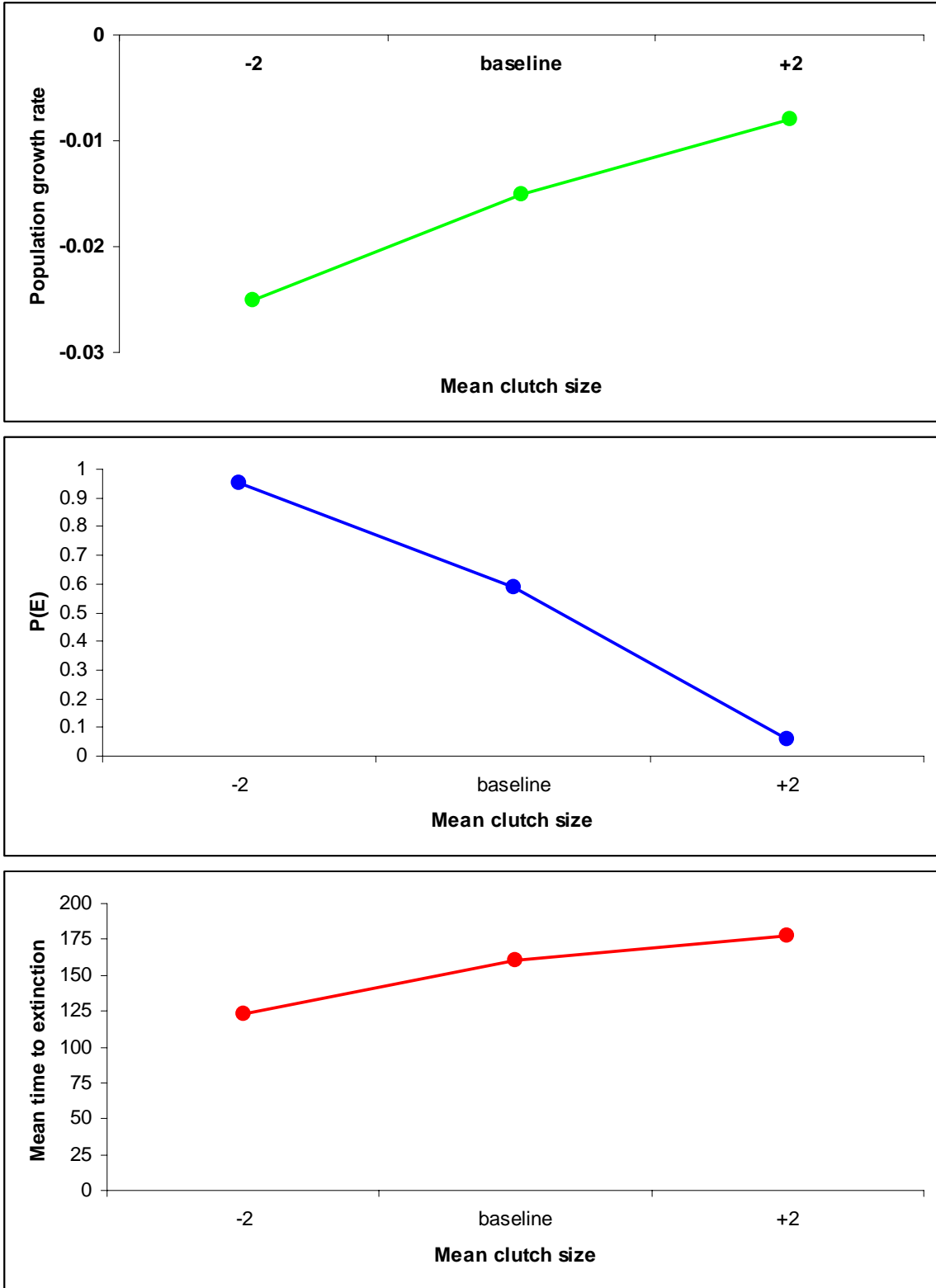


Figure 5.9. Population growth rates (top), probability of extinction within 200 years (center), and mean time to extinction (bottom) as a function of mean clutch size. The baseline clutch size is 6.75 eggs.

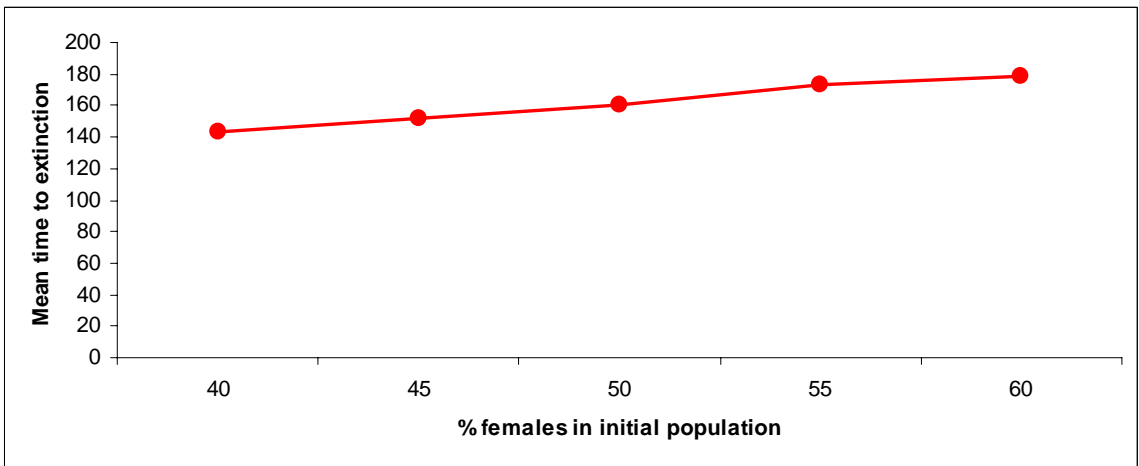
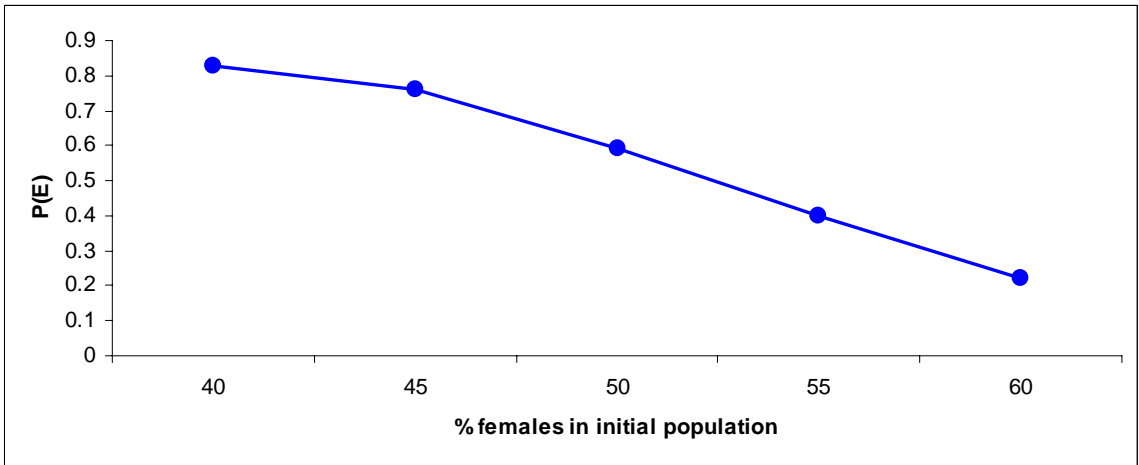
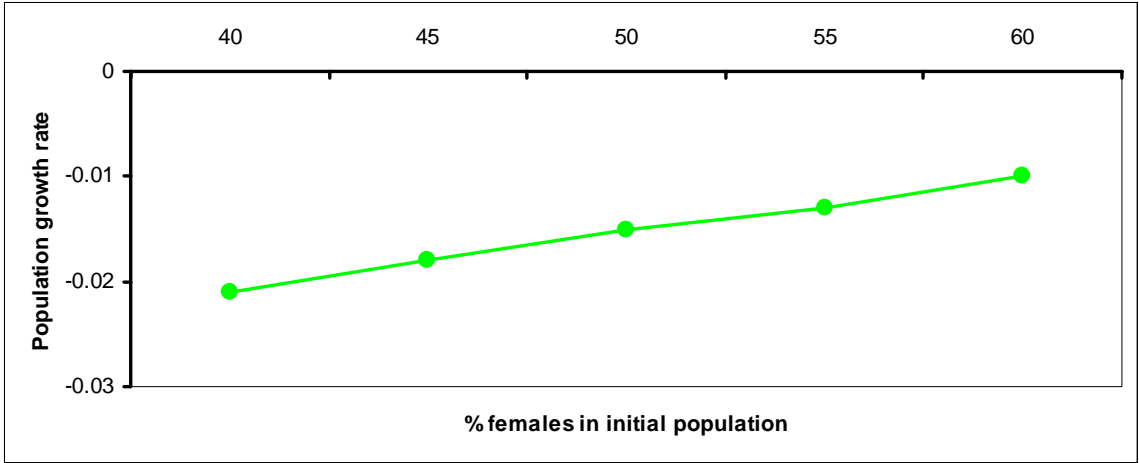


Figure 5.10. Population growth rates (top), probability of extinction within 200 years (center), and mean time to extinction (bottom) as a function of sex ratio (% females in initial population).

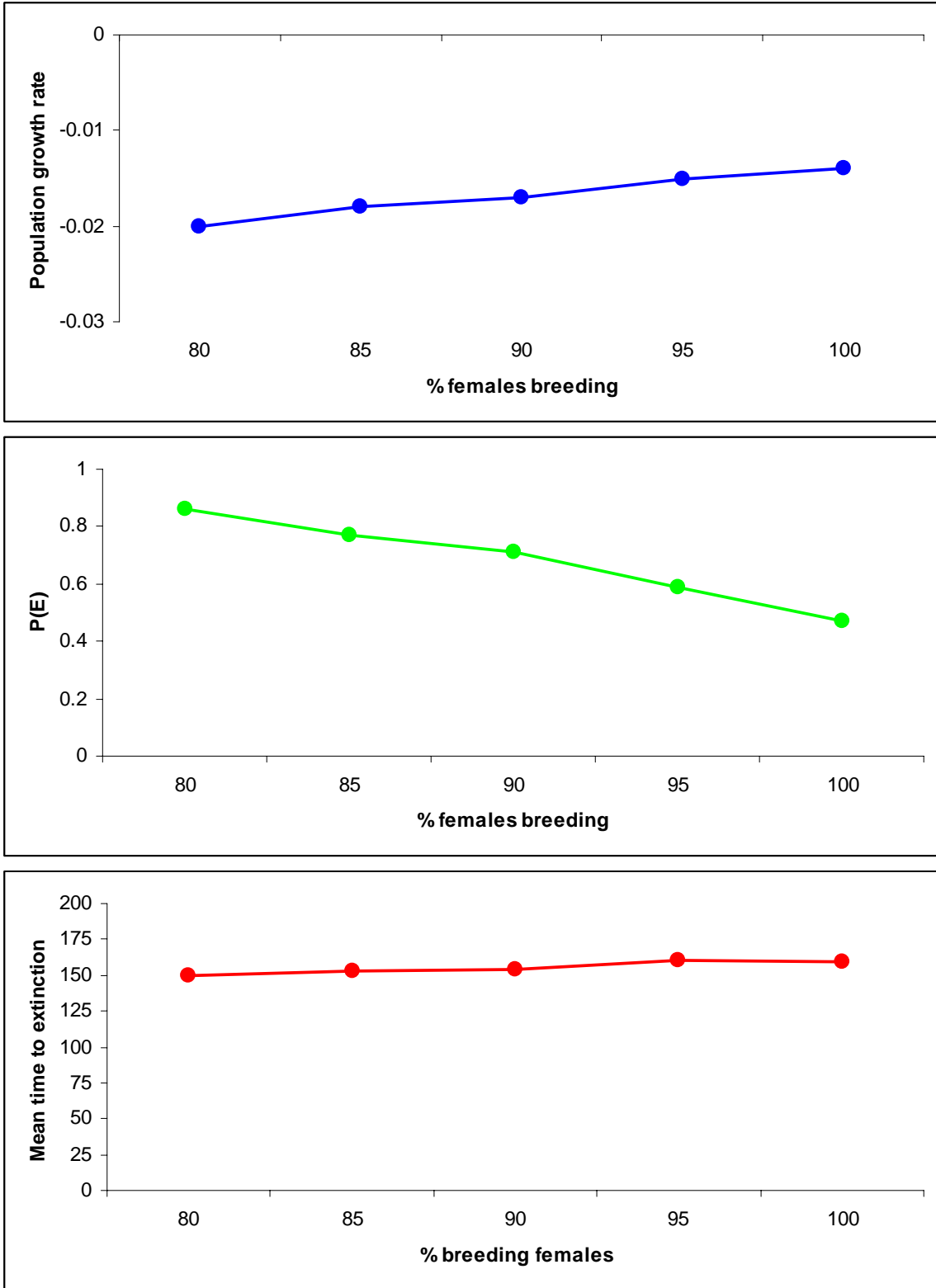


Figure 5.11. Population growth rates (top), probability of extinction within 200 years (center), and mean time to extinction (bottom) as a function of proportion of females breeding.

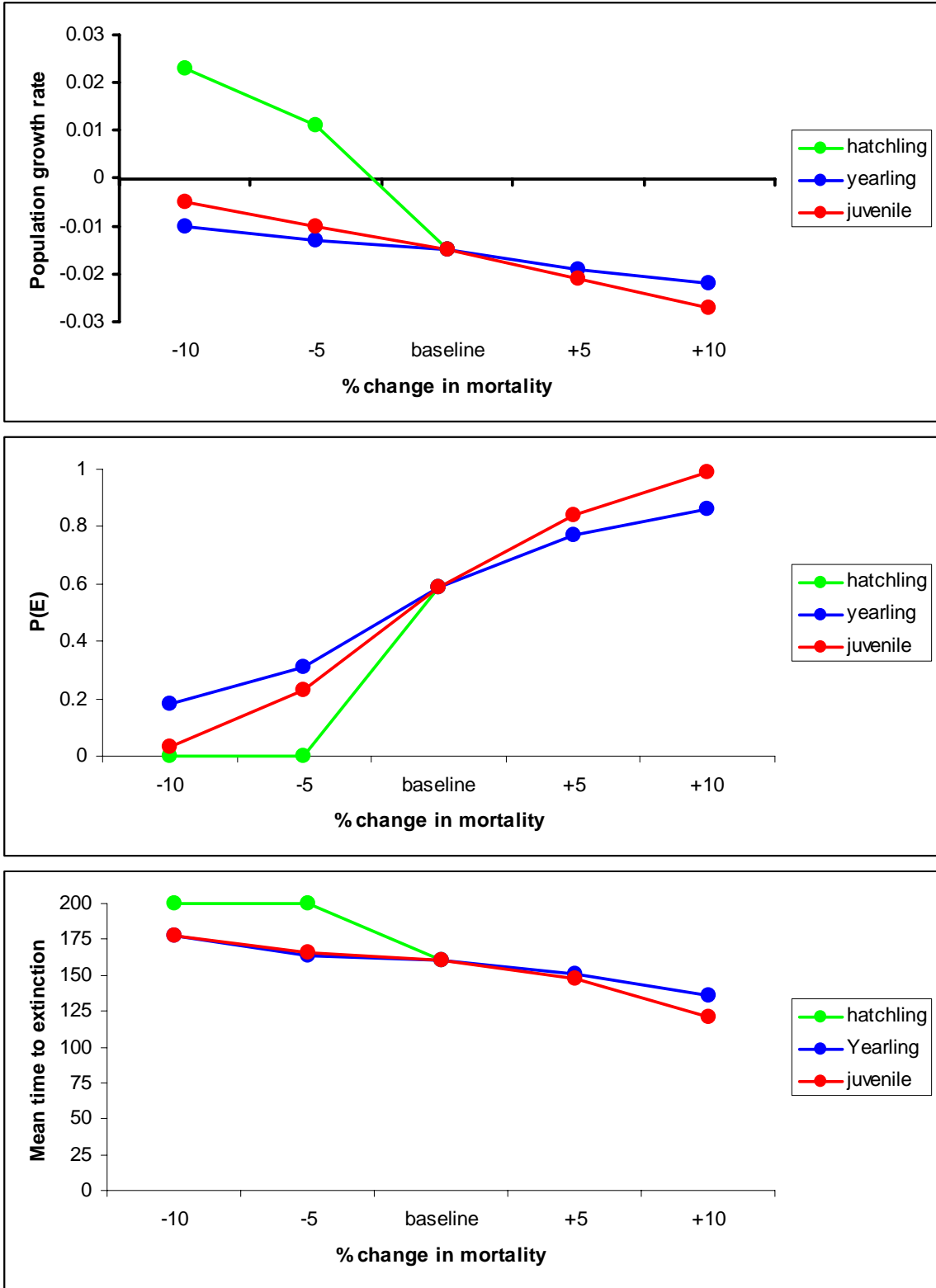


Figure 5.12. Population growth rates (top), probability of extinction within 200 years (center), and mean time to extinction (bottom) as a function of variation in hatchling, yearling and juvenile mortality rates from baseline model.

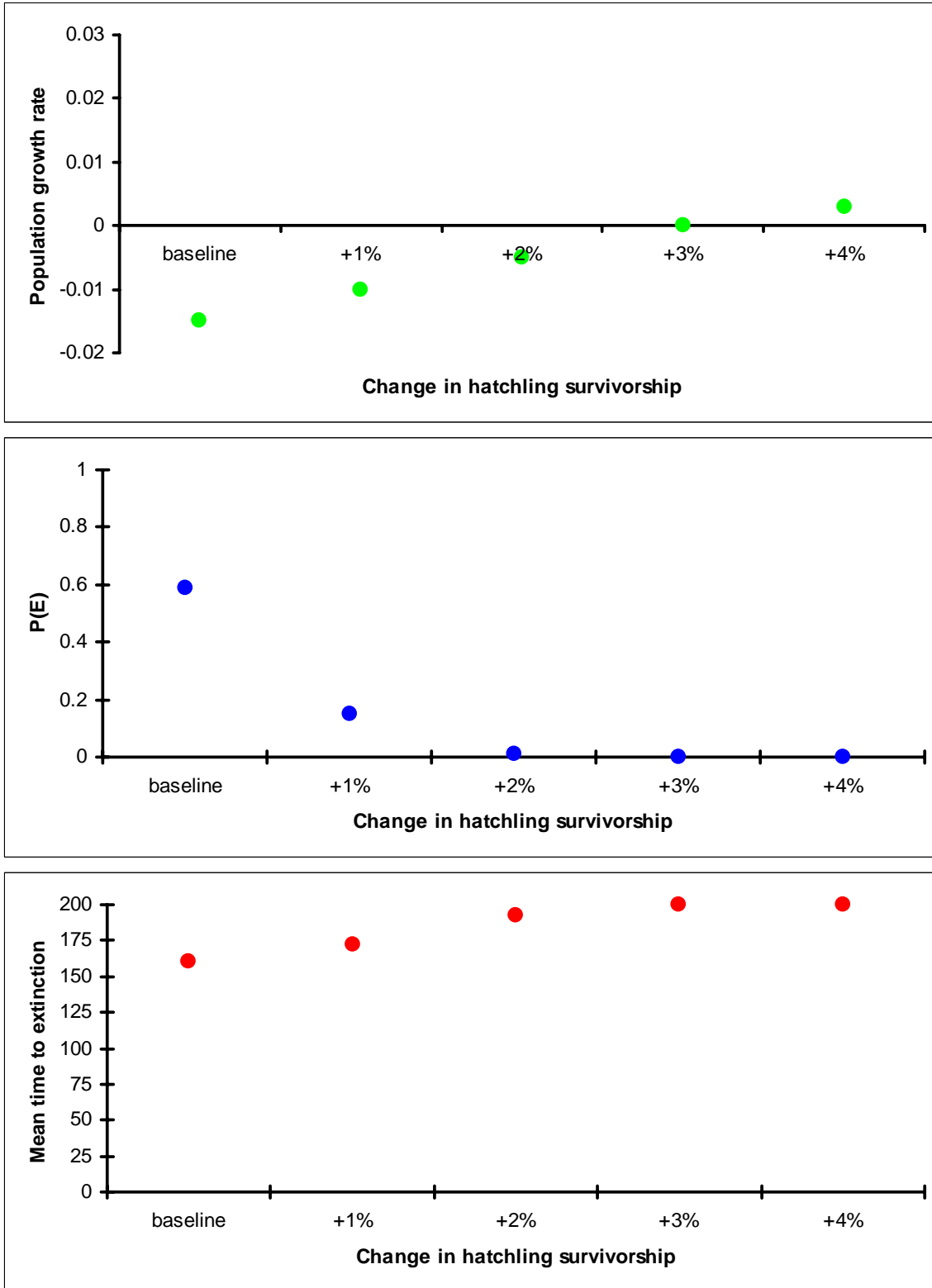


Figure 5.13. Population growth rates (top), probability of extinction within 200 years (center), and mean time to extinction (bottom) as a function of small variation in hatchling mortality rates from baseline model (baseline survivorship = 4%).



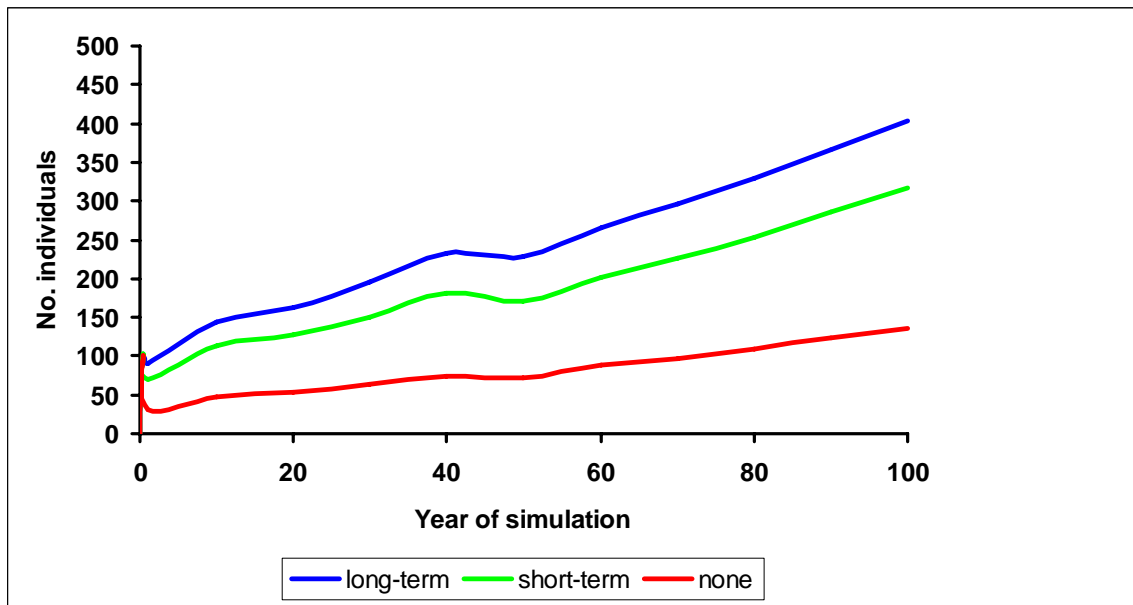


Figure 5.14. Population trajectories following translocation for founder populations of 100 tortoises released at unoccupied sites without penning (red) or following short-term (green) or long-term (blue) penning.

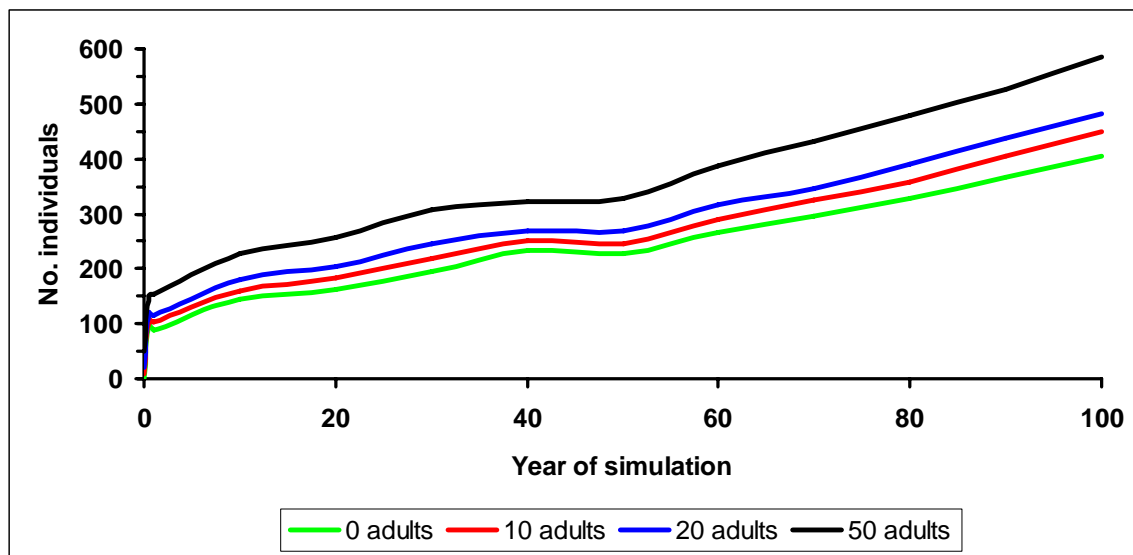


Figure 5.15. Population trajectories during 100 years following translocation for founder populations introduced at sites with 0 (green), 10 (red), 20 (blue), or 50 (black) resident adult tortoises.

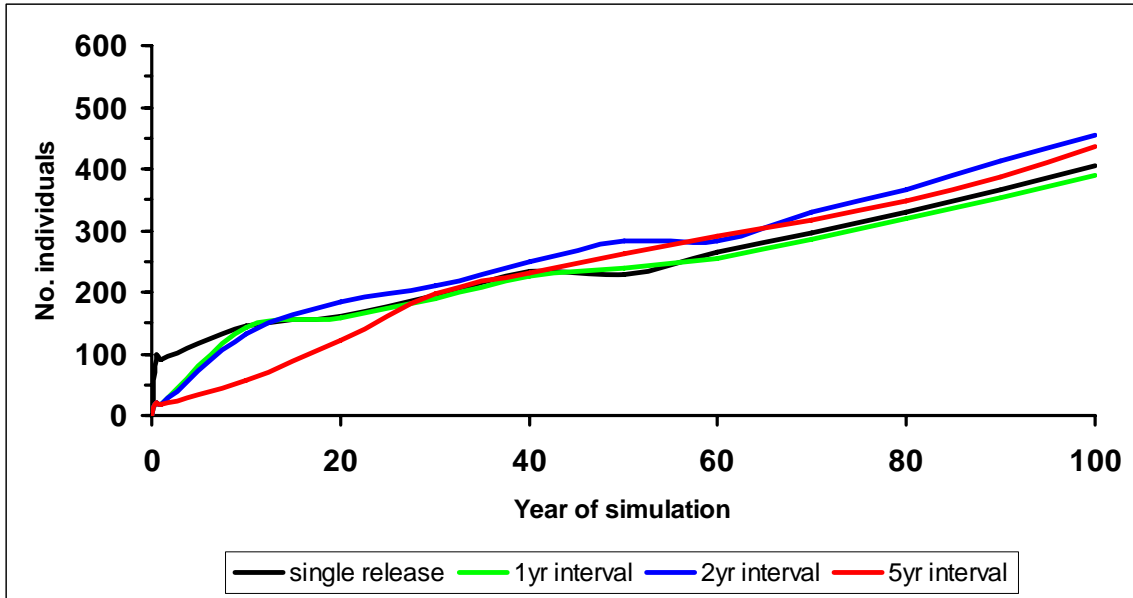


Figure 5.16. Population trajectories for founder population of 100 adult gopher tortoises released as a single release (black) or a series of five releases of 20 adults each over 1-yr (green), 2-yr (blue), and 5-yr (red) intervals.

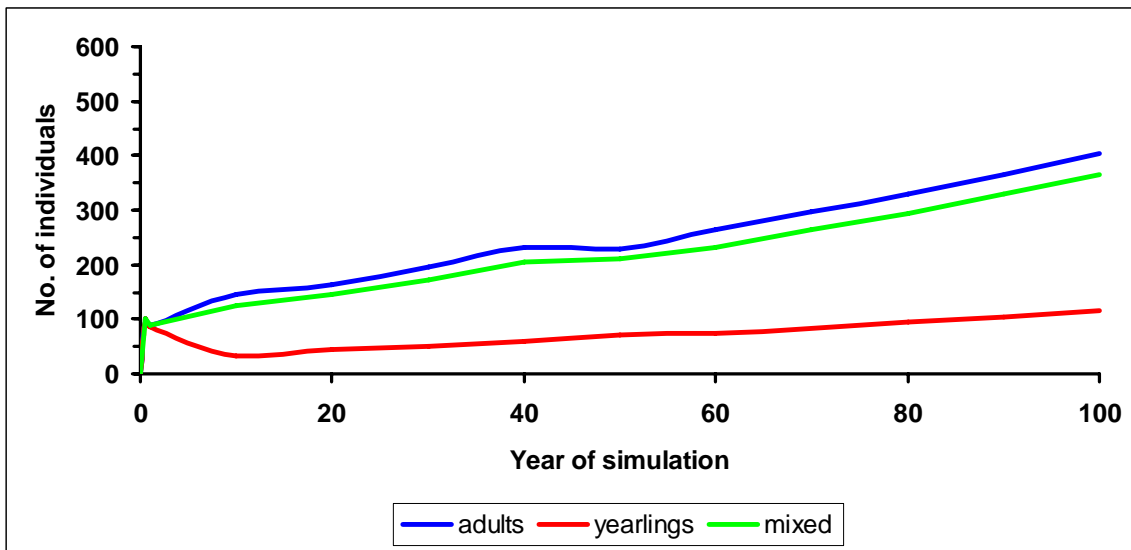


Figure 5.17. Population trajectories for founder populations established through the release of 100 adults (blue), yearlings (red), or a mixed population of adults, subadults, and juveniles (green).

Appendix 5.1. Stable age distribution calculated by VORTEX for an initial population of 100 individuals.

Age	Males	Females	Total no. indiv.
1	5	5	10
2	2	2	4
3	1	1	2
4	1	1	2
5	1	1	2
6	1	1	2
7	1	1	2
8	1	1	2
9	1	1	2
10	1	1	2
11	1	1	2
12	0	0	0
13	1	1	2
14	1	1	2
15	1	1	2
16	1	1	2
17	0	0	0
18	1	1	2
19	1	1	2
20	1	1	2
21	0	1	1
22	1	1	2
23	1	0	1
24	0	1	1
25	1	1	2
26	1	1	2
27	0	1	1
28	1	0	1
29	1	1	2
30	0	1	1
31	1	1	2
32	1	1	2
33	0	0	0
34	1	1	2
35	0	1	1
36	1	1	2
37	0	1	1
38	1	1	2
39	1	0	1
40	0	1	1
41	1	1	2
42	0	1	1
43	1	1	2
44	0	0	0
45	1	1	2

<b>Age</b>	<b>Males</b>	<b>Females</b>	<b>Total no. indiv.</b>
46	0	1	1
47	1	1	2
48	0	1	1
49	1	1	2
50	0	0	0
51	1	1	2
52	0	1	1
53	0	1	1
54	1	1	2
55	0	1	1
56	1	0	1
57	0	1	1
58	1	1	2
59	0	1	1
60	0	1	1
Total	44	56	100

Appendix 5.2. Parameter estimates used in the VORTEX baseline model for naturally occurring gopher tortoise populations. Important model assumptions include: 1) sex ratio is 1:1; 2) mortality is equal between males and females; 3) mortality is stage-based rather than age-based ; 4) fecundity does not increase with age; and 5) dispersal is equivalent to death of the individual.

Model input parameter	Parameter estimate	Justification
<b>Breeding system</b>	polygynous	
<b>Age at first reproduction (F/M)</b>		Site-specific factors (such as location within geographic range and habitat quality) will have systematic effects on tortoise growth and, as a result, age at maturity. Although length of the activity season (and opportunity for growth) varies with latitude, there is also evidence growth rates among tortoises can vary significantly among local populations as a result of habitat quality. Habitat quality can be manipulated through management; it is predicted that viability of populations at the periphery of species' range will be less resilient to marginal habitat conditions
Southern periphery - optimal habitat	13 / 12	
South periphery - marginal habitat	15 / 13	
Central range- optimal habitat	15 / 11	
Central range - marginal habitat	17 / 15	
Northern/western periphery - optimal habitat	20 / 17	
Northern/western periphery - marginal habitat	23 / 20	
<b>Maximum age of reproduction</b>	60	
<b>Annual % adult females reproducing (S.D.)</b>		Annual proportion of females in a population reproducing will be greater and less variable from year to year in optimal habitat than marginal habitat. I chose less optimistic values (even under "optimal" habitat) than the values used in Miller et al. 2001.
optimal habitat	95 (5)	
marginal habitat	80 (10)	
<b>Maximum clutch size</b>	10	
<b>Mean clutch size</b>		Mean clutch sizes are categorized according to location within geographic range. Model constraints assume that clutch sizes do not vary with age of female; although this assumption may be violated, there are no data to estimate age-specific fecundity. Individual variation (due to body size) can be modeled by constraining distribution of clutch sizes within a given year. Year to year variation in mean clutch size will be reflected in S.D.
Southern periphery	7.5	
Central range	6.75	
Northern/western periphery	5	
<b>Overall offspring sex ratio</b>	0.5	
<b>All adult males in breeding pool?</b>	Yes	
<b>% annual mortality (SD)*</b>		Annual mortalities are based on information from the literature (including Miller et al. 2001) and are assumed to be most influenced by environmental stochasticity, modeled in the S.D. There are very few data available in literature on which to base survivorship/mortality estimates. Unpublished data will need to be solicited from researchers or at least estimates need to be reviewed by experts. Craig Guyer sent Conecuh mark-recapture data set to use in calculating survivorship estimates; will also send data for two other sites - Wade Tract & Ichauway.
hatchlings	96	
yearlings	55	
juveniles (age 2-4)	25	
subadult	3	
adult	1.5	

Appendix 5.3. Manipulations of the baseline model for demographic sensitivity testing. The simulated population has an initial size of 100 individuals and occurs in optimal habitat in the central range. The original parameter values used in the baseline model are represented by “B.”

Scenario name	Variable modified	Relationship to baseline	Numeric value
ST.Scenario 17.max_longev(40)	MaxAgeRepr	B - 20	40
ST.Scenario 17.max_longev(50)	MaxAgeRepr	B - 10	50
ST.Scenario 17.max_longev(70)	MaxAgeRepr	B + 10	70
ST.Scenario 17.max_longev(80)	MaxAgeRepr	B + 20	80
ST.Scenario 17.max_longev(100)	MaxAgeRepr	B + 40	100
ST.Scenario 17.sex_ratio(1)	SexRatio	B*.8	40
ST.Scenario 17.sex_ratio(2)	SexRatio	B*.9	45
ST.Scenario 17.sex_ratio(3)	SexRatio	B*1.10	55
ST.Scenario 17.sex_ratio(4)	SexRatio	B*1.2	60
ST.Scenario 17.clutch_size(-2)	MeanProgenyPerYr	B-2	4.75
ST.Scenario 17.clutch_size(+2)	MeanProgenyPerYr	B+2	8.75
ST.Scenario 17.adult_surv(+05)	AdultSurv	B*.95	+5%
ST.Scenario 17.adult_surv(-05)	AdultSurv	B*1.05	-5%
ST.Scenario 17.adult_surv(+10)	AdultSurv	B*.90	+10%
ST.Scenario 17.adult_surv(-10)	AdultSurv	B*1.10	-10%
ST.Scenario 17.perc_repro(+10)	PercentBreed_Pop1	B*1.10	+10%
ST.Scenario 17.perc_repro(-10)	PercentBreed_Pop1	B*.9	-10%
ST.Scenario 17.perc_repro(+20)	PercentBreed_Pop2	B*1.2	+20%
ST.Scenario 17.perc_repro(-20)	PercentBreed_Pop3	B*.8	-20%
ST.Scenario 17.hatch_surv(x2)	Mortality_Age0	B*.5	2x
ST.Scenario 17.hatch_surv(x5)	Mortality_Age0	B*.2	5x
ST.Scenario 17.hatch_surv(x10)	Mortality_Age0	B*.1	10x
ST.Scenario 17.hatch_surv(+10)	Mortality_Age0	B*.9	+10%
ST.Scenario 17.hatch_surv(+20)	Mortality_Age0	B*.8	+20%
ST.Scenario 17.hatch_surv(+5)	Mortality_Age0	B*.95	+5%
ST.Scenario 17.hatch_surv(+1)	Mortality_Age0	B*.99	+1%
ST.Scenario 17.hatch_surv(+2)	Mortality_Age0	B*.98	+2%
ST.Scenario 17.hatch_surv(+3)	Mortality_Age0	B*.97	+3%
ST.Scenario 17.hatch_surv(+4)	Mortality_Age0	B*.96	+4%
ST.Scenario 17.yearling_surv(+10)	Mortality_Age1	B*.9	+10%
ST.Scenario 17.yearling_surv(+20)	Mortality_Age1	B*.8	+20%
ST.Scenario 17.yearling_surv(x2)	Mortality_Age1	B*.5	2x
ST.Scenario 17.juv_surv(+10)	Mortality_Age2to4	B*.9	+10%
ST.Scenario 17.juv_surv(+20)	Mortality_Age2to4	B*.8	+20%



Appendix 5.4. Translocation scenarios reflecting different release protocols for founder population of 100 individuals released into optimal habitat in the central range.

Scenario descriptors (user defined)	Initial population size	Supplementation option					
		Last yr	Interval	No. of yearlings	No. of juveniles	No. of subadults	No. of adults
Initial population size_ founder description_ release interval	Initial population size						
0_100adult_single_rel	0	1	1				90
0_100adult_annual_rel	0	5	1				18
0_100adult_2yr_interv	0	10	2				18
0_100adult_5yr_interv	0	25	5				18
10_100adult_single_rel	10	1	1				90
10_100adult_annual_rel	10	5	1				18
10_100adult_2yr_interv	10	10	2				18
10_100adult_5yr_interv	10	25	5				18
20_100adult_single_rel	20	1	1				90
20_100adult_annual_rel	20	5	1				18
20_100adult_2yr_interv	20	10	2				18
20_100adult_5yr_interv	20	25	5				18
50_100adult_single_rel	50	1	1				90
50_100adult_annual_rel	50	5	1				18
50_100adult_2yr_interv	50	10	2				18
50_100adult_5yr_interv	50	25	5				18
0_100yearling_single_rel	0	1	1	87			
0_100yearling_annual_rel	0	5	1	17			
0_100yearling_2yr_interv	0	10	2	17			
0_100yearling_5yr_interv	0	25	5	17			
10_100yearling_single_rel	10	1	1	87			
10_100yearling_annual_rel	10	5	1	17			
10_100yearling_2yr_interv	10	10	2	17			
10_100yearling_5yr_interv	10	25	5	17			
20_100yearling_single_rel	20	1	1	87			
20_100yearling_annual_rel	20	5	1	17			
20_100yearling_2yr_interv	20	10	2	17			
20_100yearling_5yr_interv	20	25	5	17			
50_100yearling_single_rel	50	1	1	87			
50_100yearling_annual_rel	50	5	1	17			
50_100yearling_2yr_interv	50	10	2	17			
50_100yearling_5yr_interv	50	25	5	17			
0_100mixed_single_rel	0	1	1		9	27	54
0_100mixed_annual_rel	0	5	1		2	6	11
0_100mixed_2yr_interv	0	10	2		2	6	11
0_100mixed_5yr_interv	0	25	5		2	6	11
10_100mixed_single_rel	10	1	1		9	27	54
10_100mixed_annual_rel	10	5	1		2	6	11
10_100mixed_2yr_interv	10	10	2		2	6	11
10_100mixed_5yr_interv	10	25	5		2	6	11

<b>Scenario descriptors (user defined)</b>	<b>Initial population size</b>	<b>Supplementation option</b>					
<b>Initial population size_ founder description_ release interval</b>	<b>Initial population size</b>	<b>Last yr</b>	<b>Interval</b>	<b>No. of yearlings</b>	<b>No. of juveniles</b>	<b>No. of subadults</b>	<b>No. of adults</b>
20_100mixed_single_rel	20	1	1		9	27	54
20_100mixed_annual_rel	20	5	1		2	6	11
20_100mixed_2yr_interv	20	10	2		2	6	11
20_100mixed_5yr_interv	20	25	5		2	6	11
50_100mixed_single_rel	50	1	1		9	27	54
50_100mixed_annual_rel	50	5	1		2	6	11
50_100mixed_2yr_interv	50	10	2		2	6	11
50_100mixed_5yr_interv	50	25	5		2	6	11

CHAPTER 6  
CONCLUSIONS

## SUMMARY AND CONCLUSIONS

This dissertation provides a framework for measuring translocation success that includes monitoring three processes that influence population stability – emigration, survivorship and reproduction. The preceding chapters illustrate how the framework can be applied to a target species, using the gopher tortoise (*Gopherus polyphemus*) as a case study. Collectively, the studies presented here represent one of the few attempts to comprehensively evaluate the utility of translocation as a management tool in a single species of turtle.

In Chapter 2, we experimentally tested the effects of three penning treatments on short-term site fidelity of translocated gopher tortoises following release. Tortoises subjected to prior on-site penning (i.e., soft-release) exhibited increased site fidelity compared to immediately-released tortoises (i.e., hard-release; 23.1%), with site fidelity increasing with longer penning durations (61.5% with 9-mo. penning, 91.7% with 12-mo. penning). Most initial dispersal attempts occurred shortly following release and tortoises established well-defined home ranges by the end of the first year. Immature tortoises had smaller home ranges and were less likely to disperse than adult tortoises, suggesting that life stage of release animals can affect site fidelity. In addition, propensity to disperse varied among individuals of the same life stage regardless of penning treatment, indicating that other, currently unknown factors can also influence individual responses to translocation.

In Chapter 3, we used long-term mark-recapture data to estimate apparent survival of gopher tortoises following translocation and to determine whether apparent survival changed as a function of time since release. Apparent survival of translocated tortoises (all unpenning) was lowest during the first six months following release (67%) but consistently high (98% per six-month interval, 96% annually) once tortoises became established as residents. We attributed the

initially low apparent survival to permanent dispersal of tortoises from the release area.

Apparent survival of previously established residents was not adversely affected by subsequent releases of additional tortoises.

In Chapter 4, we investigated the mating system of a translocated population of gopher tortoises established through multiple releases. Rather than quantifying recruitment levels, we examined parentage patterns by genetic analysis of offspring. During the two year study, we documented successful reproduction between tortoises from different release groups, suggesting that at least some animals from each release group had become socially integrated into the population. Reproductive success (as measured by number of offspring sired) varied among males, and successful sires were significantly larger than males to which no offspring were attributed. The three most successful males represented only 18.6% of the male breeding pool but sired 60.3% of the offspring sampled, and all three males were from the first group of tortoises released. Prior residence could influence reproductive success in translocated tortoises, but other possible explanations (e.g., age effects, temporal variation in individual reproductive success, inbreeding avoidance, chance, etc.) could not be eliminated. Further investigation is needed to identify the causes contributing to the intriguing variation in reproductive success we observed.

Finally, in Chapter 5, we used information published in the literature, data presented in Chapters 2-4, and unpublished data to construct population viability models for both naturally-occurring and translocated populations of gopher tortoises. Our models predicted that populations starting with at least 100 individuals were fairly resilient to extinction under most scenarios, although larger populations ( $\geq 250$  tortoises) were needed under the least favorable conditions (northern geographic range and marginal habitat quality) to avoid extinction during

the 100 year simulations. All baseline models for naturally occurring populations resulted in population declines. Further analyses of our parameter estimates indicate that model outcome was very sensitive to parameters for which few data were available (e.g., immature survivorship), and suggest that additional data are needed to adequately characterize the life history and population dynamics of gopher tortoises. A comparison of translocation scenarios predicted that short-term effects due to release protocols (e.g., penning treatment) could have long-term demographic consequences for translocated populations.

## RECOMMENDATIONS

Based on the research presented in this dissertation and the work of other researchers studying translocation of gopher tortoises, we make the following recommendations for evaluating translocation success in other turtle species:

- 1) Require post-translocation monitoring of the manipulated populations.
- 2) Monitor the three population processes affecting population stability – dispersal, mortality, and reproduction.
- 3) Encourage long-term studies of naturally-occurring “control” populations for comparison with translocated populations.
- 4) Replicate release and monitoring protocols or repeat previously conducted studies to verify repeatability of results.
- 5) Incorporate an experimental component into the release and monitoring protocols to test specific hypotheses.