ASPECTS OF GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) POPULATIONS IN GEORGIA: STATUS, LANDSCAPE PREDICTORS, JUVENILE MOVEMENTS AND BURROW USE

by

ASHLEY ROSE BALLOU

(Under the Direction of Steven Castleberry)

ABSTRACT

I estimated gopher tortoise population sizes using line transect distance sampling on 17 sites in Georgia, and studied whether burrow width affects detection probability. I used tortoise density data to determine which site and landscape variables affect tortoise population density. I also studied a juvenile tortoise population in southwestern Georgia to test the accuracy of juvenile gopher tortoise burrow scopes, compare juvenile and adult tortoise burrow occupancy and evaluate a new method for tracking juvenile tortoises. Population size estimates among sites ranged from 89 (95% CI: 61-129) to 1877 (95% CI: 1485-2372). I found that detection probability decreased with decreasing burrow width, from 0.78 for burrows > 23 cm to 0.67 for burrows < 12 cm in width. The best model to predict tortoise densities was the model that included evergreen and mixed forest within sites and road density in the surrounding landscape. The juvenile burrow scope was highly accurate (occupancy of 96.7% of burrows was determined correctly), and juveniles had a significantly higher burrow occupancy rate (77%) than adults (40%). Finally, I found that fluorescent powder tracking was a simple and inexpensive method for tracking juvenile gopher tortoises.

INDEX WORDS: tortoise, population, line transect distance sampling, density, detection probability

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by

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) population has declined by about 80% across the range over the past 100 years (Auffenberg and Franz, 1982). The population west of the Mobile and Tombigbee Rivers in Alabama is currently federally listed as threatened (U.S. Fish and Wildlife Service, 1987) and the eastern population is a candidate for federal listing as threatened (U.S. Fish and Wildlife Service, 2011). Florida and southern Georgia are considered the stronghold of the species (Smith et al., 2006); however, the status of many gopher tortoise populations is largely unknown. Baseline information on tortoise populations is central to setting recovery goals for the species and for measuring progress toward those goals.

The gopher tortoise is considered a keystone species in longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*), or sandhill, forests that occur in the Coastal Plain of the southeastern United States. It is considered a keystone species because of the effects it can have on habitat and other vertebrate and invertebrate species. Gopher tortoises disperse seeds, which can influence the structure of understory vegetation (Kaczor and Hartnett, 1990). Boglioli et al. (2000) found that tortoises altered the groundcover around their burrows and increased soil compaction, and hypothesized that seeds of some native legumes benefit from scarification by gopher tortoises.

history requirements. For example, gopher frog (*Rana capito*) use of tortoise burrows after metamorphosis greatly reduces mortality rate (Roznik and Johnson, 2008).

The goals of this study were to: 1) provide baseline data on tortoise populations in Georgia for future monitoring and determine how burrow width affects detection probability and tortoise abundance estimates, 2) determine site and landscape variables that affect tortoise densities, 3) test the accuracy of juvenile gopher tortoise burrow scopes, 4) determine whether juvenile burrow occupancy differs from adult burrow occupancy, and 5) test a new method for short term tracking of juvenile gopher tortoises.

LITERATURE REVIEW

Longleaf pine ecosystems

Longleaf pine occurs across a gradient of soil types from poorly drained soils in pine flatwoods to well-drained sandy soils characteristic of sandhills. Longleaf pine ecosystems are open-canopied with diverse herbaceous groundcover and few understory hardwoods (Landers et al., 1995). These ecosystems are fire-dependent, and longleaf pine and its associated species are adapted to periodic fire (Landers et al., 1995).

Longleaf pine forests once covered approximately 37 million hectares of the southeastern United States (Frost, 1993), but have experienced severe declines since European settlement. According to Noss et al. (1995), longleaf pine forests have declined more than 98% in the southeastern Coastal Plain since 1880, when they covered approximately 40% of the region. This loss was the result of many factors, including harvest, fire suppression, development, agriculture and silviculture. Today, remnants of the longleaf forest type are highly fragmented (Frost, 1993).

Fire suppression is a threat to the longleaf pine ecosystem and associated species, such as the gopher tortoise. If longleaf forests are not regularly maintained with fire, fireintolerant trees become established and eventually displace longleaf and the herbaceous plants eaten by the gopher tortoise. Many historic longleaf pine forests have been converted to pine plantations. The fire regime in pine plantations is much different than in a natural longleaf pine ecosystem. Fire is generally suppressed because off-site pine species like slash pine (*Pinus elliottii*) are vulnerable to fire (Frost, 1993; Landers, 1995). Fire suppression increases the number of shrub and midstory plants, and that, paired with the high tree densities in plantation stands, keeps sunlight from reaching the forest floor, shading out herbaceous plants (Kirkman et al., 2007).

Gopher tortoise ecology

Gopher tortoises dig burrows up to 4.6 m long and 2 m deep in well-drained sandy soils of the southeastern Coastal Plain (Hansen, 1963; Auffenberg and Franz, 1982; Hermann et al., 2002; Jones and Dorr, 2004). Preferred habitat is open-canopy upland pine stands with herbaceous ground cover and frequent fire. Burrows remain at relatively stable temperature and humidity levels throughout the year providing shelter from heat and cold. Burrows also provide refuge during the frequent fires that occur in upland pine habitats. Hundreds of other species have been documented using the burrows. Jackson and Milstrey (1989) compiled reports of burrow commensals and found 302 invertebrate and 60 vertebrate species that use tortoise burrows. Included in these are species such as the gopher frog, the federally threatened eastern indigo snake (*Drymarchon couperi*) and the eastern diamondback rattlesnake (*Crotalus adamanteus*). Tortoise burrows provide these commensals the same benefits as tortoises, including shelter from cold, heat and fire.

Gopher tortoise abundance estimation

The extent to which gopher tortoise populations have declined has been inferred based on loss of habitat (Auffenberg and Franz 1982; U.S. Fish and Wildlife Service, 2011). While the species has undoubtedly declined, actual population data for gopher tortoises throughout their range are lacking. Historically, population estimates were derived by counting burrows and using signs of activity at the burrows as an indication of the presence and abundance of tortoises on a site. Burrow surveys have proven unreliable in estimating population size (Smith et al., 2005) due to differences in burrow occupancy from site to site (Auffenberg and Franz, 1982; Doonan, 1986; Breininger et al., 1991; Ashton and Ashton, 2008).

More recently, line transect distance sampling (LTDS; Buckland et al., 2001) has been used to estimate gopher tortoise density and abundance (Nomani et al., 2008; Smith et al., 2009). Line transect distance sampling is an efficient method for estimating population abundance and density of wildlife based on observations of individuals along transects (Buckland et al. 2001). Use of a camera system during surveys allows use of actual tortoise observations rather than burrow observations to derive population estimates. When used with a camera system, LTDS is often the most effective and efficient means for estimating gopher tortoise population size (Smith et al., 2009; Stober and Smith, 2010).

Gopher tortoise habitat requirements

Little research has examined how habitat characteristics and surrounding land use and land cover affect gopher tortoise populations. Hermann et al. (2002) found that gopher tortoises in Georgia were more likely to be found in open pine habitat maintained with fire, and these habitats had the highest proportion of active burrows. Unburned sites, agricultural land and pine plantations were found to have much lower numbers of active burrows. Gopher tortoises also require sunny sites for nesting, well-drained loose soil for burrows and suitable herbaceous food plants (Auffenberg and Franz, 1982). Jones and Dorr (2004) found that active burrows in Mississippi and Alabama were located more often in deep, sandy soils, and that density of active burrows was negatively related to total canopy closure and fine loam soils with limited sand content. Boglioli et al. (2000) found gopher tortoise burrows were more frequently found in longleaf forest with sparse overstory canopy cover, low shrub density and positive slope.

Juvenile gopher tortoises

Information is lacking on juvenile gopher tortoises and how their ecology may differ from adult tortoises. Juveniles, and their burrows, can be difficult to locate due to their small size (Pike and Grosse, 2006). Juvenile tortoises generally use only one or two burrows at a time, whereas adults may use 3-7 burrows over the course of a year (McRae et al., 1981). Adult burrow occupancy rates are reported to vary from 32% to greater than 90% depending on the site (Auffenberg and Franz, 1982; Breininger et al., 1991; Ashton and Ashton, 2008); occupancy rates for juvenile tortoises are not known. A major contributing factor to the lack of information on the ecology of juvenile gopher tortoises

is the difficulty in locating burrows and challenges associated with monitoring small individuals.

To address the need for additional information regarding the status of gopher tortoise populations, I estimated gopher tortoise population sizes using line transect distance sampling on 17 sites in the Coastal Plain of Georgia and looked at factors that can affect tortoise abundance estimates. With these data I also modeled tortoise densities using site and landscape habitat variables. Finally, I studied juvenile tortoise movement and burrow use in a population at the Joseph W. Jones Ecological Research Center at Ichauway in Baker County, Georgia.

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CHAPTER 2

POPULATION AND SITE EVAULATIONS OF GOPHER TORTOISES (GOPHERUS POLYPHEMUS) ON PUBLIC AND PRIVATE LANDS IN GEORGIA

ABSTRACT

Due to range-wide declines in gopher tortoise (*Gopherus polyphemus;* Daudin) populations, determining population status is vital for management and recovery of the species. I used line transect distance sampling (LTDS) based on observations of occupied burrows to derive baseline estimates of gopher tortoise abundance and density at 17 sites representing a variety of public and private lands in Georgia. I examined detection probability by burrow size class using LTDS on the 17 sites. Population size estimates across the 17 sites ranged from 89 (95% CI: 61-129) to 1877 (95% CI: 1485-2372). I found that detection probability increased as burrow size increased, ranging from 0.67 for the smallest juvenile burrows (< 12 cm) to 0.78 for adult burrows (>23 cm). Effective strip width, which is a function of detection distance, also increased with burrow size from 7.39 m for burrows < 12 cm to13.85 m for burrows > 23 cm in width. Because of the difference in detection probability between adult and juvenile tortoises, my results indicate that burrow size should be used as a covariate in gopher tortoise surveys using LTDS to create population estimates that better represent all size classes.

INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*; Daudin) is considered a keystone species in the longleaf pine (*Pinus palustris*) forests that occur in the Coastal Plain of the

southeastern United States. Gopher tortoises disperse seeds that can influence the structure of understory vegetation (Kaczor and Hartnett, 1990; Birkhead et al., 2005), may provide necessary seed scarification of some native legumes, and alter groundcover and increase soil compaction around their burrows (Boglioli et al. 2000). Additionally, many other species depend on gopher tortoise burrows to meet their life history requirements (Jackson and Milstrey, 1989). Unfortunately, the gopher tortoise population has declined by about 80% over the last 100 years (Auffenberg and Franz, 1982). The population west of the Mobile and Tombigbee Rivers in Alabama is currently federally listed as threatened (U.S. Fish and Wildlife Service, 1987) and the eastern population is a candidate for listing as threatened (U.S. Fish and Wildlife Service, 2011). Florida and southern Georgia are the stronghold of the species (Smith et al., 2006); however, the status of many gopher tortoise populations in Georgia is unknown, especially those on private lands. Baseline information on tortoise populations is central to setting recovery goals for the species and for measuring progress toward those goals.

Line transect distance sampling (LTDS) is a method for estimating population abundance and density of wildlife based on observations of individuals along transects (Buckland et al. 2001). Studies conducted on the use of LTDS for both large-scale gopher tortoise surveys and surveys of small populations found that LTDS is often the most effective and efficient means for estimating population sizes, provided estimates are based on observations of tortoises rather than subjective estimates of occupancy based on burrow characteristics (Smith et al., 2009a; Stober and Smith, 2010). The assumptions of LTDS are that all objects on the transect are detected, objects are found at their initial location, transect length and perpendicular distance from the transect are measured

accurately, and the transects are randomly placed (Buckland et al. 2001). With gopher tortoises, observations include both tortoises above ground and occupied burrows.

There are several important considerations when using LTDS for gopher tortoises. First, variables other than distance from the transect can affect detection probability of a burrow (Margues and Buckland, 2003). Smaller burrows are presumably more difficult to detect than larger ones, and would therefore have lower detection probabilities. The width of a tortoise burrow is approximately the same as the length of the tortoise (Alford, 1980). Thus, population estimates may not fully represent juvenile tortoises in the population. Nomani et al. (2008) found no or little difference in detection probability with and without burrow width as a covariate, but results were based on a small sample size (n = 163 with burrow width; n = 262 without burrow width) and surveys took place in open sandhill habitat. There is also error associated with using a camera scope to determine occupancy status of a burrow because of obstructions in the burrow or because the burrow may be longer than the camera scope. This source of error likely results in an underestimate of population size; however, the magnitude of the error may vary depending on the size of the burrow (Chapter 3) and observer experience (Smith et al., 2005).

In addition to collecting baseline data on tortoise population size at sites across southern Georgia, I wanted to determine how burrow width affects detection probability and tortoise abundance estimates when using line transect distance sampling (LTDS; Buckland et al., 2001, Buckland et al., 2004). I also collected habitat data to describe habitat characteristics and population management options for the sites.

METHODS

Study sites

I conducted surveys on 17 study sites distributed throughout the Coastal Plain of Georgia (Figure 2.1). Sites were privately owned hunting plantations and private or public conservation lands. Habitat conditions ranged from densely planted pines to mixed pine/hardwood to longleaf pine savannas with a wiregrass understory. Sites were selected by the Georgia Department of Natural Resources based on occurrence records for gopher tortoise population locations and willingness of landowners to allow access (Matt Elliott, Georgia Department of Natural Resources, pers. comm.).

Data collection

Potential tortoise habitat was determined for each site based on aerial photographs, soil maps, landowner surveys and site visits (Matt Elliott, Georgia Department of Natural Resources, pers. comm.). All suitable habitat areas were combined to create a sampling frame for each site. Pilot surveys were then conducted at each site to determine the tortoise encounter rate, which is defined as the length of transect (m) sampled/tortoise observed. Pilot survey transect locations were initially chosen by picking arbitrary starting points in the field. However, to avoid possible bias associated with using arbitrary starting points, I later used random start points generated using Hawth's Tools extension in ArcMap (ESRI, version 9.3.1). During pilot surveys, three observers (one person on center line, and one on either side of center line approximately 5-10 m away depending on habitat conditions) walked transects searching for tortoise burrows. I elected to use three observers rather than a single observer to increase the number of observations (Buckland et al., 1993; Buckland et al., 2004). All burrows

observed were scoped using an EMS2010 burrow camera with a 6.4 cm diameter (approximately 6 m long; for adult burrows) or a 2.5 cm diameter (approximately 1.7 m long; for juvenile burrows) camera head (Environmental Management Systems[®], Canton, GA) to determine whether a tortoise was present. All burrows were categorized as: 1) tortoise observed, 2) no tortoise observed for entire length of burrow, or 3) unable to determine if occupied (i.e., undetermined). "Undetermined" burrows were those that could not be searched completely because of an obstruction, sharp curve or recent wash in. I then calculated the tortoise encounter rate for each site.

I used the encounter rate to determine the total length of transect required to obtain abundance and density estimates with a coefficient of variation (CV) < 20%. Transects were established in Distance 6.0 software (<u>http://www.ruwpa.st-</u> and.ac.uk/distance/) using systematic random placement across suitable habitat on each study site. Transects and sampling frame boundaries were uploaded to a Nomad[®] Global Positioning System (GPS; Trimble Navigation, Ltd., Sunnyvale, CA) equipped with a GPS antenna (Crescent A100, Hemisphere GPS, Inc., Mountain View, CA) with submeter accuracy (Stober and Smith, 2010).

Three observers were also used for the full surveys. The survey team used ArcPad (ESRI, version 7.1) as a data entry platform and the team leader navigated the transect center line using the Nomad. A GPS point was collected at the beginning and end of each transect to determine the actual length of transect surveyed. The team leader searched the transect center line and the area around it for tortoises and burrows. The two additional observers walked approximately 5-10 m from the center line, and looked for burrows up to 20 m on either side of the center line. When a burrow or tortoise was

observed, a GPS point was collected and burrow attributes (burrow width and tortoise presence) were recorded. ArcGIS software was used to determine the perpendicular distance from the transect centerline to the burrow opening or tortoise.

At each burrow, I used a burrow camera to determine if a tortoise was present using the same categories as the pilot surveys. I recorded the number of undetermined burrows as a potential source of error in population estimates. I considered collapsed burrows to be unoccupied. Burrow width was measured 50 cm (\pm 1 cm) inside the opening using burrow calipers; these data were used as a surrogate for tortoise size because burrow width is closely correlated with carapace length (CL) (Alford 1980). Tortoises in Georgia reach sexual maturity at 23 cm CL (Landers et al. 1982). Therefore, I considered burrows \geq 23 cm in width to be inhabited by adult tortoises, and those < 23 cm potentially occupied by juveniles and subadults. Other vertebrates observed in burrows also were recorded.

To characterize habitat at each site, I took several vegetation measurements at the start and end points of the transects including: dominant canopy type (pine, hardwood or mixed), dominant ground cover (grass, broadleaf or bare), and basal area (measured with a 10 Basal Area Factor [BAF] prism; Forestry Suppliers, Inc., Jackson, MS). I also took digital photographs in four cardinal directions at the start and end points of survey transects.

Data analysis

I calculated tortoise density (tortoises/ha) and population abundance (number of tortoises based on density and area of the sample frame) for survey sites using Distance 6.0 software. I truncated the data set by including only occupied burrows within 20 m on

either side of a transect and by excluding the furthest 5% of burrows to either side of the transect (Buckland et al., 2001). I developed six models relating tortoise density and abundance to transect length, number of observed tortoises and perpendicular distance of tortoises from the transect. The six models used were a combination of key functions (uniform, half-normal or hazard-rate) and series expansion functions (cosine or simple polynomial), and were used to fit the distribution of the perpendicular distance data. In effect, the models estimate how many tortoises are not detected based on the distribution of observations with increasing distance from the transect. I used Akaike's Information Criterion (AIC; Akaike, 1974) to select the model(s) that best fit the data.

I used burrow width measurements of occupied burrows to describe the size/age class structure of the populations (Alford 1980). I used Pearson's product moment correlation to examine the relationship between tortoise density and habitat characteristics (basal area, % of habitat points that had pine, % of transect end points that had grass, and area of tortoise habitat) at each site. I accepted statistical significance at P ≤ 0.05 .

To determine if detection varied depending on burrow width, I combined data from four sites with high burrow densities and grouped burrows into five size categories: > 23 cm in width, 20 to 23 cm, 16 to 19 cm, 12 to 15 cm and 8 to 11 cm. Each category was analyzed separately in Program Distance to determine detection probability. After analyzing burrow size categories separately, gopher tortoise data collected using LTDS were run in Program Distance for each site with and without burrow size as a covariate to test whether using a covariate would affect the precision (CV) of the results. Three models, using the half-normal and hazard-rate key functions and the same series

expansion functions as above, were examined in Program Distance and evaluated using AIC as described above, adding burrow size as an additional factor. I was unable to use burrow size as a covariate with data from one site (Arcadia) because the burrow width measurements were not taken consistently.

RESULTS

We surveyed 8435 ha of suitable tortoise habitat across 17 sites. Tortoise densities ranged from 0.29 tortoises/ha at Persons to 1.74 tortoises/ha at Tallokas (Table 2.2). Population size estimates ranged from 95 (95% CI: 59-154) at Plum Creek to 1877 (95% CI: 1485-2373) at Lentile. The percentage of burrows for which I could not determine occupancy using a camera scope ranged from 1.0% at Warbick Farm to 9.7% at Plum Creek.

The model with the lowest AIC value varied among sites (Table 2.3); however, all candidate models that truncated 5% of the burrows farthest from the center line were generally within < 2 AIC points of each other. The addition of burrow width as a covariate lowered CVs for population estimates at 12 of 16 sites (Table 2.4).

Seven sites had grass as the dominant groundcover at > 50% of habitat points whereas 11 sites had pine or mixed pine and hardwood at > 50% of habitat points (Table 2.5). Average basal area ranged from 6.2 m²/ha at Plum Creek, which had recent clear cuts, to 18 m²/ha at Ballard, which had densely planted sand pine (*Pinus clausa*). None of the variables were significantly correlated with tortoise density (Mean Basal Area, P = 0.34, R = 0.209; % Pine, P = 0.33, R = -0.169; % Grass, P = 0.90, R = 0.035; Site Area, P = 0.33, R = -0.251).

There were two sites where we did not detect any occupied burrows < 18 cm in width, and we detected 13 occupied burrows < 18 cm at one site. There was a mean of 4.1 ± 4.2 burrows/site < 18 cm in width across all sites (Table 2.6). Detection probability for adult burrows was 0.78 (n = 1382), while the smallest burrows (< 12 cm in width) had a detection probability of 0.67 (n = 22; Table 2.7).

DISCUSSION

Smith et al. (2009b) used LTDS to estimate gopher tortoise populations on 13 of 20 protected lands in Georgia, consisting mainly of natural areas, wildlife management areas, state parks and preserves. Seven of the sites sampled by Smith et al. (2009b) had extremely low densities of tortoises, which would have required considerable effort to derive estimates using LTDS (e.g., > 1000 km of survey transect on one site). In contrast, I estimated population sizes on mostly privately-owned properties (13 of 17 sites) and was able to estimate density on all 17 sites with reasonable effort. In general, population abundances on the private lands were larger than those on protected lands. This finding supports the contention that the largest populations of gopher tortoises in Georgia may occur on privately owned lands (Hermann et al., 2002). Hermann et al. (2002) found open pine habitats had the highest proportion of active burrows, and that private lands in Georgia are often good habitat for tortoises because many are bobwhite quail (Colinus virginianus) hunting plantations with frequent fire and an open pine structure. Private lands in both this study and Smith et al. (2009b) had lower mean basal area (10.8 m^2/ha) than did public lands in either study (15.7 m^2/ha), which may be an indicator of more open habitat on private lands. To increase gopher tortoise populations on public lands, management activities should include thinning and prescribed fire to decrease canopy

cover and increase herbaceous cover (Auffenberg and Franz, 1982; Jones and Dorr, 2004).

None of the habitat variables I examined (mean BA, ground cover type, over story type and site area) from the 17 survey sites were significantly correlated with tortoise density. I expected that the habitat characteristics collected would be related to tortoise density because of the tortoises' preference for open canopy pine or mixed pinehardwood habitats with sparse understory (Auffenberg and Franz, 1982). The lack of observed relationships could have been related to the location of sampling points at the edges of the sampling frame. Habitat structure within the sampling frame may have been more representative of the overall habitat conditions. Some of the habitat on the edges was not ideal for tortoises and did not take into account the varying habitat quality along transects. Also, there was a great deal of variation in BA among sampling points, and the average BAs derived for these sites were likely not representative of the structure of habitat when tortoises occurred. Information on understory and overstory tree species rather than broad vegetation categories would have provided greater detail and percent canopy cover may be a better explanatory variable than basal area. Others have found that tortoise or burrow densities are correlated with herbaceous cover (Auffenberg and Iverson, 1979), amount of bare ground or fire frequency (Ashton et al., 2008). It would be useful to look at these and other habitat variables when trying to understand how habitat affects tortoise density.

In contrast to Nomani et al. (2008), I found that detection probability decreased with decreasing burrow size. Nomani et al. (2008) concluded that detection probability did not decrease for one site and decreased on another site, but did not affect burrow

density estimates. However, their results were based on using burrow width as a covariate, rather than analyzing burrow sizes separately. Also, unlike Nomani et al. (2008), I found a difference between density estimates calculated with and without using burrow width as a covariate. My results most likely differed from theirs because they had fewer small burrows in their dataset. The lower detection probability could explain the low numbers of juveniles found on some of my sites. Arcadia, Jeffords and OISP all had low numbers of juveniles found during surveys (two or three juveniles). The lack of observations of juveniles at these sites may indicate low or negligible recruitment; however, further monitoring is needed.

One possible source of error with line transect distance sampling is scoped burrows with unknown occupancy. The percentage of scoped burrows with undetermined occupancy was high at both Blackjack Crossing (7.0%) and Plum Creek (9.7%). At both sites, many burrows were longer than on other sites, and our burrow scope was unable to reach the end of the burrow. Also, at Blackjack Crossing, many burrows had pine needles and leaves packed inside so we were unable to adequately search the burrow. Surveys of sites with a higher percentage of burrows of unknown occupancy may yield underestimated population densities and sizes (Smith et al., 2009b). Using a longer burrow scope, at least 7 m long, would help reduce this source of error in population size estimates.

I recommend taking burrow width measurements for all surveys to account for the differences in detection among burrows of different sizes and to ensure that population estimates consider juveniles, which are an important, often overlooked life stage. The difference in detection probabilities for burrows of different sizes affected the density and

abundance estimates. Detection probabilities ranged from 0.65 - 0.78 depending on the size class, and many sites had few small juveniles. A different method, such as plot-based searches specifically for small burrows, may be necessary for increasing observations of juveniles to better include this age class in surveys.

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Table 2.1. Pilot survey data for 17 gopher tortoise survey sites in Georgia, 2010 - 2012. n_o was the number of tortoises observed, and L_o was the total length of transect surveyed (m). The full survey effort (total transect length; L) was determined based on the encounter rate (L_o/n_o) and a desired coefficient of variation (CV) of <20%. Transect surveyed is the actual length of transect that was surveyed during full surveys.

| Site | no | L_o | L_o/n_o | L for 15% CV | L for 17% CV | L for 20% CV | Transect surveyed |
|--------------------|----|-------|-----------|--------------|--------------|--------------|-------------------|
| Arcadia | 12 | 2300 | 191.7 | 25556 | 19896 | 14375 | 25573.2 |
| Balfour (D) | 26 | 7400 | 284.6 | 37949 | 29545 | 21346 | 24054.0 |
| Balfour (S) | 18 | 6550 | 363.9 | 48519 | 37774 | 27292 | 35546.8 |
| Ballard | 7 | 2265 | 323.6 | 43143 | 33589 | 24268 | 26532.9 |
| Blackjack Crossing | 8 | 5700 | 712.5 | 95000 | 73962 | 53438 | 31415.1 |
| Jeffords | 32 | 5640 | 176.3 | 23500 | 18296 | 13219 | 17742.4 |
| Lentile | 8 | 2000 | 250.0 | 33333 | 25952 | 18750 | 29834.7 |
| OISP- Lower | 12 | 3100 | 258.3 | 34444 | 26817 | 19375 | 22736.9 |
| Murff | 9 | 2928 | 325.3 | 43378 | 33772 | 24400 | 33278.6 |
| Persons | 6 | 3000 | 500.0 | 66667 | 51903 | 37500 | 53904.2 |
| Plum Creek | 8 | 1850 | 231.3 | 30833 | 24005 | 17344 | 20167.4 |
| Reed Bingham SP | 16 | 1300 | 81.3 | 10833 | 8434 | 6094 | 8410.9 |
| Samara/Beadles | 25 | 6090 | 243.6 | 32480 | 25287 | 18270 | 25318.8 |
| Tallokas | 14 | 3200 | 228.6 | 30476 | 23727 | 17143 | 25886.8 |
| Thompson Brothers | 10 | 2000 | 200.0 | 26667 | 20761 | 15000 | 22909.5 |
| Warbick Farms | 9 | 4837 | 537.4 | 71659 | 55790 | 40308 | 50967.7 |
| Warnell | 7 | 1800 | 257.1 | 34286 | 26693 | 19286 | 27789.2 |

| Site | Area ¹ | ESW | D | 95% CL | N | 95% CL | Р | CV | % Unknown Burrows |
|-----------------------|-------------------|------------|------------|-------------------|-------------|------------------|-----------|-----------|--------------------------|
| Arcadia | 836 | 12.71 | 0.6 | 0.349 - 1.032 | 502 | 292 - 863 | 0.82 | 0.27 | 3.90% |
| Balfour (D) | 979 | 16.34 | 0.7 | 0.479 - 1.022 | 685 | 469 - 1001 | 0.97 | 0.191 | 1.90% |
| Balfour (S) | 1048 | 13.61 | 0.744 | 0.475 - 1.166 | 780 | 498 - 1223 | 0.89 | 0.222 | 5.50% |
| Ballard | 259 | 14.57 | 0.841 | 0.552 - 1.28 | 218 | 143 - 332 | 0.82 | 0.214 | 2.80% |
| Blackjack | | | | | | | | | |
| Crossing | 186 | 12.33 | 0.633 | 0.436 - 0.917 | 118 | 81 - 171 | 0.69 | 18.9 | 7.00% |
| Jeffords | 514 | 11.71 | 0.843 | 0.459 - 1.547 | 433 | 236 - 795 | 0.70 | 0.301 | 5.80% |
| Lentile | 1115 | 16.42 | 1.684 | 1.332 - 2.129 | 1877 | 1485 - 2373 | 0.87 | 0.116 | 6.80% |
| Murff | 532 | 16.66 | 0.307 | 0.208 - 0.452 | 163 | 111 - 240 | 1.00 | 0.196 | 5.00% |
| OISP | 95 | 13.95 | 1.238 | 0.884 - 1.734 | 118 | 84 - 165 | 1.00 | 0.171 | 2.50% |
| Persons | 358 | 17.35 | 0.315 | 0.203 - 0.491 | 113 | 72 - 176 | 0.91 | 0.226 | 3.70% |
| Plum Creek | 147 | 16.39 | 0.65 | 0.404 - 1.048 | 95 | 59 - 154 | 0.93 | 0.244 | 9.70% |
| Reed | | | | | | | | | |
| Bingham SP | 66 | 13.89 | 3.081 | 1.997 – 4.753 | 202 | 131 - 312 | 0.78 | 0.218 | 1.20% |
| Samara | 222 | 12.46 | 2.092 | 1.54 - 2.842 | 465 | 342 - 631 | 0.73 | 0.154 | 2.00% |
| Tallokas | 546 | 10.87 | 1.742 | 1.147 - 2.645 | 950 | 626 - 1443 | 0.70 | 0.206 | 6.50% |
| Thompson | | | | | | | | | |
| Brothers | 310 | 18.53 | 0.777 | 0.537 - 1.125 | 241 | 167 - 349 | 1.00 | 0.185 | 3.10% |
| Warbick | | | | | | | | | |
| Farm | 563 | 14.22 | 0.297 | 0.208 - 0.423 | 167 | 117 - 238 | 0.79 | 0.18 | 1.00% |
| Warnell | 659 | 13.69 | 0.539 | 0.304 - 0.955 | 355 | 201 - 630 | 0.74 | 0.287 | 3.50% |
| 1 Area (ha) = es | timate an | nount of s | uitable ha | bitat; ESW = effe | ctive stri | ip width (m); Cl | V = coeff | icient of | variation; Unknown burro |

Table 2.2. Gopher tortoise population density (D; tortoises/ha) and abundance (N) estimates (with 95% confidence limits [CL])

derived using line transect distance sampling (LTDS) for 17 sites in Georgia, 2010 – 2012.

were those for which we could not confirm whether or not a tortoise was present using a burrow camera scope.

| Site | Raw Data | HN_simp5% | HN_cos5% | UN_simp5% | UN_cos5% | Bootstrap |
|------------------|----------|-----------|----------|-----------|----------|-----------|
| Arcadia | 239.10 | 214.31 | 214.31 | 213.62 | 213.62 | 214.31 |
| Balfour Decatur | 345.27 | 312.63 | 312.63 | 310.67 | 310.67 | 310.67 |
| Balfour Seminole | 436.59 | 394.11 | 394.11 | 392.95 | 392.95 | 392.95 |
| Ballard | 398.69 | 374.50 | 374.50 | 374.22 | 374.86 | 374.22 |
| Blackjack | | | | | | |
| Crossing | 305.08 | 279.41 | 279.41 | 279.96 | 278.99 | 278.99 |
| Jeffords | 214.65 | 194.80 | 194.80 | 195.24 | 194.58 | 194.58 |
| Lentile | 1040.76 | 967.96 | 967.96 | 967.93 | 968.25 | 967.93 |
| Murff | 216.40 | 193.28 | 193.28 | 191.28 | 191.28 | 191.28 |
| OISP | 443.97 | 413.11 | 413.11 | 413.11 | 413.11 | 411.11 |
| Persons | 373.04 | 349.95 | 349.95 | 348.44 | 348.44 | 348.44 |
| Plum Creek | 265.17 | 248.55 | 248.55 | 246.73 | 246.73 | 246.73 |
| Reed Bingham | 450.24 | 412.95 | 412.19 | 413.36 | 412.37 | 412.19 |
| Samara | 803.79 | 738.29 | 738.29 | 738.66 | 738.42 | 738.29 |
| Tallokas | 584.17 | 531.47 | 531.47 | 532.35 | 530.63 | 530.63 |
| Thompson | | | | | | |
| Brothers | 420.51 | 387.38 | 387.38 | 385.38 | 385.38 | 385.38 |
| Warbick Farm | 265.83 | 247.83 | 247.83 | 247.74 | 248.18 | 247.74 |
| Warnell | 255.90 | 239.29 | 239.29 | 239.58 | 238.88 | 238.88 |

Table 2.3. Akaike's Information Criterion (Akaike, 1974; AIC) values of six models developed in Program Distance to determine

gopher tortoise density and abundance at 17 sites in Georgia surveyed using line transect distance sampling, 2010 - 2012.

| | | | | | | | | | % <i>CV</i> |
|--------------------|-------------------|-------|-------|---------------|------------|-------------|------|-------|-------------|
| Site | Area ¹ | ESW | D | 95% CL | N | 95% CL | Р | CV | Change |
| Balfour (D) | 979 | 15.56 | 0.748 | 0.58 - 0.965 | 733 | 568 - 944 | 0.88 | 0.121 | -36.6 |
| Balfour (S) | 1048 | 13.45 | 0.753 | 0.505 - 1.234 | 789 | 529 - 1177 | 0.88 | 0.189 | -14.9 |
| Ballard | 259 | 14.29 | 0.844 | 0.581 - 1.226 | 219 | 151 - 318 | 0.80 | 0.189 | -11.7 |
| Blackjack Crossing | 186 | 13.44 | 0.592 | 0.393 - 0.892 | 110 | 73 - 166 | 0.76 | 0.207 | -98.9 |
| Jeffords | 514 | 11.38 | 0.867 | 0.479 - 1.568 | 445 | 246 - 806 | 0.69 | 0.291 | -3.3 |
| Lentile | 1115 | 16.84 | 1.659 | 1.359 - 2.026 | 1849 | 1515 - 2258 | 0.89 | 0.096 | -17.2 |
| Murff | 532 | 18.82 | 0.279 | 0.168 - 0.259 | 149 | 90 - 247 | 0.96 | 0.259 | 32.1 |
| OISP | 95 | 14.7 | 1.235 | 0.962 - 1.586 | 118 | 92 - 151 | 0.99 | 0.124 | -27.5 |
| Persons | 358 | 16.59 | 0.33 | 0.231 - 0.47 | 118 | 83 - 168 | 0.87 | 0.178 | -21.2 |
| Plum Creek | 147 | 16.63 | 0.641 | 0.34 - 1.211 | 94 | 50 -177 | 0.94 | 0.328 | 34.4 |
| Reed Bingham SP | 66 | 13.68 | 3.128 | 2.098 - 4.665 | 205 | 138 - 306 | 0.77 | 0.199 | -8.7 |
| Samara | 222 | 12.25 | 2.127 | 1.608 - 2.814 | 472 | 357 - 625 | 0.72 | 0.139 | -9.7 |
| Tallokas | 546 | 11.46 | 1.652 | 1.106 - 2.467 | 902 | 604 - 1346 | 0.74 | 0.196 | -4.9 |
| Thompson Brothers | 310 | 14.23 | 1.013 | 0.564 - 1.817 | 314 | 175 - 564 | 0.77 | 0.301 | 62.7 |
| Warbick Farm | 563 | 12.88 | 0.343 | 0.248 - 0.473 | 193 | 140 - 266 | 0.72 | 0.162 | -10 |
| Warnell | 659 | 14.32 | 0.515 | 0.3 - 0.885 | 340 | 198 - 584 | 0.77 | 0.269 | -6.3 |

Table 2.4. Gopher tortoise population density (D; tortoises/ha) and abundance (N) estimates (with 95% confidence limits [CL])

derived using line transect distance sampling (LTDS) for 16 sites in Georgia, 2010 – 2012, with burrow width as a covariate.

¹Area (ha) = estimate amount of suitable habitat; ESW = effective strip width (m); D = density (tortoises/ha); N= abundance (tortoises

x size (ha); CV = coefficient of variation; % CV Difference = percent change in CV from Table 2.2 obtained by adding burrow width

as a covariate.

Table 2.5. Number of sample points (n), mean basal area (m^2/ha), basal area range, and percent of sample points with grass, pine, and mixed as dominant canopy cover at 16 gopher tortoise survey sites in Georgia, 2010 - 2012. No vegetation data were collected at Jeffords.

| Site | n | Mean basal area | Basal area range | % grass | % pine | % mixed |
|--------------------|-----|-----------------|------------------|---------|--------|---------|
| Arcadia | 15 | 12.2 | 6.9-18.4 | 93.3 | 93.3 | 0 |
| Balfour (D) | 29 | 9.9 | 4.6-25.3 | 6.7 | 3.3 | 23.3 |
| Balfour (S) | 30 | 9.6 | 2.3-23.0 | 3 | 93 | 3 |
| Ballard | 124 | 18.1 | 0-45.9 | 4 | 49.2 | 36.3 |
| Blackjack Crossing | 164 | 12.9 | 4.6-35.6 | 46.3 | 97 | 0 |
| Lentile | 96 | 6.7 | 0-26.4 | 35.4 | 86.5 | 12.5 |
| Murff | 223 | 12.2 | 0-39.0 | 4.7 | 50.9 | 8.5 |
| OISP - lower | 34 | 13.3 | 0-27.5 | 11.8 | 38.2 | 29.4 |
| Persons | 124 | 10.3 | 0-29.8 | 62.1 | 42.7 | 51.6 |
| Plum Creek | 125 | 6.2 | 0-34.4 | 6.4 | 36.8 | 16 |
| Reed Bingham SP | 78 | 15.4 | 2.3-39.0 | 11.5 | 47.4 | 0 |
| Samara | 127 | 15.2 | 3.4-33.3 | 63 | 99.2 | 0 |
| Tallokas | 146 | 9.0 | 0-21.8 | 58.2 | 88.4 | 0 |
| Thompson Brothers | 114 | 11.0 | 0-29.8 | 56.6 | 43.4 | 52.2 |
| Warbick Farm | 148 | 7.8 | 0-32.1 | 6.1 | 80.4 | 16.9 |
| Warnell | 63 | 17.3 | 0-34.4 | 47.6 | 33.3 | 44.4 |

| Site | <12 | 12-17 | 18-23 | 24-29 | 30-35 | 36-41 | 42-47 | >47 |
|--------------|-----|-------|-------|-------|-------|-------|-------|-----|
| Balfour (D) | 1 | 2 | 7 | 11 | 27 | 9 | 2 | 1 |
| Balfour (S) | 5 | 8 | 7 | 16 | 31 | 8 | 1 | 0 |
| Ballard | 0 | 1 | 4 | 5 | 29 | 21 | 5 | 3 |
| Blackjack | | | | | | | | |
| Crossing | 2 | 1 | 2 | 4 | 33 | 11 | 1 | 0 |
| Jeffords | 0 | 0 | 2 | 5 | 25 | 3 | 0 | 0 |
| Lentile | 2 | 9 | 15 | 30 | 62 | 46 | 3 | 1 |
| Murff | 1 | 0 | 4 | 7 | 22 | 10 | 0 | 0 |
| OISP | 0 | 1 | 2 | 13 | 32 | 24 | 4 | 6 |
| Persons | 4 | 8 | 10 | 2 | 20 | 24 | 7 | 0 |
| Plum Creek | 0 | 1 | 6 | 5 | 17 | 16 | 3 | 1 |
| Reed Bingham | 3 | 3 | 2 | 19 | 34 | 15 | 0 | 0 |
| Samara | 0 | 1 | 5 | 11 | 50 | 62 | 14 | 4 |
| Tallokas | 2 | 3 | 5 | 16 | 56 | 18 | 2 | 0 |
| Thompson | | | | | | | | |
| Brothers | 2 | 1 | 2 | 3 | 11 | 42 | 6 | 1 |
| Warbick Farm | 4 | 0 | 2 | 3 | 17 | 19 | 1 | 0 |
| Warnell | 2 | 2 | 5 | 4 | 7 | 19 | 11 | 3 |

Table 2.6. Burrow size class distribution at 16 gopher tortoise (Gopherus polyphemus) sites surveyed in Georgia surveyed from 2010-

2012. Data are presented for occupied burrows

Table 2.7. Number of burrows (n), effective strip width (ESW)¹, and detection probability (P) of gopher tortoise (*Gopherus polyphemus*) burrow width categories from line transect distance sampling at 4 sites in Georgia, 2010-2012.

| Burrow Diameter (cm) | n | ESW | Р |
|----------------------|------|-------|------|
| > 23 | 1382 | 13.85 | 0.78 |
| 20 to 23 | 103 | 12.33 | 0.71 |
| 16 to 19 | 75 | 14.41 | 0.86 |
| 12 to 15 | 37 | 10.17 | 0.65 |
| < 12 | 22 | 7.39 | 0.67 |

¹Effective strip width is the distance at which the number of animals detected outside the ESW equals the number of animals missed inside the ESW.



Figure 2.1. Locations of sites surveyed for gopher tortoise using line transect distance sampling in Georgia, 2010-2012.

CHAPTER 3

JUVENILE GOPHER TORTOISE (GOPHERUS POLYPHEMUS) BURROW OCCUPANCY AND TRACKING TECHNIQUES

ABSTRACT

The gopher tortoise (Gopherus polyphemus) is federally listed under the Endangered Species Act in the western portion of its range and is a candidate for listing in the eastern part of its range. Data on occupancy and movements of all age classes is required for management and recovery. Juvenile gopher tortoises have received less research attention than adults, primarily because juveniles and their burrows can be difficult to locate, and because they spend more time underground than adults. To address the lack of data on juvenile occupancy and movements, I used a small (2.5 cm diameter) burrow camera system to determine occupancy rates of juvenile tortoise burrows at the Jones Ecological Research Center in Georgia. I trapped burrows to confirm the accuracy of cameras for determining occupancy. I then compared burrow occupancy of juveniles and adults using data from four additional sites in Georgia. A subset of tortoises captured (n=21) were tracked using both thread trailing (n=4) and fluorescent powder (n=17) to test the effectiveness of these methods to monitor juvenile movements. Overall, cameras were 96.7% accurate for determining occupancy of juvenile tortoise burrows. Juveniles had a significantly higher burrow occupancy rate (77% occupied, n= 30) than adults (40%, n= 183) at the Jones Center; however, juvenile burrow occupancy rates varied at the other sites. Average daily movement was 0.86 ± 0.66 m for juveniles tracked using

fluorescent powder. One tortoise moved a total of 1.74 m and the other moved a total of 0.85 m. Only two of four tortoises tracked with thread trailers left trails, while 14 of 17 tortoises tracked with fluorescent powder left trails. I found fluorescent powder tracking to be a relatively simple and inexpensive method for tracking juvenile tortoises and it yielded more consistent results than thread trailing. I found juvenile burrow occupancy varied across sites, and was significantly higher than adult occupancy at two sites. Higher occupancy may be related to better quality habitats for juveniles.

INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is a keystone species in longleaf pine (*Pinus palustris*) habitats of the Southeast (Eisenberg, 1983). Gopher tortoise populations have declined mainly due to human exploitation and habitat loss (Auffenberg and Franz, 1982); however, there is also concern about juvenile survival and recruitment as a factor in population declines (Pike and Seigel, 2006). Juvenile gopher tortoises are especially vulnerable to predation because of their small size and because their shells do not harden until they are 7-10 years old (Wilson, 1991; Butler and Sowell, 1996; Pike and Seigel, 2006).

Gopher tortoises are difficult to study because they spend much of their time in burrows. However, burrow characteristics can provide useful information about age and size of the inhabitant because the width of a tortoise burrow is approximately the same as the length of the tortoise (Alford, 1980). Male tortoises in southwestern Georgia mature at 16-18 years or 23-24 cm carapace length (CL), and females at 19-21 years or around 25 cm CL (Landers et al., 1982). Based on this information, tortoises inhabiting burrows < 23 cm in width are considered immature.

Adult gopher tortoises use more than one burrow within their home range for feeding and socialization purposes, and the relationship between burrow number and population size varies by site (McRae et al., 1981). Eubanks et al. (2003) found that females used 5.2 ± 0.32 burrows and males used 10.0 ± 0.53 burrows in a 13 month study in southwestern Georgia. Also in southwestern Georgia, McRae et al. (1981) found adults of both sexes generally used ≥ 2 burrows per month, although burrow use depended on season, whereas juveniles (0-9 years old) generally used 1-2 burrows at a time. Other studies have focused on burrow occupancy rates for tortoises, and have found that occupancy rates for adults vary from site to site, from 4% to 67% of active and inactive burrows found to be occupied (Auffenberg and Franz, 1982; Doonan, 1986; Breininger et al., 1991; Ashton and Ashton, 2008). Occupancy rates for juvenile burrows have not been described.

One method for determining burrow occupancy is to use a burrow camera scope (Smith et al., 2005). Although burrow scoping currently is considered the most reliable method for determining burrow occupancy in gopher tortoises, an estimate of accuracy is necessary when using the method to estimate population size. Observer experience and obstructions such as roots or debris can influence ability to determine whether a burrow is occupied by a tortoise using a camera scope. Scoping accuracy has been tested for adult and subadult burrows (Smith et al., 2005); however, similar data for cameras small enough to scope burrows <12 cm diameter are not available. As a result, surveys to provide tortoise population estimates using a burrow camera scope have been based on observations of tortoises in burrows >12 cm, which include only larger juveniles and adult tortoises (Smith et al., 2009).

Daily and seasonal movements of tortoises have been studied using a variety of methods, but tracking juvenile tortoises presents unique challenges. The primary methods used in previous studies have included radio transmitters (Diemer, 1992a; Epperson and Heise, 2003; Pike, 2006; Pike and Grosse, 2006) or thread trailers (Pike, 2006). Radio transmitters can be expensive and only give start and end points for movement at the times they are recorded, rather than total distances moved by the animal. Telemetry studies on juvenile tortoises can also be difficult due to their small size. Transmitters that are small and light enough to use on juveniles have short-lived batteries. Thread trailers are light-weight and much less expensive than radio transmitters and can provide information about actual distance moved by the animal (Iglay et al., 2006). However, thread can easily snap or become tangled, and may not be suitable if long-term data are desired. Pike (2006) used thread trailers to track hatchling tortoises in Florida, but they lasted only 2.2 ± 2.8 days before the spool fell off or the thread broke.

Fluorescent powder is a method frequently used to track small mammals (Stokes et al., 2004), and less frequently with other taxa such as lizards (Dodd, 1992; Fox et al., 2005), snakes (Furman et al., 2001) and turtles (Stickel, 1950; Stickel, 1989; Tuttle and Carroll, 2005; Perez-Heydrich et al., 2012). The standard procedure with all of these taxa is to cover the animal with the fluorescent powder before releasing it and to follow the powder trail at night using a portable ultraviolet light. If the same individual needs to be tracked for more than one day, it must be found again and recoated with powder daily. Florescent powder has been used to track hatchling wood turtle movements by recapturing and coating with powder daily (Tuttle and Carroll, 2005). Gopher tortoises cannot be recaptured daily to re-coat them with powder due to their use of burrows, but

the method may be modified slightly to include attaching a nylon sack containing powder to allow for tracking individuals for longer periods of time (Heydrich et al., 2012).

Juvenile gopher tortoises have received little research attention primarily because of the difficulties applying methods typically used on adults. For example, analysis of line transect distance sampling data from Georgia found detection probability of adult burrows (> 23 cm) on a transect was 0.78, while the smallest burrows (<12 cm diameter) had a detection probability of 0.67 (Chapter 2). Therefore, I had three main objectives. First, I compared occupancy rates of juvenile burrows to adult burrows. Second, I tested the accuracy of using a burrow camera scope to determine occupancy of juvenile burrows. Finally, I examined average daily movement of juvenile tortoises using powder tracking, a method that, to my knowledge, has not previously been used to track juvenile gopher tortoises and compared this method to thread trailing.

METHODS

Study Site

Data on juvenile gopher tortoises were collected at four sites in Georgia including the Joseph W. Jones Ecological Research Center at Ichauway in Baker County. Ichauway is an 11,700 ha property, but my study focused a 50 ha area called Green Grove, which has a high density of gopher tortoises (Eubanks et al., 2002). The remaining three sites were among those surveyed to estimate population size (Chapter 2) and included Lentile, a 1115 ha site in Irwin county, Samara, a 222 ha site in Worth county and Balfour, a 1048 ha site in Seminole County.

Data Collection and Analysis

Burrow occupancy and scoping accuracy

I located juvenile tortoise burrows in Green Grove using an existing GIS data set of burrow locations (J. McGuire, unpubl. data) and informal burrow searches in July 2011 and April-May 2012. I measured the width of all burrows to the nearest 1 cm, at 50 cm inside the burrow entrance using hand-made calipers. Burrows < 23 cm wide were considered juvenile burrows, and burrows ≥23 cm were considered adult. Juvenile burrows were scoped using an EMS2010 burrow camera with a 2.5 cm diameter camera head (Environmental Management Systems[®], Canton, GA) and adult burrows were searched using the standard 6.4 cm diameter camera head. Each burrow scoped was classified as: 1) tortoise observed; 2) end of burrow reached, no tortoise observed; and 3) unable to determine occupancy. I placed a pitfall trap at each of the juvenile burrows to confirm occupancy (Diemer, 1992b; Tuberville et al., 2008). Pitfall traps were 3.8 or 7.6 l buckets with drainage holes in the bottom. Buckets were placed flush with the ground and covered with tissue paper and a thin layer of sand to disguise the opening. I checked traps twice daily for 30 days or until a tortoise was caught exiting the burrow. I determined whether the tortoise in the trap came from the inside or outside of the burrow by placing small sticks vertically in the burrow entrance; if the sticks were dislodged, I assumed the tortoise was captured as it exited the burrow. After trapping ended (30 days without a tortoise or a tortoise was caught) results were compared to original classification given to the burrow using the burrow scope (tortoise, no tortoise or unable to determine) to determine the accuracy of the burrow scope (Appendix 2).

I weighed and measured all captured tortoises, and each was given a unique ID number either by shell notching (Cagle, 1939) or by gluing a plastic alphanumeric tag (Northwest Marine Technologies, Shaw Island, WA) to the carapace. Straight-line measurements of carapace length, plastron length, maximum body width and thickness, anal width and notch, and gular length were taken to the nearest 0.1 mm. I weighed tortoises to the nearest g. I also counted shell growth rings on a plastral scute to determine the approximate age of the tortoise (Wilson et al., 2003). Fourteen juvenile tortoises were trapped in 2011 during a pilot study, and 21 were trapped during the 2012 field season. I used linear regression to examine the relationship between burrow width and carapace length (CL). I considered a test statistically significant at $P \le 0.05$ in all statistical tests.

Occupancy was determined at the offsite locations (Persons, Lentile and Balfour Seminole) using a juvenile burrow scope in the same manner as in Green Grove. Data from all 4 sites were used to compare occupancy rates between juveniles and adults using Fisher's exact tests.

Daily Movements

Four juvenile tortoises (mean $CL = 173.15 \pm 8.76$ mm; range = 163–181 mm), captured using methods described above, were tracked using thread trailing in July 2011. I placed thread spools inside of plastic disposable pipettes (The Lab Depot, Dawsonville, GA) and attached them to the back of the carapace using PC-Marine Epoxy (Protective Coating, Inc., Allentown, PA). The device weighed approximately 7 g and was approximately 4 cm in length. I released tortoises at their burrows and tied the end of the thread to nearby vegetation. I checked for thread trails once/day following release.

Maximum distance and total distance the tortoise moved from the burrow each day were measured, if the trail was visible. I measured trails using a measuring tape starting at the burrow entrance and following the trail to its end where the tortoise returned to the burrow entrance.

I followed seventeen tortoises (mean $CL = 123.05 \pm 27.11$ mm; range = 63.7– 158.3 mm) with a fluorescent powder tracking device in July 2011 and April – May 2012. The tracking devices consisted of pouches weighing between 3-17 g (\leq 6.7% of the tortoises' body mass) made out of nylon stockings and filled with Greenwop® (Forensic Source, Jacksonville, FL) or pink leak detection (The Cary Company, Addison, IL) fluorescent powder. I attached pouches to the back of the carapace using PC-Marine Epoxy such that the pouch would drag slightly on the ground, allowing powder to slowly fall out and leave a trail. I released tortoises into their burrow and tracked them once/day following release. I tracked tortoises at night using a 395 nM portable ultraviolet light (LED Wholesalers, Hayward, CA). I measured total and maximum distance moved by each tortoise. After measuring each trail, I washed the powder away using water to avoid confusion with trails made the following day. I used Pearson's product moment correlation to examine the relationship between average distance tortoises moved/day and CL.

RESULTS

Burrow occupancy and scoping accuracy

Thirty burrows between 8.0 and 18.8 cm in width were searched for tortoises using the camera scope in Green Grove; 23 of the burrows were classified as occupied, six as unoccupied and one was recorded as unknown occupancy. I captured tortoises at

all 23 burrows classified as occupied with the camera scope. Tortoises were captured between two and 11 days after traps were set, with a mean trap time of 5.3 ± 2.5 days. The burrow classified as unknown occupancy was confirmed to be unoccupied after 30 days of trapping. Thus, scoping with the 2.5 cm diameter camera head was 97% accurate (29/30 burrows correct). Juvenile burrow occupancy at the four sites ranged from 21-77% (Table 1). Occupancy of adult burrows at Green Grove was 39.9% (J. McGuire, unpubl. data). The proportions of adult and juvenile burrows occupied differed at Green Grove (*P* = <0.001) and Persons (*P* = 0.012), but not at Lentile (*P* = 0.057) or Balfour Seminole (*P* = 0.462) (Table 1). There was a significant relationship between burrow width and CL of juvenile tortoises captured at Green Grove (*P* = <0.0001, r = 0.745; Figure 1).

Daily Movements

For three of the four tortoises, the thread trailing device lasted only one day, and one tortoise never left its burrow during the study. Two tortoises each left one measurable trail. One tortoise moved a total of 1.74 m in one day, and the furthest distance it moved away from its burrow was 0.87 m, and the other moved 0.85 m and 0.33 m from its burrow.

Tortoises tracked using fluorescent powder left 0-3 distinguishable trails/day. A total of 59 trails were observed for the 17 tortoises tracked. Average length of each trail was 0.70 ± 0.59 m. Total average daily movement for all trails was 0.86 ± 0.66 m on days they were active. Average distance moved away from the burrow was 0.30 ± 0.21 m. Neither average distance moved away from the burrow (P = 0.575, r = 0.152; Figure 3.2) nor average distance a tortoise moved/day (P = 0.895, r = 0.036; Figure 3.3) was correlated with tortoise CL.

DISCUSSION

I was able to confirm that a 2.5 cm camera scope was 97% accurate at correctly determining occupancy of juvenile gopher tortoise burrows <18 cm in width. Smith et al. (2005) found the accuracy of burrow scoping to be 95.8% for burrows large enough to scoped with a large adult burrow camera (approximately 10 cm in diameter). In my study, traps were set during late spring when tortoises are active (Eubanks et al., 2003) and all tortoises were captured within eleven days of pitfall traps being set. In a pilot study on my study site, tortoises were trapped during summer (July), and were not all trapped within 14 days, suggesting that trapping success may vary by season. Diemer (1992b) determined that tortoise capture rates varied by years and among study sites.

Juvenile burrow occupancy varied across sites. Burrow occupancy has been reported to range from 4% to 67% among populations and may be related to differences in habitat quality (Auffenberg and Franz, 1982; Doonan, 1986; Breininger et al., 1991; Ashton and Ashton, 2008). I suspect that the high proportion of occupied burrows at Green Grove may be a result of the methodology used to locate burrows at this site. Juvenile burrows are generally more difficult to observe than burrows of adults because of their small size (Diemer, 1992b; Chapter 2). However, occupied juvenile burrows may have been more visible than unoccupied burrows because of the clear mound of sand at the entrance, which could have biased observed occupancy rates for juveniles in this study. Burrows at Persons were located systematically using line transect distance sampling rather than by chance. However, I still may have been more likely to find active burrows than inactive because of their higher visibility. Higher occupancy rates at Green Grove and Persons could also be attributed to habitat quality. Fewer burrows may be

needed on sites with higher quality habitat, which could be linked to resource availability (McCoy and Mushinsky, 2007). Juveniles at Lentile and Balfour Seminole may need to use more burrows to cover a larger home range to obtain the resources they need. Habitat data taken at these sites showed low percentage of grass understory compared to Green Grove and Persons (Chapter 2). Lower quality habitat could result in decreased burrow occupancy rates as tortoises need to travel more to obtain resources (Pike, 2006). Lower habitat quality could potentially make juvenile occupancy rates more similar to adult burrow occupancy on these sites.

Fluorescent powder tracking was effective for determining movements of juvenile gopher tortoises for short time periods (up to 12 days). Tracking tortoises for longer periods with this method would have required recapturing the tortoise and attaching a new nylon pouch with fluorescent powder. Similar to observations by Tuttle and Carroll (2005), rain events washed away powder trails as described and clumped the powder in the nylon sack so that no further powder trail was left. Nonetheless, fluorescent powder tracking was more effective for tracking tortoises than thread trailing. Thread snapped frequently and became entangled in vegetation, especially with frequent trips in and out of burrows. Pike (2006) tracked hatchling tortoises using thread trailers and was able to track between 0 and 13 days, but the mean tracking duration was 2.2 ± 2.8 days.

Consistent with previous studies, juvenile tortoises moved relatively short distances from their burrows (Diemer, 1992a; Epperson and Heise, 2003; Pike, 2006; Pike and Grosse, 2006). Mushinsky et al. (2003) hypothesized that the limited movements reported for juveniles is a function of their short foraging bouts due to rapid satiation, or vulnerability to thermal stress or predation. In a north Florida population

reported mean home range was 0.05 ha for large juveniles (immature tortoises \ge 13.0 cm carapace length) and 0.01 ha for small juveniles (< 13.0 cm carapace length) (Diemer, 1992a). In southern Mississippi, average daily movement of 48 radiotracked hatchling tortoises ranged from 2.4 m and 20.6 m (8.17 ± 4.87 m) as they dispersed from the nest (Epperson and Heise, 2003).

My results indicate that small diameter burrow camera scopes and fluorescent powder tracking are useful tools for studying juvenile gopher tortoises. The 2.5 cm diameter burrow scope was accurate for determining occupancy of juvenile burrows and should be used to include smaller tortoises in population surveys. The camera system allowed me to determine that juvenile burrow occupancy varied among sites, and was significantly higher than adult occupancy rates on two sites. Fluorescent powder tracking was useful for short-term tracking of gopher tortoises, and could also be used to monitor juvenile habitat use.

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Table 3.1. Proportion of occupied adult (\geq 23 cm) and juvenile (<23 cm) gopher tortoise burrows as determined using a burrow camera scope at four Georgia sites, 2011-2012. A Fisher's Exact test was used to compare adult and juvenile occupancy rates within sites.

| Site | Adult Occupancy | n^1 | Juvenile Occupancy | n | Р |
|---------------------|--------------------|-------|-----------------------|-----|---------|
| Green Grove | 0.40 | 183 | 0.77 | 30 | < 0.001 |
| Lentile | 0.34 | 429 | 0.21 | 113 | 0.057 |
| Persons | 0.27 | 202 | 0.45 | 47 | 0.012 |
| Balfour Seminole | 0.33 | 173 | 0.39 | 49 | 0.462 |

 $^{1}n =$ the number of burrows used to calculate occupancy



Figure 3.1. Relationship between gopher tortoise body size (carapace length; CL) and burrow width. Burrow width was measured with calipers 50 cm inside the burrow, and tortoises were captured using pitfall traps at Green Grove, Ichauway, Baker County GA, 2011-2012.



Figure 3.2. Relationship between gopher tortoise body size (carapace length; CL) and average distance moved away from the burrow/day at Green Grove, Ichauway, Baker County Georgia, 2011-2012



Figure 3.3. Relationship between gopher tortoise body size (carapace length; CL) and average distance a tortoise moved/day at Green

Grove, Ichauway, Baker County Georgia, 2011-2012.

CHAPTER 4

MODELING LANDSCAPE CHARACTERISTICS AFFECTING GOPHER TORTOISE (GOPHERUS POLYPHEMUS) DENSITIES IN GEORGIA

ABSTRACT

Information regarding the status and viability of gopher tortoise (Gopherus *polyphemus*) populations is critical to effective management of this declining species. I used tortoise densities derived from line transect distance sampling for 28 sites in Georgia to model the effect of land cover at two spatial scales. I used eight site variables and seven landscape variables within a one km buffer surrounding each site to develop models. Variables were calculated from land cover, soil and road data in ArcGIS, as well as basal area data taken on sites during surveys. Twelve models were developed using site variables, and eight models were developed using landscape variables. Akaike's Information Criterion for small sample sizes (AICc) was used to identify the model(s) that received the most support from my data. Model averaging was used for variables in the best-fitted models to create a composite, multi-scale model. The multi-scale model, which included percent of evergreen and mixed forest on the site and road density in the 1km landscape surrounding each site, was the model best fitted to the data. Model predictions using the top three models suggested that site variables better predict tortoise densities than landscape variables, and that tortoise densities increase with increasing evergreen or mixed forest habitat.

INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is a federally listed species in the western portion of its range and a candidate for listing in the eastern portion (U.S. Fish and Wildlife Service, 1987; U.S. Fish and Wildlife Service, 2011). Population declines have resulted, in part, from severe declines in quantity and quality of habitat. Therefore, management to reverse declines requires knowledge of habitat factors influencing populations.

The gopher tortoise is considered a keystone species in the longleaf pine (*Pinus palustris*) forests that occur in the Coastal Plain of the southeastern United States. However, the longleaf pine ecosystem has experienced severe declines since European settlement. According to Noss et al. (1995), longleaf pine forests have declined more than 98% in the southeastern Coastal Plain since 1880, when these forests covered approximately 40% of the region. This loss was the result of many factors, including fire suppression, development and conversion to pine plantations. Additionally, remnants of the longleaf forest type are highly fragmented.

Past research has focused on how land use and land cover affect gopher tortoise populations based on abundance of burrows (McCoy and Mushinsky, 1992; Hermann et al., 2002; Jones and Dorr, 2004; Baskaran et al., 2006). Hermann et al. (2002) found that tortoises in Georgia were more likely to be found in open pine habitat maintained with fire, and these habitats had the highest proportion of active burrows. Unburned sites, agricultural land and pine plantations were found to have much lower numbers of active burrows. Gopher tortoises require sunny sites for nesting, well-drained loose soil for burrows and suitable herbaceous food plants (Auffenberg and Franz, 1982). Jones and

Dorr (2004) found that active burrows in Mississippi and Alabama were more often in deep, sandy soils, and were negatively related to total canopy closure and fine loam soils with limited sand content. Baskaran et al. (2006) used land cover and other site factors to create a model to predict gopher tortoise habitat based on absence or presence of burrows. They found that burrows increased with the following land cover types: transportation corridor, utility swath, clear-cut or sparse, deciduous, evergreen or mixed, pasture or row crop compared to other land cover categories. They also found that the occurrence of burrows decreased with increasing distance to roads and increased with increasing distance to streams. Canopy cover and pine basal area at burrows were half that at control points in southwestern Georgia (Boglioli et al., 2000).

Little research has been conducted using tortoise density rather than burrow density to identify important habitat characteristics. I developed habitat models using estimated tortoise densities obtained using line transect distance sampling methodology (Chapter 2) at 28 sites in southern Georgia. Because of the status and role of the gopher tortoise in the Southeast, information regarding the status and viability of remaining populations is critical to effective management. The goals of this study were to determine how landscape and site level factors influence tortoise density, and to develop a model for predicting gopher tortoise density.

METHODS

Data Collection

Data were collected on 28 sites in southern Georgia (Figure 1). These sites included public and privately owned properties with land use ranging from state parks, managed pine forest, to quail hunting plantations. The sites varied in size, condition, and

amount of potential tortoise habitat. Line distance transect sampling was used to estimate tortoise densities on each site (16 sites - Chapter 2; 12 sites - Smith et al., 2009) following methods outlined in the Gopher Tortoise Survey Handbook (2009) and Stober and Smith (2010). Only the upland habitats, as determined by soils and vegetation characteristics, were surveyed for gopher tortoises at each site. To characterize habitat structure at each site, I recorded basal area (BA; measured with a 10 Basal Area Factor (BAF) prism; Forestry Suppliers, Inc., Jackson, MS) at the start and end of each survey transect. Number of basal area points ranged from 8-223 depending on the site. From these data, I calculated average BA for each site.

The remaining variables examined were calculated from 2006 National Land Cover Database (NLCD) and STATSGO (Natural Resources Conservation Service; http://soildatamart.nrcs.usda.gov/USDGSM.aspx). Land cover and soil layers were clipped to the habitat boundary for each site as well as a 1 km buffer surrounding each site using ArcGIS (9.3 and 10.0). The NLCD classification contained 15 classes, six of which (evergreen forest, mixed forest, open, low intensity developed, medium intensity developed, and high intensity developed) were selected for analysis (Table 4.1). These classes were chosen based on my hypotheses of how land cover would affect tortoise density and correlations between variables. Variables were considered correlated at $r \ge$ 0.60. Open and low intensity development classes (low developed) and medium and high intensity classes (high developed) were grouped. Percent cover of the six classes on the sites and within the 1 km buffer were calculated. Average percent clay and water table depth were determined for all sites and surrounding landscapes using the STATSGO data set. Soil variables were included because gopher tortoises prefer to burrow in sandy,

well-drained soils. I calculated road density (m/ha) in and around each site using the roads layer from the U.S. Geological Survey Digital Line Graphs.

Data Analysis

Models describing the relationship between gopher tortoise density and site variables were developed using eight site variables (basal area, road density, water table depth, average % clay in the soil, low developed, high developed, evergreen and mixed forests). The same variables, except for basal area, were used to develop models for surrounding landscapes. Basal area could only be included in site models because basal area data did not exist for the landscape level. Twelve models were developed for variables at the site level (Table 4.2), each representing a hypothesis of how gopher tortoise density is related to specific habitat or environmental variables. Eight models were developed for variables at the landscape level (Table 4.2). I used Akaike's Information Criterion corrected for small sample sizes (AIC_c, Burnham and Anderson, 2002) to identify the model(s) that received the most support from my data (Burnham and Anderson, 2002). I used model averaging (function modavg.glm; R version 2.15.1) to develop a composite model for the variables with the most support from the AICc results (models within the top 0.95 cumulative AIC_c weight) for both the site and landscape model sets. I created a multi-scale model using variables with 95% confidence intervals that did not include zero from both the site and landscape models.

I created model predictions using the top models for sites, landscapes and the composite model using modavgpred (R version 2.15.1). This function applies the parameters from my models to my data to predict tortoise density values. I compared the model predictions to estimated tortoise densities (Chapter 2) on the sites.

RESULTS

Mean tortoise density for all 28 sites was 0.89 tortoises/ha, and ranging from 0.21-3.08 tortoises/ha (Table 4.3). Basal area on the sites ranged from 5-42 m²/ha with a mean of 14 m²/ha. Road density ranged from 2.7-42.98 m/ha with a mean of 16.58 m/ha. Water table depth ranged from 0.08-1.83 m with a mean of 0.98 m. Percent clay ranged from 0.67-7.50% with a mean of 4.02%. Percent evergreen forest ranged from 0.01-0.98 with a mean of 0.45. Percent mixed forest ranged from 0-0.65 with a mean of 0.09. Low developed ranged from 0-0.12 with a mean of 0.04. High developed ranged from 0-0.03 with a mean of 0.

At the landscape level, road density ranged from 16.9-219.34 m/ha with a mean of 90.63 m/ha (Table 4.3). Water table depth ranged from 0.05-1.83 m, with a mean of 0.91 m. Percent clay in the soil ranged from 1.60-7.50%, with a mean of 4.31%. Percent evergreen forest ranged from 0.14-0.63 with a mean of 0.34. Percent mixed forest ranged from 0.05. Percent low developed ranged from 0.01-0.13 with a mean of 0.04. Percent high developed ranged from 0-0.01, with a mean of 0.

Six of the 12 site models received 0.95 cumulative weight (Table 4.4). The models that best fit the data included the model with evergreen and mixed forests, and the model that included average water table depth and evergreen and mixed forests. Evergreen and mixed forests were the most important variables from model averaging because they were the only ones where the 95% confidence interval did not include zero (Table 4.5).

There were four landscape models with the top 0.95 cumulative weight (Table 4.6). The model that best fit the data for the landscape level only included road density.

Road density was the only variable where the 95% confidence interval did not cross zero (Table 4.5).

Based on results from the site and landscape models, I created a multi-scale model that included evergreen and mixed forests site variables, and the road density at the landscape level. The multi-scale model had a lower AIC_c value than the best individual site or landscape model, with an AIC_c value of 49.82. Model predictions from the top three models (site, landscape and composite) were compared to observed tortoise densities (Table 4.7). The sum of differences between observed and predicted densities for the site and composite models were close to zero, indicating a balance between overand under-predictions of tortoise density. The predictions derived from the top landscape model, however, were much lower than observed densities, potentially indicating that tortoises are not as influenced by the surrounding landscape as they are by the site variables.

DISCUSSION

Consistent with my hypotheses, I found that evergreen and mixed forests were the best explanatory variables for tortoise density with increasing tortoise density as percent composition of these forest cover classes increased. Although evergreen and mixed forest provide suitable habitat (Auffenberg and Franz, 1982), gopher tortoises likely respond to more fine scale habitat structure than was available in the NLCD, such as dominant tree species, percentage canopy cover, midstory cover or establishment method. For example, Hermann et al. (2002) found that active tortoise burrow densities were much higher on sites with open canopy pine managed with prescribed fire than in pine plantations. Also,

the NLCD data used was from 2006, and more recent data may have better represented current conditions on the sites.

Water table depth and percent clay in the soil were poor explanatory variables in my models. I expected them to be important because gopher tortoises prefer well-drained, deep, sandy soil for burrowing (Auffenberg and Franz, 1982; Jones and Dorr, 2004; Wigley et al., 2012). All upland habitat surveyed had similar soil characteristics, so the range of data for these two variables was small, which may account for them not being important variables. It is also likely that the STATSGO data were too coarse to pick up site-level variability in soils. Further study could be done using the higher resolution SSURGO soil data, if available.

The best explanatory variable when considering the surrounding landscape was road density. Although I expected road density to have a negative correlation with tortoise density, I observed a positive relationship. Roads may increase tortoise density in poor habitat because they create an open canopy and understory that may be lacking in other areas (Wigley et al., 2012). Hermann et al. (2002) found burrows in closed canopy habitats such as planted pine were more likely found along roads and edges.

The sum of the differences between observed and predicted densities for both the site and composite models were close to zero, which is expected when the models fit the data well. However, the landscape model predictions were generally lower than the observed densities, suggesting that the landscape factors considered in this study may have been too coarse to explain the differences observed in tortoise densities. Alternatively, site level variables may be more influential in affecting tortoise densities than are landscape level variables. Maclean et al. (2011) used occupancy data and habitat
variables to predict occurrence probability of African wetland birds relative to habitat characteristics collected from remote habitat mapping. They also related the occurrence probabilities to known densities so they could estimate abundance from the habitat characteristics. They were able to use these data to follow population decline rates. A study on the mountain bongo (*Tragelaphus eurycerus isaaci*) in Kenya found several strong habitat predictors, and prediction accuracies based on remote sensing variables ranged between 73 and 89% (Estes et al., 2011). Additional habitat data from the sites in my study, such as herbaceous groundcover, fire frequency or tree species, might yield a more accurate gopher tortoise model. Studies have found burrow and tortoise densities to be correlated with herbaceous cover (Auffenberg and Iverson, 1979; Diemer, 1986) and fire frequency (Ashton et al., 2008). Also, percent canopy cover may be a better explanatory variable than basal area.

Some additional factors should be considered when modeling tortoise density. Density may not be entirely related to current habitat characteristics. For example, past land use may play a large role in determining tortoise density. Lands that are currently "good" habitat could have been recently restored from what was formerly poor tortoise habitat. Recent changes in habitat quality could take years to have a discernable affect on tortoise densities because of the low reproductive rate of this species (Alford, 1980). Additionally, tortoise populations in Georgia were subjected to harvest for food and disturbance from rattlesnake collectors (Hermann et al., 2002; Diemer, 1986). Another potential limitation of this study was that many variables used in this study were averaged over entire sites and landscapes, so variation was not taken into account. A large variation

in these habitat characteristics could possibly be detrimental to tortoise populations if there is a lot of marginal habitat, and averaged variables will not take this into account.

Models that identify important habitat variables in predicting gopher tortoise densities could be used to help with management and conservation decisions. My results suggest that to improve gopher tortoise habitat landowners should manage for pine and mixed forest and discourage hardwoods. Prescribed fire is the primary method to discourage hardwood encroachment. Additionally, prescribed fire encourages plant species that gopher tortoise eat. Also, managers should strive to create more open habitat through thinning so that tortoises are not attracted to suboptimal open habitats such as roads.

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Figure 4.1. Locations of sites surveyed for gopher tortoises using line transect distance sampling in Georgia, 2008-2012.

| Table 4.1. Descriptions of Nation | nal Land Cover | Database 2006 | classes used | for model |
|-----------------------------------|----------------|---------------|--------------|-----------|
| analysis using AIC. | | | | |

| Code | Description |
|------|---|
| Е | More than 75% of the tree species maintain |
| | their leaves all year. Canopy is never without |
| | green foliage. |
| М | Neither deciduous nor evergreen species are |
| | greater than 75% of total tree cover. |
| DL | Areas with a mixture of some constructed |
| | materials, but mostly vegetation in the form of |
| | lawn grasses. Impervious surfaces account for |
| | less than 20% of total cover. |
| DL | Areas with a mixture of constructed materials |
| | and vegetation. Impervious surfaces account |
| | for 20% to 49% percent of total cover. |
| DH | Areas with a mixture of constructed materials |
| | and vegetation. Impervious surfaces account |
| | for 50% to 79% of the total cover. |
| DH | Highly developed areas where people reside |
| | or work in high numbers. Impervious surfaces |
| | account for 80% to 100% of the total cover. |
| | Code E M DL DL DL DH |

Table 4.2. Twelve site models and eight landscape models created to determine factors associated with gopher tortoise density on 28 sites in Georgia and their associated hypotheses relative to explaining tortoise densities.

| Scale/model | Hypothesis |
|----------------------------------|---|
| Site-level | |
| E ¹ +M+WTD+C+RD+DL+DH | Global model |
| 1 | Null model |
| | Density will be positively correlated with |
| E+M | evergreen and mixed forest because these provide |
| | suitable landcover |
| E+M+WTD | Density will be positively correlated with |
| | evergreen, mixed forest, and water table depth |
| | Density will be positively correlated with water |
| WTD+C | table depth and negatively correlated with % clay |
| | in the soil |
| RD | Density will be negatively correlated with road |
| | density |
| RD+DI | Density will be negatively correlated with road |
| | density and development |
| RD+DI +DH | Density will be negatively correlated with road |
| | density and development |
| DI +DH | Density will be negatively correlated with |
| ועיםע | development |

Table 4.2 Continued

| Scale/model | Hypothesis |
|--------------------|--|
| | Density will be positively correlated with |
| BA+E+M | evergreen and mixed forest and inversely related |
| | to basal area |
| | Density will be positively correlated with |
| BA+E+M+WTD | evergreen, mixed forest, and water table depth and |
| | inversely related to basal area |
| | Density will be positively correlated with water |
| BA+WTD+C | table depth and negatively correlated with % clay |
| | in the soil and basal area |
| E+M+WTD+C+RD+DL+DH | Global model |
| 1 | Null model Density will be positively correlated with |
| E+M | evergreen and mixed forest because it is suitable |
| | landcover |
| | Density will be positively correlated with |
| E+M+WTD+C | evergreen, mixed forest, and water table depth and |
| | negatively related with % clay in the soil |
| | Density will be positively correlated with water |
| WTD+C | table depth and negatively correlated with % clay |
| | in the soil |
| PD | Density will be negatively correlated with road |
| Ν <i>μ</i> | density |

Table 4.2 Continued

| Scale/model | Hypothesis |
|-------------|---|
| | Density will be negatively correlated with road |
| RD+DL+DH | |
| | density and development |
| | |
| | Density will be negatively correlated with |
| DL+DH | development |
| | development |

 ^{1}E = evergreen; M = mixed forest; WTD = average water table depth; BA = basal area;

RD = road density; DL = low development; DH = high development; C = % clay in soil

| Variable | Range | Mean | SE |
|-----------------|--------------|-------|-------|
| Site-level | | | |
| BA | 5-42 | 14 | 7 |
| RD | 2.70-42.98 | 16.58 | 10.61 |
| WTD | 0.25-6 | 3.2 | 1.78 |
| С | 0.67-7.50 | 4.02 | 1.75 |
| E | 0.01-0.98 | 0.45 | 0.27 |
| М | 0-0.65 | 0.09 | 0.13 |
| DL | 0-0.12 | 0.04 | 0.03 |
| DH | 0-0.003 | 0 | 0.001 |
| Landscape-level | | | |
| RD | 16.90-219.34 | 90.63 | 54.74 |
| WTD | 0.17-6 | 3 | 1.68 |
| С | 1.60-7.50 | 4.31 | 1.76 |
| E | 0.14-0.63 | 0.34 | 0.13 |
| М | 0-0.17 | 0.05 | 0.05 |
| DL | 0.01-0.13 | 0.04 | 0.03 |
| DH | 0-0.01 | 0 | 0.003 |

Table 4.3. Range of values for variables on 28 sites surveyed for gopher tortoises in Georgia and the mean and SE for each. Variables are defined in Table 4.2.

Table 4.4. Twelve site models and eight landscape models created to determine factors associated with tortoise density on 28 sites in Georgia. Akaike's Information Criterion for small sample size (AIC_c) was used to evaluate the models. Variables are defined in Table 4.2.

| Model | K | AIC _c | Δ_{i} | Wi | Cum. Wt |
|------------|----|------------------|-----------------------|------|---------|
| E+M | 4 | 57.35 | 0 | 0.44 | 0.44 |
| E+M+WTD | 5 | 59.12 | 1.78 | 0.18 | 0.62 |
| 1 | 2 | 59.90 | 2.55 | 0.12 | 0.75 |
| BA+E+M | 5 | 60.25 | 2.90 | 0.10 | 0.85 |
| BA+E+M+WTD | 6 | 61.53 | 4.18 | 0.05 | 0.90 |
| RD | 3 | 62.06 | 4.71 | 0.04 | 0.95 |
| DL+DH | 4 | 64.06 | 6.71 | 0.02 | 0.96 |
| WTD+C | 4 | 64.22 | 6.88 | 0.01 | 0.98 |
| RD+DL | 4 | 64.51 | 7.17 | 0.01 | 0.99 |
| Global | 10 | 66.82 | 9.47 | 0 | 0.99 |
| BA+WTD+C | 5 | 66.83 | 9.48 | 0 | 1.00 |
| RD+DL+DH | 5 | 67.00 | 9.65 | 0 | 1.00 |

Table 4.5. Variables, model-averaged estimates and 95% confidence intervals (CI) for variables in the top 0.95 cumulative weight of the site and landscape level AICc table for models to predict gopher tortoise density at 28 survey sites in Georgia. Variables are defined in Table 4.2.

| Variable | Estimate | SE | Lower 95% CI | Upper 95% CI |
|-----------------|----------|--------|--------------|--------------|
| Site-level | | | | |
| E | 1.47 | 0.66 | 0.16 | 2.77 |
| Μ | 2.43 | 0.96 | 0.55 | 4.31 |
| WTD | -0.08 | 0.09 | -0.25 | 0.09 |
| RD | 0 | 0.02 | -0.04 | 0.03 |
| BA | 0 | 0.01 | -0.02 | 0.01 |
| Landscape-level | | | | |
| RD | 0 | 0.02 | 0 | 0.01 |
| DL | -1.42 | 5.68 | -12.12 | 9.28 |
| DH | -99.98 | 537.38 | -316.61 | 116.65 |
| С | 0.11 | 0.17 | -0.05 | 0.27 |
| WTD | -0.08 | 0.09 | -0.27 | 0.1 |

E = evergreen; M = mixed forest; WTD = average water table depth; RD = road density;

DL = low development; DH = high development; C = % clay in soil

Table 4.6. Models used to examine landscape-level factors associated with gopher tortoise density at 28 sites in Georgia. Akaike's Information Criterion for small sample size (AIC_c) was used to evaluate the models. Variables are defined in Table 4.2.

| Model | K | AIC _c | Δ_{i} | Wi | Cum. Wt |
|-----------|---|------------------|--------------|------|---------|
| RD | 3 | 58.13 | 0 | 0.50 | 0.50 |
| 1 | 2 | 59.90 | 1.76 | 0.21 | 0.71 |
| RD+DL+DH | 5 | 61.21 | 3.07 | 0.11 | 0.81 |
| WTD+C | 4 | 61.55 | 3.42 | 0.09 | 0.91 |
| DL+DH | 4 | 62.21 | 4.07 | 0.07 | 0.97 |
| E+M | 4 | 64.49 | 6.35 | 0.02 | 0.99 |
| E+M+WTD+C | 6 | 66.98 | 8.84 | 0.01 | 1.00 |
| Global | 9 | 68.55 | 10.42 | 0 | 1.00 |

| Site | Estimated Density | Site Predicted Density | Difference | SE | Landscape Predicted Density | Difference | SE | Composite Predicted Density | SE | Difference |
|----------|----------------------|------------------------------|------------|------|-----------------------------------|------------|------|-----------------------------------|------|------------|
| WBTNC | 1.47 | 0.78 | 0.69 | 0.13 | 0.59 | 0.88 | 0.45 | 0.61 | 0.11 | 0.86 |
| TWMA | 0.53 | 0.73 | -0.2 | 0.14 | 0.23 | 0.3 | 0.57 | 0.99 | 0.18 | -0.46 |
| RCWMA | 0.72 | 0.99 | -0.27 | 0.12 | 0.88 | -0.16 | 0.13 | 0.65 | 0.12 | 0.07 |
| RGDTNC | 1.03 | 0.39 | 0.64 | 0.16 | 0.4 | 0.63 | 0.58 | 0.3 | 0.12 | 0.73 |
| OTRNWR | 0.35 | 0.97 | -0.62 | 0.14 | 0.81 | -0.46 | 0.18 | 0.66 | 0.13 | -0.31 |
| OD | 0.21 | 0.4 | -0.19 | 0.16 | 0.9 | -0.69 | 0.13 | 0.19 | 0.08 | 0.02 |
| LOSP | 0.56 | 0.9 | -0.34 | 0.14 | 0.34 | 0.22 | 0.59 | 1.03 | 0.15 | -0.47 |
| SSP | 0.98 | 0.99 | -0.01 | 0.15 | 0.17 | 0.81 | 0.51 | 1.8 | 0.29 | -0.82 |
| GLSSP | 0.49 | 0.48 | 0.01 | 0.16 | 0.62 | -0.13 | 0.42 | 0.3 | 0.1 | 0.19 |
| GCSP | 1.65 | 1.68 | -0.03 | 0.56 | 0.58 | 1.07 | 0.46 | 1.76 | 0.48 | -0.11 |
| FLS | 0.26 | 0.56 | -0.3 | 0.15 | 0.61 | -0.35 | 0.43 | 0.38 | 0.11 | -0.12 |
| DRNA | 0.76 | 1.29 | -0.53 | 0.23 | 0.53 | 0.23 | 0.5 | 1.27 | 0.21 | -0.51 |
| Warnell | 0.54 | 0.5 | 0.04 | 0.16 | 0.46 | 0.08 | 0.55 | 0.39 | 0.12 | 0.15 |
| WF | 0.3 | 0.96 | -0.66 | 0.12 | 0.66 | -0.36 | 0.37 | 0.75 | 0.11 | -0.45 |
| TB | 0.78 | 0.83 | -0.05 | 0.16 | 0.47 | 0.31 | 0.55 | 0.76 | 0.14 | 0.02 |
| Tallokas | 1.74 | 1.1 | 0.64 | 0.14 | 0.52 | 1.22 | 0.52 | 1.05 | 0.12 | 0.69 |
| Samara | 2.09 | 1.44 | 0.65 | 0.33 | 0.51 | 1.58 | 0.52 | 1.52 | 0.31 | 0.57 |
| RBSP | 3.08 | 1.2 | 1.88 | 0.16 | 0.17 | 2.91 | 0.51 | 2.39 | 0.4 | 0.69 |
| PC | 0.61 | 0.6 | 0.01 | 0.15 | 0.37 | 0.24 | 0.59 | 0.57 | 0.13 | 0.04 |
| Persons | 0.29 | 0.43 | -0.14 | 0.16 | 0.63 | -0.34 | 0.41 | 0.26 | 0.1 | 0.03 |
| OISP | 1.24 | 0.8 | 0.44 | 0.14 | 0.42 | 0.82 | 0.58 | 0.77 | 0.13 | 0.47 |

Table 4.7. Observed gopher tortoise densities (tortoise/ha), predicted densities from the top site-level models, landscape-level models,

and composite model, their standard errors (SE), and the difference between observed and predicted densities from 28 sites in Georgia.

| Murff | 0.31 | 0.65 | -0.34 | 0.14 | 0.4 | -0.09 | 0.58 | 0.61 | 0.13 | -0.3 |
|---------|-------|------|-------|------|------|-------|------|------|------|-------|
| Lentile | 1.68 | 0.86 | 0.82 | 0.12 | 0.71 | 0.97 | 0.31 | 0.62 | 0.11 | 1.06 |
| BJC | 0.63 | 0.81 | -0.18 | 0.14 | 0.43 | 0.2 | 0.57 | 0.78 | 0.13 | -0.15 |
| Ballard | 0.69 | 0.69 | 0 | 0.14 | 0.27 | 0.42 | 0.58 | 0.84 | 0.16 | -0.15 |
| BS | 0.66 | 1.14 | -0.48 | 0.18 | 0.77 | -0.11 | 0.23 | 0.85 | 0.16 | -0.19 |
| BD | 0.68 | 1.33 | -0.65 | 0.27 | 0.87 | -0.19 | 0.13 | 0.97 | 0.22 | -0.29 |
| Arcadia | 0.49 | 1.25 | -0.76 | 0.18 | 0.74 | -0.25 | 0.27 | 1 | 0.15 | -0.51 |
| | Total | | 0.07 | | | 9.76 | | | | 0.75 |

CHAPTER 5

CONCLUSIONS

The gopher tortoise (*Gopherus polyphemus*) is currently federally listed as threatened under the Endangered Species Act in the western portion of its range (U.S. Fish and Wildlife Service, 1987), and it is now a candidate for listing in the eastern part of its range (U.S. Fish and Wildlife Service, 2011). Relatively little is known about population numbers throughout the range. Information on the status and habitat requirements of populations is important for management of this species.

I used line transect distance sampling to estimate population size on 17 sites in Georgia. Tortoise densities ranged from 0.29 to 1.74 tortoises/ha. Population size estimates for my sites ranged from 89 (95% CI: 61-129) to 1877 (95% CI: 1485-2372) tortoises. The percentage of burrows that had unknown occupancy from scoping were also recorded to determine the margin of error in this method. Unknown burrows ranged from 1.0% to 9.7% of the burrows scoped on a site. Using a longer burrow scope would reduce this source of error in population size estimates.

The largest populations of gopher tortoises in Georgia seem to be on privately owned lands (Hermann et al., 2002; this study) and Department of Defense lands such as Ft. Stewart and Ft. Benning (Hermann et al., 2002). Hermann et al. (2002) found open pine habitats had the highest proportion of active burrows, and that private lands in Georgia are often good habitat for tortoises because many are bobwhite quail (*Colinus virginianus*) hunting plantations, with frequent fire and an open pine structure. Private

lands in both this study and Smith et al. (2009) had lower mean basal area ($10.8 \text{ m}^2/\text{ha}$) than did public lands in either study ($15.7 \text{ m}^2/\text{ha}$), which may be an indicator of better, more open habitat on the private lands. Habitat for gopher tortoises on public lands can be increased by reducing canopy closure and increasing herbaceous ground cover of wiregrass and other native bunch grasses that provide food for gopher tortoises and fine fuels for fire (Auffenberg and Franz, 1982; Jones and Dorr, 2004).

Habitat characteristics collected at the 17 survey sites, including basal area, dominant overstory and ground cover, did not explain differences in tortoise densities among sites. Other factors such as historic land use, soil type, fire history, or fine scale vegetation structure may better explain densities on these sites (Chapter 4, Ashton et al., 2008; Jones and Dorr, 2004). Several sites (Arcadia, Jeffords and OISP) all had low numbers of juveniles (two or three juveniles) relative to the other sites, which may be indicative of a lack of recruitment in these populations. Additional monitoring may be required at these sites to determine if populations are stable or potentially declining. I found that small burrows (< 12 cm) had a lower detection probability than that of adult burrows. This difference in detection probability could partially explain the low numbers of juveniles found on some sites. Using burrow width as a covariate in line transect distance sampling analysis affected population and density estimates at each site. Therefore, I recommend taking burrow width measurements for all LTDS surveys to account for the differences in detection to ensure that population estimates consider this important, often overlooked life stage. A new method for increasing observations of juvenile burrows may also be necessary to better represent this age class in surveys.

I compared burrow occupancy of juveniles and adults across four sites. Juvenile burrow occupancy rates varied from 0.21 to 0.77, and were significantly different from adult occupancy rates at 2 of the sites. Scoping accuracy for juvenile tortoise burrows was tested using a 2.5 cm diameter burrow scope to search juvenile tortoise burrows, and then using pitfall traps to verify scoping results. Scoping was found to be 96.7% accurate, with only one of the scoped burrows recorded as unknown occupancy. Finally, I compared fluorescent powder and thread trailing methods for tracking daily movements of juvenile tortoises. Total distance the tortoise moved and maximum distance moved from the burrow were measured. Thread from the trailers snapped frequently and became entangled in vegetation, especially when the tortoise made frequent trips in and out of burrows. Fluorescent powder trailing left 0-3 distinguishable trails/day, and was more successful than thread trailing. Average distance of each trail was 0.70 ± 0.59 m. Total average daily movement for all trails was 0.86 ± 0.66 m on days they were active. Average distance moved away from the burrow was 0.30 ± 0.21 m. Neither average distance moved away from the burrow nor average distance a tortoise moved/day was strongly correlated with tortoise carapace length. I recommend fluorescent powder over thread trailing to obtain movement data for juvenile tortoises.

Small diameter burrow scopes and fluorescent powder tracking may make this age class of gopher tortoises easier to study. The 2.5 cm diameter burrow scope was accurate for determining occupancy of juvenile burrows and should be used to include smaller tortoises in population surveys. Juveniles had occupancy rates that varied from site to site, and were significantly higher than adult occupancy rates on two sites.

Fluorescent powder tracking is a relatively easy and inexpensive method for short-term tracking of any size tortoise, and can be used to assess juvenile habitat use

Using tortoise densities obtained through LTDS from 16 of my sites, as well as tortoise densities on 12 sites from Smith et al. (2009), I created models to explain tortoise density using soil and landscape characteristics on each site as well as in a 1km buffer surrounding each site (landscape level). Akaike's Information Criterion was used to identify the model(s) that received the most support from my data. The best model included evergreen and mixed forest percentages on sites as well as road density at the landscape level. Site or site and landscape variables together were more precise in their predictions of tortoise density than landscape road density alone.

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APPENDIX 1

Table 2.8. Checklist of amphibian and reptile species observed during gopher tortoise surveys in Georgia from 2010-2012. Numbers of individuals observed in burrows is indicated parenthetically.

| | Balfour (D) | Balfour (S) | Ballard | Blackjack Crossing | Lentile | Murff | OISP - lower | Persons | Plum Creek | Samara | Tallokas | Thompson Brothers | Warbick Farm | Warnell |
|--|-------------|-------------|---------|-----------------------|---------|-------|--------------|------------|------------|--------|----------|----------------------|--------------|---------|
| Agkistrodon piscivorus Aspidoscelis sexlineatus | | | | | | | | | | | 1 | | 1 (1) | |
| Bufo terrestris | | (1) | | | | | | | | | | | | |
| Bufo sp. Cemophora coccinea Coluber constrictor | (11) | (3) | (1) | | 1 | (6) | | | 1 (2) | (2) | 1 | 1 | | |
| Crotalus adamanteus Drymarchon couperi Elaphe obsoleta Gastrophryne | | (1) | (3) | (4) | (4) | | (6) | 1 (1) 1 | | | 1 (1) | 1 (3) (2) | | 1 |
| carolinensis Pituophis melanoleucus Rana sp. Terrapene carolina | (1) | (3) | | | | | | | | (2) | | | (1) | |

APPENDIX 2

Table 3.2. Juvenile gopher tortoise burrows surveyed using a 2.54 cm diameter burrow camera scope and trapped by pitfall to determine occupancy at Ichauway, Baker County, GA, 2012.

| | Tortoise | | |
|----------------------|---------------|-------------------|-----------|
| | observed with | | |
| Burrow Diameter (cm) | camera scope? | Tortoise trapped? | Trap Days |
| 13.5 | Y | Y | 5 |
| 18.8 | Y | Y | 6 |
| 15.2 | Y | Y | 2 |
| 14.0 | Y | Y | 7 |
| 12.0 | Y | Y | 6 |
| 16.2 | Y | Y | 3 |
| 8.0 | Y | Y | 5 |
| 14.6 | Y | Y | 8 |
| 11.9 | Ν | Ν | 30 |
| 14.5 | Ν | Ν | 30 |
| 18.0 | Ν | Ν | 30 |
| 13.1 | Y | Y | 9 |
| 15.3 | Y | Y | 8 |
| 18.3 | Ν | Ν | 30 |
| 16.0 | Y | Y | 3 |
| 9.3 | Ν | Ν | 30 |
| 15.5 | Y | Y | 9 |
| 14.5 | Y | Y | 6 |
| 12.8 | Y | Y | 6 |
| 10.2 | Y | Y | 11 |
| 14.7 | Y | Y | 6 |
| 16.2 | Y | Y | 2 |
| 18.8 | Y | Y | 3 |
| 15.2 | Y | Y | 4 |
| 9.8 | Y | Y | 4 |
| 15.4 | U | Ν | 30 |
| 13.1 | Y | Y | 2 |
| 8.4 | Y | Y | 3 |
| 13.5 | Y | Y | 3 |
| 11.3 | Ν | Ν | 30 |

Table 3.3. Measurements collected on juvenile gopher tortoises trapped by pitfall in Green Grove, Ichauway, Baker County, GA,

| Tortoise ID | TBL^1 | CL | PL | MBW | MBT | AW | AN | Gul | PR | BW (g) |
|-------------|---------|-------|-------|-------|------|------|------|------|----|--------|
| 1606A | 146.2 | 144.9 | 140.9 | 113.7 | 59 | 23.3 | 16.1 | 25.7 | 7 | 551 |
| 1603A | 113.8 | 112.8 | 111.1 | 87.9 | 50.5 | 17.4 | 11.8 | 16.9 | 5 | 248 |
| 1605A | 149.7 | 145.2 | 144.2 | 110.8 | 59.1 | 22.3 | 16.3 | 23.4 | 10 | 476 |
| 1541A | 128.3 | 121.1 | 118.4 | 90.6 | 53.9 | 16.9 | 10 | 16.3 | 7 | 338 |
| 1607A | 140.5 | 139.9 | 138.2 | 100.4 | 60.1 | 30.3 | 9.4 | 18 | 8 | 464 |
| 2042A | 77.2 | 76.7 | 73.3 | 60.1 | 37.8 | 10.7 | 8.6 | 12.3 | 3 | 87 |
| 1608A | 136.7 | 135.3 | 132.5 | 100.9 | 57.9 | 20.7 | 14.6 | 20.4 | 5 | 406 |
| 2044A | 96.3 | 95.2 | 91.9 | 72.6 | 45.3 | 16.2 | 9.8 | 16 | 4 | 169 |
| 2050A | 87.9 | 84.3 | 84.1 | 68.5 | 42.8 | 13.2 | 9 | 9.7 | 3 | 120 |
| 2007A | 130.2 | 125.2 | 124.7 | 99.2 | 57.8 | 21.7 | 13.6 | 18.5 | 6 | 376 |
| 2045A | 121.6 | 119 | 117.3 | 91.9 | 53.3 | 20.3 | 19 | 20.4 | 4 | 305 |
| 2046A | 135.4 | 132.5 | 132 | 97.4 | 53.8 | 19.7 | 14.9 | 20.2 | 6 | 387 |
| 031 | 74.1 | 73.9 | 70.8 | 59.8 | 36.3 | 12.2 | 6.9 | 10.6 | 2 | 77 |
| 2047A | 125.6 | 123.2 | 122.7 | 95.5 | 52.2 | 18.7 | 14.2 | 19.4 | 6 | 311 |
| 2051A | 114.1 | 113.1 | 110.2 | 87.2 | 48.1 | 16.7 | 11.1 | 18.6 | 6 | 257 |
| 045 | 72 | 70.1 | 76.9 | 57.7 | 34.2 | 9.7 | 6.3 | 11.1 | 2 | 69 |
| 040 | 67.5 | 67.2 | 63 | 55.9 | 32.7 | 10.7 | 5.6 | 9.9 | 2 | 60 |
| 2052A | 108.4 | 106.6 | 105.6 | 84.9 | 49.9 | 14 | 10 | 10.5 | 5 | 214 |
| 2060A | 108 | 105.3 | 105.7 | 81.5 | 45.1 | 15.2 | 11 | 15.5 | 4 | 210 |
| 2061A | 125.5 | 123.4 | 122.3 | 92.4 | 52.2 | 21.2 | 14.4 | 20.9 | 7 | 325 |
| 1521A | 147.4 | 143.9 | 141.3 | 111.8 | 60.1 | 23.2 | 15.4 | 23.7 | 8 | 561 |
| 1604A | 128 | 127 | 123.3 | 100.8 | 54.6 | 17.2 | 13.1 | 21.3 | 5 | 388 |
| 1521A | 142.7 | 136 | 136.5 | 108.7 | 56.3 | 23.2 | 15.3 | 21.5 | 9 | 479 |
| 1530A | 158.3 | 152.4 | 153.3 | 113.1 | 60.6 | 24.1 | 17.5 | 25.3 | 13 | 608 |

| 1540A | 143.8 | 138.1 | 137.7 | 98.6 | 53.5 | 20.9 | 12.3 | 22.2 | 6 | 419 |
|------------------------|-------------|-------|-------|-------|------|------|------|------|-----|-------|
| 1541A | 119.4 | 116.7 | 115.3 | 86.8 | 52.9 | 17.2 | 11.4 | 19.9 | 9 | 291 |
| 1542A | 137.2 | 135.1 | 130.2 | 104.2 | 59 | 21.6 | 20.3 | 22 | 5 | 406 |
| 2007A | 120 | 114.8 | 114.9 | 87.2 | 53 | 20.3 | 13.5 | 15.3 | 5 | 295 |
| 026 | 63.7 | 62 | 59.6 | 50.8 | 30.5 | 8.2 | 8.1 | 11.5 | 1 | 46 |
| 1520A | 179.9 | 174.9 | 174.3 | 124.9 | 70.4 | 29.6 | 17.6 | 29.2 | 11 | 819 |
| 1522A | 168.4 | 163 | 164 | 117.1 | 65.6 | 23.7 | 21.6 | 23.9 | 11 | 768 |
| 1524A | 168.7 | 165.6 | 162.4 | 118.1 | 66.4 | 25.8 | 20.7 | 25.5 | 12 | 759 |
| 1515A | 177.4 | 171.7 | 170.9 | 130.4 | 69 | 23.9 | 21.1 | 27.8 | 12 | 886 |
| 1172A | 181 | 172.3 | 174.8 | 132.9 | 73.9 | 26.1 | 20.2 | 29.7 | 8 | 948 |
| 1544A | 126.7 | 124.4 | 123.6 | 95 | 56 | 18.6 | 13.4 | 19.5 | 5 | 314 |
| 2057A | 143.6 | 141.5 | 142.4 | 111.5 | 60.1 | 21.9 | 17.4 | 21.3 | 7 | 530 |
| Mean | 126.8 | 123.7 | 122.5 | 94.5 | 53.4 | 19.4 | 13.7 | 19.3 | 6.4 | 388.0 |
| Standard | | | | | | | | | | |
| Deviation | 31.5 | 30.2 | 30.5 | 21.1 | 10.4 | 5.3 | 4.4 | 5.5 | 3.1 | 236.2 |
| $\pm TDI = 4 - 4 - 11$ | - J 1 41. A | | | | | | | | | |

¹TBL = total body length (mm); CL = carapace length (mm); PL = plastron length (mm); MBW = maximum body width (mm); MBT

= maximum body thickness (mm); AW = anal width (mm); AN = anal notch (mm); Gul = gular (mm); PR = plastron rings; BW =

body weight (g)