ECOLOGY OF JUVENILE GOPHER TORTOISES (GOPHERUS POLYPHEMUS) ON A GEORGIA BARRIER ISLAND.

by

BESS BROWN HARRIS

(Under the Direction of Tracey D. Tuberville and Nathan P. Nibbelink)

ABSTRACT

Little is known about the ecology of the juvenile age class of the gopher tortoise (*Gopherus polyphemus*), limiting our ability to manage the species. I evaluated the overwintering timing, temperatures, and winter activity of juvenile gopher tortoises. I also compared the juvenile growth rates of gopher tortoises at St. Catherines Island to the growth rates reported at other study sites throughout the gopher tortoise range. My results found that the timing and duration of overwintering in juvenile gopher tortoises appear to be similar to that of their adult counterparts; however, juveniles are more active than adults throughout the winter. On average juveniles emerged during the winter at ≥21ºC ambient temperatures (the minimum activity temperature observed in adults) but were also beginning activity at temperatures as low as 15.8 ºC. I also found that the St. Catherines Island juvenile tortoises exhibited the highest growth rates reported for any study sites.

INDEX WORDS: gopher tortoise, *Gopherus polyphemus*, juvenile, reptile, overwintering, activity, growth rate, barrier island

ECOLOGY OF JUVENILE GOPHER TORTOISES (GOPHERUS POLYPHEMUS) ON A GEORGIA BARRIER ISLAND.

by

BESS BROWN HARRIS

BA, Agnes Scott College, 2010

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2014

ECOLOGY OF JUVENILE GOPHER TORTOISES (GOPHERUS POLYPHEMUS) ON A GEORGIA BARRIER ISLAND.

by

BESS BROWN HARRIS

Major Professor:	Tracey D. Tuberville Nathan P. Nibbelink
Committee:	Terry M. Norton Richard F. Daniels

Electronic Version Approved:

Julie Coffield
Interim Dean of the Graduate School
The University of Georgia
August 2014

DEDICATION

I would like to dedicate this thesis to Dr. Gale Bishop. He is the friend I never knew I needed, and came into my life when I did not know I needed a friend. I have had many supporters and influences in my life, in that way I have been incredibly fortunate. However, if it was not for Gale’s friendship and support I am not sure if I could have mustered the energy to finish my thesis. Gale was the voice of reason that kept me going when pressures were high and graduation seemed like an unreachable goal. Gale taught me that when the times are hard and you’re not sure how to get from one day to the next, sometimes all you need to do is breathe deep and know that you’re not alone. There is little in this world as valuable as a good friend. Sharing coffee with a good friend is sometimes all you need to start the day on the right foot.

ACKNOWLEDGEMENTS

I would like to thank my committee, Drs. Tracey Tuberville, Nate Nibbelink, Terry Norton, and Dick Daniels, for their guidance throughout my graduate school experience.

I would also like to thank Elizabeth Hunter for her help in trapping and data collection when I was unable to be in the field myself. I also need to thank Rachel Harris, Lisa Rodriguez, and Veronica Greco, who each leant a hand with data collection, which saved me a lot of time and patience. A special thanks to Jack Tuberville, who helped to build the environmental stations that I needed for my study. Thanks again, Royce Hayes and Christa Frangiamore for all of the help and support of getting me on the island and supporting my requests. Thanks to all of the SCI Foundation guys who were always there to help whenever my field equipment or vehicles needed repairs.

Thanks to TERN-Friends of Georgia’s Nongame Wildlife, Riverbanks Zoo, and the St. Catherines Island Foundation for helping to fund my thesis research.

Finally, I would like to thank my family both those biological and emotional. Walton and Tina Harris, my parents and the greatest supporters of everything I’ve done since before I could walk, and the Kling family, for taking me in and letting me know I would always have a full belly and a warm bed.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Gopher Tortoises (*Gopherus polyphemus*) are large herbivorous reptiles inhabiting the longleaf pine ecosystem of the coastal plains region of the southeastern United States from South Carolina to Louisiana (Auffenberg and Franz, 1982). Gopher tortoises are considered a keystone species because their burrows provide refuge for over 300 different invertebrate and vertebrate species, aid in seed dispersal, and help to return leached nutrients to the surface (Eisenberg, 1983; Kaczor and Hartnett, 1990). Throughout their range, it is estimated that gopher tortoises have been reduced by about 80% in the last century. These population declines have been primarily attributed to habitat destruction resulting from urbanization and other human activities (Auffenberg and Franz, 1982). The gopher tortoise is listed as threatened in the western portion of the species' range and has only recently been designated as a candidate species in the eastern portion of the range (USFWS, 2011).

Due to the severe decline in gopher tortoise numbers and the increasing fragmentation of their landscape (Auffenburg and Franz, 1982), it is important to understand the movements, habitat use, and overall needs of the species for management and conservation. The juvenile age class has been identified as a key life stage in understanding how to conserve gopher tortoises, yet little is known about their ecology, including dispersal distances, movements, and survival rates of juveniles. Information is needed to better understand the needs and ecology of the juvenile age class (Smith et al., 2006; GTC, 2012; USFWS, 2011).

This study aims to evaluate the overwintering timing, temperatures, and winter activity of juvenile gopher tortoises and to compare the growth rates of gopher tortoises on St. Catherines Island, Georgia to the growth rates reported at other study sites throughout the gopher tortoise range. Information will be used to better understand the needs of juvenile gopher tortoises and may be used to better manage populations for increased survival of juvenile tortoises. Studies have primarily focused on adult tortoises because adult tortoises and burrows are relatively easy to locate. Few studies have documented the movements and habitat use of juvenile non-hatchling gopher tortoises. Recruitment and juvenile survivorship data for most gopher tortoise populations are insufficient (USFWS, 2011), hindering efforts to understand population dynamics in this species. In addition, encountering enough individuals of this age class to have a robust sample size. Much of the difficulty in studying juveniles results from obtaining reliable sample sizes, and as a result, most of our current understanding of this age class is based on radiotelemetry of a small number of individuals.

In an effort to fill in the information gaps regarding juvenile gopher tortoise ecology, I evaluated the juvenile gopher tortoise overwintering and growth rates on a Georgia barrier island. I fitted juvenile tortoises with temperature loggers that could be compared with those placed in the environment. The objective of the temperature loggers was to monitor overwintering timing, temperatures, and winter activity of juvenile gopher tortoises. Additionally, I compared growth rates and age at maturity of the juvenile gopher tortoises at St. Catherines Island to those reported from other study sites throughout the gopher tortoise range.

Literature Review

The gopher tortoise is well adapted for digging; they have large shovel-like forelimbs that they use for excavating their burrows. A major portion of their life is spent underground in these burrows, providing them refuge from both predators and extreme temperatures (Ernst and Barbour, 1972). Burrows are dug in well-drained sandy soil, with records of adult burrows reaching 4.6 meters long and 2 meters deep with juvenile burrows being smaller in all measures (Hansen, 1963; Wilson, 1994). Over 360 other species have been documented to use these burrows; providing these commensals a safe retreat, just as they do for the tortoise (Eisenberg, 1983; Jackson and Milstrey, 1989). Through the digging of the burrow, nutrients are brought to the surface making it available to the surrounding plants (Kaczor and Hartnett, 1990). Burrow excavations also act to form a distinct mound outside the entrance referred to as the burrow apron, which is used for the tortoise's thermoregulation needs as well as for depositing their nest.

The longleaf pine ecosystems, habitat of the gopher tortoise, have also experienced severe declines; estimating that there has been more than a 98% decline in the southeast since 1880 when it covered approximately 40% of the region (Noss et al., 1995). This habitat is very important for the gopher tortoise and the declines in this ecosystem are due to some of the same causes as the tortoise declines, namely habitat destruction and fire suppression. The longleaf pine ecosystem is maintained by fire; this keeps the fire-intolerant trees from growing up and over crowding the habitat (Diemer, 1986). Tortoises need an open savanna-like habitat to forage, bask and reproduce in; if the habitat begins to overgrow it can shade out the longleaf and the herbaceous plants that the tortoise eats. When fire is suppressed from the habitat, it can quickly become an overgrown hardwood forest, unsuitable for the gopher tortoise.

Because of the severe decline in gopher tortoise numbers and the increasing fragmentation of their landscape it is important to understand as much about the species as is possible to better benefit management and conservation. Studies have been primarily focused on the adult tortoises because their burrows are relatively easy to locate. Tortoises, like other chelonians, have low survivorship and recruitment into adulthood (Gibbons and Semlitsch, 1982) which makes this a very important life stage for populations in decline. Recruitment and juvenile survivorship data for most gopher tortoise populations are insufficient (USFWS, 2011), hindering efforts to understand population dynamics in this species. Most of our current understanding of juveniles is based on surveys of burrows (rather than the tortoises themselves) or radiotelemetry of a small number of hatchlings or juveniles (Butler et al, 1995; Diemer, 1992; McRae et al, 1981; Pike and Grosse, 2006; Wilson, 1994).

The age at sexual maturity is especially important in species that are in decline, like the gopher tortoise, because it suggests the amount of time an individual is exposed to mortality before it becomes a reproductive member of the population (Auffenberg and Iverson, 1979). Growth rate and age specific size are ways to estimate this age. Additionally, growth rates can also be used to estimate habitat quality. Growth rates are variable across the gopher tortoise range due to differences in both climate and habitat quality (Landers et al, 1982; Godley, 1989; Goin and Goff, 1941; Mushinsky et al., 1994). A difference of only a few kilometers can still result in very different growth rates if the sites have different habitat histories (Diemer and Moore, 1994; Mushinsky et al., 1994). Knowing the growth rates and estimated age of maturity at different sites helps researchers and managers to better understand the effects of different habitats.

Gopher tortoises stand out from other reptiles because they create their own retreat sites; digging extensive burrows that they excavate to provide protection from predators and temperature extremes (Ernst and Barbour, 1972). Research on gopher tortoise timing and temperatures has primarily focused on adults (DeGregorio et al., 2012). Gregory (1982) notes that there can be differences in the timing and occurrence of overwintering between the young and adults of reptile species, but what these differences are is not always comparable between species. The differences between these subgroups is due to the relationship of body size to the heating and cooling abilities of each (Hutchison, 1979; Wilson et al., 1994). Due to a lack of information regarding overwintering timing and temperatures with respect to juvenile gopher tortoises it is a clear area of need study.

Literature Cited

Auffenberg, W. and R. Franz. 1982. The status and distribution of the gopher tortoise (Gopherus polyphemus). Pages 95-126 in R.B. Bury, editor. North American Tortoises: Conservation and Ecology (Wildlife Research Report 12). U.S. Fish and Wildlife Service Washington, DC.

Auffenberg, W., and J.B. Iverson. 1979. Chapter 25: Demography of terrestrial turtles. Pages 541-569 in M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

Butler, J.A., R.D. Bowman, T.W. Hull, and S. Sowell. 1995. Movements and home range of hatchling and yearling gopher tortoises, Gopherus polyphemus. Chelonian Conservation and Biology, 1(3): 173-180.

DeGregorio, B.A., K.A. Buhlmann, and T.D. Tuberville. 2012. Overwintering of gopher tortoises (Gopherus polyphemus) translocated to the northern limit of their geographic range: temperatures, timing, and survival. Chelonian Conservation and Biology, 11(1): 84-90.

Diemer, J.E. 1986. The ecology and management of the gopher tortoise in the Southeastern United States. Herpetologica, 42(1): 125-133.

Diemer, J.E. 1992. Home range and movements of the tortoise Gopherus polyphemus in Northern Florida. Journal of Herpetology. 26:158-165.

Diemer, J. E. and C. T. Moore. 1994 Reproduction of gopher tortoises in north-central Florida. Biology of North American Tortoises, Fish and Wildlife Research 13: 129-137.

Douglass, J.F., and J. N. Layne, 1978. Activity and thermoregulation of the gopher tortoise (Gopherus polyphemus) in Southern Florida. Herpetologica 34:359–374.

Eisenberg, J.F., 1983. The gopher tortoise as a keystone species. Pages 1-4 in R.J. Bryant and R. Franz, editors. The gopher tortoise: A keystone species, Proceedings of the 4th Annual Meeting, Gopher Tortoise Council, Valdosta, GA.

Ernst, C.H., and R.W. Barbour. 1972. Turtles of the United States. University Press, Lexington, Kentucky, page 347.

Gibbons, J.W. and R.D. Semlitsch. 1982. Survivorship and longevity of a long-lived vertebrate species: how long do turtles live? Journal of Animal Ecology, 51 (2): 523-527.

Godley, J.S. 1989. Comparison of gopher tortoise populations relocated onto reclaimed phosphate-mined sites in Florida. Pages 43-58 *in* J.E. Diemer, D.R. Jackson, J.L. Landers, J.N. Layne, and D.A. Wood, editors. Gopher Tortoise Relocation Symposium. Florida Game Freshwater Fish Community Nongame Wildlife—Program Technique Report 5.

Goin, C.J. and C.C. Goff. 1941. Notes on the growth rate of the gopher tortoise, *Gopherus polyphemus*. Herpetologica, 2 (3): 66-68.

Gopher Tortoise Council. 2012. Priority research topics for the conservation of gopher tortoises—compiled from the 33rd annual meeting of the Gopher Tortoise

Council, October 13-15, 2011. The Tortoise Burrow: Newsletter of The Gopher Tortoise Council. 32(1): 12-14.

Gregory, P.T.. 1982. Reptilian hibernation. Pages 53-154 *in* C. Gans, editor. Biology of the Reptilia. Academic Press.

Hansen, K. L. 1963. The burrow of the gopher tortoise. J. Florida Academy of Science, 26:353-360

Hazard, L.C. and D.J. Morafka. 2004. Characteristics of burrows used by juvenile and neonate desert tortoises (*Gopherus agassizii*) during hibernation. Journal of Herpetology, 38(3): 443-447.

Hutchison, V.H. 1979. Thermoregulation. Pages 207-228 *in* M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

Jackson D., and E.G. Milstrey. 1989. The fauna of gopher tortoise burrows. Pages 86-98 *in* J. Diemer, D. Jack- son, L. Landers, J. Layne, and D. Wood, editors. Proceedings of the Gopher Tortoise Relocation Symposium. Florida Game and Freshwater Fish Community of Nongame Wildlife. Program, Technical. Report 5. Tallahassee, FL.

Kaczor, S.A. and D.C. Hartnett. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. American Midland Naturalist, 123(1): 100-111.

Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and Maturity of the Gopher Tortoise in Southwestern Georgia. Bulletin of the Florida State Museum, Biological Science, 27 (2): 81-110.

McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement Patterns and Home Range of the Gopher Tortoise. American Midland Naturalist, 106: 165-179.

Morafka, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. *Biology of North American Tortoises, Fish and Wildlife Research* 13: 161-174.

Mushinsky, H.R., D.S. Wilson, and E. D. McCoy. 1994. Growth and sexual dimorphism of *Goperus polyphemus* in Central Florida. Herpetologica, 50(2): 119-128.

Noss, R.F., E.T. LaRoe and J.M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI National Biological Service, Biological Report 28.

Nussear, K.E., T.C. Esque, D.F. Haines, and C.R. Tracy. 2007. Desert tortoise hibernation: temperatures, timing, and environment. Copeia, 2: 378-386.

Pike, D.A. and A. Grosse. 2006. Activity of Immature Gopher Tortoises (*Gopherus polyphemus*) with Notes on Commensal Species. Florida Scientist 69:92-98.

Smith, L.L., T.D. Tuberville, and R.A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise (*Gopherus polyphemus*), Joseph W. Jones Ecological Research Center, 16-17 January 2003: final results and recommendations. Chelonian Conservation and Biology, 5(2): 326-330.

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

Tuberville, T.D., T.M. Norton, B.J. Waffa, C. Hagen, and T.C. Glenn. 2011. Mating system in a gopher tortoise population established through multiple translocations: apparent advantage of prior residence. Biological Conservation, 144(1): 175-183.

Tuberville, T.D., T.M. Norton, K.A. Buhlmann, and V. Greco. *In press*. Head-starting as a management component for gopher tortoises (*Gopherus polyphemus*). Journal: Herpetological Conservation and Biology (Special Issue on Turtle Head-starting).

Tuberville, T.D., B.D. Todd, S.M. Hermann, W.K. Michener, and C. Guyer. *In Review*. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management.

Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Review, 1:1-29.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the gopher tortoise as threatened in the eastern portion of its range. Federal Register 76:45129-45162.

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

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1994. Home range, activity and use of burrows of juvenile gopher tortoises in Central Florida. Pages 147-160 *in* R.B. Bury and D.J. Germano, editors. Biology of North American Tortoises. Washington, DC: United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13.

Wilson, D.S., Morafka, D.J., Tracy, C.R., and Nagy, K.A. 1999. Winter activity of juvenile desert tortoise (*Gopherus agassizii*) in the Mojave Desert. Journal of Herpetology, 33: 496–501.

CHAPTER 2

GROWTH IN JUVENILE GOPHER TORTOISES ON A GEORGIA BARRIER ISLAND.

Introduction

The ecology of the juvenile gopher tortoise, like other juvenile chelonians, is not well known (Morafka, 1994; Smith et al., 2006; GTC, 2012). The lack of information regarding juveniles is due in part to their secretive behavior, low detectability, and low survivorship (Morafka, 1994; Smith et al., 2006; USFWS, 2011; GTC, 2012). However, recent studies are beginning to cover many lesser known aspects of their ecology: movements (Wilson et al., 1994; Epperson et al., 2003; Pike, 2006), activity (Wilson et al., 1994), habitat use (Pike, 2006), survivorship (Wilson, 1991; Butler and Sowell, 1996; Epperson et al., 2003; Pike and Seigel, 2006; Pike and Grosse, 2006; Tuberville et al., 2011; Smith et al., 2012), detectability (Ballou et al., 2013), and diet and foraging (Mushinsky et al., 2003; Halstead et al., 2007).

Juvenile tortoises have low survivorship because they are extremely vulnerable due to their small size (Morafka, 1994). An important characteristic that can offset the vulnerability of juveniles, and therefore increase survival, is their growth rate. Tortoises grow most rapidly as juveniles, while they are at greatest risk, and this growth rate slows upon maturity (Lewontin, 1965). Age and body size are strongly correlated during the juvenile years in turtles but once maturity is reached this relationship is non-existent

(Congdon and van Loben Sels, 1993). In addition, tortoises—like many other chelonians— generally mature at a specific size, rather than age, and thus growing more quickly is advantageous not only for outgrowing predation risk, but also for decreasing the time to sexual maturity (Congdon and van Loben Sels, 1993; Mushinsky et al., 1994; Roosenberg, 1996).

Differences in growth rates have been reported across gradients of latitude and habitat quality (Landers et al, 1982; Godley, 1989; Goin and Goff, 1941; Mushinsky et al., 1994; Diemer and Moore, 1994). At higher latitudes within the gopher tortoise's range there are fewer days for a tortoise to be active, while at lower latitudes some individuals can remain active during every month of the year due to the longer growing season (Douglass and Layne, 1978). Growth rates may even differ between populations separated by only a few kilometers; this variable growth rate is likely due to differences in habitat quality (Mushinsky et al., 1994; Diemer and Moore, 1994; Aresco and Guyer, 1999). High quality habitat for gopher tortoises has 1) an open canopy, providing optimal thermal conditions for thermoregulation and nesting; 2) abundant and diverse grasses and forbs; and 3) well-drained sandy soils for extensive burrowing (Auffenberg and Franz, 1982).

Habitat loss and degradation have been the primary sources attributed to gopher tortoise declines (Auffenberg and Franz, 1982). Encroachment of overstory and midstory growth on herbaceous groundcover attributed to fire suppression may reduce gopher tortoise numbers by 60-80% in 8 years or 100 % in 16 years (Yager et al., 2007; Auffenberg and Franz, 1982). As their natural habitat declines, gopher tortoises shift into ruderal habitats where open areas are maintained (Auffenberg and Franz, 1982; Deimer, 1986; Yager et al., 2007). Ruderal habitats are disturbed, open habitats where the natural flora has been altered (considerably) by humans, and can include old agriculture fields, abandoned pastures, roadsides, and land cleared for timber or other general purposes (Auffenberg and Franz, 1982). As it stands, we do not have a clear understanding of the relative quality of ruderal versus more natural habitats for gopher tortoises, and one metric for evaluating habitat quality is through the examination of growth rates.

The objectives of this study were to 1) calculate juvenile growth rates, 2) determine age-specific sizes, and 3) estimate age of sexual maturity for gopher tortoises residing in ruderal habitat on St. Catherines Island, Georgia and compare these findings with those from eight other study locations reported in the literature.

Methods

Study Site and Study Population

St. Catherines Island is a 5670 ha barrier island off the coast of Liberty County, Georgia (Figure 2.1). It is privately owned and run by the St. Catherines Island Foundation, whose efforts are focused on supporting research and conservation. Gopher tortoises are located on the north end of the island in a 102 ha old cattle pasture (North Pasture). North Pasture was formerly a long-leaf pine (*Pinus palustris*) forest that was logged between 1938 and 1943. After World War II, Bahia grass (*Paspalum notatum*) was planted and the pasture was grazed by free-ranging Black Angus cattle until 1982. After the cattle were removed, the pasture was burned to help control establishment and encroachment by long-leaf pine seedlings. In the 1990s, management of the pasture shifted to replace burning with mowing as the method for controlling pine establishment.

The pasture has a simplistic vegetation structure comprised of a few, widely-spaced mature pines (primarily *P. palustris* but also *P. taeda*), no midstory canopy, and an open understory made up mostly of both native and nonnative grasses and forbs (Figure 2.1). The most abundant species in the understory include Bahia grass (*Paspalum notatum*), broomsedges (*Andropogon sp.*), narrowleaf silkgrass (*Pityopsis graminifolia*), needleleaf rosette grass (*Panicum aciculare*), whip nutrush (*Scleria triglomerata*), white mouth dayflower (*Commelina erecta*), wiregrasses (*Aristida sp*), cockspur pricklypear (*Opuntia pusilla*), pine barren frostweed (*Helianthemum corymbosum*), and queen's delight (*Stillingia sylvatica*).

The gopher tortoise population is not native to St. Catherines Island but became established through multiple translocations and subsequent natural recruitment (Tuberville et al. 2008, 2011). Approximately 25-30 free-ranging tortoises were released from 1987 to 1993 from a variety of undocumented sources. In addition, a wild population of 74 gopher tortoises was translocated from Bulloch County, Georgia in 1994, at which time the mark-recapture program on St. Catherines Island was initiated (see further details below). Subsequently, at least 12 formerly captive or rehabilitated tortoises have been released on island.

Mark-Recapture

We obtained juvenile gopher tortoises from 2007–2013 through targeted trapping using live wire traps, opportunistic hand captures, and hatchlings obtained from field-collected nests (Tuberville et al. 2011). Trapping occurred primarily in May-July and, in some years, again in September. Each tortoise was given a unique identification upon first capture by notching marginal scutes (Cagle, 1939). At each capture, weight (g) and straight-line carapace length (SCL; to nearest mm) were recorded. Age was estimated by counting growth annuli on plastral scutes (Landers et al., 1982) whenever possible. Hatchlings were assigned age-0 until 1 January following hatching, after which 1 year was added to the age.

For the purposes of this study, we targeted juveniles that originated from one of two groups with different initial capture histories: direct releases and wild recruits. Direct releases were individuals originally obtained from field-collected nests and released post-hatching, therefore individual age was known. Wild recruits are juveniles that were first encountered in the field and for which age was estimated. Thus, all juveniles included in our analysis were recruited and have spent their entire lives on the island.

Data Analysis

We examined age-specific size using 375 capture records for 242 individual juveniles. All records for each individual tortoise were used where age was known or could be estimated using the growth annuli. The mean and range of sizes (SCL) were compared for each age.

Mean annual growth rates were calculated using the 80 juveniles with at least two capture records greater than 8 months apart (following Mushinsky et al., 1994), using the following formula: Growth $(\frac{\text{mm}}{\text{year}}) = \frac{\text{CL}_2 - \text{CL}_1}{\text{Year}_2 - \text{Year}_1}$. Growth rates were calculated using the 1st and most recent capture of each individual. This rate was then compared with juvenile growth rates reported from other study locations throughout the species' range (Figure 2.1).

Growing Degree Days

We wanted to evaluate how length of activity season might affect growth rates, particularly among study sites. We chose to use growing degree days (GDD) as a substitute for activity days (for which we did not have data from the other study sites) because it provides a measure of daily heat unit accumulation (Lovich et al. 2012) and is easily calculated for different locations. We calculated GDD for St. Catherines Island and each of the other study sites for which juvenile growth rates were reported. We selected a biologically relevant threshold temperature of 21.0 °C based on the minimum activity temperature reported for adult gopher tortoises (Douglass and Layne, 1978; McRae et al., 1981). To calculate GDD accumulation for each study site, we used temperature data from ACIS Web Services (http://docs.rcc-acis.org/acisws/; Accessed: 10 March 2014) collected from the airport or military installation nearest to the study site for the years that each study took place (Table 2.3).

We used a sine curve temperature approximation from the daily maximum and minimum temperatures and the methodology of Snyder (1985) and Lovich et al. (2012) for calculating GDD. When daily air temperatures were above our selected threshold temperature of 21.0 °C, accumulation of GDD was calculated using the equation:

$$DD = \frac{MAX + MIN}{2} - THR$$

where MAX and MIN are the maximum and minimum daily temperatures, respectively, and THR is the selected threshold temperature. On the days when the minimum daily temperature dropped below the threshold temperature of 21.0 °C, the equation $DD = W \times N$ was used instead, where:

$$W = \frac{MAX - MIN}{2}$$

$$R = \frac{THR - MIN}{MAX - MIN}$$

In these formulas, W is the amplitude of the sine curve and N is the fraction of the amplitude that corresponds to the relative position (R) of the threshold temperature within the sine curve. Table 1 in Snyder (1985) gives the corresponding N values for a given R. If the maximum air temperature is below the threshold temperature, then GDD = 0. GDD values were then totaled for each year and averaged across the years of the study.

Statistical Analysis

Age specific size, using 375 observations from 242 tortoises, was assessed for nonlinear fit using logistic, von Bertalanffy, and Richards growth models as well as assessing the linear fit for a simple linear and polynomial line. All linear and nonlinear model fitting of jjuvenile growth was calculated in SAS (SAS Institute Inc. 2008). A Richards Growth Model (Ricker, 1975) was included because it is a flexible adaption of the von Bertalanffy model and is used to describe a wide range of growth curves (Tjørve and Tjørve, 2010; Zhao-gang and Feng-ri, 2003). A subset of adult data was included in calculating the linear and nonlinear growth models to establish a more logical estimate of future expected growth, establishing a reasonable asymptote for the slowed growth of tortoises upon maturity.

Environmental gradients (latitude, GDD, and elevation) were evaluated using a Pearson Correlation Matrix to determine if there was a correlation among the variables (SAS Institute Inc., 2008). In program R (version 3.0.1; R Core Team, 2013) we assessed the relationships between sites and environmental gradients using linear regression analysis with the mean juvenile growth rate at a site as the response variable and used Akaike's Information Criterion to select a model that best described the variability in growth rate among sites (AICc; Burnham and Anderson, 2002). Given that we were only interested in only 3 environmental gradients for comparison for the model selection, we didn't include models if the Pearson Correlation was $p > 0.05$. There were 6 total models (Table 2.6) for our candidate models.

Results

During 2007-2013 we captured 242 individual juveniles where age was known or could be reliably estimated (Table 2.1). Juveniles ranged from hatchlings (age 0) to those in their 11th year. The age-specific size data (Table 2.1; Figure 2.8) suggest that by age 9-10 years juveniles on St. Catherines Island can reach the minimum size of sexual maturity, which is 230-240 mm CL for males and 250-265 mm CL for females (McRae et al., 1981; Landers et al., 1982; Mushinsky et al., 1994). Juvenile age-specific size fit all growth models (Table 2.2, Figure 2.4, Figure 2.5, Figure 2.6, Figure 2.7) except for the simple linear model (Figure 2.3). The juvenile age-specific size fit the more flexible Richards Growth Model best ($R^2=0.964$; Table 2.2, Figure 2.7).

Mean annual growth rate was calculated from 80 individual juveniles with at least 2 captures > 8 months apart. Of the 80 juveniles used for the calculation, 43 were from direct release group and 37 were natural recruits. We only included an individual once for this analysis. The mean annual growth rate based on these individuals was 19.2 ± 0.6 mm CL/year (Table 2.4), ranging from 8.0 – 32.0 mm CL/year.

St. Catherines Island ranked as one of the highest growth rates reported among studies (Table 2.4). GDD was negatively correlated with latitude ($r = -0.96$) among study sites, with higher GDD reported at lower latitudes (Table 2.5), St. Catherines Island had the 2nd highest latitude and the 5th highest GDD (Table 2.4). The best supported model relating environmental gradients to growth rate was the model for elevation only, with relatively high support (*w*=0.93; Table 2.6), where lower elevations were associated with higher growth rates.

Discussion

St. Catherines Island juveniles from age 0 through age 11 grew an average of 19 mm CL/year (Table 2.4), the same growth rate reported by the Mushinsky et al. (1994) study, approximately 500 km south of St. Catherines Island, in Tampa, Florida. Ruderal habitats in Southwest Georgia and Polk County, Florida reported growth rates of 16 and 13 mm CL/year and lower growth rates of 12 and 11 mm CL/year in nearby pine habitat, Landers et al. (1982) and Godley (1989) respectively. Aresco and Guyer (1999) attributed the 10 mm CL/year growth rate at Conecuh National Forest (CNF) to the closed canopy cover of the pine plantation. The lowest juvenile growth rate reported was found at the Savannah River Site where juveniles exhibited a 5 mm CL/year growth rate (Tuberville et al. *unpublished*). The Savannah River Site is a relatively closed canopy, pine forest, and the site of highest latitude. In Godley (1989) and Tuberville et al. (*unpub*.), growth rates reported are post-translocation growth rates so that only the growth accumulated at the new site was calculated.

Age-specific size of tortoises at St. Catherines Island is similar to the Mushinsky et al. (1994) findings, where juveniles grew rapidly and reached minimum mature body sizes in approximately 10 years. Tortoises at 10 years of age averaged of 230 mm CL at St. Catherines Island and 208 mm CL in Tampa, Florida Mushinsky et al. (1994). St. Catherines Island tortoises are estimated to reach sexual maturity in 8-10 years based on a size of maturity for male gopher tortoises of 230-240 mm CL and 250-265 mm CL for females (Landers et al., 1982). Tortoises from Polk County matured in 16 years in pine habitat and around 14 years in ruderal habitat (Godley, 1989). Aresco and Guyer (1999) reported that the tortoises at CNF were reaching sexual maturity in 20 or more years.

The growth of both the Mushinsky et al. (1994) and Aresco and Guyer (1999) studies fit both the von Bertalanffy and Logistic growth models. However, Aresco and Guyer (1999) found that the CNF tortoise growth fit a von Bertalanffy growth curve slightly better than a logistic growth curve, while Mushinsky et al. (1994) found the reverse to be true in their study. The von Bertalanffy and Logistic growth models are sigmoidal and express early growth comparable to exponential growth that slows or stops around sexual maturity. The St. Catherines Island juveniles did not fit the von Bertalanffy growth model, likely due to the limited number of ages examined since we only studied juvenile ages and did not include individuals of later ages that might exhibit the slowed growth indicative of sexually mature individuals. The St. Catherines Island juvenile growth, however, did fit the more lenient Richards growth model, which supports our belief that with further age classes the data would likely fit a more asymptotic length-at-age growth curve since the Richards model is an adaptation of the von Bertalanffy model. We would need to collect data on older individuals in order to determine if one of the standard sigmoidal growth models will best fit the data. Since we only examined the growth of the juvenile ages on St. Catherines Island, a linear and polynomial fit of the data is consistent rapid growth rates typically associated with juveniles such that the growth is roughly exponential.

An individual tortoise's growth is affected by the interactions of different abiotic and biotic factors (Germano, 1994). The influence of latitude and the length of activity season influence tortoise's rate of growth and age of sexual maturity (Mushinsky et al., 1994). St. Catherines Island had the 2nd highest latitude and the 5th highest GDD accumulation (Table 2.4). The best supported model for landscape variables affecting growth rate was the model with elevation alone. Although the elevation only model came out as the top model this is likely due to the relatively small sample size and the fact that we could not include habitat type (which was not available for all study sites) in our model. We were only able to examine juvenile growth at 9 study sites within the gopher tortoise range. Overall elevation varies little throughout the gopher tortoise range and it is more likely that growth rate is influenced more by the complex interactions between the climatic and habitat factors affecting an individuals growth.

Tortoise growth may be due more to the the quality of the habitat rather than length of activity season (Aresco and Guyer, 1999). Quality habitat for the gopher tortoise has an open canopy, abundant forage, and sandy soils that are easy to dig (Auffenberg and Franz, 1982). Quanitity and quality of forage as well as the amount of canopy cover are 2 charactersistcis of habitat quality that are easily manipulated through habitat management. Mushinsky et al. (1994) attributed mean annual high growth rates to the habitat management at their site, where frequent burns were used to maintain an open canopy and a rich understory. The relatively closed canopy of the CNF pine plantation may have affected tortoises' growth due to the restricted sun penetration essential for the groundcover layer required to promote growth of herbacious groundcover (Aresco and Guyer, 1999). Although we were unable to directly compare habitat quality among the study sites, St. Catherines Island, much like the Mushinsky et al. (1994) study site, is actively managed to maintain a sparse canopy ideal for growth of groundcover. The main differences between the sites are geographic location and habitat type, where Mushinsky et al. (1994) is managed sandhills habitat and St. Catherines Island is managed ruderal habitat.

A comparison of natural versus ruderal habitat is needed for understanding how variations among different sites contribute to growth of tortoises. Gopher tortoises are becoming displaced primarily due to habitat loss (Auffenburg and Franz, 1982) which has led to an increased use of ruderal habitats. The effects of these habitat types on the gopher tortoise growth is not fully understood. In this study we could not assess these differences statistically due to limited information regarding all study sites compared here. However, it appears that managed ruderal habitats had higher growth rates than nearby sites of natural habitat reported for both Southwest Georgia (Landers et al., 1982) and Polk County, Florida (Godley, 1989) studies (Table 2.4), but additionally management for habitat quality may be eassential for higher growth rates (Mushinsky et al. 1994).

There are many factors that can influence growth in tortoises, however, it is important for gopher tortoise researchers and managers to know what level of impact each factor might have on growth and age at sexual maturity. Being able to determine the level of impact requires consistent and specific data from all study sites for a suitable assessment. Increased rainfall has also been shown to benefit growth rates in desert tortoises (Germano, 1988), but Germano (1994) found precipitation and temperature do not appear to affect growth directly, so how each might affect gopher tortoises is not well known. A comparison of habitat quality in relation to the available forage can be assessed through net primary productivity (NPP) and measuring the amount of relative canopy cover at different gopher tortoise sites. Evaluation of the impact of relative habitat quality could be used to weigh sites for future tortoise translocations but also in making decisions on how to best manage the habitat for gopher tortoises when the goal is to have a tortoise population with rapid growth and earlier ages of maturity.

Literature Cited

Andrews, R.M. 1982. Patterns of growth in reptiles. Pages 273-320 in C. Gans and F.H. Pough, editors. Biology of the Reptilia, vol. 13. Wiley Publishers, New York, New York, USA.

Aresco, M.J., and C. Guyer. 1999. Growth of the tortoise *Gopherus polyphemus* in slash pine plantations of southcentral Alabama. Herpetologica, 55(4): 499-506.

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

Auffenberg, W., and J.B. Iverson. 1979. Chapter 25: Demography of terrestrial turtles. Pages 541-569 *in* M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

Ballou, A.R. 2013. Aspects of gopher tortoise (*Gopherus polyphemus*) populations in Georgia: status, landscape predictors, juvenile movements and burrow use. *Unpublished* M.S. Thesis, University of Georgia, Athens.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York.

Butler, J.A. and S. Sowell. 1996. Survivorship and predation of hatchling and yearling gopher tortoises, *Gopherus polyphemus*. Journal of Herpetology, 455-458.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia, 1939:170–173.

Congdon J.D. and R.C. Van Loben Sels. 1993. Relationships of reproductive traits and body size with attainment of sexual maturity and age in blanding's turtles (*Emydoidea blandingii*). Journal of Evolutionary Biology, 6: 547-557.

Diemer, J.E. 1986. The ecology and management of the gopher tortoise in the Southeastern United States. Herpetologica, 42(1): 125-133.

Diemer, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. Journal of Herpetology. 26:158-165.

Diemer, J. E. and C. T. Moore. 1994 Reproduction of gopher tortoises in north-central Florida. *Biology of North American Tortoises, Fish and Wildlife Research* 13: 129-137.

Douglass, J.F., and J. N. Layne, 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in Southern Florida. Herpetologica 34:359–374.

Epperson, D.E., and C.D. Heise. 2003. Nesting and hatchling ecology of gopher tortoises (*Gopherus polyphemus*) in Southern Mississippi. Journal of Herpetology, 37(2): 315-324.

Germano, D.J. 1988. Age and growth histories of desert tortoises using scute annuli. Copeia, 1988: 914-920.

Germano, D.J. 1994. Growth and age at maturity of North American tortoises in relation to regional climates. Canadian Journal of Zoology, *72*(5), 918-931.

Godley, J.S. 1989. Comparison of gopher tortoise populations relocated onto reclaimed phosphate-mined sites in Florida. Pages 43-58 *in* J.E. Diemer, D.R. Jackson, J.L. Landers, J.N. Layne, and D.A. Wood, editors. Gopher Tortoise Relocation Symposium. Florida Game Freshwater Fish Community Nongame Wildlife—Program Technique Report 5.

Goin, C.J. and C.C. Goff. 1941. Notes on the growth rate of the gopher tortoise, *Gopherus polyphemus*. Herpetologica, 2 (3): 66-68.

Gopher Tortoise Council. 2012. Priority research topics for the conservation of gopher tortoises—compiled from the 33rd annual meeting of the Gopher Tortoise Council, October 13-15, 2011. The Tortoise Burrow: Newsletter of The Gopher Tortoise Council. 32(1): 12-14.

Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and Maturity of the Gopher Tortoise in Southwestern Georgia. Bulletin of the Florida State Museum, Biological Science, 27 (2): 81-110.

Lewontin, R.C. 1965. Selection for colonizing ability. Pages 77-94 *in* H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York, New York.

Lovich, J.E., M. Agha, M. Meulblok, K. Meyer, J. Ennen, C. Loughran, S. V. Madrak, and C. Bjurlin. 2012. Climatic variation affects clutch phenology in Agassiz's Desert Tortoise (*Gopherus agassizii*). *Endangered Species Research*, 19: 63-74.

McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement Patterns and Home Range of the Gopher Tortoise. American Midland Naturalist, 106: 165-179.

Medica, P.A., R.B. Bury, and F.B. Turner. 1975. Growth of the desert tortoise (*Gopherus agassizii*) in Nevada. Copeia, 1975: 639-643.

Morafka, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. *Biology of North American Tortoises, Fish and Wildlife Research* 13: 161-174.

Mushinsky, H.R., D.S. Wilson, and E. D. McCoy. 1994. Growth and sexual dimorphism of *Goperus polyphemus* in Central Florida. Herpetologica, 50(2): 119-128.

Pike, D.A. 2006. Habitat use, and growth of hatchling tortoises, *Gopherus polyphemus*. Copeia, 2006(1): 68-76.

Pike, D.A. and A. Grosse. 2006. Activity of Immature Gopher Tortoises (*Gopherus polyphemus*) with Notes on Commensal Species. Florida Scientist 69:92-98.

Pike, D.A., and R.A. Seigel. 2006. Variation in Hatchling Tortoise Survivorship at Three Geographic Localities. Herpetologica, 62 (2): 125-131.

R Core Team. 2013. R: A language and environment for statistical computing. http://www.R-project.org.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Roosenberg, W.M. 1996. Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination? American Zoologist 36: 157-168.

SAS Institute Inc. 2008. User installation guide for SAS 9.1.3 foundation for Microsoft Windows, Cary, NC.

Shine, R. and Charnov, E. L. 1992. Patterns of survival, growth, and maturation in snakes and lizards. American Naturalist, 1257-1269.

Smith, L.L., T.D. Tuberville, and R.A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise (*Gopherus polyphemus*), Joseph W. Jones Ecological Research Center, 16-17 January 2003: final results and recommendations. Chelonian Conservation and Biology, 5(2): 326-330.

Snyder, R.L. 1985. Hand calculating degree days. Agricultural and Forest Meterology, 35: 353-358.

Tjørve, E. and K. Tjørve. 2010. A unified approach to the Richards-model family for use in growth analyses: why we need only two model forms. Journal of Theoretical Biology, 267(3): 417-425.

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

Tuberville, T.D., T.M. Norton, B.J. Waffa, C. Hagen, and T.C. Glenn. 2011. Mating system in a gopher tortoise population established through multiple translocations: apparent advantage of prior residence. Biological Conservation, 144(1): 175-183.

Tuberville, T.D., B.D. Todd, S.M. Hermann, W.K. Michener, and C. Guyer. *In Review*. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management.

Turner, F.B., P.A. Medica, and R.B. Bury. 1987. Age-size relationships of desert tortoises (*Gopherus agassizii*) in southern Nevada. Copeia, 1987: 974-979.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the gopher tortoise as threatened in the eastern portion of its range. Federal Register 76:45129-45162.

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

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1994. Home range, activity and use of burrows of juvenile gopher tortoises in Central Florida. Pages 147-160 in R.B. Bury and D.J. Germano, editors. Biology of North American Tortoises. Washington, DC: United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13.

Yager, L.Y., C.D. Heise, D.M. Epperson, and M.G. Hinderliter. 2007. Gopher tortoise response to habitat management by prescribed burning. The Journal of Wildlife Management, 71(2): 428-434.

Zhao-gang, L. and L. Feng-ri. 2003. The generalized Chapman-Richards function and applications to tree and stand growth. Journal of Forestry Research, 14(1), 19-26.

Figure 2.1. The habitat at North Pasture is made up of a few, widely-spaced mature pines (primarily *Pinus palustris* but also *P. taeda*), no midstory canopy, and an open understory made up mostly of both native and non-native grasses and forbs.

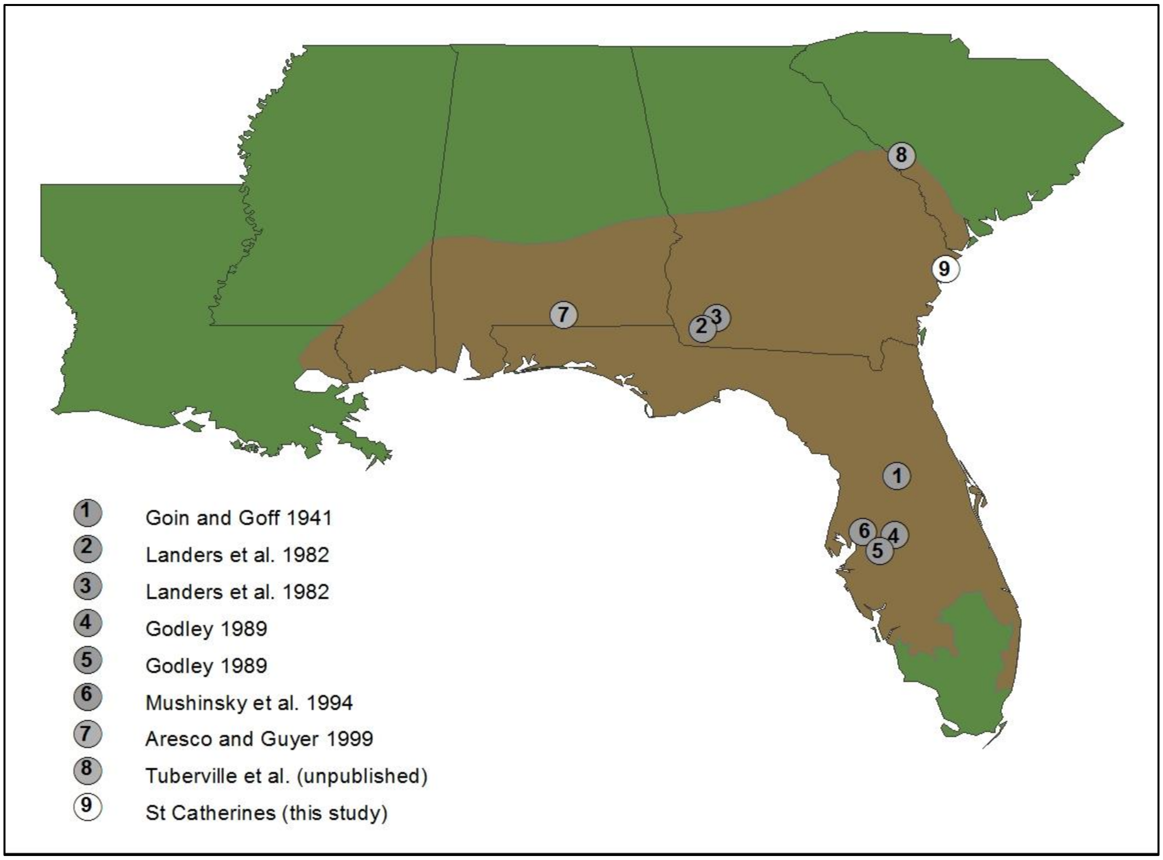

Figure 2.2. Location of studies reporting juvenile growth rates across the gopher tortoise range (brown shading). Our study on St. Catherine’s Island is the white circle labeled #9, while older studies are grey circles labeled chronologically from 1-8.

Table 2.1. The mean, range, and standard error of the carapace length (mm) at each age (years) based on 375 records of 242 individuals. Percent change of carapace lengths between successive ages was also included, where percent change at age x=[(mean CL at age X - mean CL at age X-1)/(mean CL at age X-1)] per Mushinsky et al. (1994).

Age (years)	Mean Carapace Length (mm)	Range Carapace Length (mm)	n	SE	% Change
0	51	39 – 58	171	0.03	0.0
1	70	49 – 82	32	0.15	37.9
2	92	67 – 110	23	0.24	31.5
3	109	87 – 139	22	0.30	18.5
4	131	81 – 186	28	0.38	20.9
5	152	116 – 205	24	0.36	15.6
6	164	126 – 205	21	0.43	8.3
7	180	147 – 218	15	0.49	9.0
8	194	160 – 228	19	0.46	8.1
9	218	199 – 239	8	0.48	12.7
10	230	220 – 238	7	0.25	5.4
11	241	223 – 253	4	0.64	4.5

Table 2.2. Linear (simple and polynomial) and Non-Linear (Logistic, Von Bertalanffy, and Richards) equations and R^2 for growth models.

	Growth Equation	# of Parameters	MSE	R^2
Linear:				
Simple	$L = b_0 + b_1 * Age$	2	1454	0.6757
Polynomial	$L = b_0 + b_1 * Age + b_2 * Age^2$	3	291	0.9352
Non-Linear:				
Logistic	$L = b_0 + A*(1+e^{-b*Age})^{-1}$	3	160	0.9645
Von Bertalanffy	$L = b_0 + A*(1-e^{-b*Age})$	3	178	0.9605
Richards	$L = b_0 + A*(1+e^{-b*Age})^{C}$	4	162	0.9640

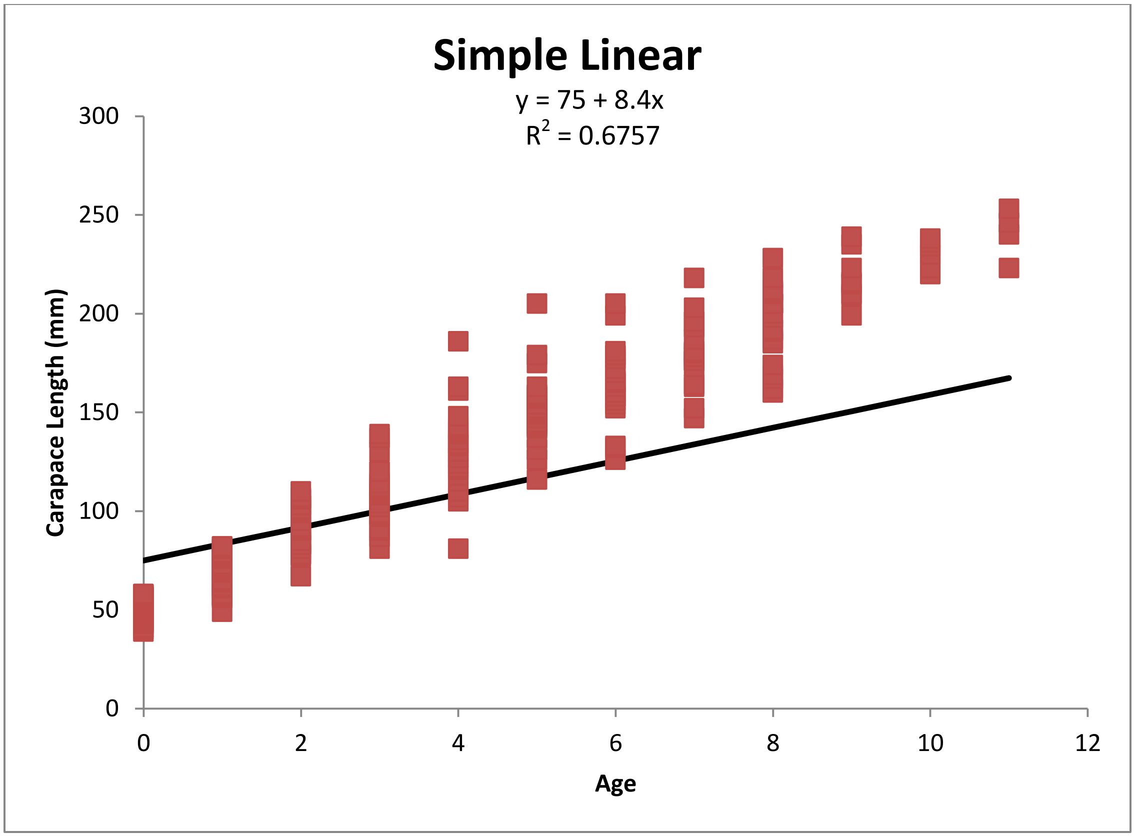

Figure 2.3. Linear fit using the equation: $y = 75 + 8.4x$ for a simple line fit ($R^2 = 0.6757$) to the juvenile age specific size of 375 juvenile records on St. Catherines Island where parameters were estimated with the inclusion of adult data to establish a more reasonable estimate of tortoise growth after maturity. Ages 0-11 were included, where age 0 represented hatchlings. Parameters were estimated in SAS (SAS Institute Inc., 2008).

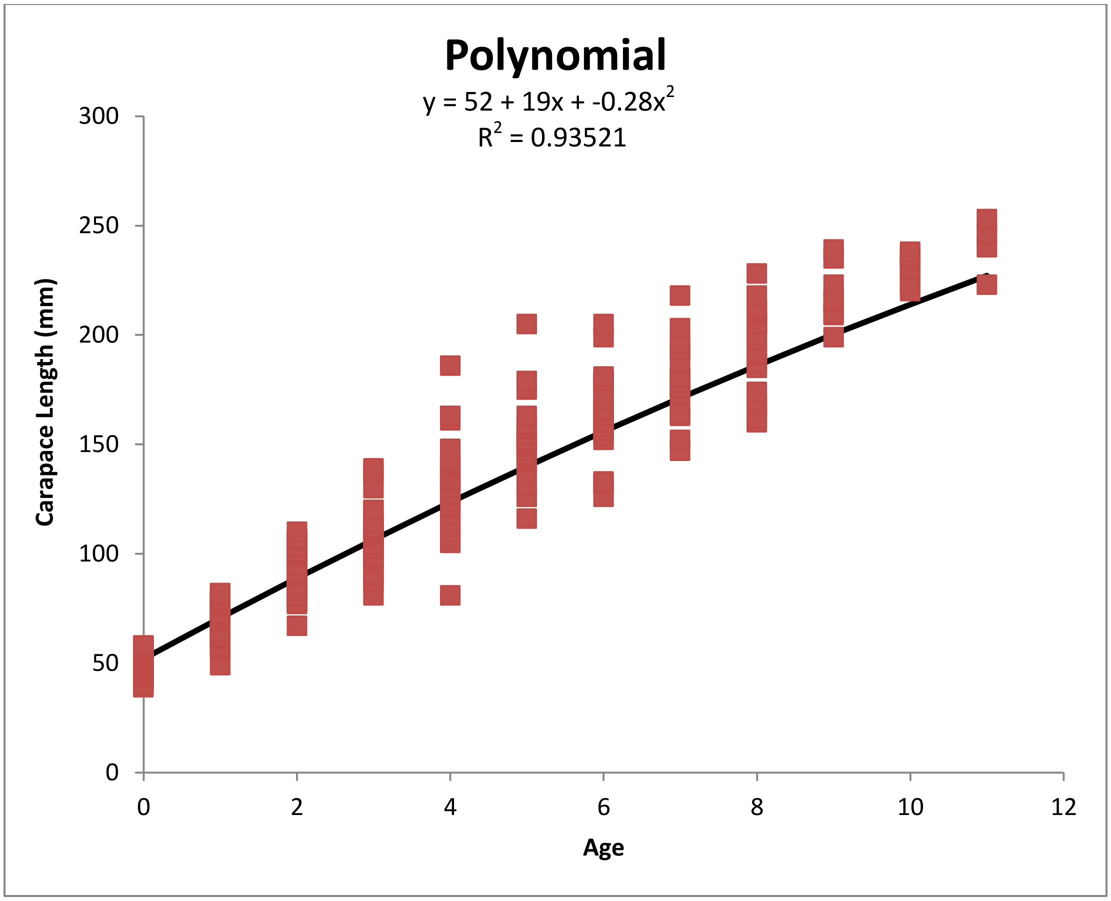

Figure 2.4. Linear fit using the equation: $y = 52 + 19x + -0.28x^2$ for a polynomial line fit ($R^2 = 0.9352$) to the juvenile age specific size of 375 juvenile records on St. Catherines Island where parameters were estimated with the inclusion of adult data to establish a more reasonable estimate of tortoise growth after maturity. Ages 0-11 were included, where age 0 represented hatchlings. Parameters were estimated in SAS (SAS Institute Inc., 2008).

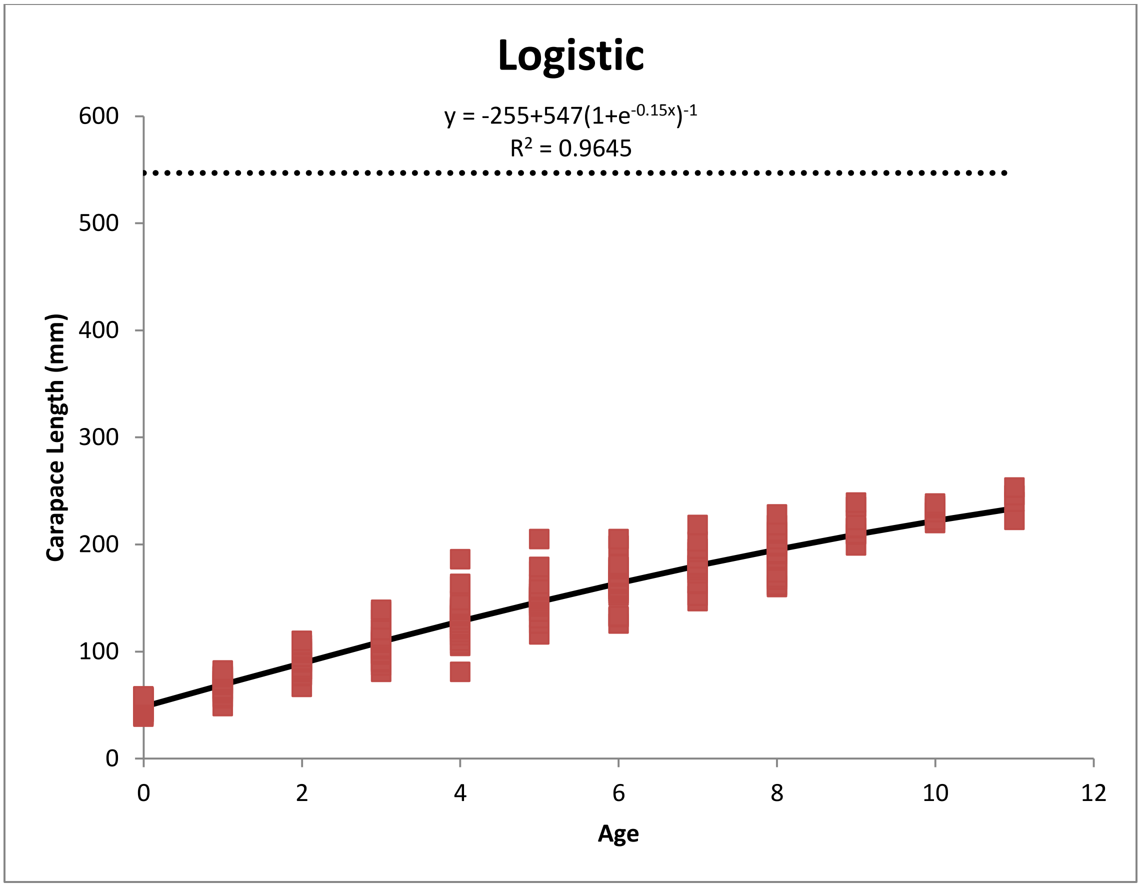

Figure 2.5. Logistic growth model fit to juvenile age specific size data ($R^2 = 0.9645$). Parameters were estimated in SAS (SAS Institute Inc., 2008) for 375 juvenile records on St. Catherines Island where with the inclusion of adult data to establish a more reasonable estimate of tortoise growth after maturity. Ages 0-11 were included, where age 0 represented hatchlings.

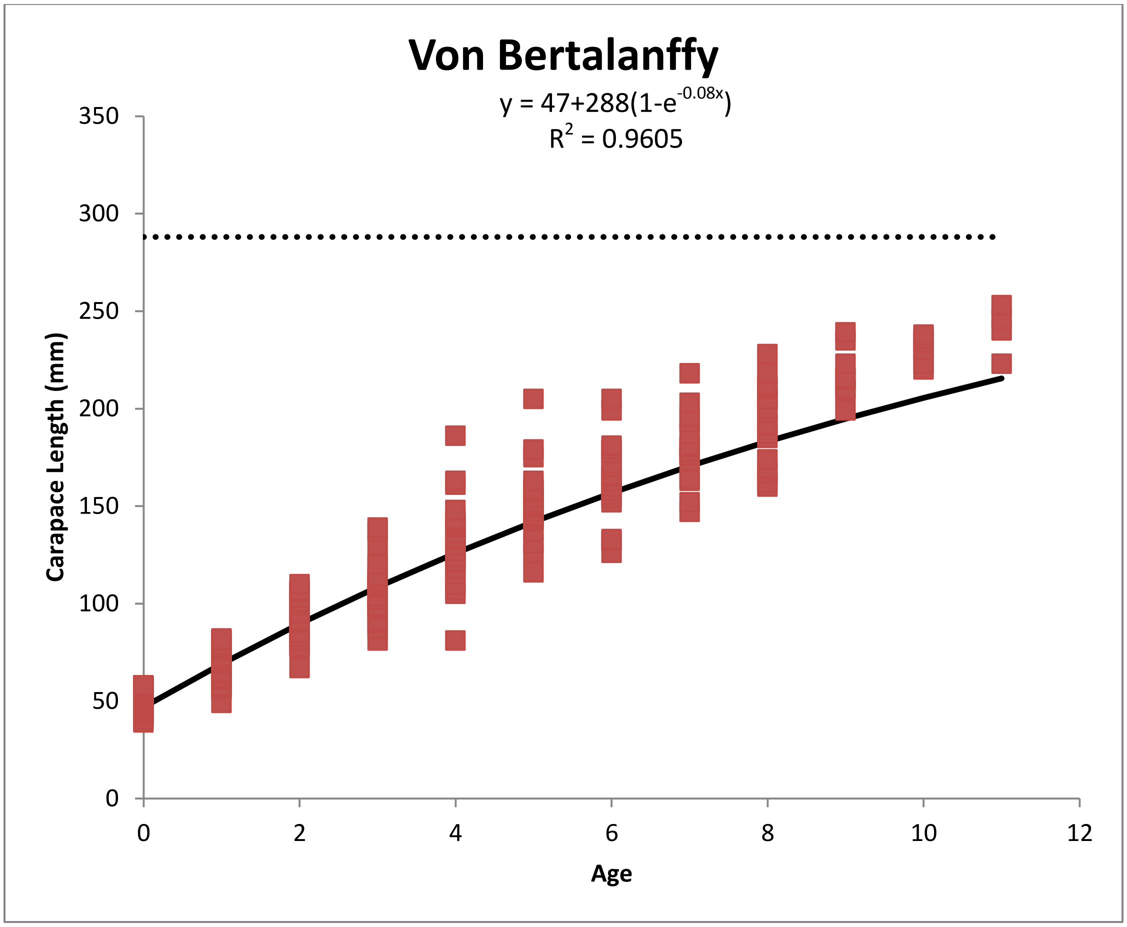

Figure 2.6. Von Bertalanffy growth model fit to juvenile age specific size data ($R^2 = 0.9605$). Parameters were estimated in SAS (SAS Institute Inc., 2008) for 375 juvenile records on St. Catherines Island where with the inclusion of adult data to establish a more reasonable estimate of tortoise growth after maturity. Ages 0-11 were included, where age 0 represented hatchlings.

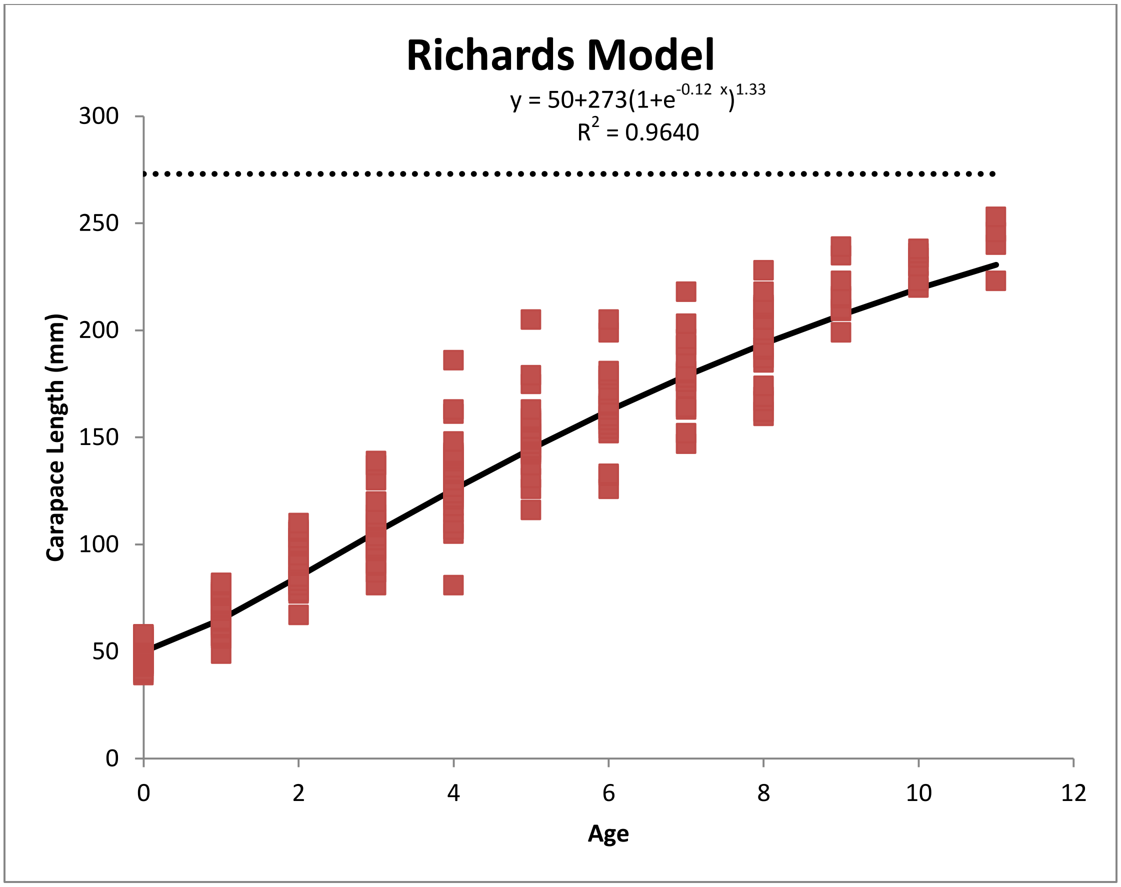

Figure 2.7. Richards growth model fit to juvenile age specific size data (R^2 = 0.9640). Parameters were estimated in SAS (SAS Institute Inc., 2008) for 375 juvenile records on St. Catherines Island where with the inclusion of adult data to establish a more reasonable estimate of tortoise growth after maturity. Ages 0-11 were included, where age 0 represented hatchlings.

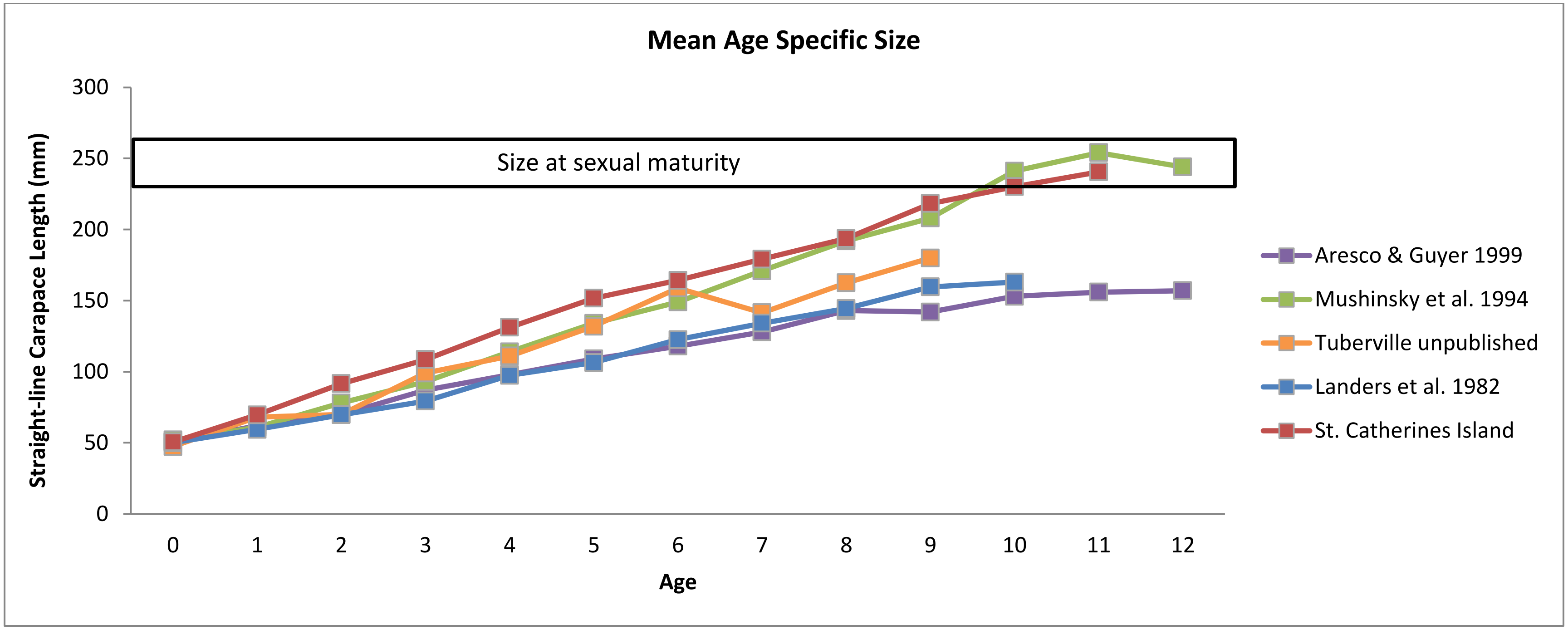

Figure 2.8. Mean age-specific size (based on carapace length; mm CL) of St. Catherines Island juveniles compared with that reported for juveniles from other study sites. The box indicates size at sexual maturity in gopher tortoises, which is 230-240 mm CL for males and 250-265mm CL for females (Landers et al., 1982).

Table 2.3. Growth studies and weather stations used for calculating growing degree-days (GDD) for each study site. Each study site's growing degree-days compared with the mean annual growth (mm CL/year) of juveniles. In Godley (1989) and Tuberville et al. (*unpub*.), growth rates reported are post-translocation.

Study	Study Years	Study Location	Weather Station	Weather Station Location	GDD	GDD rank	Growth Rate	Growth rank	Habitat
St. Catherines Island (This Study)	2007-2013	Midway, GA	KSAV	Savannah, GA	1050	5	19	1.5	ruderal
Mushinsky 1994	1982-1990	Tampa, FL	KTPA	Tampa, FL	1370	3	19	1.5	sandhill
Landers et al 1982	1978-1980	Silver Lake Station, GA	KTLH	Tallahassee, FL	980	7.5	16	3	ruderal
Godley 1989	1985-1987	Polk Co. FL	KTPA	Tampa, FL	1402	1.5	13	4	ruderal
Landers et al 1982	1978-1980	Decatur Co. GA	KTLH	Tallahassee, FL	980	7.5	12	5	natural pine
Godley 1989	1985-1987	Polk Co. FL	KTPA	Tampa, FL	1402	1.5	11	6.5	sand pine scrub
Goin and Goff 1941	1937-1938	Leesberg, FL	KORL	Orlando, FL	1222	4	11	6.5	not provided
Aresco and Guyer 1999	1991-1996	Conecuh Nat Forest, AL	KCEW	Crestview, FL	1028	6	10	8	pine plantation
Tuberville et al. (unpublished)	2001-2006	SRS, SC	KAGS	Augusta, GA	861	9	5	9	pine forest

Table 2.4. The latitude, elevation (in meters), growth degree-days (GDD), and habitat type reported from 9 growth studies on the growth rates (mm CL/year) of gopher tortoises presented in order from lowest to highest growth rate.

Study	Growth Rate	Latitude	Elevation	GDD
Tuberville et al. (unpublished)	5	33	83.14	861
Aresco and Guyer 1999	10	31	71.69	1028
Godley 1989	11	28	43.96	1402
Goin and Goff 1941	11	29	29.87	1222
Landers et al. 1982	12	31	35.44	980
Godley 1989	13	28	34.67	1402
Landers et al. 1982	16	31	39.87	980
Mushinsky et al. 1994	19	28	16.06	1370
St. Catherines Island (This Study)	19	32	7.11	1050

Table 2.5. Correlation matrix for environmental gradients and growth rate at 9 study sites using Pearson correlation coefficients**.**

	Growth Rate	**Latitude**	**Elevation**
Latitude	-0.203		
Elevation	-0.878	0.411	
GDD	-0.273	-0.962	-0.461

Table 2.6. Candidate models to evaluate effects of landscape variables (latitude, GDD, and elevation) on juvenile growth rate, including the number of parameters (K), linear regression model ranking using Akaike's Information Criterion for small sample sizes (AICc), ΔAICc, model weight (*w*), and cumulative model weight for landscape variables. Models were ranked by AICc. Models were excluded if the Pearson correlation was >0.05.

Model	**K**	**AICc**	**ΔAICc**	**AICc *w***	**Cumulative *w***
Elevation	3	48.86	0.00	0.93	0.93
Elevation + GDD	4	56.04	7.18	0.03	0.96
Latitude + Elevation	4	56.06	7.20	0.03	0.98
Null	2	57.60	8.74	0.01	1.00
GDD	3	61.52	12.66	0.00	1.00
Latitude	3	61.74	12.88	0.00	1.00

Table 2.7. AICc model summary statement for elevation only model.

	Estimate	SE	t-value	P-value	90% Confidence Interval	
(Intercept)	3.0641	0.104	29.342	1.38e-08	2.8862	3.2300
Elevation	-0.0138	0.003	-4.465	0.0029	-0.0191	-0.0089

CHAPTER 3

OVERWINTERING ECOLOGY OF JUVENILE GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*).

Introduction

Winter can be a critical time for reptiles and other ectotherms due to the drop in temperature, which may reach lethal levels for many species (Gregory, 1982). This is a stressful time for individuals because they must endure physiological changes and make behavioral changes in order to combat reduced temperatures and avoid mortality (Danks, 1987; Guppy and Withers, 1999; Ultsch, 2006). Reptiles seek places to retreat from the cold, selecting retreat sites underground, within rock crevices, in tree stumps, or even underwater where shelters can provide necessary insulation from undesired temperatures while also providing protection from predators (Gregory, 1982; Vitt and Caldwell, 2009). These retreats help in the avoidance of temperature extremes, and retreats farther from the surface may be most favorable for temperature stability (Congdon et al., 1989; Gregory, 1982; Hutchison, 1979).

The time period when an individual resides within a winter retreat can be referred to as overwintering. We use the term “overwintering” here to encompass the various states of reptiles that occur during the winter, rather than using specific behavioral and physiological terms such as hibernation, brumation, or dormancy (Hutchison, 1979; Gregory, 1982; Ultsch, 2006). Timing and duration of overwintering can be influenced by both exogenous factors, such as photoperiod and temperature, and endogenous mechanisms, such as circannual cycles (Gregory, 1982). Responding to these cues and making decisions about the onset and termination of overwintering has important consequences to the individual. An individual that begins overwintering too soon will miss out on foraging and basking opportunities and those that enter too late may risk exposure to lethal temperatures.

While many exogenous factors may influence overwintering, temperature may be the principal factor in stimulating its onset (Hutchison, 1979; Gregory, 1982). Additionally, photoperiod and temperature are highly correlated and thus effects of photoperiod are challenging to separate from temperature (Licht, 1972), however lower temperatures have been shown to inhibit the appetites of reptiles and stimulate metabolic depression (Gregory, 1989; Ultsch, 1989; Ultsch, 2006). Furthermore, when some species, like the chuckwalla (*Sauromalus obesus*), are unable to maintain a preferred body temperature they initiate overwintering (Case, 1976), suggesting that a change in temperature or temperature instability may be an important stimulus for beginning overwintering in other reptile species.

Timing and duration of overwintering may vary within a species, particularly for widely distributed species. In colder areas, species like the box turtle (*Terrapene carolina*) may overwinter for more than half of the year, while in the warmest parts of their range they may be active year round (Dodd, 2002; Gregory, 1982; Ultsch, 2006). Within a population, overwintering behavior may vary with sex or age of individuals (Gregory, 1982). For example, in some species of vipers the females and males differed in how long they overwintered (Prestt, 1971), while adults and juveniles of the orangethroated whiptail (*Cnemidophorus hyperythrus beldingi*) begin overwintering months apart (Bolstic, 1966). In juveniles, this may be due to smaller size and differing thermal requirements. The smaller body size and higher surface-to-volume ratio of juveniles allows them to reach preferred body temperatures more quickly (Miller, 1951; Gregory, 1982; Wilson et al., 1994; Wilson et al., 1999). As a result, some individuals may emerge during the winter on warm days (Woodbury and Hardy, 1940; Douglass and Layne, 1978), while others will not, resulting in variation among individuals in the degree of activity during the overwintering period (Gregory, 1989).

Overwintering has been studied extensively in freshwater turtles; however, research has been limited with regards to terrestrial turtles, particularly tortoises (Ultsch, 2006; Nussear et al., 2007). Tortoises in North America are, to varying degrees, adapted for burrowing. Burrows provide buffering from daily temperature fluctuations of the outside environment (Nussear et al., 2007). Of the North American species, gopher tortoises are the most closely tied to their often extensive burrows, which they use year round for thermoregulation, nesting, and protection from predators (Ernst and Barbour, 1972). Douglass and Layne (1978) demonstrated the temperature buffering capacity of gopher tortoise burrows, which oscillated < 1 ºC in a day, while the high summer air temperatures, varied > 30 ºC in day. However, few studies have investigated the importance of the burrow to the overwintering ecology of gopher tortoises.

Studies of overwintering in tortoises have primarily focused on adults (DeGregorio et al., 2012; Auffenberg and Iverson, 1979; Nussear et al, 2007; Bailey et al., 1995) finding that they primarily remained in their burrows during the winter. On the other hand, only a few studies have followed juvenile tortoises over the winter, finding that they appear to bask frequently during this time (DeGregorio et al., 2012; Wilson et al., 1999). DeGregorio et al. (2012) monitored only 2 juveniles in their study, but concluded that juveniles were much more likely than adults to emerge from their burrows in winter to bask for short periods. Wilson et al. (1999) monitored juvenile desert tortoises determining that the juveniles would emerge on the warm winter days to bask. These studies add to the growing body of literature that suggests the seasonal activity and overwintering ecology of juvenile reptiles may spend more time active than adults (Wilson et al., 1994; Wilson et al., 1999; Gregory, 1982).

In this study we examined the overwintering ecology of juvenile gopher tortoises on a barrier island in Georgia. Our objectives were to 1) determine the timing of the onset, termination, and duration of overwintering, 2) quantify the amount of surface activity during winter, 3) identify the temperatures tortoises experience during overwintering, and 4) identify environmental temperatures triggering winter activity in juvenile tortoises.

Methods

Study Site and Study Population

St. Catherines Island is a privately owned 5670 ha Georgia barrier island (Figure 3.1). The St. Catheriens Island Foundation manages the island to support the primary goals of research, wildlife conservation, and education. On the north end of the island, there is a 102 ha old cattle pasture, named North Pasture. The pasture (Fig. 3.2) is comprised of a few mature mixed pines (primarily *Pinus palustris* but also *Pinus taeda*), no midstory, and an open understory made up mostly of both native and nonnative grasses and forbs. The most abundant understory species include Bahia grass (*Paspalum notatum*), broomsedges (*Andropogon sp.*), narrow-leaf silkgrass (*Pityopsis graminifolia*), narrow-leaf panic grass (*Panicum aciculare*), whip nutrush (*Scleria triglomerata*), whitemouth dayflower (*Commelina erecta*), wiregrasses (*Aristida sp.*), creeping cactus (*Opuntia pusilla*), pine barren frostweed (*Helianthemum corymbosum*), and queen's-delight (*Stillingia sylvatica*). North Pasture is divided into several study sections separated by dirt roads that do not inhibit the movements of tortoises between sections. Our study took place in sections C and E, 14.13 hectares and 8.32 hectares, respectively (Figure 3.1). The pasture is managed for the gopher tortoise and is maintained with a mowing regime, rather than through burning. Both study sections were mowed in March 2012, prior to the beginning of the study.

The gopher tortoise population was established to St. Catherines Island through several translocations to the island and subsequent natural recruitment (Tuberville et al., 2008, 2011). Between 1987 and 1993 approximately 25-30 free-ranging tortoises were released from undocumented sources. In 1994, a wild population of 74 gopher tortoises was translocated from Bulloch County, Georgia, beginning the mark-recapture program on St. Catherines Island.

Data Collection

We initiated trapping 11 May 2012, targeting juvenile tortoises >200g. We defined juveniles as tortoises ≤ 230 mm CL and no signs of sexual dimorphism. Havahart® live animal traps were placed at burrow entrances, covered in burlap for shading, and checked at least twice daily. We recorded the following information for each individual captured: unique ID, weight (g), straight-line carapace length (SCL;

nearest mm) and estimated age based on counting growth annuli on plastral scutes (Landers et al., 1982). If an individual was not previously marked, it was assigned an ID and its corresponding marginal scutes notched using a triangular file (Cagle, 1939).

We fitted each juvenile tortoise with a transmitter (Holohil PD-2, 3.8 g) and temperature-logger (Thermochron iButton® 1921G, 3.3 g) that was attached to the carapace (Figure 3.3) with quick drying epoxies. Transmitters were attached to the first left costal scute with the antenna secured along the length of the tortoise's carapace within aquarium tubing secured to the shell using putty epoxy. Temperature-loggers were completely encased in putty epoxy and attached to the first right costal scute. Each temperature-logger had a resolution of 0.2 ºC, accuracy of ±0.5 ºC, and could store up to 2048 recordings. Each temperature logger was set to record temperatures every 2 hours and thus 12 times a day for 171 days until the loggers were full.

Tortoises were captured approximately every 6 months to replace transmitters and download temperature data. The temperature loggers attached to the tortoise's carapace did not measure the actual body temperature of the tortoise but rather it measured the environmental temperatures to which individuals are exposed. The temperature of the carapace is similar to body temperatures of turtles (Congdon, et al., 1989; Grayson and Dorcas, 2004; Nussear et al., 2007; Pittman and Dorcas, 2009). The temperature data we report here is limited to the winter period for 2012-2013.

Environmental temperature loggers were also deployed at 4 locations within the study area. Each location had temperature loggers to measure 1) ambient shaded air temperatures 10 cm above the ground surface (Figure 3.4 and Figure 3.5; adapted from Hubbart (2011)) and 2) burrow temperatures 1 m inside of an unoccupied juvenile burrow (Figure 3.4). Environmental temperature loggers recorded temperatures every 2 hours beginning at midnight. We report environmental data collected for the 2012-2013 winter period. Due to a prescribed fire in North Pasture, temperature data were not collected from 20-22 February 2013.

Overwintering Analysis

We inferred surface activity (i.e., an emergence event) for individual tortoises by examining the temperatures recorded by the individual's iButton. Because the maximum fluctuation in daily temperatures of burrows recorded during our study was <3.0°C, an individual was considered to have emerged on days during which its temperatures fluctuated ≥3.0°C. From these data, we determined the overwintering onset and termination dates for each individual monitored. We defined onset as the date after which a tortoise did not emerge from the burrow for the following 7 consecutive days. Termination was defined as the date after which the tortoise emerged on at least 7 days within a 14 day period. For 3 individuals, we could not determine the termination date based on their iButton temperature data alone because their iButtons stopped recording shortly before terminating overwintering. However, they were included in our analyses because 1) tortoise was trapped outside its burrow within 7 days of when its iButton stopped recording; 2) the trap was placed at the burrow prior to the temperature logger filling up, and 2) only tortoises active on the surface could be captured with the live traps. For these tortoises, we defined the termination date as the capture date. Duration of overwintering was only determined for tortoises for which both an onset and a termination date had been determined.

Furthermore, each tortoise's winter activity (emergences throughout the overwintering period) was examined to determine at what ambient air temperature each tortoise emerged from the burrow. By examining each tortoise's iButton data for the days when considered active, we determined when tortoise temperatures began increasing, indicative of leaving the stable burrow temperatures and beginning basking in the higher ambient air temperatures. From this evaluation, we were able to the ambient temperatures when tortoises emerged from their burrows and the minimum ambient temperature when tortoises became active. All data are reported in means ± 1 SE.

We encountered missing data points at some of the environmental stations due to malfunctioning or damaged iButtons. To maintain a complete record of temperatures for both ambient air and burrow temperatures, for each temperature sampling event (every 2 hrs), we averaged the available data collectedfrom the four stations. The compiled environmental data provided a complete record of temperatures for both ambient air and burrow during the 2012-2013 winter study period.

Results

Twenty juvenile tortoises were captured and released with iButtons and transmitters from 11 May – 11 July 2012. Of these, 11 tortoises had complete or nearly complete temperature records for the 2012-2013 overwintering period. Temperature loggers for 5 tortoises filled up prior to overwintering termination; however, three of these tortoises were captured within 7 days after the temperature data stopped recording and could still be used for analyses, using their capture date as the termination date. The remaining 2 tortoises were excluded from calculations of overwintering termination and duration.

Tortoises initiated overwintering over a 48 day-period (4 November to 21 December), with a median date of 14 November 2012 (Table 3.1). Termination of dormancy took place over a 32-day period (9 March to 9 April), and tortoises ended overwintering at a median date of 15 March.

Mean overwintering duration of 2012-2013 was 127 days ± 7 days (Table 3.1, Figure 3.6). Of the 9 tortoises for which we were able to calculate overwinter duration, 6 tortoises emerged on relatively few days (range 5 - 9) while the other 3 tortoises emerged frequently (19 - 22 different days) during their overwintering (Table 3.1). The three individuals with ≥ 19 overwinter emergences each had two discrete overwintering events, based on our threshold of 7 consecutive days of emergence in a 14-day period (Figure 3.6). Tortoise 720 had overwintering periods from 24 November - 1 December (8 days) and 18 December - 9 March (82 days), tortoise 761 had overwintering periods from 22 November - 1 December (10 days) and 17 December - 10 March (84 days), and tortoise 762 had overwintering periods from 21 December - 11 January (22 days) and 19 February - 10 March (20 days).

The mean temperature experienced by overwintering tortoises was 17.9 ± 0.02 °C), with a minimum tortoise temperature of 11.5 °C and a maximum of 38.5 °C (Table 3.1). The highest recorded temperatures experienced by the tortoises are associated with winter emergences (basking events). Between 1 November 2012 and 2 April 2013, the minimum ambient temperature when a juvenile tortoise emerged from its burrow to bask was 15.8 °C (Table. 3.2); however, the average minimum ambient temperature when tortoises emerged was 20.9 °C ± 1.0 °C. Juveniles were emerging frequently throughout the winter 2012-2013 and individuals are coming out of their burrows on similar days indicating that they are cueing in on the same stimuli (Fig. 3.7).

During the period coinciding with tortoise overwintering, ambient air temperatures (Figure 3.8) ranged between -6.8-36.6 °C, fluctuating on average 17.4 °C (3.5-30.8 °C) in a given day. In contrast, burrow temperatures ranged from 9.3-24.2 °C, but daily fluctuation averaged only 1.01 °C (0.0-2.8 °C).

Discussion

All juveniles in our study emerged numerous days (5-22 overwinter emergences) during the 2012-2013 overwintering period. Similarly, DeGregorio et al. (2012) reported that the 2 juveniles monitored in South Carolina emerged 4 and 5 times. Both of these studies quantitatively support the observations that juvenile gopher (Diemer, 1992; Wilson et al., 1994) and desert tortoises (Wilson et al., 1999) might be more active than adult tortoises during the winter. While adults do occasionally bask during the winter, it is not typical. DeGregorio et al. (2012) detected adults emerging only 1-2 times, although most did not emerge at all over the winter. The differences in overwintering activity between juveniles and adults are likely due to thermal differences between small and large tortoises; juveniles are able to heat and cool more quickly (Hutchison, 1979; DeGregorio et al., 2012; Wilson et al., 1994) making it easier to reach a preferred temperature on the warm winter days.

Ambient air temperatures in our study varied as much as 30 °C in a day indicating the importance of retreats that insulate from unfavorable temperature fluctuations. We found that the daily burrow temperature had an average 1 °C fluctuation, which agrees with the Douglass and Layne (1978) findings that burrows are a highly thermally stable environment where temperatures oscillated < 1 °C. Mean juvenile tortoise temperature was around 18°C during the winter 2012-2013.

Our findings indicate that juvenile tortoises were active on the surface at lower ambient air temperatures than has been reported in the literature regarding adults. Juveniles initiated basking at temperatures as low as 15.8 °C, which is a lower minimum activity temperature than is seen with adults, which only exit burrows when temperatures are > 21 °C (Douglas and Layne, 1978; McRae et al., 1981). The lower minimum temperature needed for activity we observed for juveniles supports the reported increase in winter activity seen with juvenile tortoises in this and previous studies (Diemer, 1992; Wilson et al., 1994; Butler et al., 1995; Wilson et al., 1999; DeGregorio et al., 2012).

Thermal differences between juveniles and adults that allow juveniles to heat and cool rapidly (Miller, 1951; Gregory, 1982; Wilson et al., 1994; Wilson et al., 1999) would explain why juveniles might be choosing to exit burrows at these lower temperatures. There may be advantages to the tortoises being active at lower temperatures (Naegle, 1976) including the extension of the activity season and aiding in the necessary production of vitamin D (Pritchard and Greenwood, 1968). Juveniles that have a longer activity season may be able to forage for more, accruing resources for growth. Since tortoises—like other chelonians—typically mature based on size, rather than age, gaining resources for growth would be advantageous because it would help to decrease the time to sexual maturity and help juveniles to outgrow predation risk associated with smaller sizes (Congdon and van Loben Sels, 1993; Mushinsky et al., 1994; Roosenberg, 1996).

Overwintering lasted approximately a third of a year for the juvenile gopher tortoises in our study, beginning around mid-November 2012 and ending approximately mid-March 2013. Three of the individuals we observed had 2 discrete time overwintering periods. Tortoises emerge on warm winter days for basking and activity (Keller et al., 1997; Douglass and Layne, 1978) and lower minimum activity temperature observed in juveniles in our study (relative to that reported for adults in the literature) may have contributed to the increased surface activity and discontinuous overwintering.

Previous studies on tortoise species have documented juvenile tortoises active in the winter, and some studies suggested that they might be more active than adults (Diemer, 1992; Wilson et al., 1994; Wilson et al., 1999). We found that indeed juvenile tortoises are frequently active over the winter and this may be due to their ability to be active at lower temperatures than adult gopher tortoises (Naegle, 1976). This increase in winter activity allows the tortoises opportunities to bask and possibly extend their activity season (Wilson et al., 1994). It is likely that juveniles are able to do this because they heat more quickly while basking than an adult would be able to (Hutchison, 1979; Wilson et al., 1994). Because of the importance of juvenile growth, altering behaviors that increase the active season would allow for more foraging and basking opportunities. Winter is a dangerous and stressful time (Danks, 1987; Ultsch, 2006) but the juvenile tortoise can take advantage of favorable conditions over the winter, which might otherwise be a missed opportunity.

Literature Cited

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

Auffenberg, W., and J.B. Iverson. 1979. Chapter 25: Demography of terrestrial turtles. Pages 541-569 in M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

Bailey, S.J., C.R. Schwalbe, and C.H. Lowe. 1995. Hibernaculum use by a population of desert tortoises (*Gopherus agassizii*) in the Sonoran Desert. Journal of Herpetology, 29(3): 361-369.

Bolstic, D.L. 1966. Thermoregulation and hibernation of the lizard, *Cnemidophorus hyperthyrus beldingi* (Sauria: Teiidae). Southwest Naturalist 11: 275-289.

Butler, J.A., R.D. Bowman, T.W. Hull, and S. Sowell. 1995. Movements and home range of hatchling and yearling gopher tortoises, *Gopherus polyphemus*. Chelonian Conservation and Biology, 1(3): 173-180.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia, 1939:170–173.

Case, T.J. 1976. Seasonal aspects of thermoregulatory behavior in the chuckwalla, *Sauramalus obesus*, (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology, 10: 85-95.

Congdon J.D., R.E. Gatten, Jr., S.J. Morreale. 1989. Activity of Box Turtles (Terrapene carolina) in South Carolina. Journal of Herpetology, 23(2): 179-181.

Danks, H.V. 1987. Insect dormancy: an ecological perspective. Biological Survey (Terrestrial Arthropods). Volume 1.

DeGregorio, B.A., K.A. Buhlmann, and T.D. Tuberville. 2012. Overwintering of gopher tortoises (*Gopherus polyphemus*) translocated to the northern limit of their geographic range: temperatures, timing, and survival. Chelonian Conservation and Biology, 11(1): 84-90.

Diemer, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. Journal of Herpetology. 26:158-165.

Dodd, C. K. 2002. North American box turtles: a natural history. University of Oklahoma Press.

Douglass, J.F., and J. N. Layne, 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in Southern Florida. Herpetologica 34:359–374.

Ernst, C.H., and R.W. Barbour. 1972. Turtles of the United States. University Press, Lexington, Kentucky, page 347.

Grayson, K.L. and M.E. Dorcas. 2004. Seasonal temperature variation in the eastern painted turtle (*Chrysemys picta*). Herpetologica, 60: 325-336.

Gregory, P.T. 1982. Reptilian hibernation. Pages 53-154 in C. Gans, editor. Biology of the Reptilia. Academic Press.

Guppy, M., and Withers, P. 1999. Metabolic depression in animals: physiological perspectives and biochemical generalizations. Biological Reviews of the Cambridge Philosophical Society, 74(01): 1-40.

Hubbart, J.A. 2011. An inexpensive alternative solar radiation shield for ambient air temperature micro-sensors. Natural Environmental Sciences, 2(2): 9-14.

Hutchison, V.H. 1979. Thermoregulation. Pages 207-228 in M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

Keller, C., C. Diaz-Paniagua, and A.C. Andreu. 1997. Post-emergent Field Activity and growth rates of hatchling spur-thighed tortoises, *Testudo graeca*. Canadian Journal of Zoology. Volume 75.

Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and Maturity of the Gopher Tortoise in Southwestern Georgia. Bulletin of the Florida State Museum, Biological Science, 27 (2): 81-110.

Licht, P. 1972. Problems in experimentation on timing mechanisms for annual physiological cycles in reptiles. Pages 681-710 in T.E. South, J.P. Hannon, J.R. Willis, E.T. Pengelley, and N.R. Alpert, editors. Hibernation and Hypothermia, Perspectives and Challenges. Elsevier Publishing Company, Amsterdam.

McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement Patterns and Home Range of the gopher tortoise. American Midland Naturalist, 106: 165-179.

Naegle, S.R. 1976. Physiological responses of the desert tortoise, *Gopherus agassizii*. *Unpublished* M. S. Thesis, University Nevada, Las Vegas.

Nussear, K.E., T.C. Esque, D.F. Haines, and C.R. Tracy. 2007. Desert tortoise hibernation: temperatures, timing, and environment. Copeia, 2: 378-386.

Pittman, S.E. and M.E. Dorcas. 2009. Movements, habitat use, and thermal ecology of an isolated population of bog turtles (*Glyptemys muhlenbergii*). Copeia 2009: 781-790.

Presst, I. 1971. An ecological study of the viper, *Vipera berus*, in southern Britain. Journal of Zoology, London. 164: 373-418.

Pritchard, P.C.H. and W.F. Greenwood. 1968. The Sun and the Turtle. International Turtle and Tortoise Society Journal. 34(2): 20-25.

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

Tuberville, T.D., T.M. Norton, B.J. Waffa, C. Hagen, and T.C. Glenn. 2011. Mating system in a gopher tortoise population established through multiple translocations: apparent advantage of prior residence. Biological Conservation, 144(1): 175-183.

Tuberville, T.D., B.D. Todd, S.M. Hermann, W.K. Michener, and C. Guyer. In Review. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management.

Ultsh, G.R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biological Reviews, 64: 435-516.

Ultsch, G.R. 2006. The Ecology of Overwintering Among Turtles: Where Turtles Overwinter and Its Consequences. Biological Review 1:1-29.

Ultsch, G.R., and J.F. Anderson. 1986. The respiratory microenvironment within the burrows of gopher tortoises (*Gopherus polyphemus*). Copeia, 1986: 787-795.

Vitt, L. J., and J.P. Caldwell. 2009. Thermoregulation, Performance, and Energetics. Pages 177-196 *in* Herpetology. Amsterdam: Academic/Elsevier, 3rd Edition.

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1994. Home range, activity and use of burrows of juvenile gopher tortoises in Central Florida. Pages 147-160 in R.B. Bury and D.J. Germano, editors. Biology of North American Tortoises. Washington, DC: United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13.

Wilson, D.S., Morafka, D.J., Tracy, C.R., and Nagy, K.A. 1999. Winter activity of juvenile desert tortoise (*Gopherus agassizii*) in the Mojave Desert. Journal of Herpetology, 33: 496–501.

Woodbury, A.M. and R. Hardy. 1940. The dens and behaviour of the desert tortoise. Science, N.Y. 92, 129.

Woodbury, A.M. and R. Hardy. 1948. Studies of the Desert Tortoise, *Gopherus agassizii*. Ecological Monographs 18: 145-200.

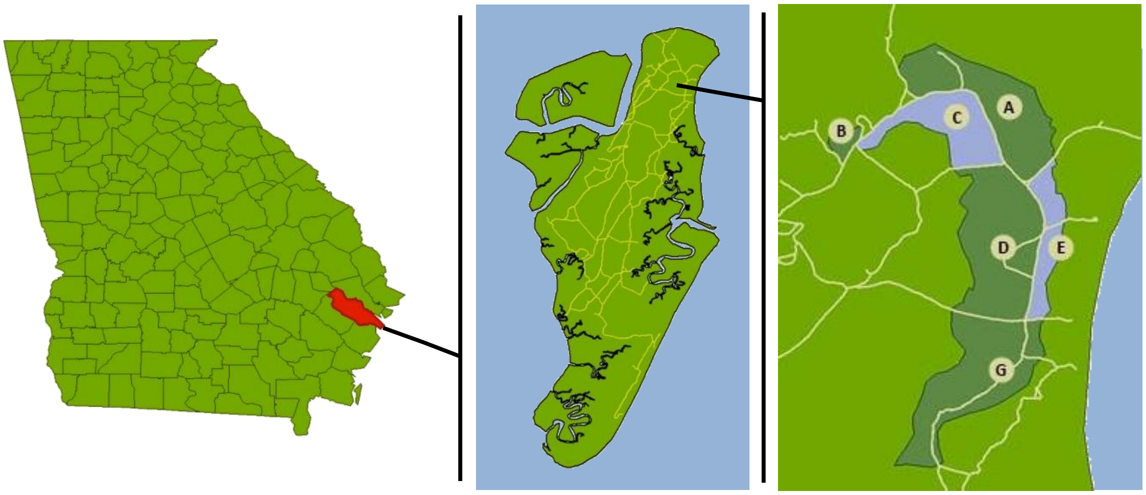

Figure 3.1. St. Catherines Island is a barrier island off the coast of Liberty County, Georgia. The gopher tortoise population occupies the north end of the island in an area named North Pasture. The pasture is separated into sections that are defined by the island roads. The overwintering study took place in sections C and E, depicted in purple.

Figure 3.2. Habitat structure in North Pasture, St Catherines Island, GA. The habitat is comprised of a sparse over-story, no mid-story, and an understory of native and nonnative grasses and forbs maintained through mechanical disturbance.

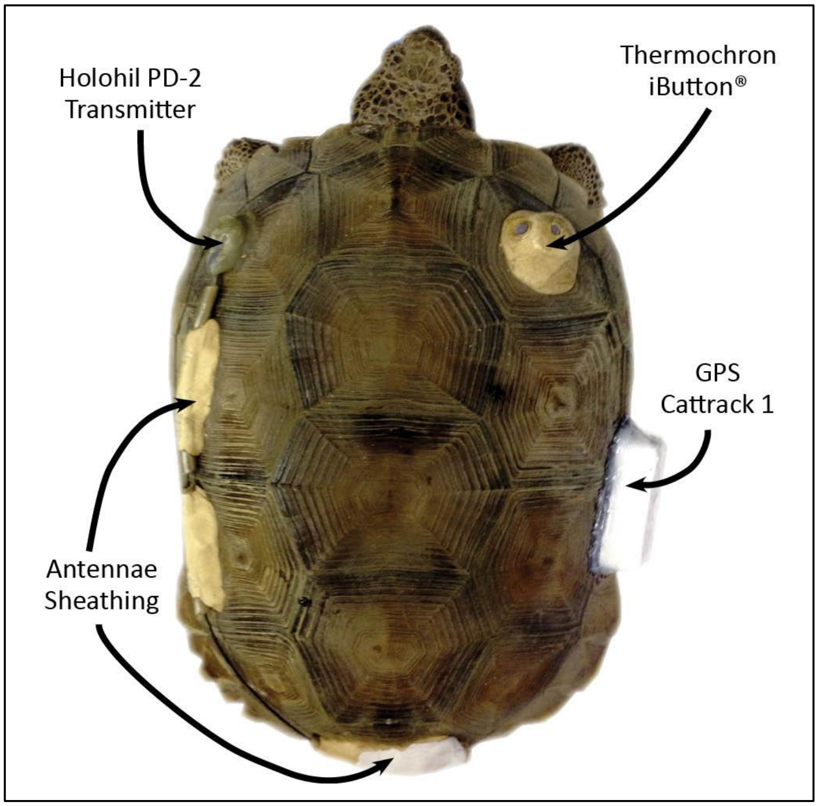

Figure 3.3. Juvenile gopher tortoise showing attachment of telemetry (Holohil PD-2 Transmitter and antennae sheathing) and temperature (Thermocron iButton®) equipment to the carapace using epoxy. In addition, the figure depicts a GPS logger (GPS CatTrack 1/CatLog), which was attached to a subset of the study tortoises.

Figure 3.4. The environmental station was setup to collect both ambient air temperatures on the surface as well as air temperatures in an abandoned juvenile gopher tortoise burrow. The ambient air temperature logger was secured 10 cm above the surface using a design adapted from Hubbart (2011). It was placed approximately 30 cm away from the entrance to the abandoned burrow where burrow temperatures were taken. The temperatures of the inside of the burrow were taken with a temperature logger secured to the end of a PVC pipe and placed approximately 1m inside the burrow. A small portion of the end of the PVC pipe remained visible at the entrance to the burrow.

Figure 3.5. The environmental station setup for collecting shaded ambient air temperatures on the surface using a design adapted from Hubbart (2011). The ambient air temperature logger was secured 10 cm above the ground’s surface. It was placed approximately 30 cm away from the entrance to the abandoned burrow.

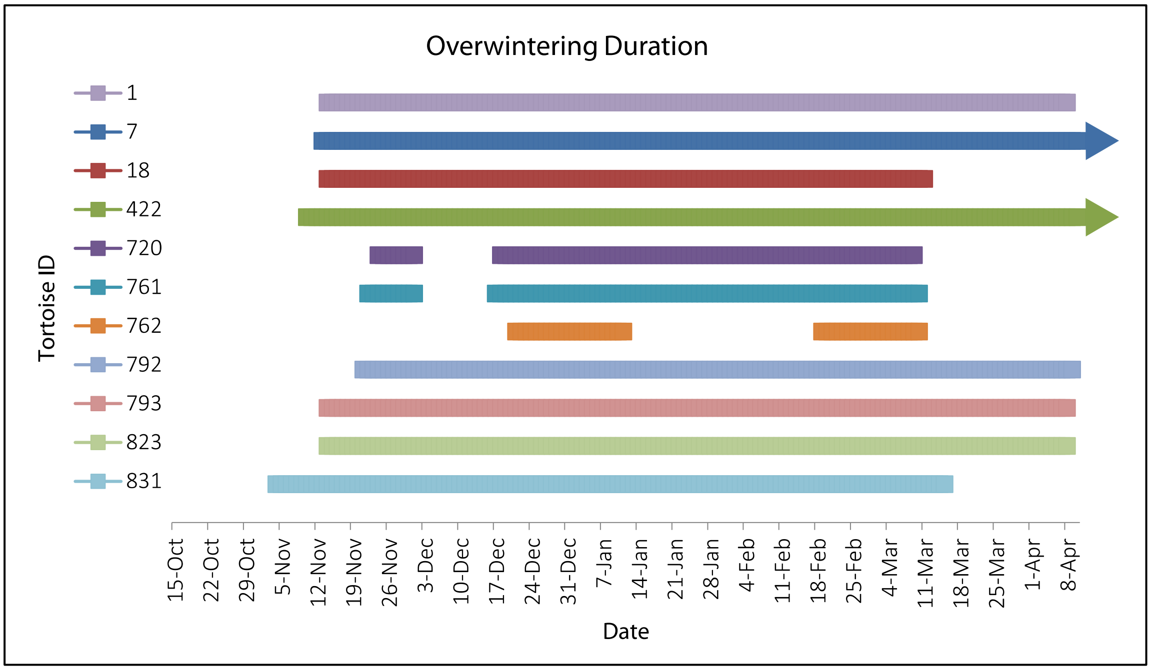

Figure 3.6. The duration of juvenile gopher tortoise overwintering events at St. Catherines Island during the 2012-2013 winter. The duration is represented from onset to termination by each solid line for each tortoise. Lines ending in arrows did not have a termination date before the temperature loggers had filled. The tortoises with broken lines are the juvenile tortoises that had discontinuous overwintering events comprised of two discrete overwintering periods.

Table 3.1. For each juvenile tortoise monitored during the 2012-2013 winter, the following data are reported: tortoise age (years) and size (straight-line carapace length; CL); first overwintering onset date, last overwintering termination date, and overwintering duration (days); mean, minimum, and maximum overwintering temperatures experienced during the overwintering period; and number of emergence days. Each tortoise with an * by the date is one for which the temperature logger became full prior to the tortoise terminating overwintering but for which capture date could be used to determine termination date. Tortoises without a calculated termination date were excluded from the duration and emergence calculations as is indicated by the –.

Tortoise ID	**SCL (mm)**	**Overwinter Onset**	**Overwinter Termination**	**Overwinter Duration (days)**	**Mean Overwinter Temperature °C (± SE)**	**Overwinter Minimum Temperature °C**	**Overwinter Maximum Temperature °C**	**Overwinter Emergence0s**
1	164	14-Nov-12	8-Apr-13 *	146	18.4 ± 0.06	15.5	35.0	8
7	217	13-Nov-12	—	—	17.4 ± 0.05	13.0	31.0	—
18	174	14-Nov-12	11-Mar-13	140	18.0 ± 0.09	11.5	38.5	8
422	215	10-Nov-12	—	—	17.4 ± 0.05	14.0	35.0	—
720	179	24-Nov-12	9-Mar-13	106	18.0 ± 0.08	12.5	34.0	20
761	142	22-Nov-12	10-Mar-13	109	18.7 ± 0.08	14.0	37.5	19
762	199	21-Dec-12	10-Mar-13	80	21.0 ± 0.09	16.0	37.5	22
792	147	21-Nov-12	9-Apr-13 *	140	16.7 ± 0.06	13.0	35.5	5
793	230	14-Nov-12	8-Apr-13 *	146	17.9 ± 0.06	14.0	33.0	9
823	140	14-Nov-12	8-Apr-13 *	146	16.6 ± 0.06	13.0	33.5	9
831	130	4-Nov-12	15-Mar-13	132	16.6 (0.1)	11.5	35.0	5

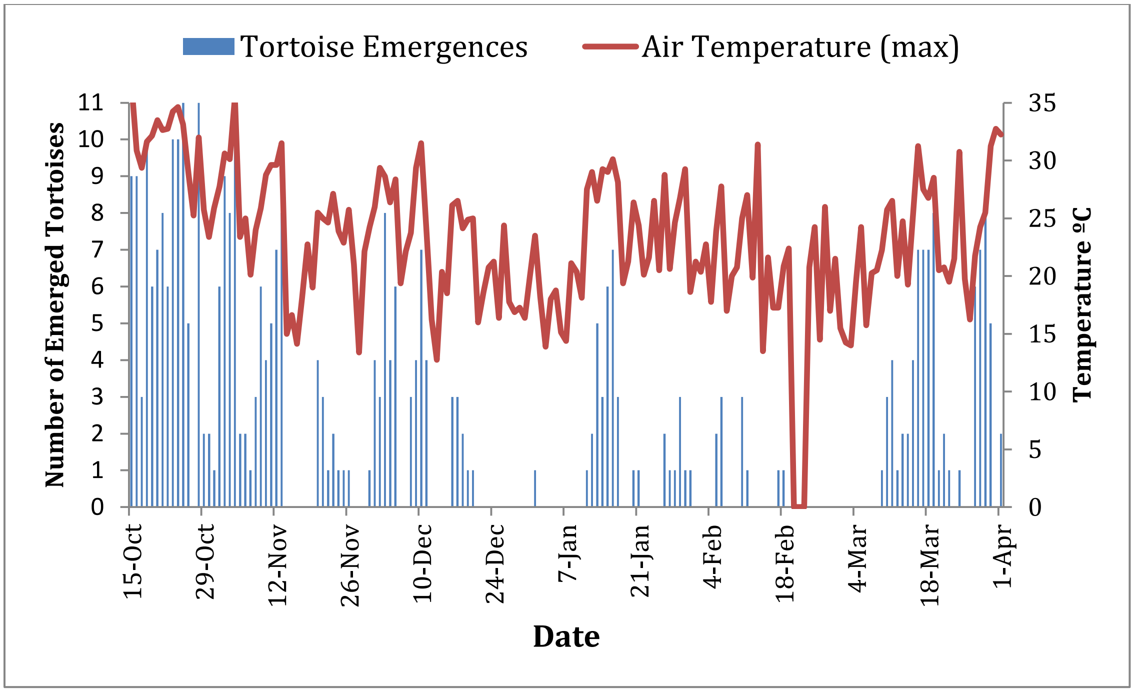

Figure 3.7. The number of tortoises that emerged each day and the maximum daily ambient temperature during the 15 October 2012- 2 April 2013. Ambient temperatures were not collected 20 February 2013 – 22 February 2013 due to a prescribed fire in North Pasture where the environmental stations were located.

Table 3.2. Table of ambient temperatures (ºC) on days when at least one tortoise emerged from its burrow during the 2012-2013 overwintering period. The number of tortoises (of the 11 monitored) that emerged at a given time and the mean, minimum, and maximum ambient temperature at the time of emergence between 1 November 2012 and 2 April 2013.

Tortoises Emerging	Mean Temperature (SE)	Minimum Temperature	Maximum Temperature
1	24.5 (0.5)	15.8	31.5
2	25.3 (0.4)	18.5	31.5
3	26.3 (0.5)	18.5	31.3
4	27.4 (0.5)	24.3	35.0
5	29.2 (0.8)	25.3	35.5
6	27.2 (0.2)	25.5	28.4

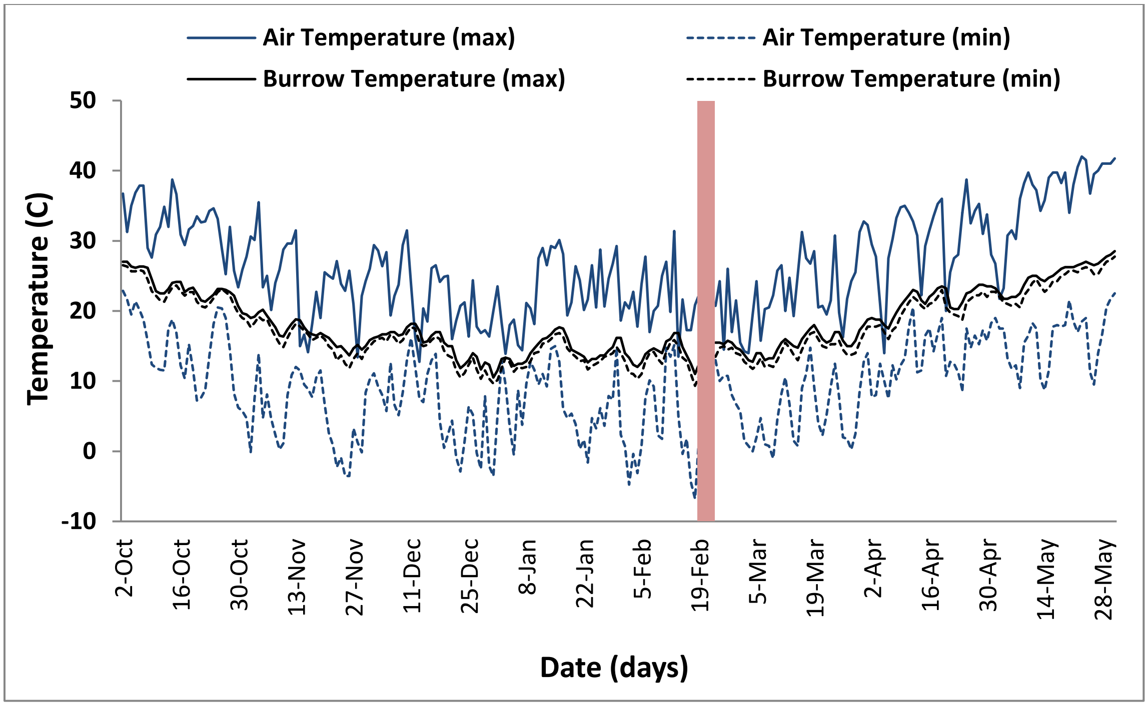

Figure 3.8. Environmental Temperatures over the winter of 2012-2013 at the St. Catherines Island study site, including daily maximum (solid grey line) and minimum (dashed grey line) ambient air temperatures, as well as daily maximum (solid black line) and daily minimum burrow temperatures (dashed black line). During 20 February 2013 – 22 February 2013 a prescribed fire was administered which required environmental stations to be pulled from the field, resulting in 3 days for which data are missing.

CHAPTER 4

DISCUSSION AND MANAGEMENT IMPLICATIONS

Basic information on the ecology of the juvenile gopher tortoise (*Gopherus polyphemus*) is needed to better inform habitat management and conservation efforts. Past research has typically focused on adult tortoises (Morafka, 1994), yet the ecology of the juvenile tortoises may differ from their adult counterparts. Understanding more about the juvenile age class is essential in better understanding the species (Morafka, 1994; Smith et al., 2006; USFWS, 2011; GTC, 2012). Due to their small body size and soft shell, juveniles are highly susceptible to the elements and predation (Diemer, 1986; Wilson, 1991). The purpose of this study was to examine the growth rates of juvenile gopher tortoises on a barrier island and compared these findings with those of other studies that occurred on the mainland. Additionally, this study investigated the overwintering period of juvenile gopher tortoises, evaluating the timing and temperatures that they experience during this critical time.

The growth rate of tortoises has been documented at several sites throughout the gopher tortoise range, but has only focused on mainland sites (Goin and Goff, 1941; Landers et al., 1982; Godley, 1989; Mushinsky et al. 1994; Aresco and Guyer, 1999; Tuberville et al., *unpublished*). More information regarding the variability in growth rates as well as the sizes and ages of maturity at the sites throughout the range of the gopher tortoise is required (Smith et al.,2006). Understanding the relative contributions of habitat type and quality towards that influences that growth rate is necessary for understanding how we might be able to improve growth rates at sites. This study examined the growth rates of juvenile gopher tortoises on a barrier island off the coast of Georgia. The results of this study found that the juveniles are growing an average of 19 mm CL/year, one of the highest growth rates reported. Age at sexual maturity also stood out from other sites at an estimated at short 9-10 years for tortoises to reach maturity, similar to that of the Mushinsky et al. (1994) site. Age at sexual maturity is especially important in species that are in decline, such as the gopher tortoise, because it suggests how long an individual is exposed to mortality before it becomes a reproductive member of the population (Auffenberg and Iverson, 1979).

The effects of environmental gradients and the relative habitat quality and type could not be fully addressed in this study due to a lack of comparable information between all of the study sites. Although location has understandable effects related to the number of activity days at a site, this did not account for the variations in growth rates observed in this study. Instead, tortoise growth may be influenced more by habitat rather than length of activity season (Aresco and Guyer, 1999). This is why I believe future work on gopher tortoise growth and age of maturity should focus on gathering comparable information among study sites. This would be useful for assessing what conditions are ideal for supporting high growth rates and the relative impact of these contributions towards tortoise growth. This information might be useful for managers making habitat decisions or when assessing sites for translocations, because understanding the relative influences that habitat characteristics contribute towards growth can help in prioritizing the needs for the tortoises.

The overwintering timing and temperatures of the juvenile gopher tortoise has received little attention. The idea that juvenile tortoises may be more active than their adult counterparts (Deimer, 1992; Wilson et al., 1994; Wilson et al. 1999; DeGregorio et al., 2012) is not new, but it had not been investigated quantitatively. I evaluated the onset, termination, duration, activity, and temperatures experienced by juvenile tortoises overwintering. My results indicate that while the gopher tortoise juveniles exhibited the same overwintering timing and duration as adults seen in the DeGregorio et al. (2012) study the juveniles do differ in their winter activity. Specifically, if adults emerge over winter they do so rarely (1-2 times; DeGregorio et al., 2012) while juveniles emerged a minimum of 5 times with some individuals emerging >19 times throughout the winter. The juveniles are likely able to be active more often because of their different thermal requirements (Hutchison, 1979; Wilson et al., 1994; DeGregorio et al., 2012) allowing them to be active at lower temperatures than adults. Although juveniles begin emerging when ambient temperatures are approximately 21.0°C on average, the minimum activity temperature of adult gopher tortoises (Douglass and Layne, 1978), they also emerged at temperatures as low as 15.8°C. This difference in the minimum activity temperature allowed for more time when a tortoise could be active throughout the year.

Winter has typically been the time when managers employ habitat management, whether it is through mechanical disturbance or prescribed fire. While this may still be the preferred time for most managers to perform the necessary habitat maintenance, it is important to consider that juveniles may still be above ground during this time and could either be injured or stressed from theses habitat disturbances, particularly on the warmer winter days.

Any future work on overwintering of gopher tortoises should address both juveniles and adults in equal number during the same study. This would help in making a comparison between these two groups, removing the variation between years and studies. I also believe it would be useful to include individuals of varying sizes to determine how size might impact the amount of activity observed overwinter. Size differences are often used to explain why juvenile tortoises might behave differently during the winter than adults (Wilson et al., 1994; DeGregorio et al. 2012), but I was unable to determine this relationship from the data at St. Catherines Island. I believe it is likely that it is not the juveniles size when compared with the adults that affects their overwintering activity, but perhaps instead the relative investment on growth versus reproduction that makes the difference. Such that juvenile tortoises may vary in the amount of time spent active during the winter but upon maturity there would be a drop in activity as the investment in growth declines.

Literature Cited

Aresco, M.J., and C. Guyer. 1999. Growth of the tortoise *Gopherus polyphemus* in slash pine plantations of southcentral Alabama. Herpetologica, 55(4): 499-506.

Auffenberg, W., and J.B. Iverson. 1979. Chapter 25: Demography of terrestrial turtles. Pages 541-569 in M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

DeGregorio, B.A., K.A. Buhlmann, and T.D. Tuberville. 2012. Overwintering of gopher tortoises (*Gopherus polyphemus*) translocated to the northern limit of their geographic range: temperatures, timing, and survival. Chelonian Conservation and Biology, 11(1): 84-90.

Diemer, J.E. 1986. The ecology and management of the gopher tortoise in the Southeastern United States. Herpetologica, 42(1): 125-133.

Diemer, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. Journal of Herpetology. 26:158-165.

Douglass, J.F., and J. N. Layne, 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in Southern Florida. Herpetologica 34:359–374.

Godley, J.S. 1989. Comparison of gopher tortoise populations relocated onto reclaimed phosphate-mined sites in Florida. Pages 43-58 in J.E. Diemer, D.R. Jackson, J.L. Landers, J.N. Layne, and D.A. Wood, editors. Gopher Tortoise Relocation Symposium. Florida Game Freshwater Fish Community Nongame Wildlife—Program Technique Report 5.

Goin, C.J. and C.C. Goff. 1941. Notes on the growth rate of the gopher tortoise, *Gopherus polyphemus*. Herpetologica, 2 (3): 66-68.

Gopher Tortoise Council. 2012. Priority research topics for the conservation of gopher tortoises—compiled from the 33rd annual meeting of the Gopher Tortoise Council, October 13-15, 2011. The Tortoise Burrow: Newsletter of The Gopher Tortoise Council. 32(1): 12-14.

Hutchison, V.H. 1979. Thermoregulation. Pages 207-228 in M. Harless and H. Morlock, editors, Turtles: Perspectives and Research. John Wiley & Sons, New York, New York, U.S.A.

Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and maturity of the gopher tortoise in Southwestern Georgia. Bulletin of the Florida State Museum, Biological Science, 27 (2): 81-110.

Morafka, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. Biology of North American Tortoises, Fish and Wildlife Research 13: 161-174.

Mushinsky, H.R., D.S. Wilson, and E. D. McCoy. 1994. Growth and sexual dimorphism of *Goperus polyphemus* in Central Florida. Herpetologica, 50(2): 119-128.

Smith, L.L., T.D. Tuberville, and R.A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise (*Gopherus polyphemus*), Joseph W. Jones Ecological Research Center, 16-17 January 2003: final results and recommendations. Chelonian Conservation and Biology, 5(2): 326-330.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the gopher tortoise as threatened in the eastern portion of its range. Federal Register 76:45129-45162.

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

Wilson, D.S., Mushinsky, H.R., and McCoy, E.D. 1994. Home range, activity and use of burrows of juvenile gopher tortoises in Central Florida. Pages 147-160 in R.B. Bury and D.J. Germano, editors. Biology of North American Tortoises. Washington, DC: United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13.

Wilson, D.S., Morafka, D.J., Tracy, C.R., and Nagy, K.A. 1999. Winter activity of juvenile desert tortoise (*Gopherus agassizii*) in the Mojave Desert. Journal of Herpetology, 33: 496–501.