LONG-TERM POPULATION ECOLOGY AND MOVEMENT PATTERNS OF GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*) IN SOUTHWEST GEORGIA

by

ALEXANDER DAVID WRIGHT

(Under the Direction of Jeffrey Hepinstall-Cymerman)

ABSTRACT

Habitat loss, fragmentation, and degradation have led to an estimated 80% range-wide decline of gopher tortoise (*Gopherus polyphemus*) populations across the Southeastern Coastal Plain. Recently, the gopher tortoise was identified as a candidate for listing under the Endangered Species Act in the eastern part of its range. To support an adaptive landscape planning and decision framework for gopher tortoise conservation, I examined the population dynamics and movement patterns of four gopher tortoise populations on a large private reserve in southwestern Georgia, where tortoises were previously marked/recaptured from 1995-2000. It is critical to understand how tortoise populations vary in space and time at large spatial and temporal scales to protect a long-lived species, such as the gopher tortoise, into perpetuity. With further understanding of the long-term population ecology and movement patterns, we can better evaluate the roles of emigration and survival within populations to inform reserve design and decision analysis for the species' conservation.

INDEX WORDS: gopher tortoise, *Gopherus polyphemus*, population dynamics

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DEDICATION

This thesis is dedicated to my late mother, Sandy Wright.

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CHAPTER 1

INTRODUCTION & LITERATURE REVIEW

Introduction

The gopher tortoise (*Gopherus polyphemus*) is a keystone species of the longleaf pine (*Pinus palustris*) ecosystem in the coastal plain of the southeastern United States (Auffenberg and Franz 1982, Eisenberg 1983). The gopher tortoise is considered a keystone species because its burrows are known to provide habitat for over 360 commensal species, including at least 302 invertebrate species and 60 vertebrate species (Eisenberg 1983, Jackson and Milstrey 1989), as well as federally threatened species, such as the eastern indigo snake (*Drymarchon couperi*). Commensal species use the burrow microhabitat as refuge from fire, predators, and the effects of extreme or variable temperature events, which may increase in frequency or duration as a result of global climate change (Pike and Mitchell 2013). In addition, gopher tortoises increase understory plant diversity through habitat modification by creating colonization sites of bare mounds of soil for early successional plant species (Kaczor and Hartnett 1990), and potentially through seed dispersal (Auffenberg 1969, Boglioli et al. 2000, Birkhead et al. 2005).

The geographic distribution of longleaf pine habitat in the southeastern United States has been reduced to small and highly fragmented forests covering <3% of its pre-1880 range when it covered 40% of the region (Noss et al. 1995). The widespread loss of longleaf pine habitat and other upland habitats occupied by tortoises, along with other factors such as disease and predation, has led to an 80% range-wide decline of gopher tortoise populations (Auffenberg and

Franz 1982). Due to these threats, the species has recently been identified as a candidate for federal listing as Threatened under the Endangered Species Act in its eastern range (USFWS 2011). Western populations (west of the Mobile and Tombigbee Rivers) are currently listed as threatened under the law (USFWS 1987), and the species is given state-level protection throughout its range (Ernst et al. 1994).

There has been significant research on home range size, reserve area requirements, behavior, and short-term population dynamics of gopher tortoises (McRae et al. 1981b, Cox et al. 1987, Diemer 1992, Smith et al. 1997, Eubanks et al. 2002, Eubanks et al. 2003, Nomani et al. 2008, Styrsky et al. 2010). However, to date, there has been only one published study on long-term population dynamics (Berish et al. 2012), and no studies on large-scale movement patterns of the gopher tortoise, a species that has an estimated lifespan of greater than 60 years (Landers 1980). It is critical to understand these processes and behaviors at large spatial and temporal scales to protect a long-lived species, such as the gopher tortoise, into perpetuity.

Objectives

To address the need for additional information, we investigated the long-term population ecology and large-scale movement patterns of gopher tortoises on and around Ichauway, the ~11,700 ha research site of the Joseph W. Jones Ecological Research Center. I conducted a mark-recapture study on four populations of gopher tortoises where individuals had been marked between 1995 and 2000. To better understand movement, we used site-wide gopher tortoise presence data and environmental variables to construct a probabilistic sampling frame to survey and trap habitat surrounding the original sites as well, on and off the reserve. We used the mark-recapture data collected in 1995-2000 from the four study populations of gopher tortoises in concurrent with our present mark-recapture efforts of the study populations and surrounding landscape matrix to address the following objectives:

1. To estimate annual apparent survival for four distinct age-classes (juveniles, sub-adults, males, and females) of gopher tortoises to understand how tortoises persist on the landscape under various site characteristics (Chapter 2).
2. To estimate annual and long-term gopher tortoise movement patterns to understand the scale at which connectivity may be relevant to gopher tortoise conservation management in both contiguous and fragmented landscapes (Chapter 3).

The results of this study are being used to inform a spatially explicit population modeling framework for gopher tortoises in the state of Georgia. This work is part of a larger collaborative effort to develop an adaptive landscape planning and decision framework to be implemented by the Georgia Department of Natural Resources for the statewide conservation of gopher tortoise populations.

Literature Review

Southeastern Coastal Plain Ecology & the Longleaf Pine Ecosystem

The largest ecoregion in the State of Georgia is the Coastal Plain, covering approximately ~9.2 million hectares. The relatively flat landscape and well-drained soils of the ecoregion developed due to the advancements and retreats of both the Atlantic Ocean and the Gulf of Mexico since the Cretaceous period, exposing intermixed layers of sands and clays (Edwards et al. 2013). Historically, the Coastal Plain ecoregion was dominated by the longleaf pine ecosystem, its range covering approximately 40% of the region (Noss et al. 1995). The longleaf pine ecosystem is an upland, fire-dependent ecosystem characterized by an open canopy and diverse herbaceous groundcover (Landers et al. 1995). Longleaf pine is a slow-growing and long-lived conifer and is usually found in a gradient of soil types ranging from poorly-drained flatwoods to well-drained sandhills (Landers et al. 1995). Historically, the ecosystem covered as much as 92 million acres throughout the southeastern U.S. (Ware et al. 1993), but has been reduced to small and highly fragmented forests covering <3% of its pre-1880 range (Noss et al. 1995). Most longleaf pine forests have been converted to agricultural and silvicultural land use, and fire suppression (Frost 1993), which allows fire-sensitive and fast-growing species to establish and compete with longleaf pine, increasing percent canopy cover which has rendered remaining longleaf pine stands unsuitable for tortoises (Landers et al. 1995). The longleaf pine ecosystem is considered one of the most globally imperiled ecosystems (Ware et al. 1993, Noss et al. 1995).

Gopher Tortoise Ecology & Natural History

The gopher tortoise is a terrestrial, herbivorous chelonian endemic to the southeastern United States, with its historic range overlapping much of that of the longleaf pine ecosystem (Auffenberg and Franz 1982). Individuals dig one or more burrows in deep, sandy soils which are, on average, 4.6 m long and at least 1 m deep (Hansen 1963, Jones and Dorr 2004). The burrows protect tortoises, and over 360 commensal species, from desiccation, fire, and predation (Auffenberg and Franz 1982, Jackson and Milstrey 1989). In addition, the gopher tortoise increases understory plant diversity through habitat modification by creating bare mounds of soil that are colonization sites for early successional plant species (Kaczor and Hartnett 1990), and potentially through seed dispersal (Auffenberg 1969, Boglioli et al. 2000, Birkhead et al. 2005).

Most activities (e.g. mating, foraging, and nesting) are centered around the burrow. Burrow use is often reported as number of burrows/year, because tortoises generally use multiple different burrows, e.g., 5.2 +/- 0.32 burrows per year for females and 10.0 +/- 0.53 burrows per year for males (Eubanks et al. 2003), but in well managed habitat gopher tortoises may retain the same burrows for decades (Guyer and Hermann 1997). In a more recent study, Guyer et al. (2012) found that tortoises, on average, use 2.5 burrows. Essential habitat characteristics for the gopher tortoise include well-drained sandy soil for burrowing, adequate herbaceous vegetation, and sunlit nesting sites (Landers 1980, Auffenberg and Franz 1982). An open canopy structure supports a diverse herbaceous ground cover by allowing light to penetrate to the groundcover layer, also creating a beneficial thermoregulatory environment by providing sunny sites for basking and nesting (Auffenberg and Franz 1982). Jones and Dorr (2004) found that active burrow occurrence was negatively related to total canopy closure and positively related to deep, sandy soils, and Boglioli et al. (2000) documented a mean 30% canopy cover within gopher tortoise habitats compared with a mean 60% canopy cover of control habitats.

Gopher tortoises are best identified by their moderatelydomed, greyish black carapace, elephantine hind limbs, and wide, flattened front limbs covered in hard scales (Jensen 2008). Adult males in southern Georgia reach sexual maturity at approximately 16 to 18 years of age and a carapace length (CL) of 230-240 mm. Females reach sexual maturity around 19 to 21 years of age and a CL of 250-265 mm (Landers et al. 1982). Tortoises in the southern portion of their range reach sexual maturity at smaller body sizes which may be related to warmer year-round temperatures, or tohigher nutrtitional forage (Diemer and Moore 1994, Small and Macdonald

2001). Other sexually dimorphic traits include a plastron concavity which aids males during copulation, an elongated gular projection which aids males in combat during territorial defense, and wider anal notch measurements in males than females (McRae et al. 1981a, Mushinsky et al. 1994). Hatchling gopher tortoises are approximately 42 mm in length (Jensen 2008), and transition into a secondary immature stage, sub-adult, at approximately 150 mm when the shell hardens (McRae et al. 1981b).

Gopher Tortoise Movement Patterns & Population Dynamics

Gopher tortoises have relatively small home range sizes, ranging from 0.08 to 1.7 hectares per tortoise (McRae et al. 1981b, Diemer 1992, Smith et al. 1997, Eubanks et al. 2002). The home range of the gopher tortoise has been shown to be inversely related to the amount of available herbaceous vegetation (Auffenberg and Iverson 1979). Gopher tortoises will frequently abandon their burrows in closed-canopy stands as understory herbaceous plants are lost (Aresco and Guyer 1999, Berish et al. 2012). McCoy et al. (2013) reported that the homing accuracy of translocated tortoises was strongly correlated to the openness of the habitat, and observed that tortoises would not enter unburned plots, but instead would move along the fire lanes that acted as plot boundaries.

Eubanks et al. (2002) calculated reserve area requirements for gopher tortoises using available home range data, with estimates ranging from 24.8 to 81.3 hectares of habitat for a population of 50 adult individuals. However, McCoy and Mushinsky (2007) estimated a reserve area of 140 to 150 hectares to support 110 to 130 individuals. Population densities are reported to range from 0.2 ± 0.04 to 3.14 ± 0.61 tortoises per hectare (Boglioli et al. 2000, Nomani et al. 2008, Smith et al. 2009, Styrsky et al. 2010, Ballou 2012, Berish et al. 2012). Guyer et al. (2012)

proposed that in populations with densities below 0.4 tortoises per hectare, movements are altered in ways that might affect population viability because of changes in social structure and gene flow.

To create effective reserves for the gopher tortoise, it is critical to understand how populations vary in space and time under various habitat and landscape conditions. Although a comprehensive understanding of demographic processes of gopher tortoises is limited, apparent survival rates of adult and hatching gopher tortoises are available (McCoy et al. 2014). Tortoises are most susceptible to predation during the hatchling life stage while the shell has not yet hardened, with survival rates ranging from 4 to 34%(Perez-Heydrich et al. 2012). Tuberville at al. (2014) estimated mean apparent survival estimates for both mature adults (males, 86.8-94.6%; females, 95.5 – 98.0%) and immature tortoises representing both juveniles and sub-adults (69.7-82.4%) of populations on protected lands. The authors hypothesize that lower apparent survival estimates of males as compared to females may reflect a difference in dispersal rates. This hypothesis seems to be supported by a radio-telemetry study in which onlyadult males were found to emigrate (Eubanks et al. 2003), which suggests that reproduction is a major stimulus for dispersal.

Long-term Movement Patterns & Population Dynamics

Our current knowledge of home range suggests tortoises have small annual home ranges; however, long-term data are lacking across different habitat types are lacking (Berish et al. 2012). In one of the longest-term published studies, Douglass (1986) reported home ranges for two individual males that were occasionally observed for five (4.2 hectares) and six (6.3 hectares) year periods. In a long lived species such as the gopher tortoise, it is important to understand the extent to which individuals move across the landscape and how their movement patterns and population dynamics change over time and space. Berish et al. (2012), found that after 27 years, 88% of marked tortoises were found within 200 meters from their previous capture sites. However, their overall recapture rate was only 8%, and the fate (emigration vs. mortality) of the other 92% of marked tortoises is unknown. Additionally, the population studied by Berish et al. (2012) was on a small tract of habitat within an industrial pine forest that had been subjected to frequent clear-cuts, site preparation, and replanting. In a study at Camp Shelby, Mississippi, Richter et al. (2011) documented only four recaptures of tortoises greater than 2.5 km from the initial capture site over a 12 year maximum capture interval. However, the authors found no evidence of distinct population structure across the ~56,000 site. The authors hypothesize the lack of population structure may relate more to recent land use change in the area than to tortoise demographic processes. So, it is critical to understand the population dynamics at large spatial and temporal scales to protect a long-lived species, such as the gopher tortoise, into perpetuity. With further understanding of the long-term population ecology and large-scale movement patterns of gopher tortoises, we can better evaluate the connectedness and viability of known populations to inform reserve design and decision analysis for the species' conservation.

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CHAPTER 2

LONG-TERM POPULATION ECOLOGY OF GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*) IN SOUTHWEST GEORGIA

Introduction

Due to population declines (Auffenberg and Franz 1982), associated threats, and its role as a keystone species (Eisenberg 1983, Jackson and Milstrey 1989, Kaczor and Hartnett 1990) of an imperiled ecosystem (Noss et al. 1995), the gopher tortoise has recently been identified as a candidate for federal listing as Threatened under the Endangered Species Act in its eastern range (USFWS 2011). Even on protected lands, there has been a documented decline of tortoise populations, such as those observed at 8 of 10 sites in Florida (McCoy et al. 2006). In light of its imperiled status, there is an increased need for an understanding of the underlying mechanisms that drive the long-term persistence of gopher tortoise populations. The life-history traits characteristic of the gopher tortoise (i.e. long-lived, late to reach sexual maturity, and low reproductive output) pose challenges to the continued growth and persistence of gopher tortoise populations under documented threats (McCoy et al. 2014).

An increased understanding of the demographic parameters, such as apparent survival, through mark-recapture efforts may provide additional insight into the decline of tortoise populations across its range. However, for a species that has an estimated lifespan of 40 to 60 years (Landers 1980), short-term studies do not adequately explain apparent survival over large enough temporal scales to guide land-management activities for the protection of the species into perpetuity, and long-term population studies are generally lacking (Berish et al. 2012, Tuberville et al. 2014). Additionally, understanding the population dynamics in relatively undisturbed habitat (e.g. not experiencing large clear cuts, site preparation, and replanting) may better represent the ecology of this organism (Dodd and Seigel 1991, Eubanks et al. 2003), and such habitats will comprise necessary conservation targets. Tortoises are most susceptible to predation during the hatchling life stage while the shell has not yet hardened, with survival rates ranging from 0.040 to 0.340 (Perez-Heydrich et al. 2012). However, recent long-term studies have focused on survival of mature and immature individuals, with both juvenile and subadults grouped into a single "immature" age-sex class.

As conservation planners and policymakers make management decisions to implement conservation actions using population viability analyses, it is important to have robust estimates of apparent survival. In this study, I investigated the long-term population ecology of gopher tortoises on Ichauway, the ~11,700 ha research site of the Joseph W. Jones Ecological Research Center. My objective was to better understand the demographic processes driving the persistence of gopher tortoise populations on the landscape. Specifically, I used mark-recapture data on gopher tortoises collected from four study populations with varying site characteristics in 1995-2000, and mark-recapture data on gopher tortoises from the same sites in 2014-2015 that I gathered to estimate annual apparent survival rates for four distinct age-sex classes (juveniles, sub-adults, males, and females).

Methods

Study Area

This research was conducted at Ichauway, the research site of the Joseph W. Jones Ecological Research Center in Baker County, Georgia, 35 km southwest of Albany, GA (Figure 2.1). Ichauway is an 11,700 ha ecological reserve mainly composed of longleaf pine – wiregrass (*Aristida beyrichiana*) habitat interspersed with small stands of planted pine, wildlife food plots, and wetlands. Ichauway is managed with prescribed burns every 1 to 2 years and hardwood removal, to restore an open canopy and a diverse herbaceous understory. Tortoises occur on all non-floodplain soils across Ichauway (an area of >6800 ha in size) and overall density is 0.7 tortoises per ha (unpublished data). My research focused on four study populations (Figure 2.2.) of gopher tortoises at Ichauway that were surveyed and trapped for mark-recapture between 1995 and 2000 (C. Guyer, unpublished data). Although, not all study populations were surveyed every year (see details below).

The four study populations (Green Grove, Sand Pond, Sandy Desert, and Slash Pine) vary in size (20-75 ha) and the initial observed population size and structure (Figure 2.3.; unpublished data, C. Guyer). 'Green Grove' and 'Sand Pond' are in the northern section of the property, in a relatively contiguous, natural longleaf habitat matrix (Figure 2.4.). Green Grove is approximately 75 hectares in size and is dominated by an open, longleaf pine overstory with a wiregrass understory (Table 2.1.). The site was surveyed and trapped every year between 1995-2000, and 322 individuals were marked during that period. Green Grove is bordered by a rural highway and the property border on its southern boundary, hardwood-dominated forest on its eastern boundary, but by dirt roads and similar longleaf pine-wiregrass habitat in all other directions. For the recent sampling, ~2 ha grids were randomly selected within the study population to account for approximately ~30% of the total area. Sand Pond is a linear strip of natural longleaf habitat covering approximately 20 hectares (Table 2.1.). The site was surveyed and trapped every year between 1995-1998, and 96 individuals were marked during that period. The site is bordered on its eastern border by a large, semi-ephemeral wetland. It is bordered by dirt roads and similar longleaf pine-wiregrass habitat in all other directions.

'Sandy Desert' and 'Slash Pine' are in the central section of the property in a relatively fragmented, and human-influenced landscape with patches of natural longleaf habitat (Figure 2.4.). Sandy Desert is approximately 25 hectare in size and is dominated mixed pine/hardwood forests with patches of natural longleaf habitat (Table 2.1.). The site was surveyed and trapped every year between 1995-1998, and 86 individuals were marked during that period. It is bordered on its southern boundary by the property boundary and a large, center-pivot agricultural field. On its western boundary, it is partially bordered by the property boundary and an unburned mixed pine-oak forest. To the northwest, it is bordered by a cypress-dominated wetland. On its eastern side, it is bordered by a pine forest matrix with interspersed wildlife food plots. To the north, it is connected with similar longleaf pine habitat. Slash Pine is a 75 year old pine plantation dominated by slash pine (*Pinus elliottii*), but is currently being experimentally restored to a longleaf pine forest (Table 2.1.). The understory in Slash Pine is not dominated by wiregrass, but by other herbaceous and woody plants. It is approximately 55 hectares in size, and was surveyed and trapped in 1998-1999 resulting in the capture of 60 tortoises. Slash Pine is bordered to the south by a busy, two-lane state highway (Highway 91), to the east by the Ichauwaynochaway Creek, to the west by a large, center-pivot agricultural field, and by administrative, research, and residential buildings to the north.

Current Tortoise Sampling Effort

Between 2014 (May-August) and 2015 (June-July), each study population was surveyed and re-trapped once. All areas were surveyed using the line transect distance sampling (LTDS) method with a double observer (Buckland et al. 2001). One observer walked along a center line of a 20-m wide transect, followed by a second, independent observer (Nichols et al. 2000, Nomani et al. 2008), searching for gopher tortoise burrows or tortoises above ground with observers switching roles on consecutive transects. All burrows were scoped with a burrow camera (Environmental Management Services, Canton, GA) to determine tortoise occupancy. Havahart® live traps (Lititz, PA) were set at the entrance of all occupied burrows and shaded with burlap to protect the trapped animal from overheating. If occupancy could not be determined from the burrow camera, a trap was set in front of the entrance and monitored for 1-2 weeks. Traps were checked twice daily and left out until the tortoise was captured. Where possible, we also hand-captured tortoises observed within the study populations. Locations of all tortoises were recorded using a F4 Tech® Flint S812 Handheld GPS Unit (Tallahassee, FL). These methods were selected to closely replicate those of the original study (Boglioli et al. 2000, Eubanks et al. 2003), in which multiple observers (1-3) would walk roughly parallel transects, marking all burrows with a handheld Trimble Global Positioning System unit (+/- 2 m). In the original study, all observed burrows were trapped to determine occupancy, and all individuals were marked by drilling marginal scutes of the carapace (Cagle 1939).

Captured tortoises were measured (carapace length, plastron length, plastron concavity, total length, gular length, anal width, anal notch, and mass) and examined to determine if the animal had been previously marked. Sex (for adults) was determined based on shell morphology (McRae et al. 1981a, Mushinsky et al. 1994), and juveniles were distinguished from sub adults based on carapace length (juveniles < 150 mm < subadults < 220-230 mm) for which sex cannot be determined. (Landers et al. 1982). Unmarked animals were individually marked by notching the marginal scutes with a Dremel® Stylus tool (Mt. Prospect, IL) (Cagle 1939, Norton et al. 2013). All equipment was cleaned with a 10% bleach solution between uses. Prior to marking, the portion of the shell to be notched was cleaned with a Clorox wipe and Bactine was applied to the area after the animal was marked. Marking and measurements were performed in the field and tortoises were released at the capture location (AUP# A2014 02-024-Y3-A1).

Statistical Analysis

I fit the capture data from both time periods to Cormack-Jolly-Seber (CJS) open population models using the RMark interface (Laake 2013) of Program MARK (White and Burnham 1999) in R (Team 2013) to estimate tortoise apparent survival (Φ), the probability an animal is alive and is located within the study area, and recapture probability (p). I modeled both parameters as functions of the factors age-sex (four classes: juvenile, subadult, male, or female), site (four sites), and time (two options: year-specific vs. constant). I considered factors in all additive combinations, and I also considered interactions for a total of 129 models. Because intervals between capture periods were unequal, the capture history record of each tortoise was annualized by including the number of years between sample periods. We fit models for juveniles and subadults only using data from the original study (1995-2000), and we fit models for adults using data from both studies (1995-2000, 2014-2015), thus restricting inference to survival within stages of age-sex class. I used an information theoretic approach, Akaike's Information Criterion (AIC) to evaluate the relative support for competing models and to identify the best fitting model (Burnham and Anderson 1998). To account for overdispersion in the data, I estimated the variance inflation factor (ĉ) of the saturated model to compute the quasi-likelihood AIC value (QAICc) for each model (White and Burnham 1999). I used the model-averaging feature in RMark to generate parameter estimates, and Program RELEASE (within MARK) to assess goodness of fit.

Results

The number of tortoises captured at each site varied greatly among different age-sex classes and by survey period, but recall I only sub-sampled Green Grove in 2015 (Table 2.2.). At Sand Pond, there were a total of 234 captures of 111 individuals over 5 capture periods, and 911 captures of 365 individuals at Green Grove over 7 capture periods. At Sandy Desert, there were a total of 209 captures of 96 individuals over 5 capture periods, and there were 110 captures of 72 individuals over 3 capture periods at Slash Pine. The goodness of fit testing revealed no violation of equal catchability or the effect of previous captures on detectability (Test 2: p-value=0.935, Test 3: p-value=0.4326). I estimated a variance inflation factor (ĉ) of my saturated model of 3.761411 and adjusted the results accordingly. The most parsimonious model (Table 2.3.) indicated additive site and age-sex class effects on apparent survival, and additive site and time effects of capture probability (accounting for W_i = 37% total weight among candidate models). Two other models were listed as having a $QAIC_c$ within two units of the top model, showing relatively equal support for those competing models. The model with the second most weight ($\Delta QAIC_c$ = 1.45, W_i = 18%) included only site as an effect of apparent survival. The model with the third most weight ($\Delta QAIC_c$ = 1.61, W_i = 16%) included site, age-sex class, and time as effects of apparent survival. Site and time affected capture probability in all of the top ten candidate models. Interactive effects were not significant contributors to apparent survival or capture probability. Model-averaged estimates of apparent survival are presented in Table 2.3. and Figure 2.5. There were no statistical differences among any site or age-sex class relationships due to overlapping confidence intervals, although some results may be of biological significance. Across all sites, apparent survival was highest for females, followed by males, subadults, and juveniles. For all age-sex classes, apparent survival was highest for Slash Pine, followed by Sandy Desert, Sand Pond, and Green Grove.

Discussion

While apparent survival of all age-sex classes was highest at Slash Pine and lowest at Green Grove,, it is important to note that apparent survival represents both the likelihood that a tortoise survives, and the likelihood that it does not emigrate from the study area (White and Burnham 1999). In a previous study, Tuberville et al. (2014), who found similar low apparent survival at Green Grove, hypothesized that Green Grove had reached carrying capacity and the increased social interactions and competition for resources may be displacing individuals. Additionally, of the four sites on Ichauway, Green Grove is bordered by natural longleaf habitat to the West and to the North, whereas Slash Pine,as described previously, is bordered by a fifth-order stream, agricultural landscapes, and urban features (e.g. roads, buildings). Thus, the lower apparent survival at Green Grove may result from higher dispersal rates from that particular study site based on the permeability of the surrounding landscape matrix and availability of suitable habitat nearby. It has been documented by McCoy et al. (2013) that tortoises do not seek good habitat but rather avoid bad habitat using visual cues (i.e. light). The authors argue this avoidance behavior will often confine individuals to small, isolated patches (such as Slash Pine), as long as the areas surrounding the occupied site offer less suitable habitat than the site itself.

Therefore, differences in apparent survival may not emerge from differences in site quality and size alone, but also from differences in dispersal rates related to habitat quality in the surrounding landscape matrix. Regardless of the habitat quality of the site, tortoises may not disperse if the habitat surrounding is seen as lower quality or impenetrable. Because the capacity of an organism to navigate in both space and time is a driving factor influencing the movement path of individuals, and is largely affected by the spatial structure of the environment (Nathan et al. 2008), this movement strategy may have a large effect on broad-scale ecological processes, such as gene flow, colonization rates, and population persistence (Bowler and Benton 2005). Therefore, maintaining contiguous landscapes for tortoises and removing impermeable barriers surrounding populations may be critical to the persistence of tortoise populations.

Among the age classes, adult female apparent survival was consistently highest, followed by adult males, subadults, and juveniles. It has been shown that males have significantly larger mean home range sizes than females (McRae et al. 1981b, Diemer 1992, Smith et al. 1997, Eubanks et al. 2003) which may have affected detection in my study, particularly when the home range centers of individuals lie near or outside the boundary of the study area. Recent studies focusing on gopher tortoise demography have analyzed juvenile tortoises and subadult tortoises as one group, immatures (Tuberville et al. 2008, Berish et al. 2012, Tuberville et al. 2014). We analyzed the two groups separately due to the increased predation risk of juvenile tortoises (carapace length of < 150 mm) related to the hardness of their shell (Landers et al. 1982). Although standard error estimates were high for juveniles (Table 2.4.), evidence to separately analyze juveniles and subadults is supportive, and we believe the separation of the two groups is more representative of the biology of the organism and its developmental stages.

Other studies have investigated annual apparent survival of gopher tortoises, in both naturally-occurring populations (Tuberville et al. 2014) and translocated populations (Ashton and Burke 2007, Tuberville et al. 2008). Interestingly, Tuberville et al. (2014) had analyzed mark-recapture data collected at Green Grove during the years of 1995-1999. Although I found a smaller difference in apparent survival among males and females (0.025) as compared to their study (0.087). This information may demonstrate that shorter-term studies may be adequate to describe apparent survival of gopher tortoises, although these studies may miss 'pulse' recruitment or dispersal events if they occur. Additionally, the results from my other three sites most closely resemble apparent survival of males and females at Conecuh National Forest (0.946 $\pm$ 0.039 and 0.980 $\pm$ 0.028, respectively; Tuberville et al. 2014) and of adults at St. Catherines Island, a translocated population (0.98 $\pm$ 0.01; Tuberville et al. 2008). Conecuh National Forest is located in south-central Alabama and the area studied is largely composed of slash pine plantations (Aresco and Guyer 1999). The study area at St. Catherines Island represents the primary area of suitable habitat in an old field on the northern half of the island. This may support the hypothesis that apparent survival is more sensitive to the influence of the habitat matrix surrounding the study areas (through the facilitation of emigration) than to habitat structure of the site itself. Further research on emigration patterns of gopher tortoises at sites of various management strategies is necessary to better understand this critical aspect of tortoise ecology.

Low apparent survival of tortoises 50-150 mm, as observed in this study, may indicate increased vulnerability of this age class. Conservation management tools, such as head-starting or predator removal, may be viable options to protect this vulnerable age-class for the persistence of gopher tortoise populations. Smith et al. (2013) found that mean nest survival and hatchling survival was significantly higher in mammalian predator-exclosure plots as compared to control sites. Green Grove had the highest proportion of both juveniles and subadults in the captured sample, whereas the other three sites had low proportions of both juveniles and subadults (Table 2.2.). This may potentially indicate either an overall lack of recruitment, or high natal dispersal. Additionally, juvenile and hatchling tortoises are harder to detect than larger individuals which may lead to their disproportionate under-representation among the distribution of individuals by age-sex class (Smith et al. 2009). Further research into the movement patterns of juvenile and subadult tortoises, and how recruitment varies across sites and management strategies, is necessary to ensure the long-term viability of gopher tortoise populations.

Consideration of the gopher tortoise as a candidate species for Threatened status under the U.S. Endangered Species Act has prompted long-term viability analyses to evaluate listing criteria and to design effective management strategies. Results of this study provide estimates of a key demographic parameter, apparent survival, reflecting the life history characteristics of the organism (i.e. long lived, slow to reach sexual maturity, low reproductive output, etc.) to aid these exercises. The findings of this study represent populations of various sizes with varying site characteristics that share a consistent management strategy, which remained relatively static throughout the duration of the entire study. This study adds to a set of similar studies across the range of the tortoise on a gradient of management strategies and habitat conditions (Ashton and Burke 2007, Tuberville et al. 2008, Berish et al. 2012, Tuberville et al. 2014) to offer a comprehensive understanding of how tortoises persist on the landscape.

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Table 2.1. The landscape composition of each study population (in hectares) by landcover type at Ichauway, Baker County, Georgia. SAP = Sand Pine, GRG = Green Grove, SAD = Sandy Desert, and SLP = Slash Pine.

	LANDCOVER TYPE (hectares)						
SITE	**Longleaf pine forest**	**Longleaf pine/ Hardwood forest**	**Other pine spp. / Hardwood Forest**	**Hardwood forest**	**Conifer plantation**	**Shrub/ scrub**	**TOTAL (ha)**
SAP	16.95	0.09	0.52	0.69	0	0	18.25
GRG	66.21	4.41	0.94	0.28	1.87	0.54	74.25
SAD	5.83	10.96	9.87	1.92	0	0.13	28.71
SLP	0	0	1.28	0.90	49.31	0	51.49

Table 2.2. The number of gopher tortoises caught at each site by age/sex class during the original study (1995-2000) and this study (2014-2015) at Ichauway, Baker County, Georgia. J=Juveniles, SA=Subadults, M=Males, and F=Females. SAP=Sand Pond, GRG= Green Grove, SAD=Sandy Desert, and SLP=Slash Pine. RECS=# of Recaptures in this trapping period (2014-2015) of individuals that were originally marked in the original study.

	1995-2000				**2014-2015**				
SITE	**J**	**SA**	**M**	**F**	**J**	**SA**	**M**	**F**	**RECS**
SAP	4	5	39	47	2	1	14	16	19
GRG	111	27	104	80	15	8	13	20	20
SAD	6	4	45	31	4	0	13	10	17
SLP	9	0	29	26	2	0	18	12	22

Table 2.3. The ten best-fitting candidate Cormack-Jolly-Seber models of apparent survival (Φ) and capture probability (*p*) of gopher tortoises for four study populations trapped during 1995-2000 & 2014-2015 at Ichauway, Baker County, Georgia. Parameters include time, age-sex class (Sex), and Site, and their interactions. A variance inflation factor (ĉ) of 3.76141 was used.to compute the quasi-likelihood AIC value (QAICc) for each model. The model structure (Model), number of parameters (K), quasi-likelihood AIC value ($QAIC_c$), differences in $QAIC_c$ values from the top model ($\Delta QAIC_c$), and weight for each model (*w*) are provided.

Model	**K**	**$QAIC_c$**	**$\Delta QAIC_c$**	**W_i**
Φ(~Site + Sex)p(~Site + time)	17	661.99	0.00	0.37
Φ(~Site)p(~Site + Sex + time)	17	663.44	1.45	0.18
Φ(~Site + Sex + time)p(~Site + time)	23	663.60	1.61	0.16
Φ(~Site + Sex)p(~Site + Sex + time)	20	664.10	2.11	0.13
Φ(~Sex)p(~Site + time)	14	665.01	3.02	0.08
Φ(~Site + Sex + time)p(~Site + Sex + time)	26	666.91	4.91	0.03
Φ(~Sex)p(~Site + Sex + time)	17	669.41	7.41	0.01
Φ(~Site * Sex)p(~Site + time)	25	670.01	8.01	0.01
Φ(~Site + time)p(~Site + Sex + time)	23	670.05	8.05	0.01
Φ(~Sex + time)p(~Site + time)	20	670.77	8.78	0.01

Table 2.4. Model-averaged estimates of apparent survival of gopher tortoises at four study populations from data collected from two mark-recapture studies (1995-2000, 2014-2015) on Ichauway, Baker County, Georgia. The age-sex class (Sex), study population (Site), average apparent survival with the associated standard error (Estimate +/- SE), total duration in years of the study (Duration), and the number of sampling occasions (K) are provided for comparison.

Sex	**Site**	**Estimate +/- SE**	**Duration**	**K**
Juveniles	Sand Pond	0.820 ± 0.161	20	4
Subadults	Sand Pond	0.916 ± 0.084	20	4
Males	Sand Pond	0.951 ± 0.042	20	5
Females	Sand Pond	0.963 ± 0.032	20	5
Juveniles	Green Grove	0.690 ± 0.143	20	6
Subadults	Green Grove	0.827 ± 0.079	20	6
Males	Green Grove	0.883 ± 0.028	20	7
Females	Green Grove	0.908 ± 0.027	20	7
Juveniles	Sandy Desert	0.869 ± 0.157	20	4
Subadults	Sandy Desert	0.943 ± 0.077	20	4
Males	Sandy Desert	0.968 ± 0.038	20	5
Females	Sandy Desert	0.977 ± 0.029	20	5
Juveniles	Slash Pine	0.889 ± 0.152	17	2
Males	Slash Pine	0.976 ± 0.037	17	3
Females	Slash Pine	0.982 ± 0.028	17	3

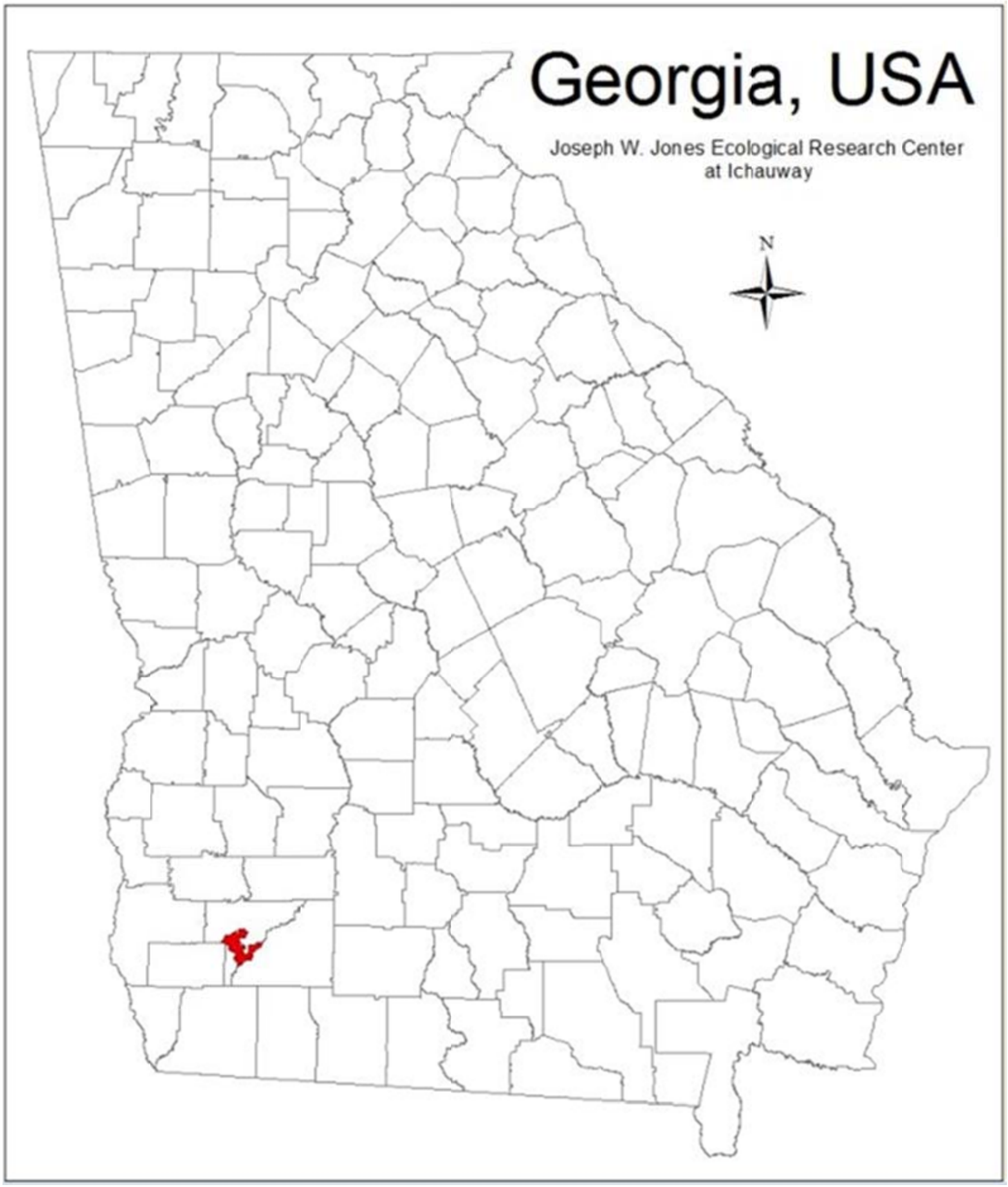

Figure 2.1. Location of my study area, Ichauway, the ~11,700 ha research site of the Joseph W. Jones Ecological Research Center in Baker County, Georgia.

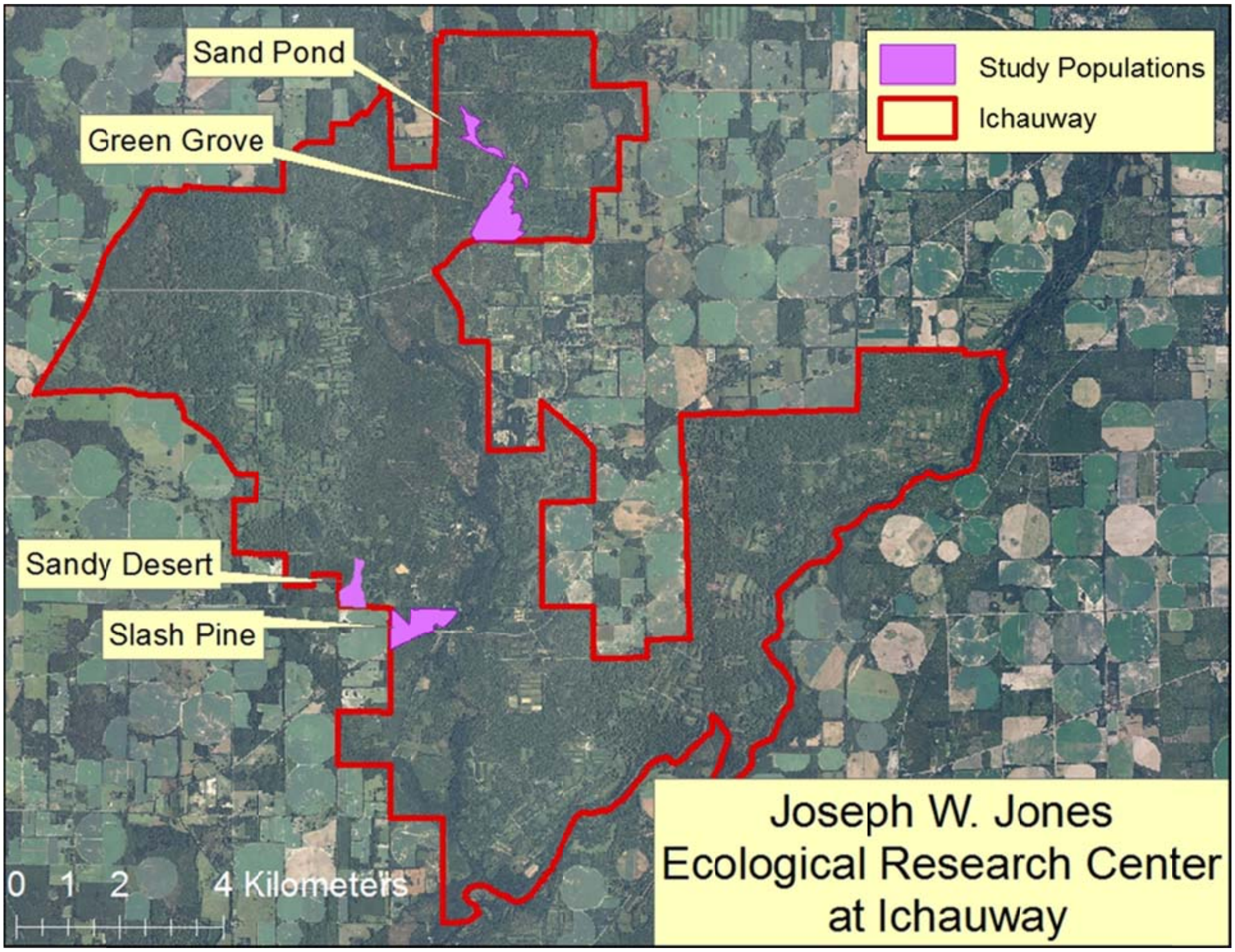

Figure 2.2. Locations of the four study populations where gopher tortoises had originally been marked/recaptured in between the years of 1995-2000 on Ichauway in Baker County, Georgia.

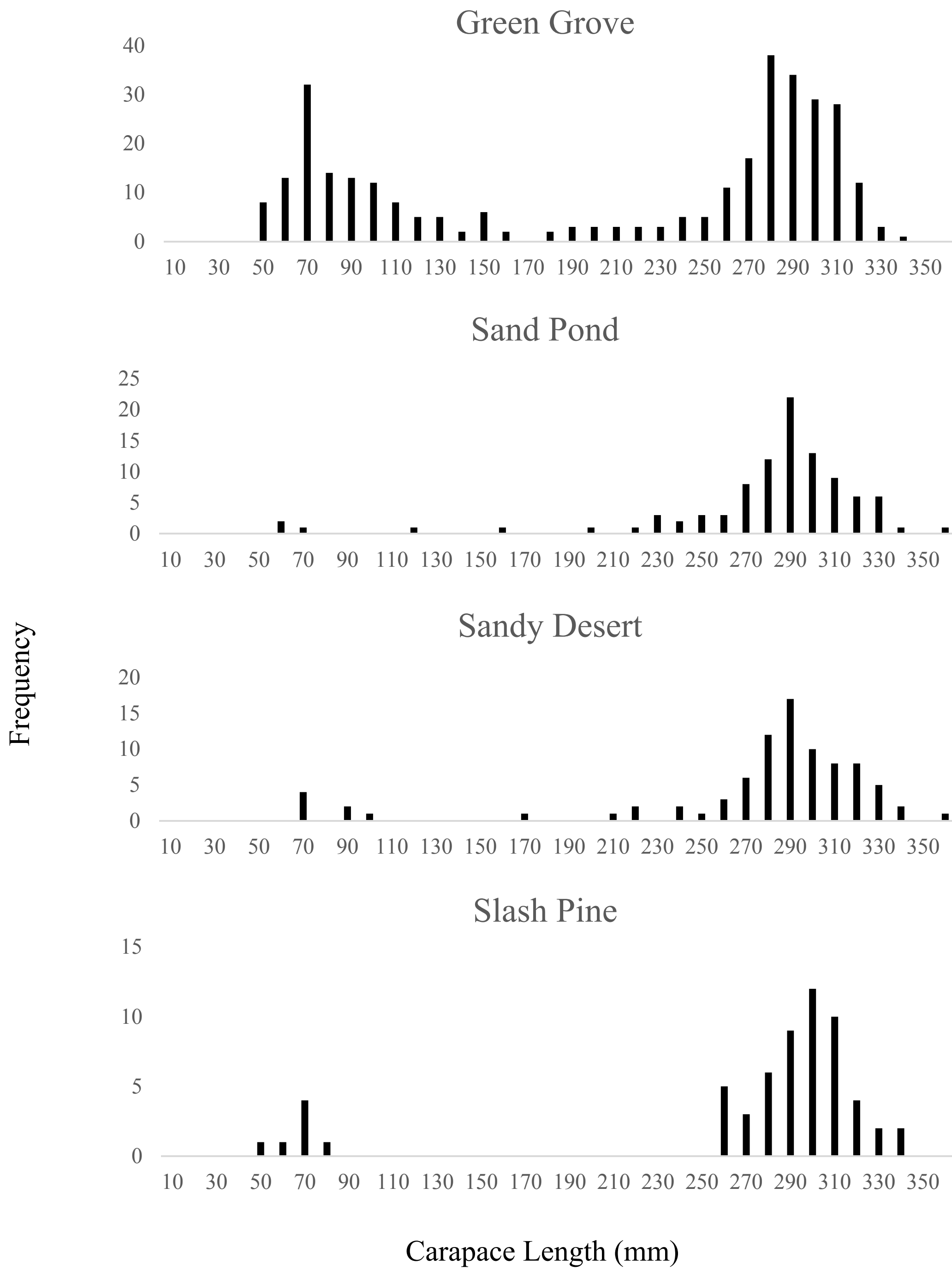

Figure 2.3. Size-class distribution (carapace length in mm) of observed gopher tortoises at each of the four study population during the original mark-recapture study (1995-2000) on Ichauway, Baker County, Georgia.

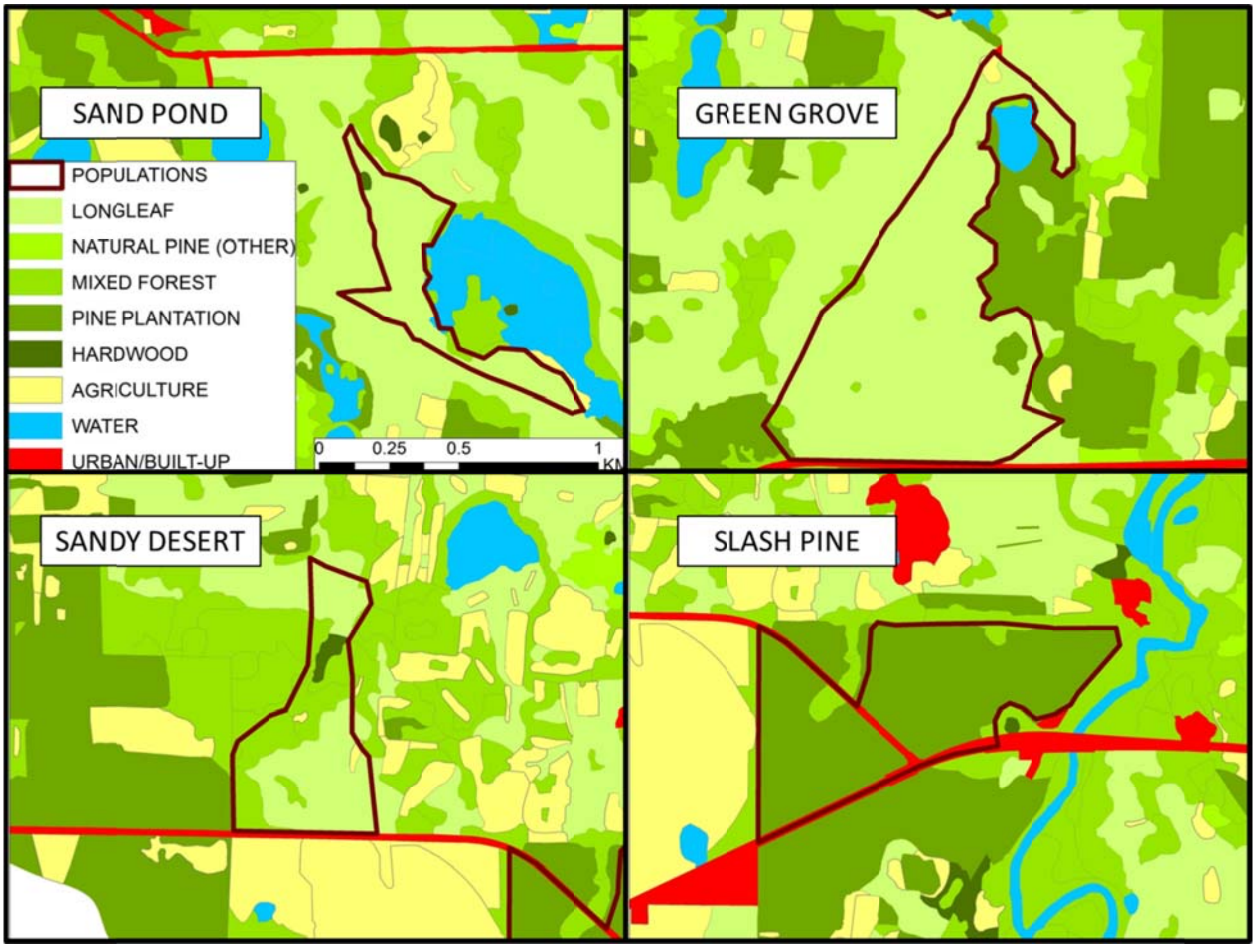

Figure 2.4. Land cover/land use classifications of the four study populations where gopher tortoises had originally been marked/recaptured in between the years of 1995-2000 on Ichauway in Baker County, Georgia.

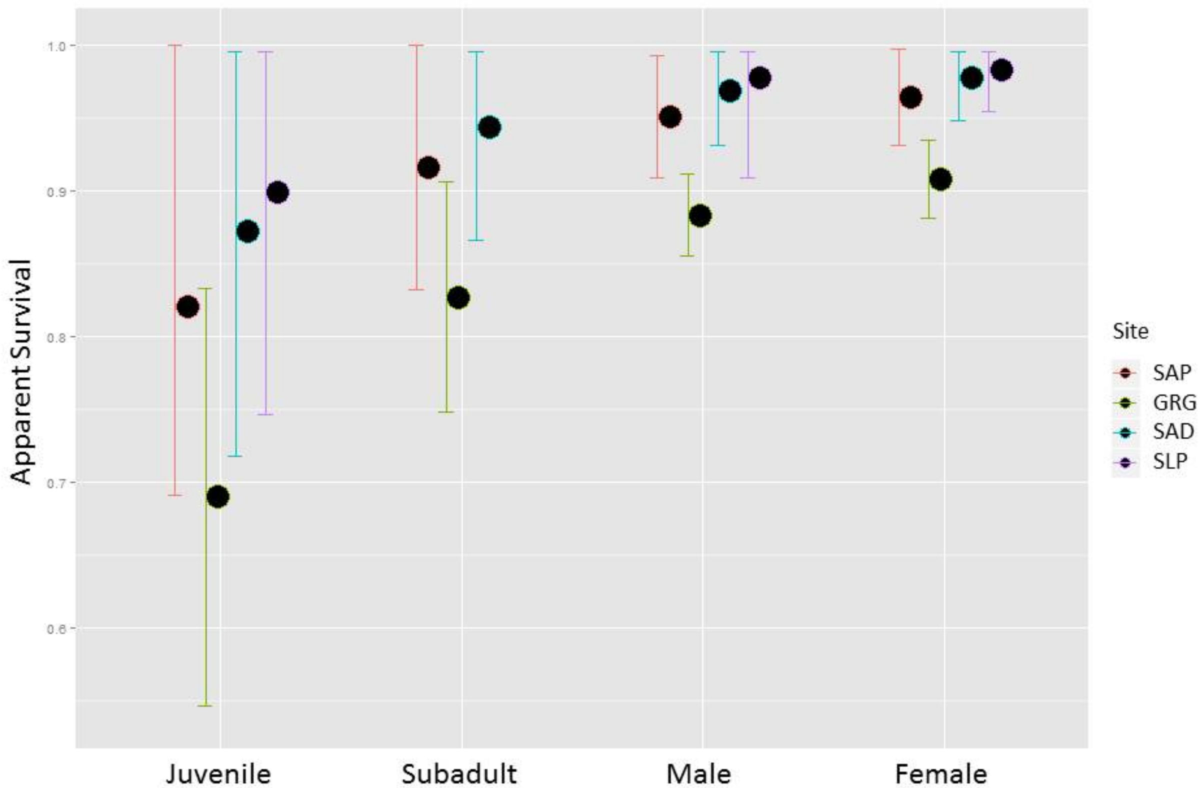

Figure 2.5. Model-averaged estimates of apparent survival (Φ) and the standard error for each age-sex class and site combination for gopher tortoises at four study populations on Ichauway, Baker County, Georgia. SAP = Sand Pond, GRG = Green Grove, SAD = Sandy Desert, SLP = Slash Pine. Note: no subadults were captured at Slash Pine.

CHAPTER 3

LONG-TERM MOVEMENT PATTERNS OF GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*) IN SOUTHWEST GEORGIA

Introduction

The geographic distribution of longleaf pine habitat in the southeastern United States has been reduced to small, highly fragmented forests covering <3% of its pre-1880 range when it covered 40% of the region (Noss et al. 1995). The widespread loss of longleaf pine habitat, along with other factors including fire suppression and human depredation, has led to an 80% range-wide decline of gopher tortoise (*Gopherus polyphemus*) populations (Auffenberg and Franz 1982). The gopher tortoise is considered a keystone species as its burrows provide refuge for over 360 commensal species (Eisenberg 1983, Jackson and Milstrey 1989), and federally threatened species such as the eastern indigo snake, *Drymarchon couperi*. Due to its decline, associated threats, and role as a keystone species, the gopher tortoise has recently been identified as a candidate for federal listing as Threatened under the Endangered Species Act in its eastern range (USFWS 2011). The gopher tortoise's imperiled status and habitat loss have led to concerns over how to manage remaining habitat, restore other habitat, and facilitate connections of currently protected areas.

Although researchers have addressed home range size and short-term movement patterns of the gopher tortoise (McRae et al. 1981b, Diemer 1992, Eubanks et al. 2003), information is currently lacking for these processes at large spatial and temporal scales, an issue for a species that has an estimated lifespan of 40-60 years (Landers 1980). Broad-scale ecological processes, such as gene flow, colonization rates, and population persistence, often depend on the successful movement of individuals among habitat patches over time (Bowler and Benton 2005). However, most research on gopher tortoise movement patterns has focused on within patch movements (but see Eubanks et al. 2003, McCoy et al. 2013). The capacity of an organism to navigate in space and over time is a driving factor influencing the movement path of individuals, and is largely affected by the spatial structure of the environment (Nathan et al. 2008). In a synthesis of a global set of manipulative, fragmentation experiments, Haddad et al. (2015) found that inter-patch movements and recolonization were reduced among fragments of increased isolation. In addition, the authors found that abundance was generally lower in fragments of reduced area and increased isolation. This may indicate that in landscapes composed of smaller and more isolated fragments, the ability of a species to persist will be lower.

To implement effective conservation management and reserve designs for a long-lived and imperiled species, such as the gopher tortoise, there is a need for an empirical understanding of the movement behavior and patterns within various landscape conditions (e.g. contiguous vs. fragmented), particularly at large spatial and long temporal scales. This may better inform actions of conservation planners to the extent at which movement may be relevant to the connectivity of tortoise populations. To address the need for additional information, we investigated the short (annual) and long-term (>10 years) movement patterns of gopher tortoises on and around Ichauway, the ~11,700 ha research site of the Joseph W. Jones Ecological Research Center. Our objective was to document movement of gopher tortoises by age-sex class and landscape types (e.g. contiguous and fragmented) throughout two studies conducted 1995-2000 and 2014-2015 of four long-term study populations. This will allow us to gain an implicit understanding of the functional connectivity (i.e. how an organism moves among patches) of this long-lived and imperiled species to facilitate conservation planning.

Methods

Study Area

This research was conducted at Ichauway, the research site of the Joseph W. Jones Ecological Research Center in Baker County, Georgia, 35 km southwest of Albany, GA (Figure 2.1). Ichauway is an 11,700 ha ecological reserve comprised mainly of longleaf pine – wiregrass (*Aristida beyrichiana*) savanna with variable canopy of oaks (*Quercus spp.*), along with small stands of planted pine, wildlife food plots, and wetlands. The reserve is actively managed with prescribed burns every 1 to 2 years and hardwood removal, helping to maintain a diverse plant understory. Deep, sandy soils, ranging from moderately well-drained to poorly drained, overlay heavily-weathered limestone bedrock. Tortoises occur on all non-floodplain soils across Ichauway (an area of >6800 ha in size) and overall density is 0.7 tortoises per hectare (unpublished data). I focused on four gopher tortoise study populations at Ichauway (Figure 2.2.) that were surveyed using mark-recapture methods between the years of 1995-2000 (C. Guyer, unpublished data).

The four study populations were originally selected for study because they had high densities of tortoises relative to other tracts of forest at Ichauway (C. Guyer, pers. comm); however, they varied in size (18-75 ha), landscape composition (Chapter 2, Table 2.1., Figure 2.4.), and the size-class distribution of tortoises (Figure 2.3.). 'Green Grove' and 'Sand Pond' are in the northern section of the property, in a relatively contiguous, natural longleaf habitat matrix (Figure 3.1.). Green Grove is approximately 75 hectares in size and is dominated by an open, longleaf pine overstory with a wiregrass understory (Chapter 2, Table 2.1.). The site was surveyed and trapped every year between 1995-2000, and 322 individuals were marked during that period. Green Grove is bordered by a rural highway and the property border on its southern boundary, hardwood-dominated forest on its eastern boundary, and by dirt roads and similar longleaf pine-wiregrass habitat in all other directions. For the current sampling, ~2 ha grids were randomly selected within the study population to account for approximately ~30% of the total area. Sand Pond is a linear strip of longleaf pine habitat covering approximately 20 hectares (Chapter 2, Table 2.1.). The site was surveyed and trapped completely every year between 1995-1998, and 96 individuals were marked during that period. The site is bordered on its eastern border by a large, semi-ephemeral wetland. It is bordered by dirt roads and similar longleaf pine-wiregrass habitat in all other directions. To differentiate between landscapes that were primarily contiguous habitat from those with more fragmented and patchy habitat, I classified each site as either “contiguous” or “fragmented”. I considered the landscape type of these two study populations to be contiguous.

‘Sandy Desert’ and ‘Slash Pine’ are in the central section of the property in a relatively fragmented, and human-influenced landscape with patches of natural longleaf habitat (Figure 3.1.). Sandy Desert covers approximately 25 hectares and is primarily composed of mixed longleaf/hardwood habitat (Chapter 2, Table 2.1.). The site was surveyed and trapped every year between 1995-1998, and 86 individuals were marked during that period. It is bordered on its southern boundary by the property boundary and a large, center-pivot agricultural field. On its western boundary, it is partially bordered by the property boundary and an unburned mixed pine-oak forest. To the northwest, it is bordered by a cypress-dominated wetland. On its eastern side, it is bordered by a pine forest matrix with interspersed wildlife food plots. To the north, it is connected with similar longleaf pine habitat. Slash Pine is a 75 year old pine plantation dominated by slash pine (*Pinus elliottii*), and is currently being experimentally restored to a longleaf pine forest (Chapter 2, Table 2.1.). Its understory is not dominated by wiregrass, but by other herbaceous and woody plants. It is approximately 55 hectares in size, and was surveyed and trapped in 1998-1999 resulting in the capture of 60 individuals. It is bordered to the South by a busy, two-lane state highway (Highway 91), to the East by the Ichawaynochaway Creek, to the west by a large, center-pivot agricultural field, and by administrative, research, and residential buildings to the north. I considered the landscape type of these study populations to be fragmented.

To detect large-scale movements of tortoises outside of the original study area, I selected grid cells (120 m x 120 m), referred to as "outer sampling areas", located within 3 kilometers of the populations (on property, and on adjacent properties) to locate migrant, marked tortoises from the original mark/recapture study that may have moved. Outer sampling area grid cells were selected using a probabilistic sampling frame that was weighted towards the selection of cells likely to harbor dispersing tortoises. The purpose of this selection method was to maximize the capture of migrant, marked tortoises while sampling efficiently across a large area. Grid cells in the outer sampling area were chosen at random in proportion to a measure weighted by habitat suitability (0.75) and cost-distance (0.25). Habitat suitability values were assigned to 64 unique land cover-soil combinations using burrow presence data from a line transect distance sampling (LTDS) systematic survey of Ichauway conducted in 2011. A total of 395 transects, each transect separated by 400 meters with a length of 250 meters and a width of 30 meters, yielded observations of 474 occupied burrows (Lora L. Smith, personal communication). The landcover-soils combinations were created from four classes of soils ranked by suitability for tortoises

(USFWS and NRCS 2012) and 16 land cover classes defined by the 2011 National Land Cover Database (Homer et al. 2015). Suitability values were defined as the proportion of total occupied burrows that were found in each landcover-soil combination scaled relative to the amount of each landcover-soil combination represented in the transects surveyed. Resistance was estimated as the inverse of the habitat suitability value to calculate cost-distance, the least accumulative cost for each cell to the nearest core population over a resistance surface, in ArcGIS (ESRI, Redlands, CA). For landcover-soil categories in which the habitat suitability was 0 or less than 0.01 (such as developed and open-water areas), resistance was set at a maximum resistance value of 100.We surveyed and trapped 119 grid cells of a potential set of ~6,000 cells which represented approximately 2% of the total possible area (Figures 3.2. & 3.3.).

Tortoise Sampling

Between 2014 (May-August) and 2015 (June-July), each study population (core area) was surveyed and re-trapped once. From May to October 2015, the 119 outer sampling area grid cells were surveyed and trapped. All areas were surveyed using the line transect distance sampling (LTDS) method with a double observer (Buckland et al. 2001). One observer walked along a center line of a 20-m wide transect, followed by a second, independent observer (Nichols et al. 2000, Nomani et al. 2008), searching for gopher tortoise burrows or tortoises above ground with observers switching roles on consecutive transects. All burrows were scoped with a burrow camera (Environmental Management Services, Canton, GA) to determine tortoise occupancy. Havahart® live traps (Lititz, PA) were set at the entrance of all occupied burrows and shaded with burlap to protect the trapped animal from overheating. If occupancy could not be determined from the burrow camera, a trap was set in front of the entrance and monitored for 1-2 weeks. Traps were checked twice daily and left out until the tortoise was captured. Where possible, I also hand-captured tortoises observed with the sampling areas. Locations of all tortoises were recorded using a F4 Tech® Flint S812 Handheld GPS Unit (Tallahassee, FL). These methods were selected to closely replicate those of the original study (Boglioli et al. 2000, Eubanks et al. 2003), in which multiple observers (1-3) would walk roughly parallel transects, marking all burrows with a handheld Trimble Global Positioning System unit (+/- 2 m). In the original study, all observed burrows were trapped to determine occupancy, and all individuals were marked by drilling marginal scutes of the carapace (Cagle 1939).

Captured tortoises were measured (carapace length, plastron length, plastron concavity, total length, gular length, anal width, anal notch, and mass) and examined to determine if the animal had been previously marked. Sex (for adults) was determined based on shell morphology (McRae et al. 1981a, Mushinsky et al. 1994), and juveniles were distinguished from sub adults based on carapace length (juveniles < 150 mm < subadults < 220-230 mm) for which sex cannot be determined. (Landers et al. 1982). Unmarked animals were individually marked by notching the marginal scutes with a Dremel® Stylus tool (Mt. Prospect, IL) (Cagle 1939, Norton et al. 2013). All equipment was cleaned with a 10% bleach solution between uses. Prior to marking, the portion of the shell to be notched was cleaned with a Clorox wipe and Bactine was applied to the area after the animal was marked. Marking and measurements were performed in the field and tortoises were released at the capture location (AUP# A2014 02-024-Y3-A1).

Modeling tortoise survival, movement, and recapture

The data were fit to spatially explicit Cormack-Jolly-Seber open population models to estimate tortoise survival (φ), probability of capture (p), and movement (σ). Annual probability of tortoise survival was assumed to be unrelated to annual distance moved. Given that a tortoise was alive and in the study area (core areas + 3-km buffer) in year t, its probability of surviving and remaining in the study area in year t+1 was represented by φ. Conditional on the tortoise's survival, the tortoise's movement between locations X_t and X_{t+1} was assumed to follow a bivariate normal distribution with covariance matrix $I\sigma^2$ (i.e., uncorrelated, equal variance). Finally, the tortoise's probability of capture p in year t+1 was conditional on its arrival (survival and movement) in a spatial unit surveyed that year (i.e., in a core area or an outer sampling area). Because searches within spatial units were active (as opposed to passive encounters of tortoises at fixed trap locations), it was reasonable to assume probability of capture was uniform within boundaries of a spatial unit. Should the tortoise survive and move to a spatial unit not sampled, its probability of capture was $p = 0$. Similarly, capture probability was fixed at 0 for any year in which no surveying or trapping was conducted, meaning that the model accounted for survival and movement during the inter-study period (2001-2013) despite the absence of capture data.

I examined a candidate set of biologically-relevant models incorporating a fixed effect of site (i.e. study populations), a fixed effect of landscape (e.g. contiguous or fragmented), and/or a fixed effect of age-sex class (e.g. juvenile, subadult, male, and female) on the movement parameter (σ). Effects for survival (φ) and capture probability (p) were based on the top candidate models from a non-spatial Cormack-Jolly-Seber analysis done in Chapter 2, and these effects were maintained in each competing model for movement. Survival was assumed to depend on fixed site and age-class effects. Probability of capture depended on fixed site and age-class effects, and a random time (year) effect. Survival and capture probability were modeled as linear functions of the relevant predictor variables via a logistic link. Movement distance was modeled as a linear function of the candidate variables via a log link. In all cases, parameter values were sampled from vague normal prior distributions.

Parameter estimation and model assessment

Analyses were conducted in Program JAGS (Plummer 2003), using the package 'rjags' (Plummer 2013) in the R user interface (R-Core-Team 2013). All parameters were given vague, uninformative priors. We used the Deviance Information Criterion (DIC), a Bayesian method for model comparison, within rjags (Plummer 2013) to identify the most parsimonious model. We used Gelman and Rubin's convergence diagnostic (Gelman and Rubin 1992) in rjags (Plummer 2013) to estimate a potential scale reduction factor for each variable to diagnose convergence issues. Convergence was determined for each parameter if the upper limit (95%) was close to 1.

Results

Over the course of the entire study, we had capture histories for 621 individuals that had recorded geographical locations. Of the 568 individuals that were captured and recorded with geographic location in 1995-2000, 84 were recaptured in the 2014-2015 study (~15%). Twelve of the 84 recaptured tortoises were caught outside the boundaries of the study population in which they were originally captured (~14%). Three individuals that had originally been marked in Sand Pond were found in Green Grove. Nine individuals were recaptured outside the original core study populations and within the outer sampling area matrix. All twelve individuals found outside their study area of first capture were in the 'contiguous' landscape type, while none of the tortoises in the 'fragmented' landscape type were found outside of their study area of first capture in the grid cells sampled in the outer sampling area (3 kilometer buffer).

The most parsimonious model (Table 3.1.) indicated landscape type and age-sex class effects of the movement parameter (ψ). No other models were listed as having a DIC within ten of the top model, indicating no clear support for the other competing models, and no parameters were identified to have convergence issues (Table 3.2.). The standard deviation of the bivariate normal distribution predicting a tortoise's location (movement parameter) for each time period was larger for individuals captured in the contiguous landscape as compared to individuals in the fragmented landscape for all age-classes (Table 3.3; Figure 3.4.). In each landscape, the overlap of credible intervals (Table 3.3.) does not suggest statistically significant difference between average movement distances of juveniles and subadults, but sexually immature individuals (e.g. juveniles and subadults) had significantly smaller values than sexually-mature individuals (e.g. males and females). Average movement distances differed significantly for females and males in the contiguous landscape, but not in the fragmented landscape. For a range of annual distances moved bounded within a 90% credible interval, see Figure 3.5.

Although our top candidate model for a previous non-spatial analysis (Chapter 2, Table 2.1.) demonstrated support for an effect of site on apparent survival, we found no statistical difference among estimates of the effect of site on survival after incorporating movement into the analysis (Figure 3.6.). It is important to note that apparent survival represents both the likelihood that a tortoise survives, and the likelihood that it does not emigrate from the study area. This may be explained by the further displacement distance, the distance moved from first capture to the final year of the study if still alive, of individuals in the contiguous landscape as compared to those in a more fragmented landscape (Figure 3.7.) Apparent survival differed among age-classes (Figure 3.4.).

Discussion

Tortoises in the core study populations within a contiguous landscape were shown, on average, to move greater distances on an annual basis than tortoises from study populations in a more fragmented landscape. Individuals marked in the original study from 1995-2000, and predicted to be alive in 2015, were estimated to be < 500 m from their original capture location in the fragmented landscape. A 500 m movement would represent only an intra-patch movement (within a study population). Conversely, individuals captured in the contiguous landscape were estimated to be up to 2500 m from their original capture location, representing both intra- and inter-patch movements (within and among study populations) (Figure 3.7.). Estimating the long-term movement distances of individuals across different landscapes provides a better understanding of the functional connectivity of the organism, or 'the degree to which landscapes facilitate or impede the movement among resource patches' (Taylor et al. 1993).

In a translocation experiment, habitat degradation and fragmentation was shown to lead to the restriction of gopher tortoises to small areas of marginal quality when the surrounding landscape matrix is of relative, lower habitat quality (McCoy et al. 2013). This process may be driven by tortoises exhibiting avoidance of dense vegetation (specifically, cogon grass (*Imperata cylindrica*) and unburned plots). Therefore, maintaining contiguous landscapes for tortoises by maintaining permeable habitat surrounding populations may be critical to maintain broad scale ecological processes, such as gene flow and recolonization. Additionally, the effect of the surrounding landscape matrix on movement patterns may explain the difference in estimates of apparent survival of gopher tortoises across studies (Ashton and Burke 2007, Tuberville et al. 2008, Tuberville et al. 2014, this study), in addition to their management histories.

Sexually immature tortoises (juveniles and subadults) have been shown to move shorter distances on an annual basis than sexually mature tortoises (males and females). Pike (2006) found hatchling tortoises moved increasingly further from their nest in their first year, but the mean distance from nest at the end of the study was only ~70 m. In a radio-telemetry study of tortoises at one of our study sites, Green Grove, in 1997-1998, Eubanks et al. (2003) documented two male, adult tortoises emigrating out of the study area (estimated annual dispersal rate of ~3%). One of the individuals traveled a total distance of 4.8 km before his transmitter signal was lost at the edge of the property approximately 1.2 km from his original location. The other individual moved a total of 6.4 km before settling in an area approximately 1.5 km from his original location. Interestingly, two of the tortoises we had captured in the outer sampling area were found in the same general area. Foraging activity of gopher tortoises has been shown to be limited to within 15-50 m of the burrow (Auffenberg and Iverson 1979, McRae et al. 1981b), which may indicate that long-distance movements are influenced by mate-seeking and nest searching (Berish and Medica 2014).

If long distance movements by tortoises are related to mate-seeking or nest site selection, adults would be more likely than immature tortoises to move larger distances, as supported by my data. Although, Diemer (1992) documented a 0.74 km movement (the largest movement among tortoises in her study) by a subadult on a pine plantation in Northern Florida. McRae et al. (1981b) suggested that aggressive interactions of adult males towards subadults may influence individuals at or near sexual maturity to disperse to sparsely populated areas. Additionally, the authors found that movements of juveniles were directed toward the periphery of the population, suggesting that juveniles may be major dispersers. However, myresults did not support this hypothesis.

In a long-term demographic study, Berish et al. (2012) recaptured 8% of all tortoises marked ~20 years earlier. Most of those individuals (88%) were found within 200 m of their original location. However, within the span of the two studies the site had experienced intensive silvicultural activity (i.e. clear-cutting, replanting, tree thinning, etc.). Although gopher tortoises have been shown to exhibit high rates of site fidelity, research suggests anthropogenic disturbances and fire suppression (canopy closure) may influence tortoise movement patterns (Diemer 1992, Aresco and Guyer 1999). Our four study populations were sampled over a time period where landuse remained relatively static, and the sites were managed with prescribed fire on an approximate 2 year burn cycle. Of the 84 tortoises recaptured in our study (~15%), the majority (~75%) were recaptured within 200 m from their original location, similar to the Berish et al. 2012 study. Although for logistical reasons, I only resampled approximately 30% of one of the study areas, Green Grove. The recapture of only 12 marked individuals (~14 %, 2.1 % of total individuals) outside of the boundaries of the original study populations was somewhat surprising. Upper-respiratory-tract-disease has been documented in gopher tortoises at the study sites (>90% prevalence of antibodies, McGuire et al. 2014). Severe infection with URTD was shown to alter movement patterns of gopher tortoises, either greatly decreasing or increasing home range size and maximum distance moved (McGuire et al. 2014). None of the tortoises captured in our study exhibited severe signs of URTD; however the implications of disease on our results is not known.

The finding that the eastern populations of the gopher tortoise warrant listing as Threatened under the U.S. Endangered Species Act has led to an increased attention on developing effective management and empirically-based conservation planning to mitigate the effects of the major threat to the species, habitat loss (USFWS 2011). However, there has been a lack of understanding of the rate and distance at which tortoises move across the landscape, which may have implications for gene flow, colonization rates, and population persistence (Bowler and Benton 2005). Previous studies have addressed home range size and short-term movement patterns of the gopher tortoise (McRae et al. 1981b, Diemer 1992, Smith et al. 1997, Eubanks et al. 2003, McGuire et al. 2014), yet these studies were short-term and relatively small scale. The findings of our study extend the current understanding of tortoise movement patterns in both time and space to give conservation scientists and tortoise biologists a better understanding of the functional connectivity of the organism andhow an organism moves across the landscape. This will allow decision makers and conservation practitioners to better evaluate the scale and extent to which connectivity is relevant to gopher tortoise management. For an organism with an estimated lifespan of 40-60 years, this information is important and timely for the continued persistence of tortoise populations on the landscape.

Acknowledgements

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Table 3.1. The five candidate Cormack-Jolly-Seber models of survival (Φ), capture probability (p), and movement (σ) of gopher tortoises of four study populations at Ichauway, Baker County, Georgia during 1995-2000 & 2014-2015 ranked in order. Parameters that vary across movement include landscape, site, and sex (i.e. age-class). Model structure for survival and capture probability was held fixed across competing models for movement. The model structure (Model), Deviance Information Criterion value (DIC), differences in DIC values from the top model (ΔDIC), and rank for each model (Rank) are provided.

Model	DIC	ΔDIC	Rank
σ (~ Landscape + Sex) Φ(~Site + Sex)p(~Site +Sex + time)	21210.95	0	1
σ (~ Landscape) Φ(~Site + Sex)p(~Site +Sex + time)	21349.45	138.5	2
σ (~ Site) Φ(~Site + Sex)p(~Site +Sex + time)	21371.57	160.62	3
σ (~ Sex) Φ(~Site + Sex)p(~Site +Sex + time)	21490.38	279.43	4
σ (~ Null) Φ(~Site + Sex)p(~Site +Sex + time)	21969.4	758.45	5

Table 3.2. The potential scale reduction factor for each parameter of Φ (survival) and σ (movement) to diagnose convergence which was estimated using Gelman and Rubin's convergence diagnostics function in rjags. Convergence was determined for each parameter if the upper limit (95%) was close to 1.

Parameter	Point Estimate	Upper C.I.
Φ – Intercept	1.061	1.173
Φ – Age-class Effect (Juvenile)	1.022	1.058
Φ – Age-class Effect (Subadult)	1.001	1.002
Φ – Age-class Effect (Male)	1.06	1.169
Φ – Age-class Effect (Female)	1.032	1.095
Φ – Site Effect (Sand Pond)	1.02	1.047
Φ – Site Effect (Green Grove)	1.04	1.109
Φ – Site Effect (Sandy Desert)	1.049	1.14
Φ – Site Effect (Slash Pine)	1.008	1.015
σ – Intercept	1.02	1.059
σ – Age-class Effect (Juvenile)	1.034	1.09
σ – Age-class Effect (Subadult)	1.014	1.038
σ – Age-class Effect (Male)	1.015	1.042
σ – Age-class Effect (Female)	1.012	1.032
σ – Landscape Effect (Contiguous)	1.018	1.052
σ – Landscape Effect (Fragmented)	1.026	1.073

Table 3.3. The movement parameter, the standard deviation sigma, in meters, of the bivariate normal distribution predicting a tortoise's location for each time period, of tortoises in our mark-recapture study on Ichauway in Baker County, Georgia. The age-class (Age-class), landscape type (Landscape), mean estimate (Point Estimate), and 90% credible interval (Credible Interval) is provided.

Age-class	**Landscape**	**Point Estimate (m)**	**Credible Interval**
Juveniles	Contiguous	81.1	71.8 – 92.4
Juveniles	Fragmented	38.5	33.1 – 45.1
Subadults	Contiguous	87.5	77.7 – 99.1
Subadults	Fragmented	41.6	35.8 – 48.2
Males	Contiguous	172.3	163.8 – 181.3
Males	Fragmented	81.8	74.9 – 89.3
Females	Contiguous	151.9	143.8 – 160.3
Females	Fragmented	72.1	66.5 – 78.2

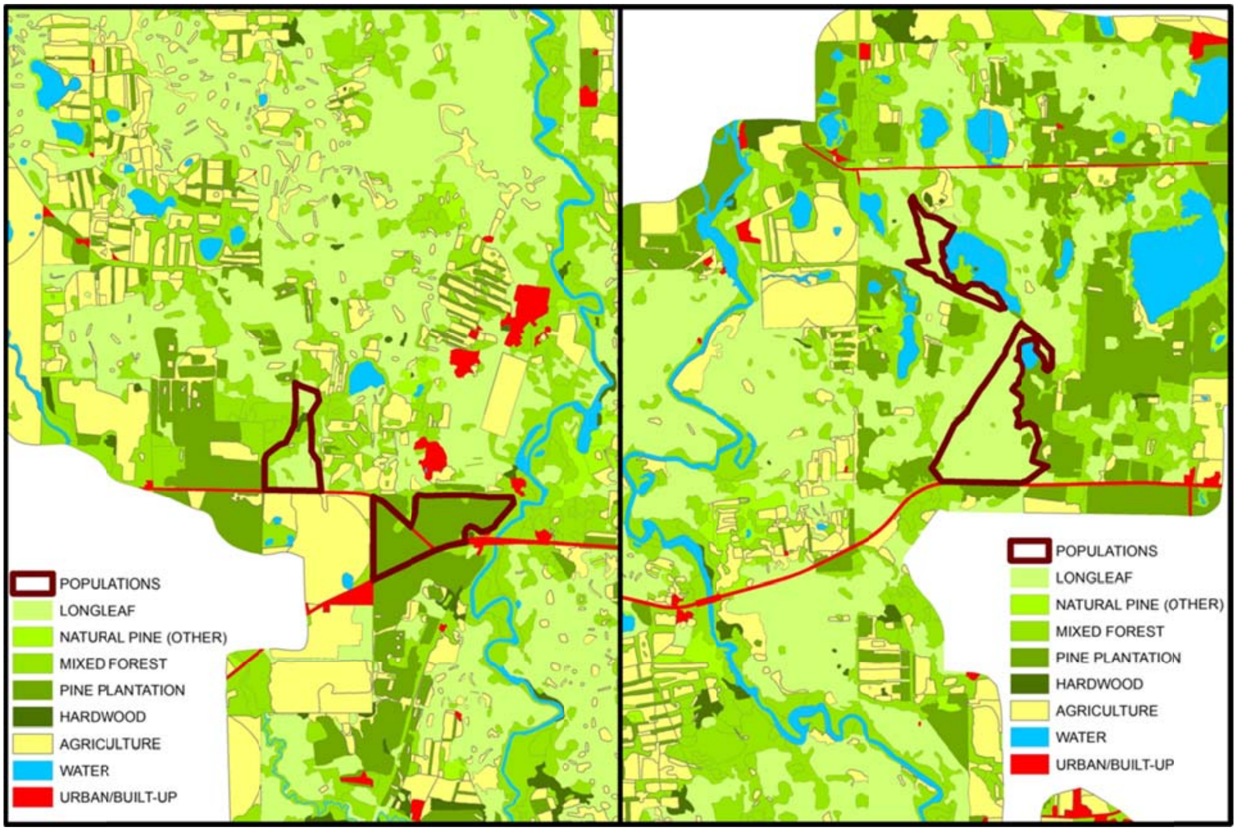

Figure 3.1. The land use/cover classifications in and around the four study populations of gopher tortoises at Ichauway, Baker County, Georgia. Slash Pine and Sandy Desert are depicted on the left in the fragmented landscape, and Green Grove and Sand Pond are depicted on the right in the contiguous landscape.

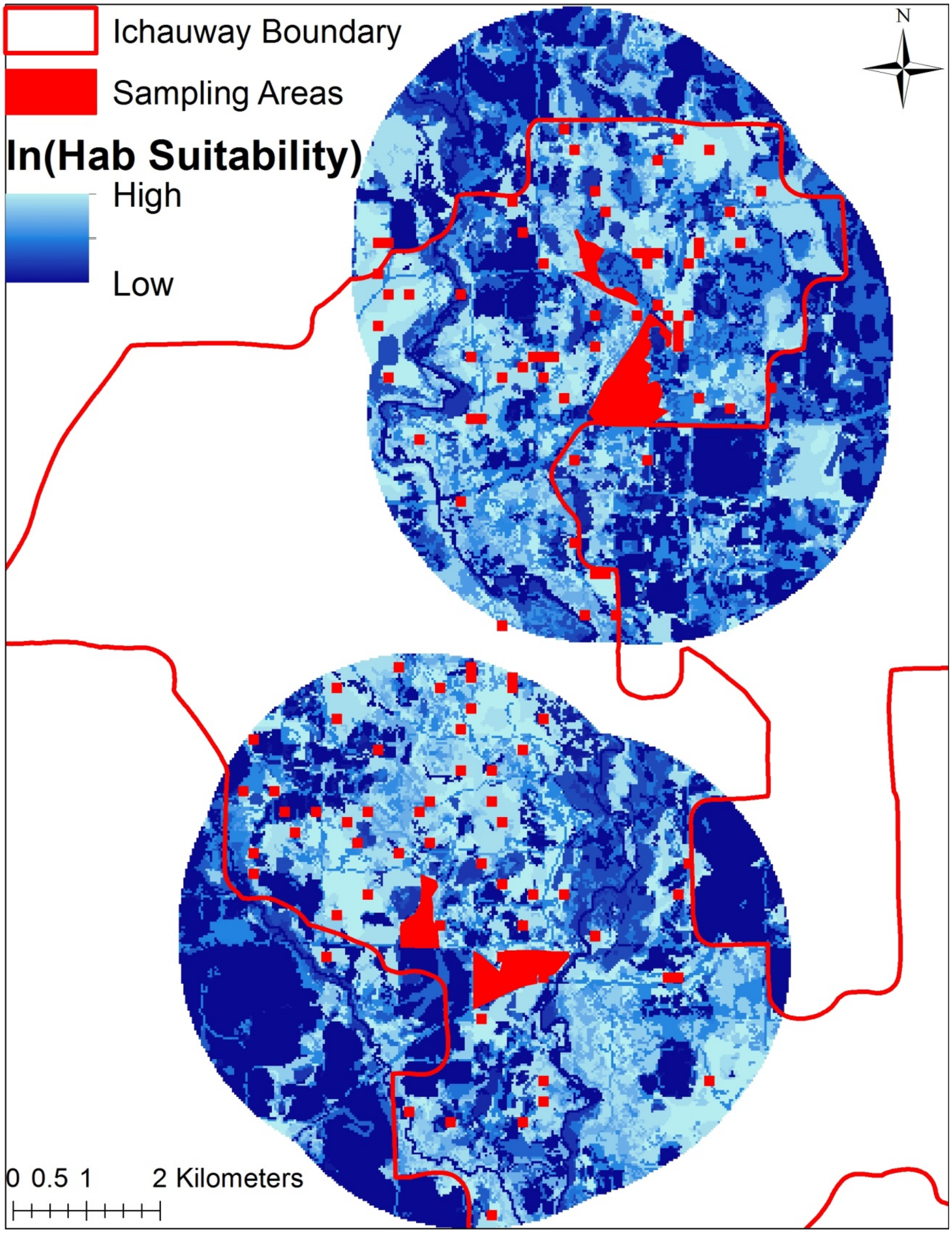

Figure 3.2. Location of our sampling areas, both core populations and outer sampling area grids, and habitat suitability values (log-transformed) used in our probabilistic sampling frame on and around Ichauway, Baker County, Georgia.

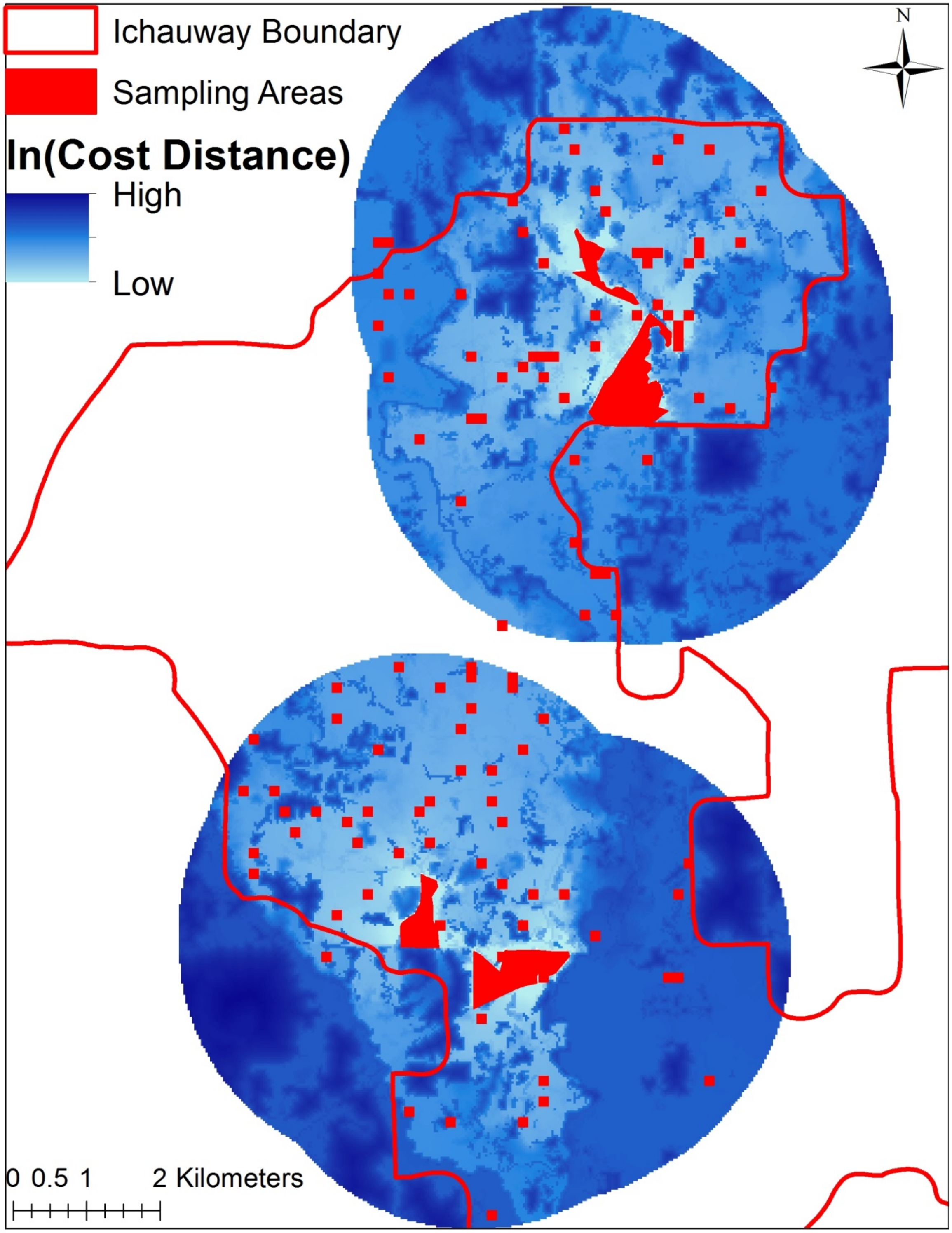

Figure 3.3. Location of our sampling areas, both core populations and outer sampling area grids, and cost distance values (log-transformed) used in our probabilistic sampling frame on and around Ichauway, Baker County, Georgia.

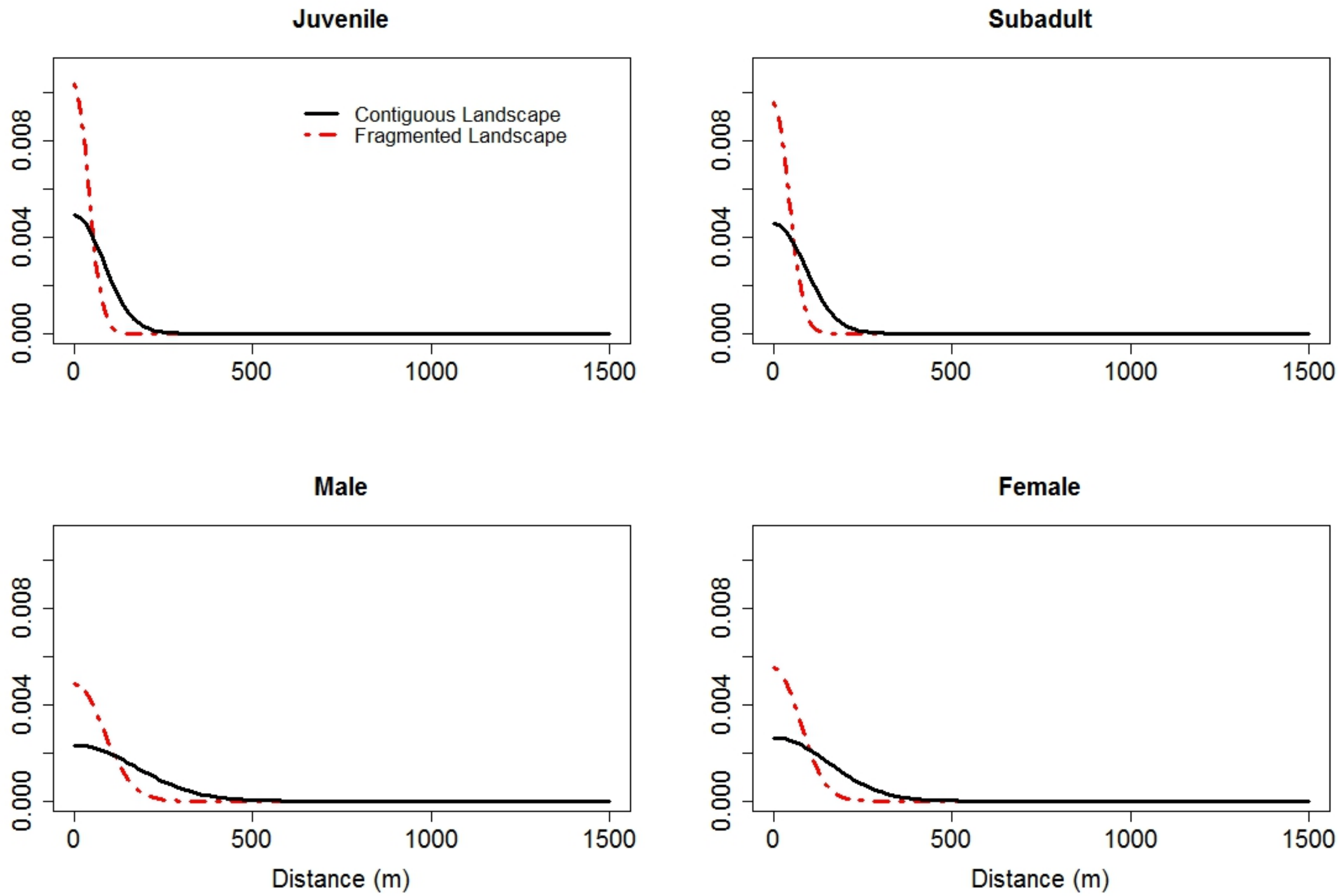

Figure 3.4. The estimated precision parameter (sigma – movement distance) of the bivariate normal distribution predicting gopher tortoise's locations in a given year for individuals of all age-classes in both the contiguous and fragmented landscapes, for tortoises captured between 1995-2000 & 2014-2015 at Ichauway, Baker County, Georgia.

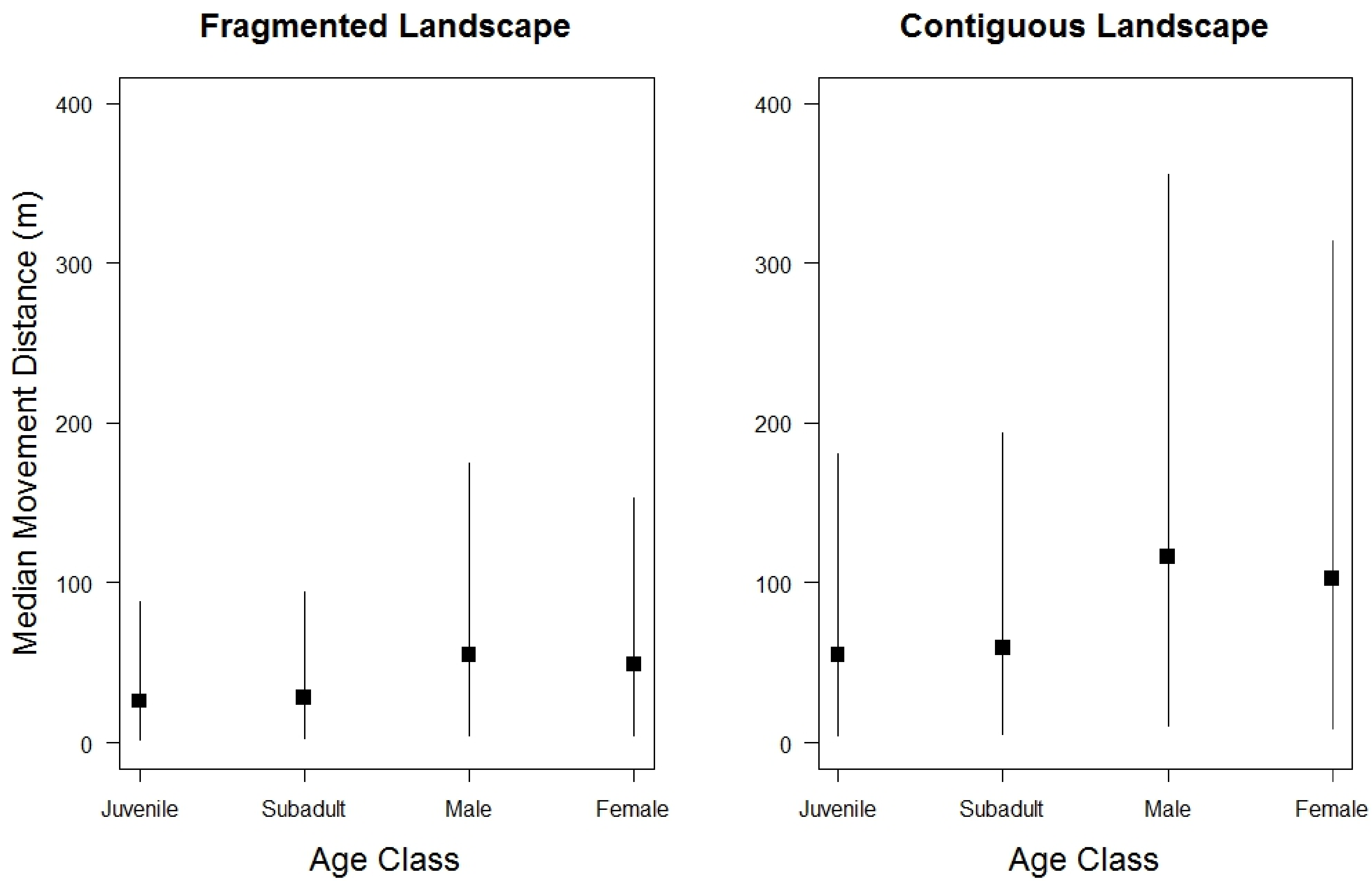

Figure 3.5. The median (50% credible interval) annual movement distance, bounded by 90% credible intervals of the range of annual movement distances, of gopher tortoises by age-class and landscape of tortoises captured 1995-2000 & 2014-2015 at Ichauway, Baker County, Georgia.

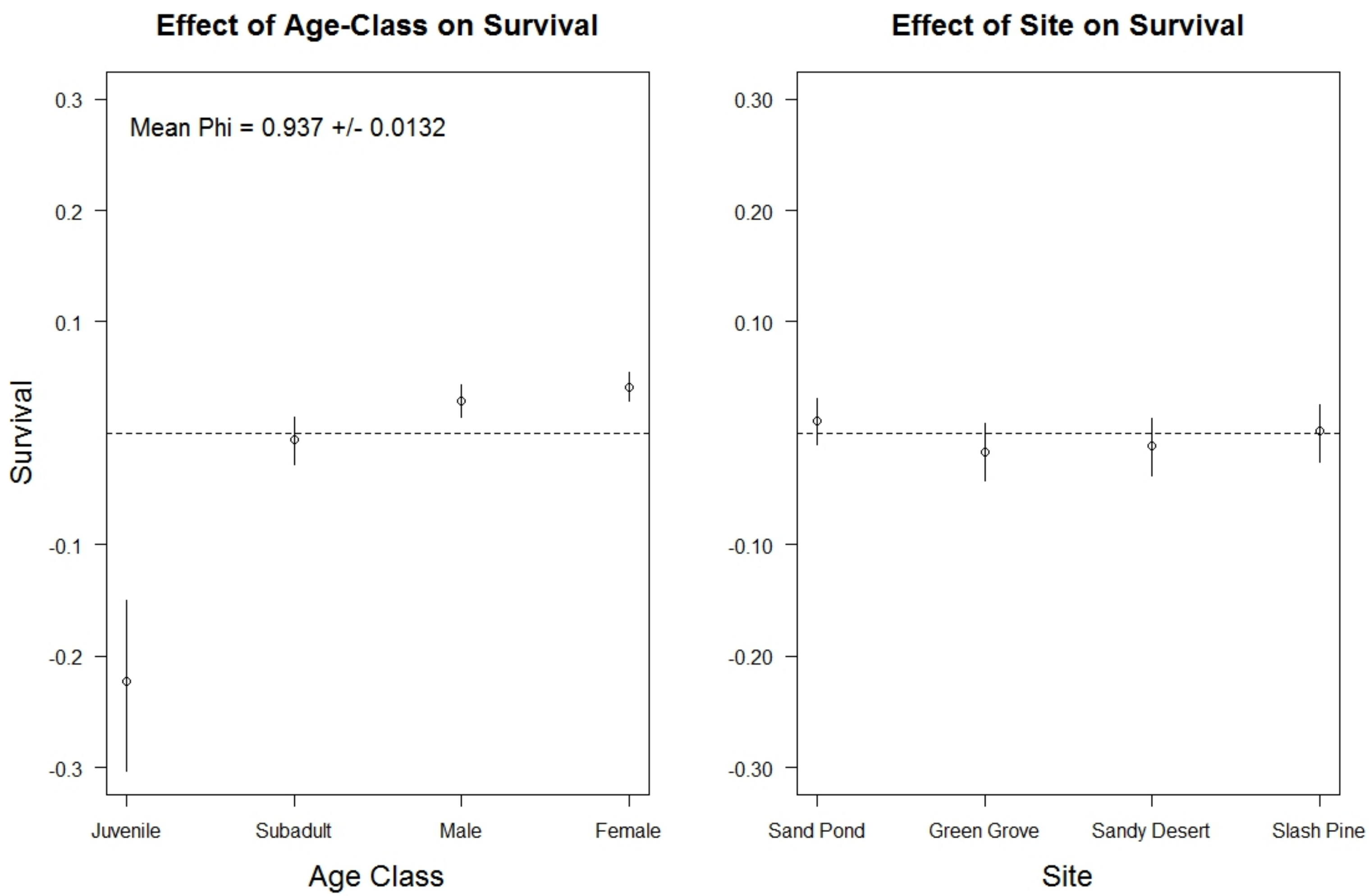

Figure 3.6. The estimated mean effects of age-class and site on survival, with 90% credible intervals, of our top candidate model (Table 3.1.) for individuals captured 1995-2000 and 2014-2015 at Ichauway, Baker County, Georgia.

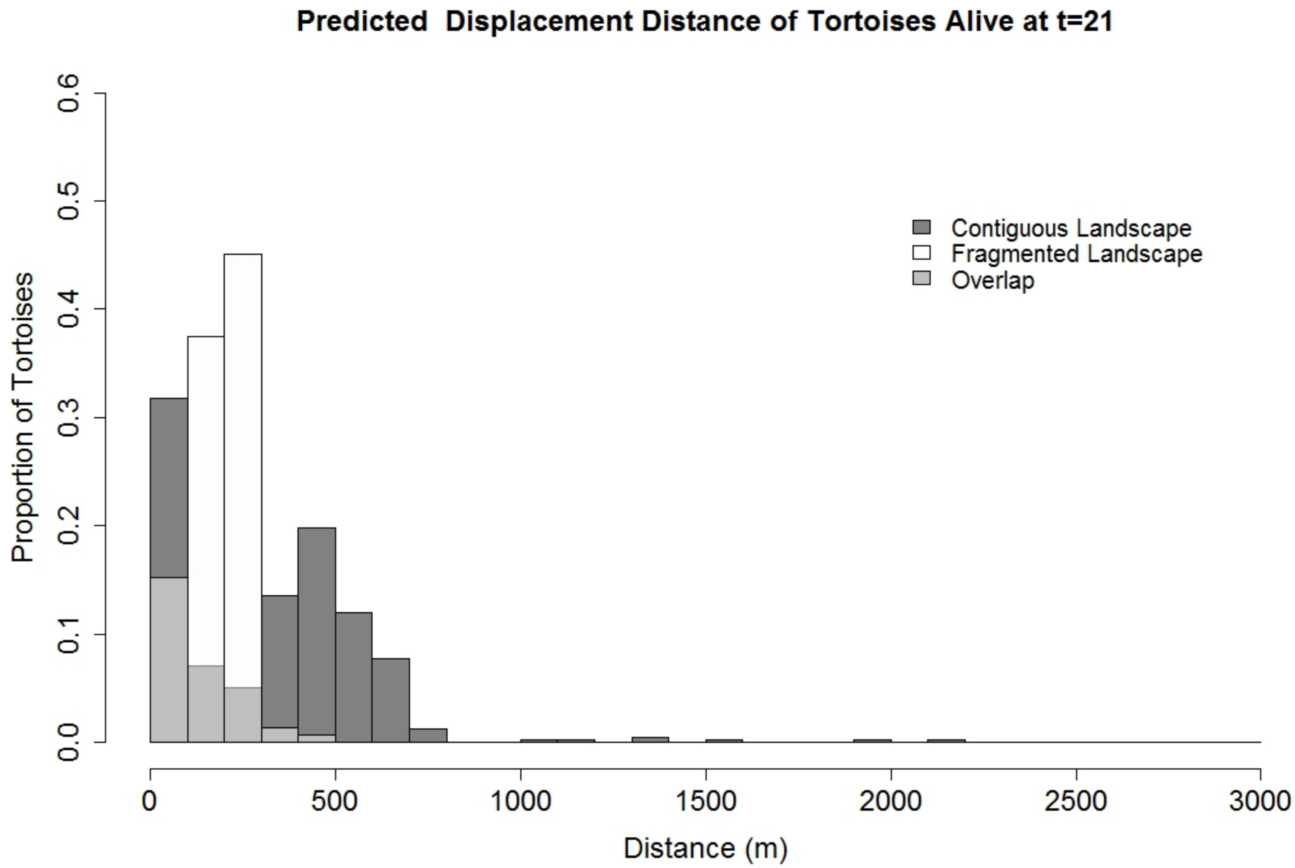

Figure 3.7. The estimated mean displacement distance of individuals in both the contiguous and fragmented landscapes, for gopher tortoises that were originally captured in 1995-2000 and are predicted to be alive in the final year of trapping (2015) at Ichauway, Baker County, Georgia.

CHAPTER 4

CONCLUSIONS & MANAGEMENT RECOMMENDATIONS

Due to the widespread decline of gopher tortoise populations (Auffenberg and Franz 1982), the species has recently been identified as a candidate for federal listing as Threatened under the U.S. Endangered Species Act (ESA) in its eastern range (USFWS 2011). The current listing of the gopher tortoise as a candidate species under the ESA has prompted long-term population viability analyses to evaluate listing criteria and management implications on population persistence. However, long-term population studies are lacking (Berish et al. 2012), and studies that investigate tortoise biology and behavior may not be representative of the lifespan of the organism, which is estimated to be at least 40 – 60 years (Landers 1980). My results provide robust estimates of a key demographic parameter reflecting the life history characteristics of the organism (i.e. long lived, slow to reach sexual maturity, low reproductive output, etc.) to aid these exercises. The focus of this study was to understand the underlying demographic mechanisms driving the persistence of tortoises on the landscape, and to understand the scale at which connectivity may be relevant to gopher tortoise populations. By better understanding how populations may vary in space and time, conservation managerw and practitioners may better evaluate the connectivity and viability of populations to inform reserve design and decision analysis for the species' conservation. Specifically, these results will aid in an ongoing a spatially explicit population modeling exercise for gopher tortoises in the state of Georgia. This work is part of a larger collaborative effort developing an adaptive landscape planning and decision framework to be implemented by the Georgia Department of Natural Resources for the statewide conservation of gopher tortoise populations.

To address the need for additional demographic information, this study investigated the long-term population ecology and movement patterns of gopher tortoises on Ichauway, the ~11,700 ha research site of the Joseph W. Jones Ecological Research Center. I conducted a mark-recapture study on four study populations of gopher tortoises where individuals had been previously marked between 1995 and 1999. Additionally, I used site-wide gopher tortoise presence data and environmental variables to construct a probabilistic sampling frame to survey and trap habitat surrounding the original sites as well, to better understand emigration processes. I used the mark-recapture data collected from the four study populations of gopher tortoises in 1995-2000 concurrent with the present mark-recapture efforts of the study populations and surrounding landscape matrix to address these research gaps. Specifically, I estimated annual apparent survival for four distinct age-classes of gopher tortoises on four long-term study population to better understand how tortoises persist on the landscape. Additionally, I estimated annual and long-term movement patterns of gopher tortoises on these study populations which occur on two different landscapes (e.g. contiguous and fragmented) to gain an implicit understanding of the functional connectivity of the organism.

Recently, gopher tortoise population dynamics have been investigated on a range of management strategies to assess the effects on apparent survival and demographic changes on naturally-occurring populations (Berish et al. 2012, Tuberville et al. 2014), to which my findings add additional information. My results reported apparent survival estimates of long-term apparent survival among the four distinct tortoise age-sex classes across relatively undisturbed sites of similar management regimes that vary in size and habitat composition. Apparent survival of all age classes was highest at Slash Pine and lowest at Green Grove. This was contradictory to my assumption that apparent survival values would be highest at Green Grove and lowest at Slash Pine due to their differences in landscape composition. Although, I believe this is influenced by the permeability and quality of the surrounding landscape matrix, as well as general site characteristics. For each site, apparent survival differed among age-classes as well. Adult male apparent survival was consistently highest, followed by adult males, subadults, and juveniles. Recent studies focusing on gopher tortoise demography have analyzed juvenile tortoises and subadult tortoises as one group, immatures (Tuberville et al. 2008, Berish et al. 2012, Tuberville et al. 2014). I analyzed the two groups separately due to the increased predation risk of juvenile tortoises (carapace length of < 150 mm) related to the hardness of their shell (Landers et al. 1982). Apparent survival of juveniles was markedly lower than subadults across all four sites. This research highlights the increased vulnerability of tortoises of a carapace length in between 50 to 150 mm (i.e. juvenile tortoises), and demonstrates the importance of conservation management tools, such as head-starting (Tuberville et al. 2015) or predator removal, to protect gopher tortoise populations.

Although researchers have addressed home range size and short-term movement patterns of the gopher tortoise (McRae et al. 1981, Diemer 1992, Eubanks et al. 2003), my study expands the scientific knowledge of gopher tortoise movement patterns in both time and space.. Broad-scale ecological processes, such as gene flow, colonization rates, and population persistence, often depend on the successful movement of individuals among habitat patches (Bowler and Benton 2005). The capacity of an organism to navigate in both space and time is a driving factor influencing the movement path of individuals, and is largely affected by the spatial structure of the environment (Nathan et al. 2008). In a synthesis of a global set of manipulative, fragmentation experiments, Haddad et al. (2015) found that inter-patch movements and recolonization were reduced among fragments of increased isolation. In addition, the authors found that abundance was generally lower in fragments of reduced area and increased isolation. This may indicate that in landscapes comprised of smaller and more isolated fragments, the ability of species to persist will be lower.

Tortoises in the northern populations (contiguous landscape) were shown, on average, to move larger distances at a higher rate on an annual basis than tortoises in the southern populations (fragmented landscape). Over the course of the entire study, individuals originally marked between 1995-2000, and predicted to be alive in 2015, were estimated to be less than 500 m from their original capture location in the fragmented landscape, which would represent only intra-patch movements (movements within the study population of original capture), whereas individuals captured in the contiguous landscape were estimated to be up to 2500 m from their original capture location (representing movements within and among study populations). In addition, the effect of the surrounding landscape matrix on movement patterns may explain the difference in estimates of apparent survival of gopher tortoises across studies (Ashton and Burke 2007, Tuberville et al. 2008, Tuberville et al. 2014) in addition to their management histories. Sexually immature tortoises (juveniles and subadults) were shown to move shorter distances on an annual basis than sexually mature tortoises (males and females). I believe these results suggest that the lack of juveniles and subadults in a population may be due to a lack of recruitment, and not due to an increase in dispersal of immature individuals (specifically juveniles).

The listing of the gopher tortoise as a candidate species as Threatened under the Endangered Species Act has led to an increased need for effective management and empirically-based conservation planning (USFWS 2011), to which this study adds key demographic information. In a recent study, researchers found a long-term population decline at eight of ten sites on protected lands in Florida. Consequently, understanding these demographic processes on both naturally-occurring populations on large, contiguous habitat patches of high quality and small, isolated habitat patches of marginal quality, such as this study, may allow conservation managers to better understand and manage protected gopher tortoise landscapes, and not just isolated populations.

While this study investigated tortoise survival and movement on four long-term study populations across various site and landscape characteristics, future research should focus on more manipulative-focused studies to determine the effects of site size, suitability, and the landscape matrix on survival and movement. Although survival did not vary much from population to population, the lack of juveniles and subadults at some of our study populations is cause for concern. Understanding the characteristics that increase social interactions (reproductive behaviors) and decrease predator effects (mortality of nests, hatchlings, and juveniles) is critical to inform better land management to promote recruitment. I did expand our understanding of tortoise demographic parameters (survival and movement) in both space and time. However, to ensure population persistence, a clear understanding of how large landscapes, of various composition and configuration, affect tortoise abundances over time on a broad-scale is needed. Line-transect distance sampling across large areas of the state of Georgia, and throughout the range of the tortoise, may give the necessary insight to how to manage landscapes of tortoises, and not just isolated populations surrounded by marginal habitat.

For conservation managers, I believe our findings suggest the clear vulnerability of juveniles and hatchlings as compared to other, more developmentally mature age-classes.

Creating tortoise pens around areas of known occurrence of juveniles, or forcible removing known predators, may increase survival of this age-sex class. Additionally, head-starting individuals to augment tortoise populations may be an appropriate method to bolster recruitment. Prescribed fire and mechanical removal of woody vegetation in the habitat intervening patches, or populations, of tortoises to maintain large, contiguous longleaf landscapes may be a necessary requirement to maintain gene flow, successful colonization, and population persistence., and may be more representative to the environmental conditions in which the species evolved (Dodd and Seigel 1991, Eubanks et al. 2003).

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