THE EFFECTS OF BURROW COLLAPSE ON THE GOPHER TORTOISE

(Gopherus polyphemus)

Except where reference is made to work of others, the work described in this thesis
is my own or was done in collaboration with my advisory committee.
This thesis does not include proprietary or classified information.

Richard. L. Beauman

Certificate of Approval:

Craig Guyer
Professor
Biological Sciences

Mary T. Mendonça, Chair
Associate Professor
Biological Sciences

Sharon M. Hermann
Visiting Assistant Professor
Biological Sciences

George T. Flowers
Interim Dean
Graduate School

THE EFFECTS OF BURROW COLLAPSE ON THE GOPHER TORTOISE

(*Gopherus polyphemus*)

Richard L. Beauman

A Thesis

Submitted to

the Graduate Faculty of

Auburn University

in Partial Fulfillment of the

Requirements for the

Degree of

Master of Science

Auburn, Alabama
May 10, 2008

THE EFFECTS OF BURROW COLLAPSE ON THE GOPHER TORTOISE

(Gopherus polyphemus)

Richard L. Beauman

Signature of Author

Date of Graduation

THESIS ABSTRACT

THE EFFECTS OF BURROW COLLAPSE ON THE GOPHER TORTOISE

(Gopherus polyphemus)

Richard L. Beauman

Master of Science, May 10, 2008
(B.A. St. Joseph's College, 2002)

59 Typed Pages

Directed by Mary T. Mendonça

The gopher tortoise (*Gopherus polyphemus*) is a species in decline due, in part, to loss of habitat and altered land use. One particular area of concern is the use of vehicles during urbanization and agriculture practices that may collapse their burrows, entombing the tortoise and potentially causing it harm. Few studies have examined the consequences of burrow collapse and entombment on gopher tortoises. We collapsed 42 burrows using logging and military vehicles in 2003 and 2004 at several sites on Fort Benning in southwest Georgia. We measured the extent of collapse, documented the amount of time it took each tortoise to self-excavate, and determined the distance from the original burrow opening to the excavation exit hole. After the tortoises self-excavated, we tracked their movements to determine burrow usage patterns and compared this to what was observed pre-collapse. We returned in 2005 to again track movements of the experimental tortoises as well as a group of control tortoises that were captured. In our study, 41 of 42 tortoises self-excavated, although there was considerable variation in the time to self-excavation (several hours to 85 days). Physical factors that appeared to adversely affect the time until self-excavation were soil type and precipitation prior to the collapse. We also observed a far higher rate of burrow abandonment by tortoises that self excavated than has previously been documented for un-manipulated tortoises. Although none of the entombed tortoises were harmed during our study (including the one that did not self-excavate) and there was no changes in movement behavior, some of them were entombed during a time of year when mating occurs. This lost mating opportunity, the negative impact of soil type and precipitation on excavation times, in addition to the high rate of burrow abandonment, suggests that the process of burrow collapse and entombment may negatively impact this declining species.

ACKNOWLEDGEMENTS

I thank my committee members, Dr. Craig Guyer and Dr. Sharon M. Hermann, for their help with ideas and revisions. They helped me to think about things in ways that were novel to me. I especially thank my major professor Dr. Mary T. Mendonça for sticking with me when things got difficult and continuing to support me even though I moved away from Auburn. She gave me a chance to start the pursuit of my dreams by allowing me into her lab and I will be forever indebted to her.

I thank my family for believing in me and for their encouragement. It is truly humbling when you are told that you “were always the smart one”. It helped give me the determination I needed to find a way to get it done.

Most of all, I thank my wife, Jennifer Beauman, for all her love, help and support during this entire process. Her help was instrumental from the beginning to the end. She was my friend, editor, field tech (both paid and unpaid) and motivator. She made a very difficult ordeal much less difficult.

Journal format used: Copeia

Software used: Microsoft Word 2003; Statview

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

LIST OF FIGURES:

LIST OF TABLES:

FACTORS AFFECTING BURROW COLLAPSE AND TIME TO SELF-EXCAVATION IN GOPHER TORTOISES *(Gopherus polyphemus)*

The gopher tortoise (*Gopherus polyphemus)* is a fossorial turtle that is found only in the Coastal Plains of the southeastern United States. The species has a geographic range from South Carolina to Florida along the Atlantic coast and from Florida west to Louisiana along the Gulf Coast (Ernst et al, 1994). The species is listed as a federally threatened in the western part of its range (i.e. west of the Mobile and Tombigbee rivers), and a species of concern in the remainder of its range (Diemer, 1986; U.S. Fish and Wildlife Service, 1987).

The gopher tortoise is considered a keystone species and a specialist in its environment largely because of their burrows (Guyer and Bailey, 1993). Tortoise burrows can extend as much as five meters in depth and 15 meters in length (Diemer, 1986; Hansen, 1963) and provide shelter and refuge to over 360 animal species (Jackson and Milstrey, 1989). In addition to this, while digging these burrows; tortoises change the composition of the forest by bringing large amounts of soil to the surface. This excess soil is then distributed in front of the opening of the burrow allowing for higher plant species richness (Kaczor and Hartnett, 1990).

Gopher tortoise populations are shrinking and have declined by over 80% in the last century (Auffenberg and Franz, 1982; Hermann et al., 2002). Two of the most cited reasons for this decline are the loss of gopher tortoise habitat (longleaf pine ecosystem) and altered land use (Noss, 1988). Roughly 80% of habitat in the gopher tortoise's listed range has been lost due to urbanization and agriculture (U.S. Fish and Wildlife, 1990) caused by increased activity in home construction, forestry practices, and some military use. Because of the importance of gopher tortoises and their burrows, any increase in land use may be problematic if it increases gopher tortoise mortality or negatively impacts their habitat. The vehicles used in these activities (construction, logging and military) can accidentally collapse burrows, potentially causing physical harm as they entomb resident tortoises. Even if burrow collapse fails to cause direct injury, it may still disrupt normal activity of the occupants. It is because of this increase in risk to tortoises that studies are needed to document the effect that these practices have on resident tortoise populations.

Few studies have examined the consequences of burrow collapse on resident gopher tortoises. Some speculated that tortoises would die as a result of the burrow collapse (Auffenberg and Franz, 1975). However, Landers and Buckner (1981) observed 18 active burrows that were collapsed after roller chopping and found that 11 tortoises self-excavated within three weeks. The remaining seven burrows were manually excavated and were found to be uninhabited. Diemer and Moler (1982) monitored three tortoises after their burrows were collapsed and found that all self-excavated within eight weeks. In the most extensive study to date, Wester (2004) monitored 33 burrows collapsed by small tractors. All but one adult and subadult tortoises managed to self-excavate within a range of two to 107 days. However, one tortoise failed to excavate and, after manual excavation, was discovered dead in its burrow.

Our study further investigates the reaction of gopher tortoises to burrow collapse in two different seasons and examines factors that potentially contribute to the variation in self-excavation times. Specifically, we documented the physical factors affecting extent of burrow collapse itself (i.e., vehicle type, angle of approach) as well as those affecting the tortoises' self-excavation times (i.e. soil type, ambient temperature and rainfall amounts). We also documented whether or not the collapsing of burrows has an effect on the rate of burrow abandonment.

Materials and Methods

Study Site.— The study site was on Fort Benning, which is located in southwest Georgia. The habitat consists of a mixed loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) community with some hardwoods. It is being managed to encourage restoration of a longleaf pine ecosystem through application of prescribed fire at a return interval of three years (Dilustro et al., 2002). There were a total of three locations for the study. In 2003, two sites were used where the community is mixed pine and upland hardwoods with soils consisting of Troup sandy loam (1-10% clay). The habitat is fairly xeric with an extremely sparse canopy. In 2004, one site was used where the habitat is mostly loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) with some hardwoods. Soils at this site consist of Esto (35-60 % clay), Troup (1-10 % clay), Troup-Esto and Wagram (2-10 % clay) sandy loams. Of the three sites, the 2004 site is much less xeric than the two used in the 2003 study. In addition to the streams that run within the area, the site also has a greater percentage of hardwoods and canopy cover.

In 2003, the two sites, training compartment D12 (14 burrows) and compartment K20 (6 burrows), were approximately 8.2km apart. Located in the central portion of Ft. Benning, D12 is approximately 31ha, while K20 is approximately 2ha and is located in the north-east section of the base. In 2004, the one study site in the Oscar training area is located in the north-west portion of the base and it is approximately 138 ha in size.

The study took place from September to October of 2003 and June to September of 2004. In 2003, surveys were conducted in May to identify and map (using GPS) active burrows in locations feasible for performing burrow collapses (i.e. those that could be easily accessed by heavy equipment). A total of 20 burrows were collapsed, 10 on September 3 with an armored personnel carrier (APC) and the remaining 10 on September 6 with a logging skidder. In 2004, surveys were conducted in April and May to identify active burrows, which were also mapped. Again, the burrows (n = 22) were collapsed on two separate dates: 11 burrows on June 12 and 11 burrows on June 19. On this occasion, all burrows were collapsed with the logging skidder.

Handling.— Active burrows were located and after being marked and mapped, had a wire live trap (Tomahawk Live Trap) placed at the mouth to trap the tortoises. The traps were then covered with burlap to make them appear to be an extension of the burrow. The burlap also prevented captured tortoises from overexposure to the sun. Traps were checked twice daily (0900 and 1600) until the tortoise was captured.

Since these tortoises were part of a larger study exploring the effects of burrow collapse on several physiological factors, a blood sample was taken immediately after each captured tortoise was removed from a trap, both upon initial capture and after they had self excavated. A total of 1ml of blood was sampled from a tortoise's femoral vein using a 1ml heparinized syringe with a 25 gauge needle. Blood obtained at capture (before and after burrow collapse) was placed in a microcapillary tube, centrifuged, and hematocrit determined by the scale on an Adams Readacrit microcapillary centrifuge. After initial capture, tortoises were weighed using a 10 kg spring scale (accurate to 0.1 kg) and straight-line plastron, and carapace lengths (in mm) were taken using tree calipers. A condition index (CI) was obtained by calculating the residuals of a regression of tortoise mass on carapace length (Schultze-Hostedde et al., 2005). Tortoises were not weighed again except for the last two animals to self-excavate in 2004. After initial capture, tortoises were painted with an identifying number on their carapace, permanently marked with a file, and fitted with a radio transmitter (American Wildlife Enterprises, Monticello, Florida). Animals were returned to the burrow of capture the following day.

Collapse Study.—Immediately prior to collapsing the burrows, tortoises were located using telemetry equipment to confirm they were within a particular burrow. These occupied burrows were then collapsed with either a M113 armored personnel carrier (APC), a John Deere Skidder (in 2003) or a Timberjack 460D logging skidder (in 2004). The APC weighs approximately 10,900 kg and distributes its weight evenly on tracks exerting a ground pressure of 8.6 psi. The skidders weigh approximately 15,180 kg and exert a tire pressure of 6.8 psi. The direction and angle of the approach of the machine was dependent on the layout of the burrow and the surrounding vegetation. The approach of the machine was from the front or back in respect to the mouth and the path of the burrow (the direction of the tunnel from the mouth to the burrow chamber). In addition, burrows were run over at a perpendicular (across the path), parallel (directly over or above the path) or 45 degree angle in regards to the path of the burrow tunnel.

In 2003, five burrows were collapsed (four with the skidder and one with the APC) by passing the vehicle perpendicular to the path of the burrows, taking one to three passes at each burrow. The remaining 15 burrows were collapsed (six with the skidder and nine with the APC) parallel to (i.e. directly over or above) the path of the burrows, again taking one to three passes at each of the burrows. We did not measure the actual amount of the collapse. However, visual examination was used to determine that the burrows were indeed collapse sufficiently.

In 2004, eight burrows were collapsed parallel to and directly over the path of the burrow. Of these eight, five were collapsed from the back and three were collapsed from the front in respect to the burrow opening. Six burrows were collapsed perpendicular to the path of the burrow either from the right or left. Eight burrows were collapsed at approximately a 45 degree angle to the mouth and path of the burrow. Of these eight, six were from the back and two were from the front. Extent of burrow collapse was measured this time. Prior to collapsing a burrow, a long wood rod was used to place a string with a 7.6 cm steel washer attached to the end into the burrow. The string had markings at one meter intervals. The stick was removed, leaving the graduated string and washer in place. The burrows were then collapsed. After the collapse, the string was gently pulled from the burrow mouth until resistance was met, enabling us to calculate the length of the burrow that had collapsed.

After collapse, each burrow was monitored twice a day (0900 and 1600 hrs) for signs that the entombed tortoise had self-excavated. Upon self-excavation, tortoises were tracked to establish if they stayed at the collapsed burrow or moved to a previously used burrow, a previously unused existing burrow, or a freshly dug one. Burrows were categorized as “abandoned” if they were no longer revisited by the tortoise and showed no signs of tortoise activity. In 2003, collapsed burrows were monitored every three days for 3-4 weeks after self-excavation and then re-monitored weekly throughout the 2004 active season. In 2004, all collapsed burrows were monitored daily after self-excavation for the remainder of the study. Abandonment status was confirmed in a 2005 study (Beauman, unpublished data).

Soil Analysis.—Soil data were obtained for the study sites from Fort Benning’s data repository in the form of Soil Survey Geographic (SSURGO) GIS maps. Additionally, soil samples were collected from each burrow to determine a fine-to-coarse particle ratio to confirm the data in the SSURGO soil maps. To obtain these samples, small bore holes were hand augured 10cm to the left of the burrow apron to a depth of 1m and a total of five samples were collected at 20cm intervals. These five samples were collected to attempt to establish a soil profile through the collapse zone of each burrow. Individual samples were air dried, strained through a 2mm sieve to remove large debris, and 10g collected. These sub-samples were mixed with a dispersing agent (sodium metaphosphate) to prevent clumping, placed on a shaker for 4h and washed through a 53 micron sieve to separate fine from coarse materials. The remaining material was re-dried and weighed again to obtain a fine-to-coarse ratio used as a crude measure of clay content.

Weather Data.—Temperature and precipitation data for both 2003 and 2004 were obtained from the Columbus, GA weather station, which is ~10 km from Ft. Benning.

Data Analysis

Amount of collapse caused by direction and angle of the machine during collapse was compared using a one-way analysis of variance (ANOVA). One way ANOVAs were also used to compare self-excavation times by collapse dates, sex, and exit distances between abandoned and active burrows. We could only examine the effect of soil type on days until self-excavation for burrows from 2004 because this was the only site that, according to the SSURGO soil map, had more than one soil type. Soil samples from all burrows assayed during 2004 were collected and processed as described above, and the values for the 5 sub-samples were averaged for a mean fine-to-coarse soil percentage. These soil values were placed into a priori assigned (based on SSURGO maps) high (35-60%) vs. low (1-10%) clay categories and compared using an ANOVA. Self excavation time from these different categories was also compared by ANOVA. Additionally, we conducted a regression analysis of the relationship between the number of days to self-excavation and physical factors (e.g. extent of the collapse) and physiological (i.e. pre and post collapse hematocrit, pre-collapse CI) factors as well as the relationship between extent of collapse on excavation exit point and burrow abandonment.

Results

Amount of Collapse.—In 2003, by visual examination, the logging skidder appeared to effectively collapse all the burrows by running over either the track or the mouth of the burrow. The burrow's path caved in and the mouth became closed off. In comparison, the

APC did not seem to effectively collapse the burrows. This was the case whether it passed over the track or the mouth of the burrow. Although the mouth was still closed off, only minimal, if any, damage was done to the burrow tunnel itself of all the burrows.

In 2004, the extent of collapse ranged from 0.5 to 2.25m ($n = 22$). There was no difference in the amount of collapse based on the direction or angle of collapse (front vs. back, $df = 1$, $F = 1.7$, $p = 0.2$; perpendicular vs. parallel vs. angle, $df = 2$, $F = 0.07$, $p = 0.9$).

Extent of collapse was not significantly correlated with time to self-excavation ($Y = 4.598 + 10.956 * X$, $r^2 = 0.05$, $p = 0.34$). However, there was a significant, positive correlation between amount of collapse and emergence point from the original burrow mouth ($Y = -0.6 + 0.714 * X$, $r^2 = 0.30$, $p = 0.01$).

Days to Self-Excavation.—In 2003 (September 3-29), all 10 of the tortoises in the burrows collapsed by the APC excavated themselves within three to 13 days, with seven of the 10 taking only five to six days (Fig. 1A). The average time to self-excavation of this group was 5.70 ± 0.88 days. It appeared that none of the 10 tortoises were physically harmed in the APC burrow collapse.

Nine of the 10 tortoises in burrows collapsed by the skidder excavated themselves. They did so within two to 13 days, with approximately half of them (four of nine) taking 13 or more days to do so, compared to five to six days for APC tortoises ($\bar{x} = 9.00 \pm 1.96$ days, Fig. 1A). One tortoise was manually excavated on the 23rd day due to the lateness in the season. Upon excavation, the tortoise appeared healthy. There was no significant difference in days to self-excavation between the sexes (females vs. males, respectively: $\bar{x} = 9.00 \pm 2.07$ days; $\bar{x} = 6.25 \pm 1.31$ days, $p = 0.3$).

In 2004 (June 12 – September 12), times to self-excavation in the first collapse group (12 June 2004) ranged from under two hours after collapse to 41 days (Fig. 1B); however, the majority of animals (six of eleven) had emerged within seven days of burrow collapse ($\bar{x} = 10.91 \pm 3.78$ days).

The second collapse group (19 June 2004) exhibited a different profile. The first tortoise emerged three days after collapse. The majority of animals (six of eleven) emerged within 16 days after collapse. The penultimate tortoise to emerge did so on day 51. Finally, the last tortoise of this group emerged 85 days after collapse (Fig. 1B). Average time ($\bar{x} = 26.55 \pm 7.46$ days) to self-excavation in this group differed significantly ($p = 0.018$) from those found the previous fall (September 3 and September 6, 2003) as well as the group collapsed a week earlier the same spring (June 12, 2004, Fig. 2). As in 2003, there was no significant difference between sexes, males vs. females, ($\bar{x} = 14.33 \pm 3.59$ vs4.00 ± 8.71 days; $p = 0.29$) in the time until self-excavation in 2004.

Condition Index and Hematocrit.—There was no significant relationship between pre- or post-collapse hematocrit or pre-collapse CI and the number of days until self-excavation in 2003 ($r^2 = 0.04$, $p = 0.47$; $r^2 = 0.01$, $p = 0.70$; $r^2 = 0.0002$, $p = 0.98$, respectively) or 2004 ($r^2 = 0.006$, $p = 0.75$; $r^2 = 0.006$, $p = 0.75$; $r^2 = 0.008$, $p = 0.68$, respectively).

Burrow Usage.—In 2003, upon self-excavation, two tortoises continued using their burrows after the collapse, while 14 moved to a neighboring, previously used burrows, and three dug new burrows within the immediate area. Of the 20 collapsed burrows, nine (46%) were no longer observed to be used in 2003, 2004 or during a 2005 study (Beauman, unpublished data).

In 2004, 11 tortoises stayed at the collapsed burrow, 10 moved to an existing burrow, not previously used in the 30 days prior to burrow collapse and one moved to a previously used burrow. Of the 22 burrows, nine (41%) were no longer used in 2004. Additionally, burrows that were classified as abandoned were those which had significantly higher self-excavation distances from the original burrow mouth than those that had remained active (Fig. 3).

Weather.—In 2003, weather profiles were similar for the two collapse dates. In 2004, temperature during the seven-day period prior to the two collapse dates did not differ. However, precipitation the week before the first collapse date (June 6 -12, 2004), was 0.9cm, which was roughly 6.4% of the total rainfall for the month of June. In the week before the second collapse date (June 13-19, 2004), 9.9cm of precipitation fell on the site, more than ten times as much as that of the preceding week and 69.7% of the total rainfall for the month.

Soil.—In the 2003 study, according to the GIS SSURGO maps, all of the collapsed burrows in D12 and K20 were in Troup sandy loam (1-10% clay).

In 2004, based on the same GIS SSURGO soil maps, the collapsed burrows in the Oscars were in Troup loamy sand (1-10% clay), Wagram loamy sand (1-10% clay), Troup and Esto loamy sand (35-60% clay), or Esto sandy loam (35-60% clay). Of the five burrows in which tortoises took longer than 30 days to self-excavate, four were in high clay content soils (Esto 35-60%), while the remaining one was in low clay (1-10%). When we compared the amount of fine material at the high and low clay content burrows using a coarse to fine ratio, the burrows that were categorized as high clay had a significantly higher amount of fine material ($\bar{x}$ = 15.43 ± 0.46% vs. $\bar{x}$ = 12.66 ± 0.17%; p = 0.0004 respectively) than those categorized as low clay, which helped to give some credence to the soil maps. When all 2004 burrows were divided into two categories based on soil type (high and low clay content) indicated by the SSURGO soil map, clay content had a significant effect (p = 0.03) on how long it took tortoises to self-excavate (Fig. 4). When we compared soil type's effect on self-excavation time, we found that the tortoises from burrows categorized as high clay content soils (which were really only present in the June 19 collapse) exhibited a significantly longer time until self-excavation (p = 0.03) than those from burrows categorized as low clay content (Fig.5).

Discussion

Auffenberg and Franz (1975) speculated that if gopher tortoise burrows were collapsed, entombed tortoises would die. However, in three previously conducted burrow collapse studies (Landers and Buckner, 1981; Diemer and Moler, 1982; Wester, 2004), there has only been one documented fatality (Wester, 2004). In our study, 41 out of 42 tortoises self-excavated. The one tortoise that did not self-excavate was entombed 23 days, from September 7 to September 30, 2003. This tortoise was manually excavated on that date to prevent it from entering the colder portion of the year while entombed. At the time that this decision was made, the 19 other tortoises in 2003 had self-excavated and it appeared that the remaining tortoise may have been in difficulty. However, given the results of the 2004 study, in which six of 22 animals were entombed for longer than 23 days (up to 85 days) and all survived, it seems unlikely that this tortoise was in distress.

Since time to self-excavation varied from several hours to 85 days, we examined physical factors that might account for the variation in time to self-excavation among the tortoises. The extent of the collapse (determined by actual measurement) did not differ based on the angle or approach of the skidder. However, some of the variation observed in the extent of collapse (i.e. 0.5 – 2.25m) may have been caused by overlooked factors such as the angle of the burrow itself and/or the amount of vegetation in the top layers of soil. Despite the variation in the collapse extent, this factor did not exhibit a significant relationship with the time to self-excavation. There was a significant relationship on the site of self-excavation ($r^2 = 0.30$, $p = 0.01$); the greater the length of the burrow collapse, the further from the burrow mouth the tortoise exited. Importantly, there was also a significant ancillary effect of exit point on the subsequent abandonment status of the collapsed burrow; burrows that were abandoned had a significantly greater average distance from self-excavation exit point to the original burrow mouth. Additionally, 46% and 41% (2003 and 2004, respectively) of the collapsed burrows were abandoned, frequencies that were approximately twice of that documented by Aresco and Guyer (1999), who observed a natural burrow abandonment rate of 21% in poor quality habitat.

Physical factors that did appear to affect the time until self-excavation were soil type and, possibly, precipitation, through its effects on soil characteristics. Thirty of 31 burrows in the first three groups (the two 2003 collapse dates and the first 2004 collapse date) were found in soil that was categorized as low in clay content (i.e., 1-10% clay). These were also the groups in which there was no significant difference in time until self-excavation. Tortoises in the second 2004 collapse group took significantly longer to self-excavate than the three previous groups (Fig 2). Interestingly, six of the 11 burrows that were in the 2004 collapse group were in soils that the SSURGO maps indicated had high clay content (Esto 35-60% clay). When we tested by soil analysis to see whether the burrows designated as "high clay content" soil actually were significantly higher in clay than those designated as "low clay content", we found that they, indeed, did have a significantly higher fine to coarse soil ratio. When we compared the times to self-excavation of tortoises whose burrows were in these "high clay" versus those whose burrows were in "low clay content", we found that the excavation times of tortoises from high clay content burrows were, again, significantly longer. The mean time to self-excavation associated with the low clay content burrows during this second collapse were slightly, but not significantly, longer than those observed for similar burrows in the 2003 study as well as the first collapse date in the 2004 study (Fig. 5).

This second collapse period in 2004 also differed from the other collapse periods in that there was a large amount of precipitation just before the second collapse date of the 2004 study. Kozlowski (1999) documented that some soils compact to a depth of more than 1m under heavy traffic loads and when clay soils are wet, they compact more readily. The rain may have contributed to the prolonged periods of entombment in burrows in the higher clay content soils.

This potential compaction of the higher clay content soils could potentially limit the percolation and porosity of the soil **(**Dickerson, 1976**)** and might result in lower O_2 and higher CO_2 levels within the burrow. If there was lower porosity, tortoises might attempt to excavate sooner from burrows collapsed in high clay content soils, but instead, they took significantly longer. This may be because heavily compacted clay is difficult to dig through. Unfortunately, we were unable to determine whether the tortoises had been actively trying to self-excavate through compacted clay for some time, or if they had remained quiescent in the burrow until some physiological or physical factor (hunger, thirst, excessive CO_2) caused them to emerge. Tortoises are known to be fairly tolerant of hypoxic and hypercarbic conditions (Ultsch and Anderson, 1988) and may use the calcium carbonate found in their shells and bones as a buffer against lactic acid build-up (Jackson et al., 2000). Additionally, Means (1982) and Diemer (1992) both regularly observed that tortoises remained below the water line in flooded burrows, again suggesting extreme tolerance to low oxygen levels. Thus, while tortoises may have been trying to emerge over some time from the collapsed burrows in high clay content soil, it is also plausible that they remained in their burrow until they were triggered to emerge, which then they rapidly proceeded to do.

The amount of time that tortoises were entombed is within the normal behavioral range for these animals to remain in their burrows and that this inactive period does not result in sufficient weight loss to cause tortoises to self-excavate. In a telemetry study, Diemer (1992) observed a tortoise that did not emerge from its burrow for five months.

Additionally, a desert tortoise (*Gopherus agassizii*) that was pinned within its burrow by a fallen rock for 11 months, without food or water, only lost 4.2% of its body weight and only exhibited minimal changes in standard blood chemistry measures (Christopher, 1999). So, even a three month entombment period (the longest we observed), may not constitute a great challenge for these animals. However, while gopher tortoises may naturally remain in burrows without eating for an extended time period, presumably tortoises in collapsed burrows are in more hypoxic and water deprived states than normally quiescent tortoises. Due to a methodological fault, we did not take a weight measurement of the tortoise just before the collapse date but, instead, took it early in the active season (just after the winter period). It could be that tortoises gained weight in the intervening time period and this is why we did not see a relationship between condition index and days to self-excavation. This idea is substantiated by the self-excavation weights of the two tortoises that were entombed the longest. The weight of the tortoise that was entombed for 85 days decreased from 5.2kg to 4.4kg, but, the tortoise entombed 51 days was surprisingly heavier post self-excavation as its weight increased from 4.2kg to 4.5kg.

We also did not see a significant relationship between hematocrit and days until self-excavation. It may be that there is sufficient water vapor in a burrow, sustained by the porosity of the soil, to prevent dehydration. Alternatively, this result, again, could be a methodological artifact. We did not capture tortoises immediately upon emergence. Although we placed a trap within a day of emergence at the mouth of the burrow to which the animal relocated, there was a short time period in which the animal could have potentially foraged or drunk. This activity may have been enough to restore normal hematocrit levels. However, the range of variability for this parameter was very small which would indicate every tortoise was able to re-hydrate in a very short time, although this occurrence seems unlikely.

In our study, we found that burrow collapse and the subsequent entombment period caused a higher than normal rate of burrow abandonment. An extended entombment period could also potentially interfere with the normal tortoise mating activity, which occurs primarily in the late summer and fall months (Boglioli, 2003). In addition to these consequences, there may be physiological ones as well. More studies need to be conducted to understand how burrow collapse and other detriments of land use affect this declining species. If tortoise populations are shrinking as a direct or indirect effect of having their burrows collapsed, current military and forestry land management policies will have to be assessed (Seigel and Dodd, 2000).

LITERATURE CITED

Alford, R. A. (1980). Population structure of *Gopherus polyphemus* in Northern Florida. *Journal of Herpetology* **14**:177-182.

Aresco, M. and C. Guyer. (1999). Burrow abandonment by Gopher Tortoises in slash pine plantations of the Conecuh Forest. *Journal of Wildlife Management* **63(1)**:26-35.

Auffenberg, W. and R. Franz. (1975). The status and distribution of *Gopherus polyphemus. United States Fish and Wildlife Service Report* **48**.

Auffenberg, W. and R. Franz. (1982). The status and distribution of the Gopher Tortoise (*Gopherus polyphemus*). In: Burry, R. B. (ed.), *North American Tortoises: Conservation and Ecology. U.S. Fish and Wildlife Service*, Wildlife Research Report **12**. United States Department of the Interior, Fish and Wildlife Service, Washington, D.C. 95-126.

Boglioli, M. D., C. Guyer, and W. K. Michner. (2003). Mating opportunities of female Gopher Tortoises, *Gopherus polyphemus,* in relation to spatial isolation of females and their burrows. *Copeia* **4**:846-850.

Christopher, M. M. (1999). Physical and biochemical abnormalities associated with prolonged entrapment in a Desert Tortoise. *Journal of Wildlife Diseases* **35**:361-366.

Dickerson, B. P. (1976). Soil compaction after tree-length skidding in northern Mississippi. *Soil Science Society American Journal* **40**:965-966.

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(2):158-165.

Diemer, J. E. and P. Moler. (1982). Gopher Tortoise response to site preparation in northern Florida. *Proceedings of the Annual Conference of Southeast Association of Fish and Wildlife Agencies* 634-637.

Dilustro, J. J., B. S. Collins, L. K. Duncan, and R. R. Sharitz. (2002). Soil texture, land-use intensity and vegetation of Fort Benning upland forest sites. *Journal of the Torrey Botanical Society* **129**(4):289-297.

Ernst, C. H., J. E. Lovich, and R. W. Barbour. (1994). Gopher Tortoise (*Gopherus polyphemus).* In: Ernst, C. H. Lovich, J. E. and Barbour R. W. (eds), *Turtles of the United States*. Smithsonian Institution Press, Washington, D. C. and London 466-478.

Guyer, C. and M. A. Bailey. (1993). Amphibians and reptiles of longleaf pine communities. In: Hermann S. M. (Ed.), *The longleaf pine ecosystem: Ecology, restoration and management.* Proceedings of the 18th Tall Timbers Fire Ecology Conference 139-158. Tall Timbers Research, Inc., Tallahassee Fl.

Hansen, K.L. (1963). The burrow of the Gopher Tortoise. *Quarterly Journal of the Florida Academy of Science* **26**:353-360.

Hermann, S.M., C. Guyer, J. H. Waddle, and M. G. Nelms. (2002). Sampling on private property to evaluate population status and effects of land use practices on the Gopher Tortoise, *Gopherus polyphemus*. *Biological Conservation* **108**:289-298.

Jackson, D.R., and E. G. Milstrey. (1989). The fauna of Gopher Tortoise burrows. Gopher Tortoise Relocation Symposium Proceedings. *Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program, Technical Report No. 5.* Tallahassee, Florida. 86-98.

Jackson, D. C., A. L. Ramsey, J. M. Paulson, C. E. Crocker and G. R. Ultsch. (2000). Lactic acid buffering by bone and shell in anoxic Softshell and Painted Turtles. *Physiological and Biochemical Zoology* **73(3)**:290-297.

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**: 100-111.

Kozlowski, T. T. 1999. Soil compaction and growth of woody plants. *Scandinavian Journal of Forest Research* **14**:596-619.

Landers, J. L., and J. L. Buckner. (1981). The Gopher Tortoise: Effects of forest management and critical aspects of its ecology. *Southlands Experimental Forest Technical Note* **56**:7.

Means, D. B. (1982). Responses to winter burrow flooding of the Gopher Tortoise (*Gopherus polyphemus* Daudin). *Herpetologica* **38(4)**:521-525.

Noss, R. F. (1988). The Longleaf Pine landscape of the southeast: Almost gone and almost forgotten. *Endangered species update* **5(5)**:1-8.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G .J. Hickling. (2005). Restitution of mass/size residuals: Validating body condition indices. *Ecology* **86**:155-163.

Seigel, R. A., and C. K. Dodd, Jr. (2000). Manipulation of turtle populations for conservation 218-238. In*:* M. Klemens (ed.) *Turtle Conservation*. Smithsonian Institute Press.

Ultsch, G. R., and J. F. Anderson. (1988). Gas exchange during hypoxia and hypercarbia of terrestrial turtles: a comparison of a fossorial species (*Gopherus ployphemus*) with a sympatric nonfossorial species (*Terrapene carolina*). *Physiological Zoology* **61**:142-152.

U.S. Fish and Wildlife Service. (1987). Endangered and threatened wildlife and plants; determination of threatened status for the gopher tortoise (*Gopherus polyphemus*): Final rule. *Federal Register* **52(129)**:25366-25380.

U.S. Fish and Wildlife Service. (1990). *Gopher Tortoise recovery plan*. Atlanta, GA.

Wester, E.E. (2004). Impact of natural gas pipeline operation and maintenance on long-term population viability of the threatened gopher tortoise (Gopherus polyphemus). Report to Florida Gas Transmission Company. Southern Ecosystems Research, Auburn, AL.

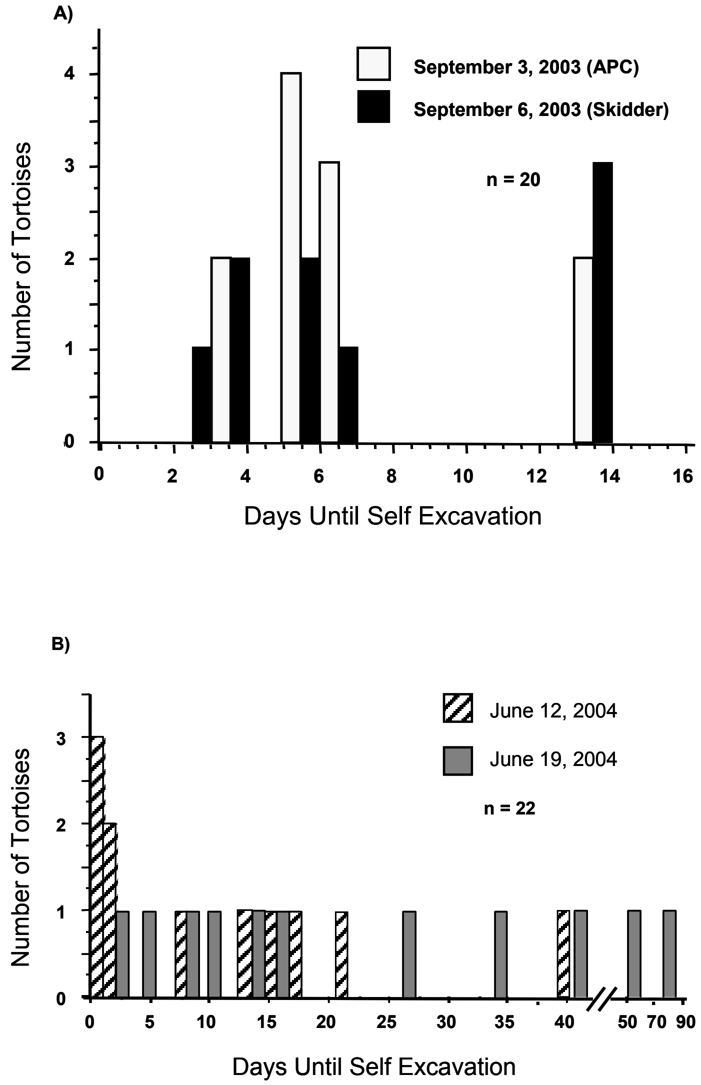

Figure 1: A) Number of tortoises that self-excavated by day after each collapse event in the Fall, 2003 study B) Number of tortoises that self-excavated by day after each collapse event in the Summer, 2004 study.

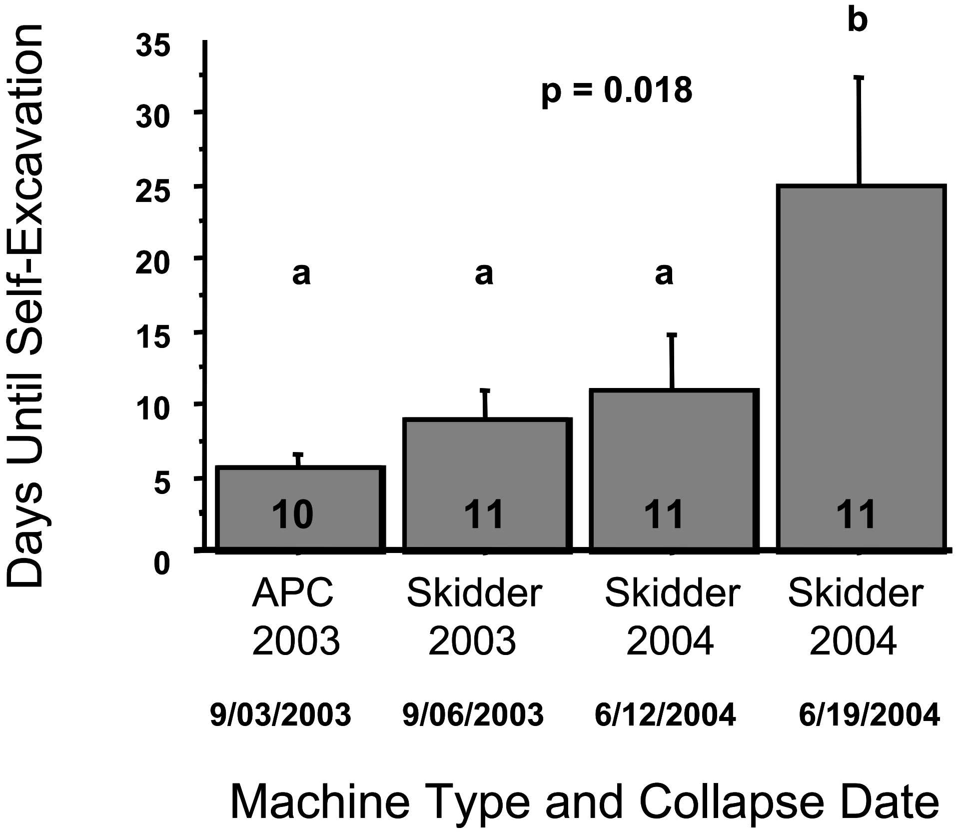

Figure 2: Mean excavation times by collapse date and machine type for the 2003 and 2004 studies. Tortoises from Group 2 in 2004 took significantly longer ($p = 0.01$) than the other three collapse dates. Error bars represent 1 SE.

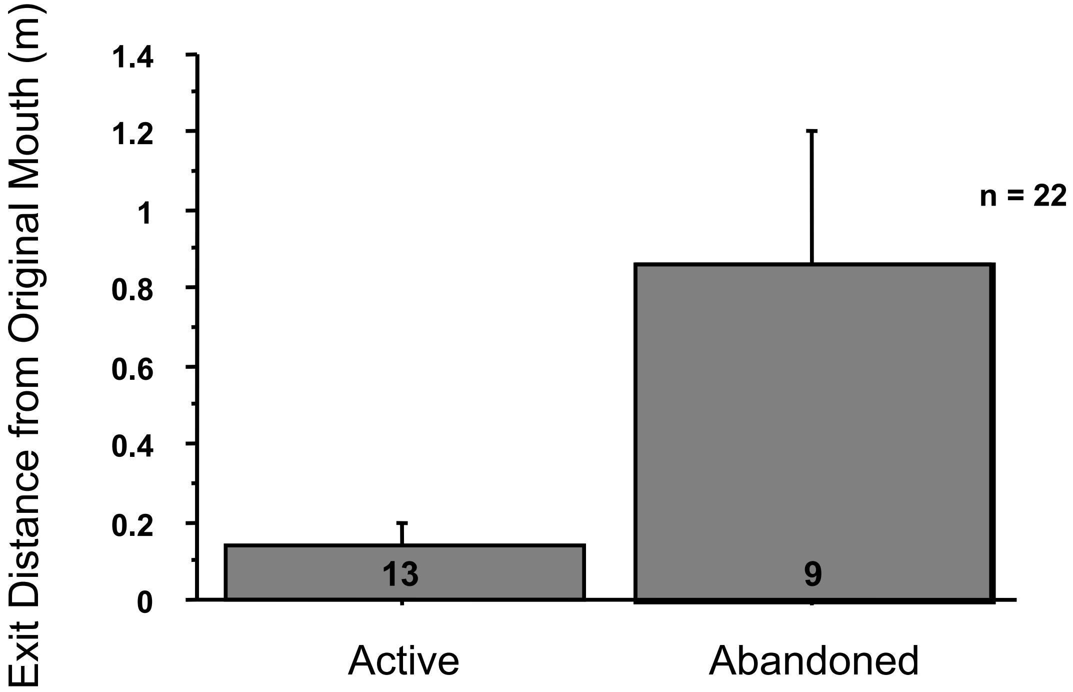

Figure 3: Mean distance between self-excavation point and original burrow mouth in burrows that remained active vs. those that were abandoned, Summer 2004. Error bars represent 1 SE.

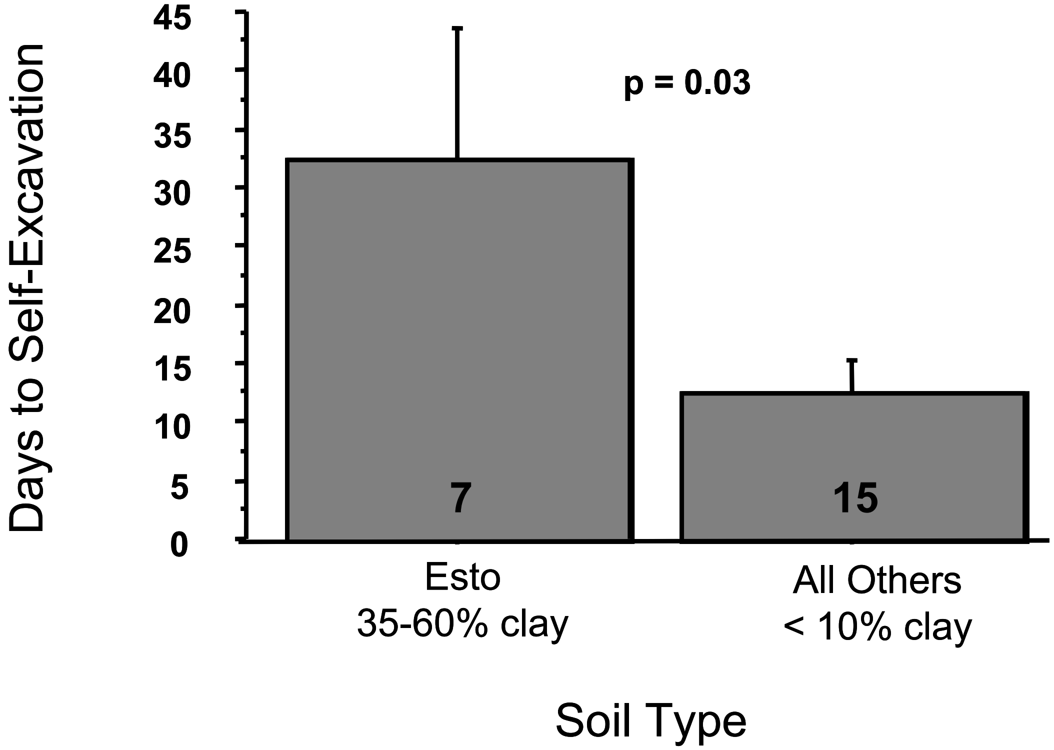

Figure 4: Mean number of days until self excavation for tortoises whose burrows were in soils determined to be high vs. low clay content, Summer, 2004. Error bars represent 1 SE.

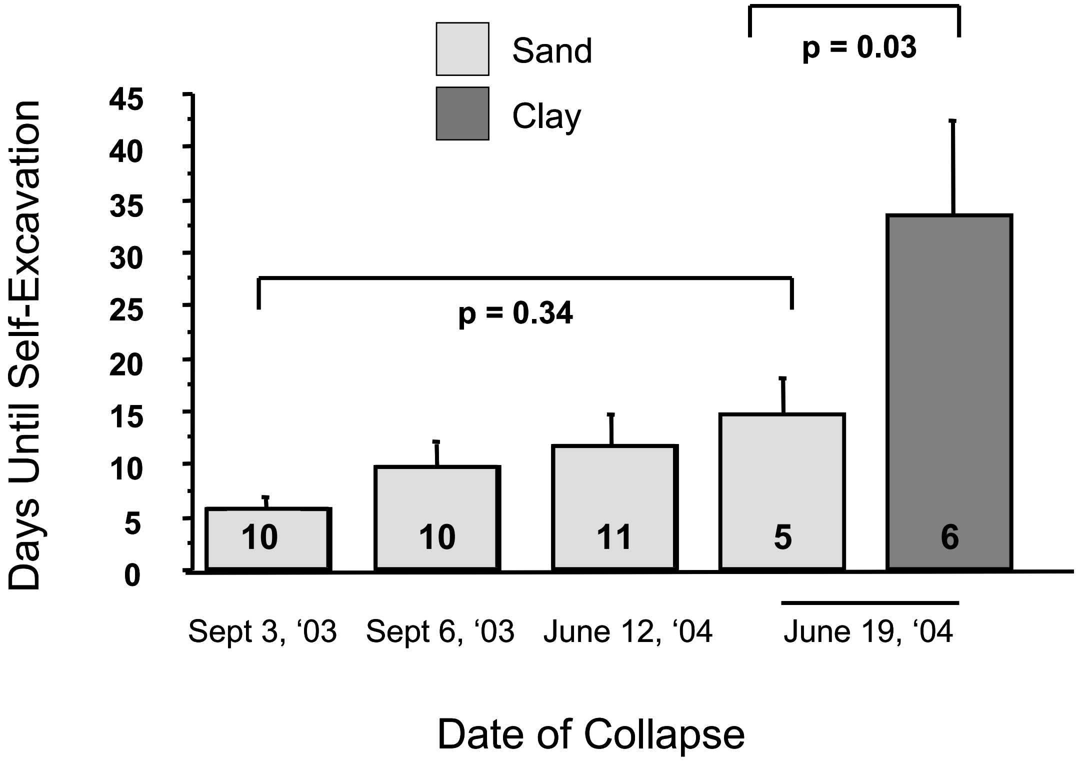

Figure 5: Mean number of days until self-excavation by collapse event for tortoises whose burrows were classified using SSURGO soil maps as "clay" (> 34% clay) and "sandy" (≤ 10% clay). There was 9.9 cm of rainfall between the two 2004 burrow collapses. Error bars represent 1 SE.

EFFECTS OF BURROW COLLAPSE ON MOVEMENT BEHAVIOR AND BURROW ABANDONMENT BY THE GOPHER TORTOISE

(Gopherus polyphemus)

The decline of the gopher tortoise (*Gopherus polyphemus)* has been well documented. Auffenberg and Franz (1982) and Hermann et al. (2002) noted that gopher tortoise populations are shrinking and have declined by over 80% over the last century. Gopher tortoises are found only in the Coastal Plains of the southeastern United States from South Carolina to Florida and from the Atlantic coast west to Louisiana (Ernst et al., 1994). They are listed as a federally threatened species in the western part of their range, along the Gulf Coast extending west of the Mobile and Tombigbee rivers to Louisiana. They are also a species of concern in the eastern part of their range, which encompasses the Coastal Plains habitat from South Carolina to Florida (Diemer, 1986; U.S. Fish and Wildlife Service, 1987).

Two of the most cited reasons for this decline are the loss of the longleaf pine ecosystem, which is the primary habitat of the gopher tortoise, and land use (Noss, 1988). Roughly 80% of habitat in the gopher tortoise's listed range has been lost due to urbanization and agriculture (U.S. Fish and Wildlife, 1990) caused by increased activity in home construction, forestry practices, and military use.

However, despite recognition of the damaging effects of current land use practices and mitigation policies on gopher tortoise populations, few studies have examined one of the most immediate consequences of heavy land use in tortoise habitat: burrow collapse.

Burrow collapse and the resulting entombment is a complex event for a gopher tortoise. Tortoise burrows can extend as much as five meters in depth and 15 meters in length (Diemer, 1986; Hansen, 1963) and provide a refuge from the weather extremes and a place to overwinter. Due to the complex relationship between gopher tortoises and their burrows, more research is necessary to understand to what extent a tortoise's movement and behavior are affected if its burrows are collapsed during heavy land use.

Although numerous studies have documented gopher tortoise home range and movement patterns in adults as well as juveniles and hatchlings (McRae et al., 1980; Diemer, 1992; Smith et al., 1997; Eubanks et al., 2003; and Pike, 2006), few studies have investigated how burrow collapse may affect subsequent tortoise movement behavior. The existing research on burrow collapse is limited to observations on tortoises to determine if they were able to self excavate after their burrows were collapsed (Landers and Buckner, 1981; Diemer and Moler, 1982; and Wester, 2004). No short-term or long-term monitoring has been done to examine physiological or behavioral consequences of a period of entombment and potential loss of a burrow. In this study, we investigated whether a burrow collapse event disrupts subsequent gopher tortoise movement behavior and home range on a short-term (within the same season) or long-term (inter-year) basis.

Materials and Methods

Study Site.— The study was conducted over three years (2003-2005) on Fort Benning, which is located in southwest Georgia. Upland habitat consists of a mixed loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) community with some hardwoods. It is managed to encourage restoration of a longleaf pine ecosystem through application of prescribed fire at a return interval of three years (Dilustro et al., 2002). Further information on location and habitat characteristics of the two study sites are detailed in Beauman et al., (submitted).

Trapping.—Active burrows (those with signs of fresh soil or tracks) at the two Fort Benning sites were initially located and mapped using GPS in May 2003 and April 2004 (n = 21 and 22, respectively). Trapping began in August of 2003 and April of 2004. A wire live trap (Tomahawk) was placed at the mouth of each burrow to trap the tortoises. The traps were then covered with burlap in order to make the trap appear to be an extension of the burrow and to prevent captured tortoises from overexposure to the sun once they were in the trap. Traps were checked twice daily (at 0900 and 1600 hrs) until the tortoise was captured. After the initial capture, tortoises were painted with an identifying number on their carapace, permanently marked with a file (Cagle, 1939) and fitted with a radio transmitter (American Wildlife Enterprises), as detailed in Eubanks et al. (2003). Animals were returned to their original burrows and monitored as detailed below for a period of time before their burrows were collapsed and after self-excavation.

For the long-term monitoring portion of this study, seven tortoises from 2003 and 17 from 2004 were re-trapped (as described above) at the start of the active season in

2005 (April) and fitted with new transmitters. In addition to these animals, 15 other tortoises (five from the 2003 site and 11 from the 2004 site) whose burrows had not been collapsed were also captured in the same manner, outfitted with American Wildlife Enterprises transmitters and had their movements monitored.

Radiotelemetry.—Tortoises were tracked daily using a receiver and a six element Yagi antenna (Wildlife Materials International, Carbondale, IL) for 30 days prior to the collapse of their burrows; this was done three times a week in 2003 and daily in 2004. During this time, number of burrows used, number of times tortoises moved from burrow to burrow, and mean distance moved were documented. Home range (HR) was calculated using the minimum convex polygon (MCP) method (Mohr, 1947).

Immediately prior to collapsing the burrows, tortoises were located using telemetry equipment to confirm they were within a particular burrow. These occupied burrows were then collapsed. In 2003, the burrows were collapsed in September with either an M113 armored personnel carrier (APC) or a logging skidder. In 2004, the burrows were collapsed in June with only a logging skidder (Beauman et al., submitted). After burrows were collapsed, they were monitored twice a day (at 0900 and 1600 hrs) until the entombed tortoise had self-excavated. Upon self-excavating, tortoises were located using telemetry equipment to establish whether they had stayed at the collapsed burrow or moved to a previously used burrow, a previously unused existing burrow, or a new, freshly dug burrow. Burrows were categorized as "abandoned" if the original tortoise stopped using them and they showed no signs of use by any tortoise. We used the classification of Aresco and Guyer (1999) in determining burrow status. A burrow was deemed “active” if the opening was shaped like a tortoise and the entrance had plastral skid marks and footprints, while “abandoned” had eroded outlines and no evidence of tortoise use.

In both collapse years, tortoises were tracked daily upon self-excavation for 14 days, at which point tortoises were re-trapped for measurements for another study examining physiological parameters in these tortoises. Again, number of burrows used, number of times moved, mean distance moved and home range were documented. We used the minimum convex polygon method to calculate post-collapse home range of each tortoise. To make this comparison, tortoises must have used a minimum of three burrows both pre- and post- burrow collapse. We were unable to calculate home range comparisons pre- and post-collapse for 2004 due to the limited number of burrows that the tortoises used post-collapse. Immediately following self-excavation collapsed burrows were monitored every three days for four weeks in 2003 and every day for 12 weeks in 2004. The 2003 collapsed burrows were re-monitored weekly throughout the 2004 and 2005 active seasons (April - October), while the 2004 burrows were re-monitored weekly in 2005.

In addition to monitoring movements immediately after self-excavation, in 2005 we tracked a subset of tortoises that had had their burrows collapsed one or two years earlier (seven from 2003; 17 from 2004) as well as 16 new tortoises not subjected to burrow collapse from the same sites (five and 11 animals respectively). We again determined the abandonment status of the collapsed burrows and the number of burrows used, number of times and the mean distances the tortoises moved, and home range.

Data Analysis

Minimum convex polygon (MCP) home range was calculated for each tortoise by using ArcView GIS 3.2 and the Animal Movement extension (Mohr, 1947; Hooge and Eichenlaub, 1997).

We used a repeated measures analysis of variance (ANOVA) to analyze differences between pre- and post-burrow collapse movement parameters (i.e. number of burrows used, number of times moved, mean distance moved and, where appropriate, home range) within the 2003 and 2004 studies. We also used a one-way ANOVA to compare the 2005 movement measures (same as described above) between recaptured 2003 and 2004 tortoises and control tortoises (those whose burrows had not been collapsed). Abandonment rate was calculated as a percentage of collapsed burrows that showed no signs of tortoise activity. A two-way repeated measures ANOVA was used to compare the difference in pre- and post-collapse movements in 2003 and 2004 of males and females. A two-way ANOVA was used to investigate the difference in movements, by sex, of the experimental and control animals in 2005. A Fisher's Exact Test was used to examine the differences in the percentage of animals that initially reused their collapsed burrows (2003 vs 2004).

Results

2003.—Immediately upon self-excavation, only two of 20 tortoises continued using their original, collapsed burrows. These reused, formerly-collapsed, burrows were modified by each tortoise and a functional burrow-mouth was re-created. Fifteen tortoises moved to a neighboring burrow, which they had been observed to have used in the month prior to burrow collapse, and three tortoises dug new burrows within their home range area. Of the 20 collapsed burrows, nine (46%) were not observed to be used by any tortoise in 2003, 2004 or 2005 and there were no signs of tortoise activity.

Table 1 indicates the means, SEs, and ranges as well as number of tortoises observed for the various movement parameters for tortoises before their burrows were collapsed and after self-excavation. When we compared the mean movement parameters before and after the burrow collapse in 2003, there was no significant difference in the number of burrows used (F = 1.52, df = 1, p = 0.23), number of times moved (F = 0.08, df = 1, p = 0.78), mean distance moved (F = 1.65, df = 1, p = 0.22) or home range area (F = 0.74, df = 1, p = 0.55). There was also no significant difference in the number of burrows used (F = 0.16, df = 1, p = 0.69), number of times moved (F = 1.10, df = 1, p = 0.30) or mean distance moved (F = 0.17, df = 1, p = 0.69) by sex.

2004.— In 2004, immediately upon self-excavation, 11 of the 22 (50 %) tortoises stayed at their collapsed burrow, compared to two of 20 (10%) that stayed at the collapsed burrow for 2003. These reused, formerly collapsed, burrows were modified by their specific tortoise and a functional burrow mouth was re-created. Unlike 2003, only one tortoise (4.5%) moved to a burrow that was observed to have been used in the 30 days prior to the collapse. Instead, 10 tortoises (45.5%) moved to an existing burrow not observed to have been used in the 30 days prior to collapse. Also unlike, the 2003 study, no tortoise dug a new burrow. However, like 2003, a similar percentage of the burrows (9 of 22, 41%) were never observed to be used by the original tortoise in 2004 or 2005 and there were signs that that they were no longer active.

Extent of collapse significantly affected the exit point of the tortoise, $r^2 = 0.30$; $p = 0.01$; $n = 22$ (Beauman et al., Submitted). The greater the burrow was collapsed the further back from the original mouth the tortoise exited upon self-excavation. The exit distance from the original mouth significantly affected whether the burrow would be abandoned, $p = 0.02$; $n = 22$ (Beauman et al., Submitted). The greater the distance the tortoise exited (self-excavated) the collapse borrow the more likely it was to be abandoned.

Table 1 also presents 2004 pre- and post- burrow collapse mean movement measures. There was no significant difference in the number of burrows used ($F = 1.00$, $df = 1$, $p = 0.33$), number of times moved ($F = 3.49$, $df = 1$, $p = 0.08$), mean distance moved ($F = 2.23$, $df = 1$, $p = 0.15$) or home range area ($F = 1.00$, $df = 1$, $p = 0.50$) for the tortoises when comparing pre- and post-collapse movements. There was also no significant difference in the number of burrows used ($F = 0.11$, $df = 1$, $p = 0.75$), number of times moved ($F = 0.61$, $df = 1$, $p = 0.44$) or mean distance moved ($F = 0.08$, $df = 1$, $p = 0.78$) by sex.

2005.—Table 2 presents means, SEs, ranges, and N for the 2005 movement measures of tortoises recaptured from the previous studies and tortoises whose burrows had not been collapsed. When movement behavior of the tortoises that were in the 2003 burrow collapse study were compared to that of the control tortoises (burrows not collapsed in 2003), there were no significant differences in the number of burrows used (F= 0.42, df = 1, p = 0.57), number of times moved (F = 2.51, df = 9, p = 0.15), mean distance moved (F = 0.31, df = 1, p = 0.63) or home range area (F = 0.06, df = 1, p = 0.81). There was also no significant difference in the number of burrows used (F = 0.37, df = 1, p = 0.56), number of times moved (F = 0.83, df = 1, p = 0.39), mean distance moved (F = 0.42, df = 1, p = 0.54) or home range area (F = 0.0002, df = 1, p = 0.99) by sex.

When the 2005 movement data of the tortoises from the 2004 burrow collapse study were compared to that of the tortoises whose burrows had not been collapsed in 2004 (controls), there was again no significant difference in the number of burrows used (F = 0.002, df = 1, p = 0.97), number of times moved (F = 0.22, df = 1, p = 0.64), mean distanced moved (F = 0.33, df = 1, p = 0.65), or home range area (F = 1.73, df = 1, p = 0.20).. There was also no significant difference in the number of burrows used (F = 0.36, df = 1, p = 0.56), number of times moved (F = 0.22, df = 1, p = 0.64), mean distance moved (F = 1.63, df = 1, p = 0.21) or home range area (F = 0.08, df = 1, p = 0.78) by sex.

Discussion

We predicted that burrow collapse and the resulting entombment would affect the movement behavior of tortoises, either in the short-term or the long-term, after they had self-excavated from their collapsed burrow. However, our study found no evidence of this. Movements (as characterized by number of burrows used, number of times moved, mean distance moved and home range area) did not differ significantly pre- and post-collapse for either 2003 or 2004. Additionally, our observed pre- and post-collapse movements were consistent with other studies, which found that there is a large natural variance among tortoises in number of movements, number of burrows used, mean distance moved, and home range (McRae et al., 1981; Diemer, 1992; Eubanks et al., 2003). The extent and pattern of movements we documented after burrow collapse and self-excavation are all well within those observed in other non-invasive studies.

For example, McRae et al. (1981) documented the mean number of burrows used for tortoises per month to be between 1.5 and 3.0 for the months of May through September. They also documented number of times moved per month and found the mean to be between 0.4 and 3.5. In both our collapse years, 2003 and 2004, our tortoises exhibited similar patterns to those observed by McRae et al. (1981) for burrow usage and number of times moved. Similarly, in 2003, the mean number of burrows used and times moved before the collapse (August) were 3.3 and 3.1, respectively, while after the collapse (September) means for each of these parameters were 2.0 and 1.2. In 2004, pre-collapse (May – June) means were 2.1 burrows used and 1.6 times moved, while post-collapse (June – September) means were 1.5 and 1.0, respectively.

Although, we did not observe short-term changes in movement patterns, we still expected that a collapsed burrow might have a long-term effect on the tortoises' behavior. However, movement data for the experimental tortoises in 2003 and 2004 were not compared to data collected in 2005 for these same individuals because it was thought that inter-year variation of environmental parameters (i.e., temperature, rainfall) might make comparison of these data problematic. For example, Mitchell (2005), found an increase in movements as rainfall increased. Since there was more rain per month in 2005 than 2003 and 2004 for all the months of the study, this difference alone could have affected inter-year comparisons in movement patterns. Instead, therefore, in 2005, we compared movement patterns of tortoises whose burrows had been previously collapsed to those who had been un-manipulated, and found no significant difference in movement patterns between the two groups.

Although we did not see a change in movements or home range area, we did find an increase in burrow abandonment, where 46% and 41% (2003 and 2004, respectively) of the collapsed burrows were abandoned, frequencies that were approximately twice those found for tortoises in habitat of relatively poor quality (i.e 22%, Aresco and Guyer,1999). This increased rate of abandonment was directly influenced by the amount of collapse caused to the burrow (at least in 2004, the only year we metrically quantified the actual extent of the collapse). It is unknown what impact this increased rate of burrow abandonment has on the tortoise. Tortoises have and can use many different burrows within their home range and little is known about the energetic cost of creating a new burrow. Although these abandoned burrows may have been in favorable locations for foraging, basking, and nest building, the detriment of moving to a neighboring burrow in their same home range area may ultimately turn out to be negligible.

Another difference observed was the movement behavior of the 2003 and the 2004 tortoises in their use of the collapsed burrows immediately following self-excavation. Although the overall rate of burrow abandonment was similar between the two years (46% and 41% in 2003 and 2004, respectively), there was a significant difference between years (Fisher's Exact Test $p = 0.007$) in the percentage of animals that initially reused the collapsed burrows (2003 vs 2004, 10% vs 50%, N= 20 and 22, respectively). There were also differences in the number of new burrows dug by the 2003 compared to 2004 tortoises. In 2003, three of the 20 tortoises (15%) dug new burrows following self-excavation, whereas in 2004, none of the tortoises dug new burrows, instead all moved to pre-existing neighboring burrows.

This discrepancy could be due to the weather (amount of rainfall) and soil type. The 2003 collapse site was located in an area where soil was categorized as low-clay content, whereas the majority of the burrows in the 2004 collapse site were in a high-clay content area (Beauman et al, submitted). This second collapse period in 2004 differed from the other collapse periods in that there was a large amount of precipitation just before the collapse date. Kozlowski (1999) documented that some soils compact to a depth of more than 1m under heavy traffic loads and when clay soils are wet, they compact more readily. The rain may have contributed to the compaction of the high-clay soil, making it more difficult for the tortoises to dig out (and, thus, contributing to longer self-excavation times). Using that same rationale, it could be argued that once the 2004 tortoises had self-excavated from their potentially compacted burrows, these burrows were stronger and more stable post-collapse than the 2003 tortoises' low-clay, less compacted burrows, making them more conducive to further use. This argument could also be used to explain why none of the 2004 tortoises dug a new burrow after self-excavation, which is supported by Guyer and Hermann (1997) who found that some types of clay are at the high end of friability for tortoises to excavate and that burrows in clay are less likely to be given up (abandoned). If the soil had high clay content and was difficult to dig through, the tortoises might have avoided the expenditure of energy necessary to dig a new burrow and moved to an existing burrow in their home range.

Although tortoises did not exhibit significant changes in movement behavior or home range area after their burrows were collapsed, this result does not necessarily suggest that the event of a burrow collapse does not pose a threat to tortoises' well being. Entombment caused by burrow collapse may interrupt the normal activity of tortoises, as they typically emerge almost every day for a short period of time (Douglass and Layne, 1978; Guyer et al., 1996). Most tortoises self-excavated within 14 days in 2003 and within 60 days in 2004 (Beauman et al, submitted) although, in 2004, some tortoises were entombed for nearly two and three months (e.g. 51 and 85 days, Beauman et al., submitted). This entombment period would have limited their foraging opportunity at a time when they should have been enhancing their body condition before over-wintering. In addition to forgoing the majority of a growing season, these tortoises could potentially have missed mating opportunities, which occur primarily in the late summer and fall, (Ott et al., 2000; Guyer et al, 2006).

The impact of an increase in abandoned burrows and the potential of lost mating and foraging opportunities are difficult to measure. Even tortoises that abandoned their burrows moved to a location within their home range. Additionally, a lost mating season may not be as important to a species that are long lived, since the females can store sperm and, even in ideal conditions, hatchlings only have less than a 10 percent survivor rate (Butler and Sowel, 1996; Witz et al., 1992). Conversely, it could be argued that, for a species that is in decline, any drop in reproduction due to moving burrow locations or losing a mating or nesting opportunity may be a factor in continuing that decline. Of greater concern may be the loss of eggs that were not laid in a nest due to being entombed or the crushing of already laid eggs by a construction, military, or logging vehicle. One of these events would eliminate the estimated 10 percent survivorship of that particular clutch. In addition to the lost recruitment, another danger to tortoises is the crushing of the animals themselves. Although our study didn't observe either of these phenomenons, Wester (2004) reported one death due to crushing by a vehicle and Guyer et al. (1996) reports a decrease in the number of smaller tortoises on impacted areas.

Overall, burrow collapse does not seem to significantly affect the tortoises' movements or home range area in our study. However, it is clear that the outcome of these events is highly variable. Further studies are needed in order to fully understand how burrow collapse affects the movement, burrow use, and behavior of gopher tortoises and to definitively ascertain the effects of having their burrows collapsed.

LITERATURE CITED

Aresco, M. and C. Guyer. (1999). Burrow abandonment by Gopher Tortoises in slash pine plantations of the Conecuh Forest. *Journal of Wildlife Management* **63(1)**:26-35.

Auffenberg, W. and R. Franz. (1982). The status and distribution of the Gopher Tortoise (*Gopherus polyphemus*). In: Burry, R. B. (ed), *North American Tortoises: Conservation and Ecology. U.S. Fish and Wildlife Service*, Wildlife Research Report **12**. United States Department of the Interior, Fish and Wildlife Service, Washington, D.C. 95-126.

Beauman, R.L., P. F. Kahn, H. Balbach and M. T. Mendonça. (Submitted). Factors affecting burrow collapse and time to self-excavation in Gopher Tortoises *(Gopherus polyphemus*). *Copeia*.

Butler, J. A., and S. Sowell. (1996). Survivorship and Predation of Hatchling and Yearling Gopher Tortoises, *Gopherus polyphemus*. *Journal of Herpetology*. **30**:455-458.

Cagle, F. R. (1939). A system of marking turtles for future identification**.** *Copeia* (3):170-173.

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(2)**:158-165.

Diemer, J. E. and P. Moler. (1982). Gopher Tortoise response to site preparation in northern Florida. *Proceedings of the Annual Conference of Southeast Association of Fish and Wildlife Agencies*. 634-637.

Dilustro, J. J., B. S. Collins, L. K. Duncan, and R. R. Sharitz. (2002). Soil texture, land-use intensity and vegetation of Fort Benning upland forest sites. *Journal of the Torrey Botanical Society*. **129(4)**:289-297.

Douglass, J. F. and J. N. Layne (1978). Activity and thermoregulation of the Gopher Tortoise (*Gopherus polyphemus*) in southern Florida. *Herpetologica* **34(4)**:359-374.

Ernst, C. H., J. E. Lovich, and R. W. Barbour. (1994). Gopher Tortoise (*Gopherus polyphemus*), pp 466-478. In: Ernst, C. H., Lovich, J. E., and Barbour R. W. (eds.) *Turtles of the United States*. Washington, DC, and London: Smithsonian Institution Press.

Eubanks, J. O., W. K. Michener and C. Guyer. (2003). Patterns of Movement and Burrow Use in a Population of Gopher Tortoises (Gopherus polyphemus). *Herpetologica* **59(3)**:311-321.

Guyer, C., R. Birkhead, and H. Balbach. (2006).Effects of Tracked-Vehicle Training Activity on Gopher Tortoise (*Gopherus polyphemus)* Behavior at Fort Benning, GA. ERDC/CERL TR-06-10 ADA467989. Champaign, IL: U.S. Army Engineer Research and Development Center.

Guyer, C. & S. M. Hermann. (1997). Patterns of size and longevity of gopher tortoise (Gopherus polyphenus) burrows: Implications for the longleaf pine ecosystem. *Chelonian Conservation and Biology* **2(4)**: 507-513.

Guyer, C., K.E. Nicholson, and S. Baucom. (1996). Effects tracked vehicles have on gopher tortoises (Gopherus polyphemus) at Fort Benning Military Installation, Georgia. *Georgia Journal of Science* **54**:195-203.

Hansen, K.L. (1963). The burrow of the Gopher Tortoise. *Quarterly Journal of the Florida Academy of Science* **26**:353-360.

Hermann, S.M., C. Guyer, J. H. Waddle, and M. G. Nelms. (2002). Sampling on private property to evaluate population status and effects of land use practices on the Gopher Tortoise, Gopherus polyphemus. *Biological Conservation* **108**:289-298.

Hooge, P. N., And B. Eichenlaub. (1997). Animal Movement extension to arcview.ver.1.1. Alaska Science Center–Biological Science Office, U.S. Geological Survey, Anchorage, Alaska.

Kozlowski, T. T. (1999). Soil compaction and growth of woody plants. *Scandinavian Journal of Forest Research* **14**:596-619.

Landers, J. L., and J. L. Buckner. (1981). The Gopher Tortoise: Effects of forest management and critical aspects of its ecology. *Southlands Experimental Forest Technical Note*. **56**:7.

McRae, W. A., J. L. Landers and J. A. Garner. (1981). Movement patterns and home range of the Gopher Tortoise. *American Midland Naturalist* **106(1)**:165-179.

Mitchell, M. (2005). Home range, reproduction, and habitat characteristics of the female Gopher Tortoise (*Gopherus polyphemus*) in southeast Georgia. A Thesis Submitted to the Graduate Faculty of Georgia Southern University.

Mohr, C.O. (1947). Table of equivalent populations of North American small mammals. *The American Midland Naturalist* **37**:223-249.

Noss, R. F. (1988). The longleaf pine landscape of the southeast: Almost gone and almost forgotten. *Endangered Species Update* **5(5)**:1-8.

Ott, J. A., M. T. Mendonça, C. Guyer and W. K. Michener. (2000). Seasonal changes in sex and adrenal steroid hormones of Gopher Tortoises (*Gopherus polyphemus)*. *General and Comparative Endocrinology* **117**:299-312.

Pike, D. (2006). Movement patterns, habitat use, and growth of hatchling tortoises, *Gopherus polyphemus*." *Copeia* **(1)**: 68-76.

Smith, R. B., D. R. Breininger, and V. L. Larson. (1997). Home range characteristics of radiotagged gopher tortoises on Kennedy Space Center, Florida. Chelonian *Conservation and Biology* **2**:358-362.

U.S. Fish and Wildlife Service. (1987). Endangered and threatened wildlife and plants; determination of threatened status for the gopher tortoise (*Gopherus polyphemus*): Final rule. *Federal Register* **52(129)**:25366-25380.

U.S. Fish and Wildlife Service. (1990). Gopher Tortoise recovery plan. Atlanta, GA.

Wester, E.E. (2004). Impact of natural gas pipeline operation and maintenance on long-term population viability of the threatened gopher tortoise (*Gopherus polyphemus*).

Report to Florida Gas Transmission Company. Southern Ecosystems Research, Auburn, AL.

Witz, B. W., D. S. Wilson, and M. D. Palmer. (1992). Estimating Population Size and Hatchling Mortality of *Gopherus polyphemus*. *Florida Scientist*. **55**:14-19.

Table 1. Movements and home range (2003 and 2004). Means, SEs, ranges and N for the various movement parameters for tortoise before their burrows were collapsed and after self-excavation

Year	Collapse Status	Burrows Used $\bar{x}$ ± SE (Range)	Times Moved $\bar{x}$ ± SE (Range)	Mean Distance Moved (m) $\bar{x}$ ± SE (Range)	Home Range (ha) $\bar{x}$ ± SE (Range)
2003	Pre-	2.3 ± 0.2 (1.0-7.0) n = 20	1.7 ± 0.3 (0.0-7.0) n = 20	61.1 ± 6.2 (0.0-222.2) n = 19	0.25 ± 0.34 (0.003-1.2) n = 11
	Post-	1.9 ± 0.2 (1.0-4.0) n = 20	1.8 ± 0.2 (0.0-4.0) n = 20	65.4 ± 7.2 (0.0-161.0) n = 19	0.19 ± 0.18 (0.06-0.6) n = 4
2004	Pre-	1.4 ± 0.1 (1.0-4.0) n = 22	1.6 ± 0.4 (0.0-6.0) n = 21	49.1 ± 12.9 (0.0-231.9) n = 22	0.24 ± 0.08 (0.02- 0.56) n = 7
	Post-	1.2 ± 0.1 (1.0-3.0) n = 22	1.0 ± 0.2 (0.0-2.0) n = 22	70.7 ± 16.0 (0-293.2) n = 22	0.24 ± 0.09 (0.16 – 0.34) n = 2

Table 2 Movements and home range (2005) Means, SEs, ranges, and N for the 2005 movement measures of tortoises recaptured from the previous studies and tortoises whose burrows had not been collapsed

Year	**Tortoise Status**	**Burrows Used** $\bar{x}$ **± SE** **(Range)**	**Times Moved** $\bar{x}$ **± SE** **(Range)**	**Mean Distance Moved (m)** $\bar{x}$ **± SE** **(Range)**	**Home Range (ha)** $\bar{x}$ **± SE** **(Range)**
2005 **(2003 -** **Tortoises)**	Experimental	4.5 ± 0.7 (3.0-7.0) n = 6	6.3 ± 0.9 (4.0-10.0) n = 6	125.3 ± 53.4 (49.0-387.0) n = 6	0.81 ± 0.40 (0.05-2.51) n = 6
	Control	4.0 ± 0.3 (3-5) n = 5	4.2 ± 1.0 (2.0-7.0) n = 5	91.6 ± 15.0 (61.0-141.0) n = 5	0.96 ± 0.46 (0.03-2.61) n = 5
2005 **(2004 -** **Tortoises)**	Experimental	4.2 ± 0.3 (3-7) n = 17	4.9 ± 0.7 (2.0-11.0) n = 17	143.3 ± 22.8 (13.0-335.0) n = 16	1.88 ± 0.85 (0.008 – 13.69) n = 16
	Control	4.2 ± 0.5 (2-7) n = 10	5.5 ± 1.2 (1.0-11.0) n = 10	122.8 ± 26.9 (41.0-297.0) n = 10	0.36 ± 0.12 (0.04 – 1.03) n = 9