Home Range, Reproduction, and Habitat Characteristics of the Female Gopher Tortoise (Gopherus Polyphemus) in Southeast Georgia

Maggie Jo Mitchell
Georgia Southern University

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HOME RANGE, REPRODUCTION, AND HABITAT CHARACTERISTICS OF THE FEMALE GOPHER TORTOISE (*Gopherus polyphemus*) IN SOUTHEAST GEORGIA

by

MAGGIE MITCHELL

(Under the Direction of David C. Rostal)

ABSTRACT

The relationship among female gopher tortoise home range, size, reproduction, habitat characteristics and season were studied for a two-year period (May 2002-May 2004) on Ft. Stewart Army Reserve (FSAR) in southeast Georgia. Tortoises were studied in four sectors or regions on Ft. Stewart that contain the longleaf pine/wiregrass ecosystem. Vegetation characteristics were consistent between the different areas that tortoises inhabited. Soil types were similar between areas and consisted of Blanton, Bonifay, Fuquay, Albany Sand, Chipley, Echaw, Centenary, Stilson and Tifton soil types. Vegetation, temperature, and rainfall data were collected and compared with female home range. Reproductive data were collected for the same females for three consecutive reproductive seasons (n=35). Yearly variation in reproductive output was observed within females but was not correlated with habitat characteristics or home range. Rainfall and temperature were monitored with a negative relationship observed between rainfall and reproduction. Female size was not correlated with home range. Home range was also not correlated with clutch size or habitat characteristics measured. Cumulative home range did tend to increase with study duration (one year vs. two-year).

INDEX WORDS: Gopher tortoise, *Gopherus polyphemus*, home range, reproduction, habitat characteristics, Ft. Stewart Army Reserve
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FEMALE GOPHER TORTOISE (*Gopherus polyphemus*) IN SOUTHEAST GEORGIA

by

MAGGIE MITCHELL

B.S., Georgia Southern University, 2002

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

MASTER OF SCIENCE

STATESBORO, GEORGIA

2005
HOME RANGE, REPRODUCTION, AND HABITAT CHARACTERISTICS OF THE
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MAGGIE MITCHELL

Major Professor: David C. Rostal

Committee: Ray Chandler
           Susan Langley

Electronic Version Approved:
December 2005
DEDICATION

To my parents, Richard and Mary Beth Mitchell for all their love and support.
ACKNOWLEDGMENTS

I would like to thank my graduate professor David C. Rostal for all his guidance throughout my project and for sharing his extensive knowledge of the gopher tortoise and the sandhill habitat in which it lives. I not only learned about tortoises, but he also taught me about many other reptiles and amphibians from other projects that he is involved with. I also want to thank Matt G. Hohmann and The Corps of Engineers Research Laboratory (CERL) for funding this research. I would especially like to thank Matt G. Hohmann from the Corps of Engineer’s research laboratory, for his guidance on project design, in particular the vegetation plots and counts. I also received funding from the Georgia Southern University Graduate Student Professional Development Fund and the Georgia Southern Excellence Grant. I would also like to thank my committee members Dr. C. Ray Chandler and Dr. Susan Langley who advised me on many aspects of my research.

I want to thank Dirk Stevenson, a fish and wildlife biologist at Ft. Stewart, for helping me obtain GIS data, weather data, and soil data related specifically to the areas on Ft. Stewart that were used for this project. I also want to show my appreciation to all the people who helped me collect data in the field: Hugh Moye, Kandice Eason, Jed Vickers, Anne Marie LeBlanc, Andy O’Neil, Lester Helm, Rachel Dubberly, Elaine Miller, Tyessa Parks, Becki Clifton, Matthew Miller, Grant Mangum, Matthew Schlosser and Bill Hammrik. I could not have collected all the data without you.
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INTRODUCTION

As a keystone species in the longleaf pine / wiregrass ecosystem, the gopher tortoise (*Gopherus polyphemus*) is important in the survival of approximately 60 vertebrate and 300 invertebrate species. (Rostal and Jones, 2002; Auffenberg and Franz, 1982; Ott Eubanks et al., 2003; Hermann et al., 2002). These species depend largely on gopher tortoise burrows both for habitat and protection. The gopher tortoise is one of the four species of extant tortoises in North America. Its range extends throughout the southeastern coastal plain from South Carolina to Louisiana (Diemer, 1986). The gopher tortoise is a long lived species (Kaczor and Hartnett, 1990; Diemer, 1986; Iverson, 1980; Landers and Speake, 1980; Landers et al., 1980; Mushinsky et al., 1994; Rostal and Jones, 2002) and is estimated to live 60-80 years in the wild (Rostal and Jones, 2002; Iverson, 1980; Landers et al., 1980). Most studies only capture a small portion of the life of this long lived animal.

The gopher tortoise has specific habitat criteria such as loose sandy soils, an open canopy, and herbaceous ground cover for foraging (Aresco and Guyer, 1999; Rostal and Jones, 2002). Once habitat quality degrades, the gopher tortoises will either extend their range to find more suitable habitat or leave the site altogether in search of better habitat (McRae et al., 1981; Landers and Speake, 1980). For some species the distribution of resources necessary for survival and reproduction determine the amount of energy the animal uses (O'Conner et al., 1994). Gopher tortoises expend valuable energy searching for burrow sites and digging new burrows, therefore less energy may be available for growth and reproduction (Aresco and Guyer, 1999).
It has been shown that the clutch size of the gopher tortoise can vary between states and regions and sometimes even between sites within the same region (Diemer and Moore, 1994; Rostal and Jones, 2002). Studies have also shown that carapace length is positively correlated with the size of the clutch (Iverson, 1980; Diemer and Moore, 1994; Rostal and Jones, 2002); however some of the differences in clutch size between states or regions may be partially attributed to slight differences in carapace length between the regions.

Home range studies on the gopher tortoise vary in duration from a few months to a year (McRae et al., 1981; Diemer, 1992b; Smith et al., 1997; Ott Eubanks et al., 2003). Along with home range it is important to study other aspects of the ecology of the gopher tortoise through long-term studies such as specific habitat characteristics and reproductive characteristics of this animal (Rostal and Jones, 2002; Cox et al., 1987). It has been recognized that home range may serve as an indicator of multiple functions: activity, energy balance, resource availability, and opportunities for reproduction and social interaction. It is very difficult to tease apart the different effects of environmental resources on home range and reproduction (O'Connor et al., 1994), but it is important to attempt to understand how these factors relate to each other. Radiotelemetry is one method used by researchers to help clarify and estimate individual movements and home range (Porter and Dooley, 1993).

Tortoise habitat is small and highly fragmented, and increasing development pressure has forced the relocation of gopher tortoises to non-native areas such as private land or reserves (Eubanks et al., 2002; Diemer, 1986; Auffenberg and Franz, 1982). Home range is an important issue for management of the gopher tortoise because it can
be used to estimate the size a reserve needs to be to sustain a certain number of tortoises (Ott Eubanks et al., 2003). It is important to acquire a multi-year home range; the home range of an individual may not be fixed from year to year due to differing environmental conditions. It is also possible that an individual may have a single-year home range that is the same size as their multi-year home range. It is critical to develop accurate reserve area estimates to ensure that existing reserves and future reserves are large enough to maintain viable populations of tortoises in the face of increasing habitat loss (Eubanks et al., 2002). Improvement in battery life for radiotags can allow us to look at individual movements in detail and mark-recapture studies also provide the concept of a home range as an area traversed during an animal’s normal activities between dispersal movements (Kenward et al., 2001). Through the use of location data collected from mark-recapture studies a long-term home range can be created as an indicator of the area an animal might need to survive long-term.

How the gopher tortoise divides its energy resources is significant for the management of these animals. If the tortoise has to travel long distances for food or appropriate nest sites it may reduce the amount of energy it can put into reproduction. If relationships exist between these factors they may provide insight on how the gopher tortoise uses its habitat and how we can improve or manage habitat to fit the needs of this tortoise species.

Using a two-year radiotag we want to obtain an average multi-year (May 2002-May 2004) home range for the female gopher tortoise at Ft. Stewart Army Reserve (FSAR). This study is one of few studies that include a large sample of females over a two-year period to determine an approximate home range for the female gopher tortoise.
Reproductive data were also collected for all females to determine factors that may influence the reproduction of this animal. Radiotagged female tortoises were captured each May during the study to obtain average clutch size and reproductive output for these animals in different years. We also wanted to assess the habitat quality, ground cover, and canopy cover for four sectors at FSAR to find out if habitat quality correlates to home range and/or reproduction. Rostal and Jones (2002) found that tortoises at FSAR were selecting burrow locations with lower than site average mean percent canopy and higher than site average mean herbaceous ground cover. Using our habitat data we wanted to see if this trend still existed with tortoises at FSAR.
METHODS AND MATERIALS

Study Site

Four sectors at Fort Stewart Army Reserve (FSAR) were used in this study. FSAR is approximately 113,400 ha and is broken up into sectors labeled by a letter and a number. The sectors used in this study were E12, E21, F11 and F12 (Figure 1), the total area of all five sectors equaled 4044 ha. Individual sector sizes which include some habitat not used by tortoises were: E12 = 826 ha, E21 = 1538 ha, F11 = 639 ha, F12 = 1197 ha. Sector E21 was composed of a sandridge that contains what are possibly two populations of gopher tortoises, one on the north end of the ridge and one on the south end of the ridge (Figure 2). These sectors were chosen because they contained previously studied populations of gopher tortoise in which mark-recapture data have been collected. All sectors (E12, E21, F11 and F12) chosen contained sufficient tortoise numbers (in excess of 50 individuals) and could be easily accessed throughout the year.

The areas studied at FSAR are dominated by longleaf pine / wiregrass. There is an active management plan to restore longleaf pine to FSAR. There is minimal soil disturbance, aside from road repair after use for military maneuvers, and all areas are maintained with prescribed burns on a 3-5 year interval. Aside from the occurrence of occasional logging, these areas retain characteristics of tortoise populations that are similar to those of ancestral habitat (Hermann et al., 2002). These characteristics are present in all areas used in this study, however there is a slight geographic difference between the Echo areas and the Foxtrot areas. These areas were selected for the range of habitat included in each and how these differing habitats might influence the ecology of the gopher tortoise. The Echo areas are dominated mostly by pine trees with few
Figure 1. Aerial photo of the western portion of Ft. Stewart Army reservation showing the location of study sectors.
Figure 2. Aerial photo of Sector E21 on Ft. Stewart Army Reserve. Note the separation between the northern concentration of tortoises and the southern concentration of tortoises within this sector.
hardwoods, and the Foxtrot areas dominated by hardwoods in the early stages of succession with pine trees distributed thinly throughout.

Soil types for FSAR were provided by Dirk Stevenson, a Fish and Wildlife Biologist at Ft. Stewart. The series types were found through a draft from the University of Florida Cooperative Extension Service Institute of Food and Agricultural Sciences (Jokela and Long, 1999). The soil series types vary slightly by sector (Table 1); all sectors contain soil from the soil series type F which includes Bonifay, Fuquay, and Stilson. These soils are found in upland areas and generally have moderate to good drainage and reasonably good moisture relations because of their topographic position. They have a sandy surface layer with a sandy clay horizon found deeper than 50.8 cm. E21 N contained only soils from series type F. E12 and E21 S contain Chipley soil in the soil series type G. These soils are deep, coarse-textured, droughty, and low in nutrient reserve. The sand surface layer is at least 254 cm thick and their drainage is excessive. E12 and F11 contain the soil Tifton, from the soil series type E. This soil type is also found in upland areas and has a sandy surface that is underlain by a red to yellow fine textured (clayey) subsoil within 50.8 cm of the surface. These soils have a good capacity to retain moisture and nutrients and are excellent soils for loblolly pine sites. E21 and F12 contain Albany sand from the soil series type B. These soils are typically found in nearly level depressions such as stream terraces and broad wet flats. The drainage is very poor to somewhat poor and there is a sandy surface layer greater than 50.8 cm thick with a finer textured soil horizon below. E12 contains Echaw and Centenary soils from the soil series type D. These soils are found in flatwoods and drainage is ranged from somewhat poorly to moderately well. Below the sandy surface layer there is a spodic horizon, which represents a zone where iron, aluminum, and organic matter have
Table 1. Soil types and their Cooperative Research in Forest Fertilization (CRIFF) soil series type (Jokela and Long 1999) for each sector in the study.

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<td>Bonifay</td>
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<tr>
<td>Fuquay</td>
<td>F</td>
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<td>F</td>
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<td>F</td>
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<tr>
<td>Albany Sand</td>
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<td>B</td>
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<tr>
<td>Chipley</td>
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<tr>
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<td>Centenary</td>
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<td>Stilson</td>
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accumulated under this layer is another sandy layer. In some cases the spodic zone may become weakly cemented when dry (Jokela and Long, 1999).

**Animal Capture, Care and Reproduction**

Tortoises were caught at burrows using bucket traps (Brieninger et al., 1991); once a tortoise was caught it was identified as a recapture or a new capture. Straight carapace length (SCL) was measured on all tortoises to the nearest 1.0 mm using a set of calipers, and tortoise were sequentially marked with a floy tag (Floy Model FTF-69 Pennant, Floy Tag & Mfg., Seattle, WA) (Rostal and Jones, 2002), and notched on their marginal scutes with a file using the Cagel method (Cagle, 1939). The notching on the tortoises corresponded to the number on the floy tag in case the tag or notching becomes lost or unreadable. In addition to the two other methods, starting in 2002 all tortoises were tagged in the right shoulder using a P.I.T. (Passive Integrated Transponder, AVID Identification Systems Inc., Norco, Ca).

All female tortoises were trapped in May, taken to a lab at Georgia Southern University, and each female tortoises reproductive status was determined by ultrasound (Rostal et al., 1994). If the female was determined to be gravid, she was then x-rayed to determine clutch size (Gibbons and Greene, 1979). Ultrasound was used to view the status of the egg before the x-ray was taken (Figure 3) in order to determine if eggs were calcified and would be visible on an x-ray and could be counted (Figure 4). In the figure, plate A and B show follicular development; note the difference in diameter size in each plate (A is 2.19 cm, B is 2.28 cm). Plate C shows a shelled egg, the outer calcified layer is visible along with the albumin layer which is between the shell and the yolk and plate D is an atretic follicle, or a follicle that was not ovulated and is being reabsorbed. If eggs were not well calcified they would not show up on an x-ray and tortoises thought to be
underproductive may have in fact had eggs that were not yet visible through x-ray creating a misinterpretation of female clutch size and reproductive output of tortoises in a population. Using ultrasound also reduced the number of times a female was x-rayed so that on average, females would only have to be x-rayed once per season.

Reproduction was analyzed in different ways and was defined as either clutch size, reproductive output or residual clutch size. Clutch size was defined as the number of eggs counted for only those females that produced a clutch in the given year. Reproductive output was defined as the average number of eggs per female, for all females captured, including females that did not produce a clutch in a given year, for which this could be verified using ultrasound. Residual clutch size refers to the residuals from the regression of clutch size on straight carapace length in order to account for tortoise body size in correlations between home range and habitat characteristics. Residual clutch represents variation in clutch size that is independent of variation in carapace length. This was used to account for body size in following regressions of clutch size and other variables.

Home Range

In May 2002, 54 female tortoise were fitted with a radiotag (Wildlife Materials Inc., Carbondale, Il) that was mounted (using epoxy putty and glue) on the right shoulder with the antenna wrapping around the left shoulder and side of the shell (Figure 5). Each radiotag weighed approximately 0.082 kg which is 0.02% of the average weight of the tortoises used in this study (4.88 kg). After the tags were mounted and checked, the tortoises were released within 48 hours at the burrows where they were captured. The tortoises were then tracked using a TRX-1000S PLL Synthesized Tracking Receiver and a YAGI Three Element Directional Antenna (Wildlife Materials, Inc., Carbondale, Il).
Figure 3. Ultrasound scans of female gopher tortoises (*Gopherus polyphemus*). A) Ultrasound image of a small follicle in the ovary. B) Ultrasound image of a larger more developed follicle in the ovary. C) Ultrasound image of a shelled egg, with calcified shell, non-echogenic Albunin layer and echoic yolk in the middle. D) Ultrasound image of an atretic follicle that is being reabsorbed by the female since it was not ovulated.
Figure 4. An example of an x-ray of a female gopher tortoise (*Gopherus polyphemus*) showing five well calcified oviductal eggs.
Figure 5. Photograph of a radiotagged female gopher tortoise in a natural burrow. Note the location of the radiotag placement on the right shoulder region which minimized obstruction in the burrow. Photo taken by Dr. David C. Rostal.
Each year, from May to August the tortoises were tracked twice a week. In August, tracking was reduced to once a week and then starting in November they were tracked once every two weeks until the weather started to get warmer. In March, tortoises were tracked once a week until May. The location of each tortoise was recorded by burrow number and/or a complete description of the above-ground location and a GPS reading was taken at each location a tortoise was found, whether in a burrow or above ground. The GPS location was taken using a Magellan Mark X, Santa Clara, CA. The locations of the tortoises were then mapped using ArcView Software (ESRI, Redlands, CA), and the minimum convex polygon home range was calculated using an extension to ArcView called Movement 2.0 (Selkirk and Bishop, 2002). The 2002 home range includes locations from May 2002 to December 2002 and 2003 home range includes locations from May 2003 until December 2003. Multi-year home range refers to the locations included from May 2002 until May 2004.

Of the 54 tortoises originally tagged, one female was found dead on her back on 6/14/02 and was not used in any analysis for this study. From winter 2003 to summer 2004 four tortoises were found “emaciated,” above ground. These tortoises were picked up and after they died a necropsy was performed. These females were larger and displayed a well worn carapace and plastron which is an indication of older animals (Pers. Obs.). Results from necropsy showed they died from a fungal pneumonia. Data from these animals was not used in most analyses. One tortoise had only two locations, which happened to be burrows, throughout the whole study so a home range could not be determined. Due to tag failure, sample sizes varied for different analyses from year to year. Animals that died, the tortoise that had only two locations, and animals that were lost due to tag failure were excluded from analysis. A total of 42 animals were used in
analysis out of the original 54 tortoises that were tagged. Severe weather in the form of rain during 2003 hampered trapping, and reproductive data could not be collected on all females. Complete home range and reproductive data for all three consecutive reproductive seasons of the study were collected on 35 females.

**Vegetation**

Vegetation data in 2001 and 2002 were collected at 10 active burrows in each sector used in the study; in 2003 vegetation data were collected at 36 burrows known to be used by females with radiotags and 36 plots that were chosen randomly using ArcView and its extension, Movement 2.0. Data was collected on the percent canopy cover and the percent ground cover at each plot. Percent canopy cover was assessed using a convex sphere crown densiometer 2m from the burrow mouth in the cardinal directions (Lemmon, 1957). At each cardinal location the canopy was then counted in that locations four cardinal directions which resulted in 16 readings at each burrow (Figure 6). The percent ground cover was counted at eight locations around the burrow mouth. Four counts were 8 meters from the mouth in the four cardinal directions and four counts were 4 meters from the mouth in the 4 semi-cardinal directions (Figure 6). The counts were done using two 1-m² grids placed at the exact compass locations mentioned above. Within this grid the amount of grass cover, forb cover, shrub cover, bare area and (in 2003) litter cover was counted and calculated into percent cover. Grass counts included wiregrass, and all other grass species found. Forb counts included annual flowering plants and shrub counts included woody perennials less than two meters tall or any plant with a woody base. Bare was any exposed sand or soil. Leaf litter was counted as coverage by leaves, bark or tree stumps. For both canopy cover and ground cover, the counts at the different compass readings were averaged to obtain a mean percentage of
cover. All trees within a 16-m radius from the burrows and/or random points were measured. The diameter at breast height was measured in cm using calipers, and trees were categorized as deciduous (e.g., Turkey oak), pine (e.g., slash pine or longleaf pine), or snag (dead but still standing).

**Data analysis**

Data did not have equal variances and did not have a normal distribution so non-parametric tests were used. Kruskal-Wallis was used when comparing more than two groups such as the difference between all sectors or years to find overall significance. A Mann-Whitney-U test was used when two groups were being compared, such as differences between two sectors or years. Linear regression was used to find predictive relationships between two variables such as tortoise size and clutch size, tortoise home range and clutch size and tortoise movements and rainfall. Principal component analysis (PCA) was used for 2003 vegetation data for comparison to 2004 reproductive output, 2004 clutch size and 2003 home range.

I obtained weather data from the forestry department on FSAR. All data were entered into excel spreadsheets and analyzed using the capabilities of Excel and the statistical software JMP IN (SAS Institute, Cary, NC). Data were graphed using the statistical software Sigma Plot (Systat Software Inc., Richmond, CA.).
Figure 6. A visual representation of the vegetation data collection methods. The GC refers to the locations the percent ground cover data was collected. The C refers to location where the canopy cover readings were taken.
RESULTS

Female straight carapace length (SCL) ranged from 25.9-32.5 cm with a mean of 30.22 cm. Female SCL did not vary between sectors: E12 ranged from 25.9-33.4 cm with an average of 30.3 ± 0.5 SE (n=11), E21 ranged from 27.02-31.4 with an average of 30.4 ± 0.32 SE (n=15), F11 ranged from 28.7-31.6 with an average of 30.2 ± 0.33 SE (n=12) and F12 ranged from 29.1-32.1 with an average of 30.6 ± 0.26 SE (n=11).

Home Range

Home range was calculated using the minimum convex polygon (MCP) method. MCP home ranges were found for 2002 home range, 2003 home range and the 2002-2004 home range for all female tortoises in the study. Sample plot MCP home ranges for four tortoises, with each year having a different color, are presented in Figure 7. Home range varied from 0.008 ha to 9.167 ha in 2002 with an average of 0.785 ± 0.28 ha SE (n=37, where 16 home ranges could not be determined because tortoises used only one or two burrows). In 2003 home range varied from 0.008 ha to 9.623 ha with an average of 1.224 ± 0.319 ha SE (n=40, 6 tortoises used only one or two burrows, 3 had signal failure and could not be found, 4 animals died and one animal’s tag fell off). The multi-year (2002-2004) home range varied from 0.008 ha to 13.489 ha with an average of 1.863 ± 0.447 ha (n=43 and one tortoise whose home range could not be determined because only two burrows were used during the entire study). Home range was observed to increase from 2002 to 2003. The multi-year average home range (2002 to 2004) differed significantly from 2002 (U=980, df=73, p=0.002) home range and was larger than 2003 average home range but was not significant.
Figure 7. Sample plots of home ranges for four radiotagged female gopher tortoises from May 2002 to May 2004.
Home range in 2002 did not differ significantly between sectors. In 2003, home range in E12 was significantly larger than home range in F11 (U=65, df=16, p=0.026) and F12 (U=61, df=15, p=0.016). The 2002-2004 home range in E12 was significantly larger than home range in F11 (U=73, df=17, p=0.019) and F12 (U=74, df=16, p=0.003) (Figure 8). There was no difference found for home range between the north and south ends of the sandridge in E21 (Figure 9). When all sector home ranges were combined for an overall home range, there was an increase from 2002 to 2003 and 2002-2004 home range was larger than both 2002 and 2003 home ranges.

No relationship was observed between home range and female size (Figure 10). Larger females did not have significantly larger home ranges in any year. Average home range by year for this study was compared to home ranges reported by previous studies (Table 2). Our multi-year home range was greater than twice the size reported for any previous studies.

Reproduction

There was a decrease in all aspects of reproduction for the gopher tortoise from 2002 to 2004. The overall percent of females that reproduced decreased from 92% in 2002 to 82% in 2003 to 67% in 2004. Average clutch size also decreased from 2002 to 2004 with an average of 6.21±0.51 (range 2-11; n=49) in 2002, 6.84±0.64 (range 3-11; n=4339) in 2003 and 5.54±0.65 (range 1-10; n=42) in 2004. The percent of females that reproduced decreased from 2002 to 2004 in all sectors (Figure 11). Sector E21 showed one of the greatest decreases in the percent of females that reproduced. There was a difference between the percent of females that reproduced between the north ridge and the south ridge (Figure 12).
Figure 8. Average minimum convex polygon (MCP) home range for female gopher tortoises for each year of the study sorted by sector. Letters refer to significant differences, values are mean ± SE.
Figure 9. Home range of the female gopher tortoise (*Gopherus polyphemus*) for the north and south ends of the sand ridge in sector E21. Values are mean ± SE.
Figure 10. Straight carapace length versus home range for radiotagged female gopher tortoise (*Gopherus polyphemus*).
Table 2. A comparison of average home range in this study to the average home range found in previous studies on the gopher tortoise in Florida and Georgia.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Location</th>
<th>Source</th>
<th>Duration</th>
<th>Sample Size</th>
<th>HR (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ford colony, Silver Lake Station</td>
<td>Decatur, Ga</td>
<td>McRae et al., 1981</td>
<td>09/1978-10/1979</td>
<td>5</td>
<td>0.08 ± 0.002</td>
</tr>
<tr>
<td>Lachloosa wildlife Mgmt Area</td>
<td>Alachua Co., Fl</td>
<td>Diemer, 1992</td>
<td>05/1985-05/1987</td>
<td>5</td>
<td>0.31</td>
</tr>
<tr>
<td>Katherine Ordway Preserve</td>
<td>Putnam Co., Fl</td>
<td>Smith, 1992; 1995</td>
<td>05/1990-10/1991</td>
<td>14</td>
<td>0.48 ± 0.11</td>
</tr>
<tr>
<td>Happy Creek, Tel-V Kennedy Space Center</td>
<td>Brevard Co., Fl</td>
<td>Smith et al., 1997</td>
<td>07/1988-03/1990</td>
<td>4</td>
<td>0.65 ± 0.20</td>
</tr>
<tr>
<td>Fort Stewart Army Reserve Year 1</td>
<td>Southeast, Ga</td>
<td>This study</td>
<td>05/2002-12/2002</td>
<td>33</td>
<td>0.78 ± 0.28</td>
</tr>
<tr>
<td>Fort Stewart Army Reserve Year 2</td>
<td>Southeast, Ga</td>
<td>This study</td>
<td>5/2003-12/2003</td>
<td>38</td>
<td>1.22 ± 0.32</td>
</tr>
<tr>
<td>Fort Stewart Army Reserve Overall</td>
<td>Southeast, Ga</td>
<td>This study</td>
<td>05/2002-05/2004</td>
<td>43</td>
<td>1.86 ± 0.45</td>
</tr>
</tbody>
</table>
Figure 11. Percent of female gopher tortoises that reproduced and their corresponding sample sizes sorted by sector. This figure does not include the five animals that were found wasting away and later died.
Figure 12. Percent of female gopher tortoises that reproduced sorted by the north and south sandridge in sector E21.
The south ridge actually had an increase in percent reproduced from 2003, while the north ridge had a significant drop in the number of females that reproduced.

Reproductive output differed significantly among years (H=14.42, df=2, p=0.001). There was no difference in reproductive output between 2002 and 2003, however there was a significant decline in 2004 with fewer females reproducing in 2004 than in 2002 (U=1441, df=88, p=0.0004) and 2003 (U=1103.5, df=78, p=0.003) (Table 3). Clutch size also differed between years (H=8.78, df=2, p=0.012) following the same trend as reproductive output. Clutch size in 2002 and 2003 were not significantly different, while clutch size in 2004 was significantly lower than clutch size in 2002 (U=797, df=70, p=0.034) and 2003(U=620.5, df=57, p=0.004) (Table 3). Note that clutch size did not include data for animals that did not reproduce. Clutch size and reproductive output did not differ significantly between sectors in 2002, 2003, or 2004 (Table 3). Interestingly it was observed that reproduction was different within one sector (E21) where the population is separated geographically into a north and south ridge subpopulation. In E21 there was no difference between the north ridge and south ridge for average clutch size but there was a significant difference in reproductive output in 2004 between the south ridge and the north ridge (U=35, df=11, p=0.03) (Figure 13). Reproductive output was significantly higher in the southern subpopulation then the northern subpopulation.

A correlation between clutch size and SCL was found each year individually and when 2002-2004 clutch size and SCL were averaged(2002: r^2=0.275, df=46, F=17.44, p=0.0001; 2003: r^2=0.212, df=29, F=7.82, p=0.009; 2004: r^2=0.441, df=25, F=19.69, p=0.0002 (Figure 14); and for all years: r^2=0.293, df=45, F=18.66, p=0.0001) (Figure 15).
We compared the residual clutch size to home range to assess the relationship between size-independent clutch size and home range. We found no significant correlation between SCL / clutch size to home range (Figure 16).

**Vegetation**

The Echo area consists of a longleaf pine / wiregrass ecosystem that is fairly undisturbed while the Foxtrot area consists of mainly oak with patches of pines throughout, this area has signs of human disturbance such as clear cutting and other activities (Figure 17). A seasonal pattern was found for ground cover characteristics in both the Echos and the Foxtrots (Figure 18). Bare ground, forb cover, and grass cover were greatest in the summer when the tortoise is most active. Canopy cover only varied slightly throughout the year with peak cover in the Fall, which would be before the leaves fall from the trees (Figure 19).

Comparing vegetation characteristics for burrows in 2002 and 2003, vegetation differences were found between forb cover, grass cover and bare ground cover. There was a significant decrease in forb cover ($U=1153$, $df=74$, $p<0.0001$) and grass cover ($U=1112$, $df=74$, $p<0.0001$) in 2003, which would account for the significant increase in bare ground cover ($U=1161$, $df=74$, $p<0.0001$) in the same year (Figure 20).

In 2002, no differences were found between ground cover characteristics and canopy cover between sectors (Figure 21). In 2003 the only difference found between sectors was a higher percentage of grass cover in F12 than in F11 ($U=78$, $df=17$, $p=0.01$) (Figure 21). This difference may possibly be attributed to the lower percent of canopy cover in F12, which could encourage more grass to grow there. There was also a difference between the north and south ridge of E21 for 2003. More shrubs were found
in the north ridge than in the south ridge, which could be attributed to the soil difference between the two ridges (Figure 22). In 2003 random points were sampled in each sector. No difference was found between canopy cover and ground cover characteristics for burrows versus random points in 2003 (Figure 23).

In 2002 there was no significant difference between the Echos and the Foxtrots when comparing all sectors combined for ground cover characteristics (forbes, grass, shrubs, and bare) (Figure 24). Canopy cover in the Echos was significantly greater than canopy cover in the Foxtrots (U=419, df=48, p=0.019) (Figure 24). There was no significant difference found between the Echos and the Foxtrots in 2003 when comparing all sectors combined for ground cover characteristics (Forbes, Grass, Shrubs, Litter and Bare). Canopy cover in the Echos was significantly greater than canopy cover in the Foxtrots (U=977, df=70, p=0.0002) (Figure 24). Differences were not observed between the two major regions and there were no generalized patterns found in the differences of vegetation characteristics among sectors.

The tree data collected supports the habitat differences in the Echos versus the Foxtrots. The Echo area is an undisturbed longleaf pine/wiregrass habitat and had significantly more pine trees than the Foxtrot area (U=465.5, df=48, p=0.001), and the Foxtrots contained more snag trees (U=623.5, df=48, p=0.023), which is probably a result of the logging and clearcutting that occurs in this area (Figure 25). Note that in 2003 there was a change in location of plots and vegetation data were not collected at the same burrows as in 2002. In 2003 the significance of pine trees being greater in the Echos continues (U=1622, df=70, p<0.0001), but the number of snag trees is no longer significant (Figure 25). This could be because of the change in location of plots, or a
Table 3. Average clutch size and reproductive output for the female gopher tortoise sorted by sector and by year. Clutch size was
defined as the number of eggs counted for only those females that produced a clutch in the given year. Reproductive output was
defined as the average number of eggs per female, for all females captured, including females that did not produce a clutch in a given
year, for which this could be verified using ultrasound.

<table>
<thead>
<tr>
<th>Reproductive Output</th>
<th>Clutch Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2002</td>
</tr>
<tr>
<td>E12</td>
<td></td>
</tr>
<tr>
<td>Reproductive Output</td>
<td></td>
</tr>
<tr>
<td>E12</td>
<td>7.18±0.61</td>
</tr>
<tr>
<td>N=11</td>
<td>N=8</td>
</tr>
<tr>
<td>E21</td>
<td>5.23±0.53</td>
</tr>
<tr>
<td>N=14</td>
<td>N=11</td>
</tr>
<tr>
<td>F11</td>
<td>5.58±0.67</td>
</tr>
<tr>
<td>N=12</td>
<td>N=11</td>
</tr>
<tr>
<td>Overall</td>
<td>5.83±0.35</td>
</tr>
<tr>
<td>N=48</td>
<td>N=38</td>
</tr>
<tr>
<td>F12</td>
<td>5.45±0.96</td>
</tr>
<tr>
<td>N=11</td>
<td>N=8</td>
</tr>
</tbody>
</table>
Figure 13. Average clutch size and average reproductive output for female gopher tortoises in E21 sorted by the south ridge and the north ridge. Sample sizes are given above each bar.
Figure 14. Regression of straight carapace length (SCL) versus clutch size for 2002, 2003 and 2004. Female body size does have an effect on clutch size.
Figure 15. Regression of average straight carapace length (SCL) and average clutch size of radiotagged females that had at least two reproductive seasons of data out of the three seasons from the study.
Figure 16. Home range versus residual clutch size to account for female body size for 2002, 2003 and 2004 home ranges.
Figure 17. Photograph A was taken in E12 and represents the relatively undisturbed longleaf pine / wiregrass ecosystem that makes up the Echo area. Photograph B was taken in F11 and represents the Foxtrot area which has been disturbed by clearcutting for pine trees and oak trees were removed using the hack and squirt herbicide method to reduce hardwoods.
Figure 18. Seasonal vegetation for the Echo and Foxtrot areas on Ft. Stewart Army Reserve, sorted by season from October 2001 to April 200
Figure 19. Seasonal canopy cover for Echo and Foxtrot areas on Ft. Stewart Army Reserve, sorted by season from October 2001 to April 2003.
Figure 20. Ground cover and canopy cover for 36 active burrows in 2002 and 36 active burrows in 2003 at Ft. Stewart Army Reserve. There were significant differences in all aspects of ground cover except shrub cover and canopy cover.
Figure 21. Ground cover and canopy cover for the summers of 2002 and 2003 at tortoise burrows on Ft. Stewart Army Reserve.
Figure 22. Ground cover vegetation for burrows on the north and south ridge in E21 for the summer of 2002 and 2003. Values are mean ± SE.
Figure 23. Burrows versus random points for canopy cover and ground cover characteristics for Ft. Stewart in the summer of 2003. Values are mean ± SE.
Figure 24. Echos versus Foxtrots for ground cover and canopy cover for the summer of 2002 and 2003. Values are mean ± SE.
Figure 25. The number of deciduous, pine and snag trees in 2002 and 2003 for the Echos (E) versus the Foxtrots (F) on Ft. Stewart Army Reserve for the sectors used in this study. Values are mean ± SE.
result of snag trees falling or as a result of increased rainfall and storms during winter 2003. All other parameters were the same suggesting uniform habitat within the sectors.

Principal Component Analysis (PCA) was used to condense 2003 habitat characteristics and compare the habitat to tortoise reproductive output, clutch size and home range. No relationship was found between PCA1 versus reproductive output 2004, clutch size 2004, and home range 2003 (Figure 26). Comparison of vegetation characteristics important to tortoises and the corresponding percent of reproductive females and average clutch size by sector are shown in Figure 27 for 2002, and Figure 28 for 2003. It should be noted that reproduction results in the spring following hibernation, hence the difference in year for habitat data versus reproduction.

Weather

Average yearly rainfall at FSAR showed a dramatic drop from 136.47 cm in 1997 to 86.63 cm in 2001. The average yearly rainfall in 2002 increased to levels similar to 1999 levels and in 2003 the average yearly rainfall increased to an amount higher than it had been observed since 1995 (1995=134.13 cm, 1996=103.83 cm, 1997=136.47 cm, 1998=129.64 cm, 1999=117.74 cm, 2000=100.69 cm, 2001=86.63 cm, 2002=121.84 cm, 2003=151.63 cm) (Figure 29). Monthly rainfall and temperature were analyzed relative to the significant decline in percent females reproducing and clutch size in 2004. In 2004 the average monthly rainfall increased and the average monthly air temperature decreased (Table 1A in appendix A). Figure 30 is a graphical representation of weather changes throughout the study period. Notice how the rainfall is greatly increased during the late summer and early fall months when follicular development begins in the female gopher tortoise.
Figure 26. Regression of 2004 home range, clutch size and reproductive output, versus PCA1 which is the vegetation characteristics for 2003.
Figure 27. Comparison of habitat characteristics by sector for summer 2002 with average clutch size and percent females reproducing per sector in May 2003.
Figure 28. Comparison of habitat characteristics by sector for summer 2003 with average clutch size and percent females reproducing per sector in May 2004.
Figure 29. Average yearly rainfall at Ft. Stewart Army Reserve in southeast Georgia from 1995 to 2003.
Figure 30. Average monthly rainfall and average monthly temperatures on Ft. Stewart Army Reserve from May 2002 to May 2004. Green asterisks mark the nesting month of each year.
Movement patterns were compared to temperature and rainfall to determine their effect on tortoise activity. Linear regression was used to compare average monthly temperature to average monthly movement patterns and results showed the two were not correlated. However, there was a significant correlation between average monthly rainfall and average monthly movements ($r^2=0.350$, df=16, p=0.010) (Figure 31).
Figure 31. Average monthly rainfall versus average monthly movements of female gopher tortoises. Months without movements (e.g. hibernation months) were not included in these analyses.
DISCUSSION

This study represents the second largest radiotracking study of tortoises to date. All previous studies tracked fewer than 15 females. Eubanks et al. (2003) tracked 53 females for one year, whereas in our study we tracked 43 females for 2 consecutive years (May 2002 – May 2004). In addition, reproductive data were collected for 3 consecutive seasons for 35 females. The multi-year home range found in this study (1.86 ± 0.45 ha) was over twice the size of the largest female gopher tortoise home range (0.65 ± 0.20) found in previous studies (Table 2). An overall decrease in reproduction was also observed from 2002 to 2004 with fewer females reproducing in 2004. A seasonal pattern was found among the vegetation at FSAR. In the summer months, when the tortoises are most active in Georgia (McRae et al., 1981) there is an increase in the percent cover of forbs and grasses, which is a large part of the gopher tortoise diet (Diemer, 1986).

Home range

It has been proposed that there is a relationship between home range, food availability (the amount of herbaceous ground cover), and the overall quality of the habitat (Diemer, 1992b; McRae et al., 1981; Landers and Speake, 1980; Aresco and Guyer, 1999). Home range has also been related to reproduction although it typically refers to tortoises searching for mates, especially in male tortoises, or nest site selection in female tortoise (McRae et al., 1981; Ott Eubanks et al., 2003; Douglass, 1986; Eubanks et al., 2003).

There are four North American tortoise of the genus *Gopherus*. The Bolson tortoise, *Gopherus flavomarginatus*, is the largest of the four and also the least studied (Germano, 1994). The desert tortoise (*Gopherus agassizii*) is smaller than the gopher
tortoise, although it occupies the largest geographical and ecological range of the four
North American tortoises in the genus *Gopherus* (Germano, 1994) with a home range that
averages from $8.7 \pm 1.08$ ha (range 5.9-11.23ha) (O'Conner et al., 1994) to 9.7 ha
(Freilich et al., 2000). The Texas tortoise (*Gopherus berlandieri*) was thought to have a
very small home range compared to the gopher tortoise and the desert tortoise with an
average of 0.17 ha for a two-year study and 0.34 ha for a five-year study (Judd and Rose,
1983). A more recent study on the home range of the Texas tortoise found a much larger
home range. The study completed by Richard Kazmaier et al. in 2002 found that in a
managed thornscrub in Southern Texas the home range for the texas tortoise in an
ungrazed area was $6.8\pm2.1$ ha and in a grazed area home range was $5.0\pm1.4$ ha using
100%MCP. This difference in home range between the two studies can be attributed to
many things such as area constraints of available habitat, low densities or research
methods(Kazmaier et al., 2002). In our study there was little difference in home range
among sectors although individual home range varied from 0.008 ha to 13.49 ha. Joan
Diemer (1992) also found considerable individual variation in her study on the
demography of the gopher tortoise in northern Florida with an average home range of
$0.358$ ha $\pm$ 0.211 (range 0-1.182).

Comparing home range for 2002 and 2003 we found no significant difference. However, when we compared each year separately to the 2002-2004 multi-year home range we found that the multi-year home range was significantly larger. Our study is
only one of few that tracked animals for a duration of two-years so we compared our
home range to the results of previous studies (Table 2). We found that our multi-year
home range was much greater than what was found in other studies on female gopher
tortoise home range. The difference in home range between sites is enough to question the blanket use of an average value for home range for the gopher tortoise (Eubanks et al., 2002). Home ranges, in general, are not static and may continually expand due to excursions or drift across the landscape, it is important to investigate effects of the environment in different seasons and years to get an approximate average home range (Kenward et al., 2001).

Although there was no significant difference in home range between 2002 and 2003, we did see an increase in home range in 2003. The increase in home range that was observed in 2003 could be attributed to the heavy rainfall that caused burrow flooding (Pers. Obs.) and increased tortoise movements (Figure 29 for weather information). We saw the greatest increase in home range in sector E12, which also happened to be where we saw the most burrow flooding occur. The flooding could be attributed to the fact that sector E12 contains soil series B and D that drain poorly, whereas the other sectors contain mostly soil series F that contain moderate to well drained soils. Short-term flooding can even occur in deep sandy soils during prolonged heavy rains (Means, 1982). We attribute the increase in home range in all sectors to the heavy rainfall that occurred during the fall in 2003. This could be supported by the significant positive regression that we found between the number of movements and amount of rainfall. The increase in 2003 home range, which we attribute to the weather, was the foundation for our large multi-year home range. The 2002 home range of 0.78 ha (n=33) was more similar to that reported by Ott (1999) where home ranges reported from other studies ranged from 0.08 ha to 0.65 ha (Ott, 1999).
We did not find a relationship between home range and body size for female gopher tortoise at FSAR, however, this relationship is hard to detect. The size of the tortoises used in home range studies is restricted by the need for tortoises large enough to carry the radiotag. Eubanks (2003) also found no correlation between the size of the female gopher tortoise and its home range at Ichauway Ecological Reserve in southwestern Georgia (Ott Eubanks et al., 2003). However, Auffenberg and Weaver (1969) found a relationship between body size and home range for the Texas tortoise, while a study of home range and movements of desert tortoises found no relationship between body size and home range (O'Conner et al., 1994). The tortoises used in our study were also selected because we wanted to collect reproductive data and they needed to be large enough to be reproductively mature.

Reproduction

Although we did not find a correlation between body size and home range, we did find a positive correlation between female straight carapace length (SCL) and clutch size for each reproductive season in this study, and all seasons averaged. This same correlation was also found in several other studies on the gopher tortoise (Iverson, 1980; Landers et al., 1980; Diemer and Moore, 1994; Rostal and Jones, 2002). We also wanted to see if there was a relationship between home range and clutch size to determine whether females with larger home ranges could possibly have smaller clutch sizes because of energy allocation. Using residuals from the Clutch/SCL regression to account for body size, we found that home range does not influence clutch size for the female gopher tortoise on Ft. Stewart.
The reproductive data gathered in this study is important to the study of reproduction in the female gopher tortoise because, unlike most studies, we were able to get reproductive data on 35 females tortoises for three consecutive reproductive seasons. Previous studies have suggested that female gopher tortoises may not reproduce every year (Landers et al., 1980; Smith et al., 1997; Cox et al., 1987), and only data from a large number of female tortoises, collected over consecutive years can support or refute this suggestion.

We saw a decrease in the percent of females that reproduced from 2002 to 2004 and a decrease in average clutch size and reproductive output from 2002-2004. It is important to distinguish between clutch size and reproductive output because we saw a slight decrease in clutch size but a very large drop in reproductive output in 2004. This means that not only were clutch sizes smaller but there were also fewer females reproducing, which would greatly lower the chances for recruitment since fewer nests were being laid.

We did not find a significant difference in clutch size (the number of eggs in a clutch for animals that produced a clutch in the given year) and reproductive output (number of eggs for all females captured including animals that did not produce a clutch in a given year) between sectors for all three seasons of the study. Rostal and Jones (2002) found that females at FSAR produced an overall mean of 6.52 ± 0.33 eggs over three consecutive reproductive seasons from 1994 to 1996. The average clutch size for this study in 2002 (6.21 ± 0.51 eggs) and 2003 (6.84 ± 0.64 eggs) were very close to that reported by Rostal and Jones (2002), however 2004 clutch size (5.54 ± 0.65 eggs) was smaller.
Tortoises in the Echos showed the greatest reduction in the percent of females that reproduced in 2004 with E12 showing the largest decrease in clutch size and reproductive output. The largest increase in home range was observed in E12 as well. We believe the decrease in clutch size and reproductive output that we saw in all sectors in 2004 may have resulted from the increase in rainfall that occurred the previous fall. With the burrow flooding in the Echos, animals were forced to move out of their burrows which would increase stress on the animal along with increasing the energy used to locate a new burrow. Our weather data shows that increased rainfall occurred in months critical to follicular development. The process of follicular development, or Vitellogensis, occurs between late July to early October and follicular enlargement occurs from July until late April, slowing only during the winter months (unpublished data). The maintenance of a high body temperature was found to be associated with both digestive processes and gestation in snakes (Gregory et al., 1999). Air temperatures did not differ greatly from the previous summer however with rain comes clouds and because of this we believe that the tortoises did not have enough opportunities to properly thermoregulate and therefore they could not allocate enough energy for vitellogenesis. In addition, the Ft. Stewart populations are near the northern edge of the species range where temperatures are slightly cooler than the more southern parts of the gopher tortoise range.

**Vegetation**

The seasonal pattern that was found for ground cover characteristics in all sectors of the study is important to understanding the ecology of the gopher tortoise at Ft. Stewart. In the summer when tortoises were most active and needed readily available food to eat the forb cover and grass cover was at its greatest. In the fall and spring bare
ground cover is greatest which is important at this time for the increased need of tortoises to thermoregulate since temperatures tend to be lower than they are in the summer and tortoises still need to be physiologically active.

Canopy cover remained fairly constant throughout the year which is important to the ecology of the gopher tortoise. The gopher tortoise is a herbivore and an ectotherm, as a result canopy cover and soil type become important because of their effects on the diversity of forage type. The type and amount of forage will affect the overall health of the tortoise and therefore its reproductive output (Rostal and Jones, 2002). Canopy closure in a pine plantation may reduce forage along with potential nest sites an increased canopy may force tortoises to move greater distances to find nest sites with sufficient sunlight (Aresco and Guyer, 1999). Open canopy is important especially around the burrow mouth so the tortoise can bask in a safe location and also for proper temperature incubation of nests at the burrow entrance. Rostal and Jones (2002) showed that gopher tortoises actively choose burrow locations where open canopy and good forage is available. Canopy cover also affects the temperature of the soil; therefore, the soil must be able to maintain critical incubation temperatures, while providing appropriate drainage for the nest (Roosenburg, 1996). Soil temperatures at Ft. Stewart were 5-10 degrees lower than they were in 2002 and 2003 (pers. Comm. Rostal). This decrease in soil temperature may have reduced the ability of some females to actively thermoregulate and therefore they may not reach a required body temperature needed for ovarian follicular growth.

The areas at FSAR used in this study have the characteristically low canopy cover that tortoises will select to dig their burrow. Our data also showed that canopy cover was
significantly greater in the Echo area than the Foxtrot area for both 2002 and 2003, although canopy still averaged less than forty percent cover. The increased canopy cover in the Echos can be attributed to the fact that the Echos also contain a significantly greater number of pine trees then the Foxtrots. The Foxtrots are dominated more by deciduous trees that do not contribute as much canopy cover as pine trees. There was no difference in canopy cover between burrows and random points, in fact the average canopy at burrows (22.9 ± 2.62%, n=36) and random points (21.9 ± 2.9%, n=36) were quite similar. The similarity between burrows and random points leads us to believe that the habitat at FSAR is fairly contiguous. Rostal and Jones (2002) also studied tortoises and habitat structure on Ft.Stewart and found that canopy cover at burrows (25.8 ± 2.19%, n=50) and random points (40.3 ± 2.51%, n=50) differed by about 15%. They also measured habitat structure at George L. Smith State Park which is a site that is less contiguous then FSAR with a higher canopy cover at random points (76.4 ± 1.79%, n=50) then at burrows (26.1 ± 2.06%, n=50) (Rostal and Jones, 2002; Aresco and Guyer, 1999; Hermann et al., 2002). Boglioli et al. (2000) studied tortoise habitat in Baker county, southwest Georgia and found a higher canopy cover at random points (60%), or control points as they called them, then at burrows (30%).

Canopy cover did not differ significantly between 2002 and 2003. The areas at FSAR that were sampled had very little canopy cover and the majority of the ground cover was in fact bare ground. It has been suggested that an open canopy and open, or litter free ground cover are important for the growth of grasses and forbs which are important parts of the gopher tortoise diet (Macdonald and Mushinsky, 1988; Mushinsky et al., 2003; Rostal and Jones, 2002; Aresco and Guyer, 1999; Landers and Speake, 1980; Diemer,
1986; Lohoefener, 1981). Rostal and Jones (2002), found a higher then site average mean of grasses cover and forbs cover (herbaceous ground cover) on Ft. Stewart from 1994-1996. This present study found a higher than site average mean of grass cover but not a higher than site average mean of forb cover. The difference in forb cover between the two studies could be due to the tortoises foraging mostly at burrows before we sampled, or to the increased rainfall we observed during that season. We also found no difference between canopy at burrows and random points, in fact, the percent cover at both was very similar but being slightly higher at burrows.

In 2003, forbs and grasses were significantly lower then they were in 2002 and the amount of bare ground cover, although not significant, increased in 2003. This decrease in ground cover that are a major component to the diet of the gopher tortoise (Macdonald and Mushinsky, 1988; Mushinsky et al., 2003; Aresco and Guyer, 1999; Lohoefener, 1981) could have been a factor in the decrease of clutch size and reproductive output that we saw in 2004. This reduction in food items could also be the source of the larger home range in 2003, gopher tortoise densities and movement patterns can be influenced by the abundance and quality of forage vegetation (Auffenberg and Franz, 1982; Aresco and Guyer, 1999; McRae et al., 1981). This decrease in forbes and grasses could possibly be attributed to the weather. Flooding of a relatively brief interval for any one year can affect species composition if seedlings cannot tolerate the saturation (McDermott, 1954). Growth of many plants is also adversely related to temporary or continuous flooding (Kozlowski, 1984).

The open canopy and high percent of bare ground is attributed to the fire management protocol on FSAR where all sectors are burned on a three year basis. This burning
regime is not only important for the growth of these forbs and grasses (Rostal and Jones, 2002), burning can also increase the nutrient value and palatability of grasses which are important to the gopher tortoise diet (Lohoefener, 1981).

**Weather**

The current geographic ranges of the gopher tortoise is subject to substantial variation in climactic factors such as temperature and rainfall (Mushinsky et al., 1994). This variation could have a substantial effect on a variety of attributes of the gopher tortoise, being a reptile and an ectotherm this animal depends greatly on these particular weather conditions.

As a reptile the box turtle regulates its body temperature within a relatively narrow range using physiological and behavioral means (Amaral et al., 2002). The gopher tortoise can regulate its body temperature by going into its burrow to get out of the sun or bask outside the burrow entrance to warm itself up. This is important because temperature affects all aspects of physiological performance and might influence the distribution and ecology of ectothermic species (Sartorius et al., 2002). An open canopy at the burrow site is also crucial to allow the tortoise to bask and find sunlit nesting sites (Diemer, 1986).

A study that was done on the factors affecting population estimates of desert tortoises found that in years with low rainfall they caught fewer tortoises. They believe that the year you survey a population may actually change the results that you find or misrepresent the densities that you calculate (Freilich et al., 2000). This study included a period of heavy rainfall which may have influenced the larger home range we saw in 2003. A linear regression of average monthly movements with average monthly rainfall
showed that as rainfall increased so did the number of movements of the female gopher tortoise. The increase in movements may have been influenced by burrow flooding that was observed in the Echo area.

After a period of drought from 1998 to 2002, the gopher tortoises on FSAR were reproducing at levels that they had before the drought began. Rostal and Jones (2002) reported an average clutch size for 1994, 1995 and 1996 as $6.52 \pm 0.33$ with a range of 2-12 eggs for tortoises at FSAR. Our three year average clutch size was $6.28 \pm 0.17$ with a range of 2 to 11 eggs. For the last year of the drought, the first season of our study, the clutch size was $6.21 \pm 0.51$ with a range of 2-11 eggs. In 2003 clutch size increased to $6.84 \pm 0.64$ with a range of 3-11 eggs but in 2004 clutch size greatly decreased to $5.54 \pm 0.65$ with a range of 1-10 eggs. The drought did not seem to affect the reproduction of the gopher tortoise however the heavy rainfall may have caused a reduction in reproduction. This is the first observation of a possible effect of heavy rainfall directly on the reproduction of the female gopher tortoises. The heavy rainfall also affected the eggs laid in May 2003. When nests were checked for hatching many eggs were found not to have hatched. A type of fungus or mold was observed on the outside of the shell which could indicate that the nest environment was too wet and the eggs essentially drowned before development could occur (Pers. Obs.).

Burrow flooding was observed in the Echo sectors during the Summer and Fall of 2003 due to increased rainfall after a five-year drought. Tortoise activity such as foraging can cause soil compaction (Boglioli et al., 2000), which may have hindered drainage of the soil in and around the burrows and therefore causing some of the nest to hold water.
Management implications

The gopher tortoise appears to be a species of special concern that falls into a category of animals that benefit from management focusing on ecosystem processes and habitat structure (Hermann et al., 2002). There has been increased interest in preserving habitat in southern Georgia because of its ecological importance to the gopher tortoise and endangered species like the Indigo snake (*Drymarchon corais couperi*) that are associated with this habitat (Landers and Speake, 1980). Habitat quality has an effect on population structure of tortoises (Hermann et al., 2002; Diemer, 1992a; Guyer and Herman, 1997; Cox et al., 1987). Tortoise respond more to a suite of physical features than to specific plant associations, the habitat as a whole must contain the presence of well drained sandy soils, and abundance of herbaceous ground cover and a generally open canopy and sparse shrub cover. It is important that these conditions persist in the long-term, gopher tortoise conservation requires active habitat management, and any recommendations need to include a description of management activities to be conducted on the preserves (Cox et al., 1987). Our study was conducted on lands that are actively managed and through our seasonal vegetation data we can see that the habitat conditions for healthy tortoise populations remain constant over many seasons and years. Management resulting in semi-natural vegetation structure and function should be able to support a self-sustaining population of gopher tortoises. Long-term studies of the species are needed to validate these statements (Hermann et al., 2002).

Approximately 90% of upland pine lands are private and data is lacking on the land use practices on these sites where populations of tortoises could be sustained (Hermann et al., 2002). Studies have found that management for bobwhites and white
tailed deer can favor burrow dwelling animals like the gopher tortoise. Slash pine plantations can also support gopher tortoises and other sandhill reptiles if they are properly managed (Landers and Speake, 1980).

With the increase in the need for relocation sites for tortoises there needs to be research into areas that can be used to support populations of these animals. Current literature indicates that the use of a blanket home range size as a basis for reserve area size are questionable because of the variation in home ranges found between different sites (Eubanks et al., 2002). When studying the home range of the gopher tortoise other factors such as sample sizes and environmental factors (habitat characteristics and weather) must be taken into account. This study concentrates on the female gopher tortoise but it is important to consider both males and females equally. We concentrated on females because we wanted a large sample size so that we could better understand the ecology of the female gopher tortoise. We were able to track 43 females for two consecutive years and collect 3 consecutive seasons of reproductive data on 35 females.

The home range data we collected is important for tortoise management and estimating reserve area because we were able to see that home range increased in the second year of tracking, and the multi-year home range was larger than both years. Not only does home range need to be looked at on a yearly basis but it is important to look at it as a multi-year range to include any areas used in one year but not in another year which may expand the home range estimate of an individual animal or the population as a whole. Home range data collected in previous studies has greatly underestimated the possible home range of the female gopher tortoise because of limited study duration.
It is important to study an area for many years to be able to take into account any environmental factors that may occur years apart from each other that could have a great affect on tortoise survival. As we saw in our study, changes in year to year environmental conditions will typically create considerable variation in survival parameters (Cox et al., 1987). The heavy rainfall we saw in 2003 may have caused adult female deaths from a fungal pneumonia in four of our tortoises since it created very moist environment that gopher tortoise are not used to. The rainfall also may have caused the decrease in clutch size and reproductive output and it very likely affected the survival of eggs in certain years.

LITERATURE CITED


MEANS, B. D. 1982. Responses to winter burrow flooding to the gopher tortoise (Gopherus polyphemus Daudin). Herpetologica. 38:521-525.


OTT, J. A. 1999. Patterns of movement, burrow use and reproduction in a population of gopher tortoises (Gopherus polyphemus): applications to the conservation and
management of a declining species., p. 28. In: Department of Zoology. Auburn University, Auburn, Auburn.


Appendix A

Monthly rainfall and temperature data from Ft. Stewart Army Reserve from 2002-2004. Rain is in centimeters and temperature is in degrees Celsius.

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Figure B1. Ground cover and canopy cover for the summer of 2002 sorted by sector. Values are mean ± SE.
Figure B2. Ground cover and canopy cover, burrows versus random points by sector for the summer of 2003. Values are mean ± SE.
Figure B3. Average percent of canopy cover and ground cover of random points for the summer of 2003 at Ft. Stewart Army Reserve. Values are mean ± SE.
Figure B4. Burrows versus random points for the summer of 2003 at Ft. Stewart Army Reserve. Shrubs in F12 were the only significant differences found between burrows and random points in all sectors. Values are mean ± SE.
Appendix B

Figure B5. The number of deciduous, pine, and snag trees in 2002 sorted by sector on Ft. Stewart Army Reserve for the sectors used in this study. Values are mean ± SE.
Appendix B

Figure B6. The number of deciduous, pine, and snag trees in 2002, sorted by sector. Values are mean ± SE.
Figure B7. Average tree size for deciduous, pine, and snag trees in 2002, sorted by sector. No difference was found in average tree size for all types among sectors. Values are mean ± SE.
Figure B8. The number of deciduous, pine, and snag trees in 2002 sorted by sector on Ft. Stewart Army Reserve for the sectors used in this study. Values are mean ± SE.
Appendix B

Figure B9. Average tree size for deciduous, pine, and snag trees sorted by sector for the summer of 2003. Values are mean ± SE.
Figure B10. The number of deciduous, pine, and snag trees around burrows and the number of those trees in each size class for 2003. Values are mean ± SE.
Figure B11. Average tree size for deciduous, pine, and snag trees in the Echos versus the Foxtrots for 2002 and 2003. Values are mean ± SE.
Figure B12. Average number of trees around burrows for each size class for deciduous, pine, and snag trees in the Echos and the Foxtrots for the summer of 2002. Values are mean ± SE.
Figure B13. Average number of trees around burrows for each size class for deciduous, pine, and snag trees in the Echos and the Foxtrots for the summer of 2003. Values are mean ± SE.
Figure B14. Burrows versus random points for average deciduous, pine, and snag tree size in 2003. No difference was found between burrows and random points for average tree size. Values are mean ± SE.
Figure B15. The number of deciduous, pine, and snag trees for burrows versus random points in 2003. No difference was found between burrows and random points for all categories. Values are mean ± SE.