EXPLORING THE RELATIONSHIP BETWEEN HABITAT STRUCTURE AND THE GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) IN SOUTHWEST GEORGIA.

by

MCKAYLA C. SUSEN

(Under the Direction of Steven B. Castleberry)

ABSTRACT

The gopher tortoise (*Gopherus polyphemus*) is a keystone fossorial species that has faced severe population declines due to habitat loss, degradation, and fragmentation. My objectives were to assess the effects of soil texture on burrow structure and temperature, examine fine-scale burrow site selection, and investigate the effects of fencing on tortoise movement. My results indicate that burrows length and depth decreased with increasing percent clay. However, temperature did not vary suggesting that soil texture influences depth required to reach stable temperatures. Tortoises selected burrow sites with sandy soils, low canopy and midstory cover, and herbaceous ground cover although they selected sites along a wider gradient of conditions than has generally been reported. Movement patterns were influenced by fence presence, with home ranges showing greater overlap, although we saw no difference in home range size. These results can inform management decisions on targets for habitat condition and use of fences.

INDEX WORDS: Gopher tortoise, soil texture, burrow site selection, home range, fencing, GPS loggers

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MCKAYLA C. SUSEN

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MCKAYLA C. SUSEN

Major Professor:	Steven B. Castleberry
Committee:	Lora L. Smith Daniel Markewitz

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
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CHAPTER 1

INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is the only tortoise species found in the southeastern United States (Bramble and Hutchinson 2014; Edwards et al. 2016). Gopher tortoises occur in temperate to subtropical climates of eastern Louisiana, Mississippi, Alabama, Georgia, Florida, and South Carolina (Auffenberg and Franz 1982; Bramble and Hutchinson 2014). They are found in upland habitats including longleaf pine (*Pinus palustris*) savannas, sandhills, xeric oak hammocks (*Quercus* spp.), scrub, and pine flatwoods (Auffenberg and Franz 1982; Kaczor and Hartnett 1990; Nussear and Tuberville 2014). Gopher tortoise populations have experienced over an 80% decline in the last century due to habitat loss, fragmentation, and degradation (Landers and Speake 1980; Auffenberg and Franz 1982; Diemer 1992a). As a result, the gopher tortoise was under consideration to be federally listed as a threatened species throughout its range. The U.S. Fish and Wildlife Service recently announced that the gopher tortoise will remain federally listed only in the western portion of their range (i.e., west of the Tombigbee and Mobile rivers in Alabama and Louisianna; U.S. Fish and Wildlife Service 2022). Throughout the remainder of their range (i.e., eastern Alabama, Georgia, Florida, and South Carolina), gopher tortoises are protected at the state level.

Burrow excavation and structure

Gopher tortoises are known as ecosystem engineers in longleaf pine forests because they alter habitat structure through burrow excavation (Kinlaw and Grasmueck 2012). These burrows provide refuge from extreme temperatures, fire, and predation for tortoises as well as over 360 commensal species (McRae et al. 1981; Alexy et al. 2003; Pike et al. 2013). Gopher tortoise burrows consist of a half-moon shaped entrance and a long descending tunnel with a mound of soil outside the entrance (i.e., apron). Burrow structure (i.e., width, length, and depth) is dependent on tortoise size and soil characteristics. Burrow width is indicative of tortoise length and has been used to assign age classes (Doonan and Stout 1994). Burrow length varies with soil type ranging from 1 – 6 m and averaging 2 m in depth (Hallinan 1923; Ultsch and Anderson 1986; Smith et al. 2005). In general, burrows are shorter and shallower in soils with high proportions of clay while burrows in sandy soils are longer, deeper, and more complex (i.e., more turns; Ultsch et al. 1986; Hallinan 1923; Doonan and Stout 1994).

Burrow temperature varies with latitude, season, and depth. Temperature fluctuates close to the entrance (Douglass and Layne 1978; DeGregorio et al. 2012; Pike and Mitchell 2013) and decreases as the burrow descends and stabilizes at about 3 m inside the burrow where it fluctuates less than 2°C (Douglass and Layne 1978; DeGregorio et al. 2012; Pike and Mitchell 2013). Burrows experience temperatures ranging from 25 – 27°C in summer and 12 – 17°C in winter (Douglass and Layne 1978; DeGregorio et al. 2012; Pike and Mitchell 2013; Harris et al. 2015). Tortoises in the northern portion of their range (i.e., South Carolina) experience lower winter and summer temperatures compared to populations farther south (i.e., Florida). Overall, the temperature within the burrow is cooler in the summer and warmer in the winter compared to ambient air temperatures.

Burrow site selection

Gopher tortoise burrow site selection is influenced by soil and vegetation characteristics. Gopher tortoises are capable of burrowing in soils with varying soil texture (i.e., relative proportions of sand, silt, and clay; Sun et al. 2004). However, the probability of encountering a gopher tortoise burrow decreases with increasing percent clay in the top meter of soil, demonstrating a preference for sandy soils (Jones and Dorr 2004; Baskaran et al. 2006; Kowal et al. 2014). Previous research has demonstrated that gopher tortoises can burrow in a variety of soil types but have not examined the effects of soil texture on burrow structure and environment. Clay and sand particles possess widely differing properties that affect both water retention and insulating properties of soil (Hendricks 1942; Grim 1962; Brady 1984; Ikari and Kopf 2011; Kumari and Mohan 2021). Clayey soils have greater insulating properties compared to sandy soils because they lack pore space which decreases air flow (i.e., higher insulation) through the soil and affects burrow structure (Grim 1962; Mana et al. 2017) but may not alter burrow environment. Fine scale soil texture and vegetation characteristics may help discern detailed patterns of burrow site selection by capturing within site variation. Gopher tortoises are most abundant in areas with well drained sandy soils, thick herbaceous ground cover, and low canopy cover (Auffenburg and Franz 1982; Aresco and Guyer 1999; Boglioli et al. 2000). Specifically, tortoise burrows are found in areas with canopy cover ranging from 30 – 60% and herbaceous ground cover between 28 – 40% (Auffenberg and Franz 1982; Aresco and Guyer 1999; Boglioli et al. 2000; McIntyre et al. 2019). Tortoises abandon burrows as tree density, total basal area, and canopy cover increase (Aresco and Guyer 1999; Jones and Dorr 2004). However, populations of gopher tortoises can still be found in habitats lacking one or more of these characteristics, but typically at lower densities (Castellón et al. 2012). For example, southern Florida is primarily composed of mesic flatwoods which lack well-drained soils and scrub communities with lower abundances of herbaceous ground cover, but both support stable low-density gopher tortoise populations (Castellón et al. 2020).

Gopher tortoise activity

Gopher tortoise movement patterns vary with latitude, season, and time of day. In the northern portion of their range gopher tortoises are inactive for extended periods during the cooler winter months (i.e., overwintering; Harris et al. 2015), whereas gopher tortoises in the southern portion of their range (i.e., Florida) remain active year-round (Douglass and Layne 1978). Seasonally, gopher tortoises are most active from May through October (Douglass and Layne 1978; McRae et al. 1981; Smith 1995). Gopher tortoise movements are generally restricted to daylight hours (0700 – 2000 h; Douglass and Layne 1978) and activities include daily foraging, nesting, and breeding (McRae et al. 1981; Smith 1995; Berish and Medica 2014). Daily forays can be unimodal or bimodal, with tortoises generally most active during the warmest time of the day (Douglass and Layne 1978; McRae et al. 1981).

Foraging activities generally occur within 30 m of the burrow. (McRae et al. 1981; Smith et al. 1995). Mating and nesting activities often require longer forays away from the burrow, and home range size (Burt 1943) varies with the age and sex of the tortoise. Due to mate seeking behavior, adult male gopher tortoises tend to make more frequent movements, use more burrows, and have larger home ranges than adult females and juveniles (Douglass and Layne 1978; McRae et al. 1981; Diemer et al. 1992b; Smith et. al 1995; Eubanks et al. 2002; Eubanks et al. 2003; Castellón et al. 2018). Male gopher tortoises have been reported to utilize up to ten burrows (i.e., preexisting, or new excavation) in one active season while females use up to five burrows (Eubanks et al. 2003).

Home range size of male and female gopher tortoises varies from 0.001 – 15.9 ha and 0.001 – 8.9 ha, respectively (McRae et al 1981; Smith 1995; Eubanks et al 2003; Guyer et al 2012). Individual home ranges can overlap, creating areas in the landscape in which multiple tortoises utilize the same geographic space and resources. Males tend to have home ranges that overlap with more individuals (regardless of age or sex) compared to females (McRae et al. 1981; Diemer 1992b; Eubanks et al. 2002). Other studies have reported differences in home range overlap between sexes and habitat types. For example, Castellón et al. (2018) found that females in Florida flatwoods had a higher degree of overlap compared to females in Florida scrub habitat. Meanwhile, males experienced the same degree of overlap across habitat types. Gopher tortoise movement patterns are also influenced by social interactions (Johnson et al. 2009; Guyer et al. 2014). Gopher tortoises form social networks comprised of subgroups known as cliques that share geographic space but do not interact socially with members of other cliques (Guyer et al. 2014). These social networks can be disrupted by changes in habitat and tortoise density. Guyer et al. (2012) demonstrated that in areas of decreasing density, individuals within cliques expanded their home ranges to maintain interactions with other clique members.

In addition to social networks, changes in habitat structure and the presence of anthropogenic features can disrupt natural movement patterns of gopher tortoises. Increased human development and urbanization has created anthropogenic barriers (i.e., roads, fencing, and buildings) which affect habitat connectivity (Forman and Alexander 1998; Peaden et al. 2017). The presence of roads has been shown to elongate movements (i.e., dispersal 0.6 – 2.6 km; McRae et al. 1981) by acting as a movement corridor to more suitable habitat or influence burrow site selection as individuals opt to permanently reside along roadsides (Rautsaw et al. 2018). Gopher tortoises may select roadsides for burrow sites because they typically have lower canopy cover and increased sunlight penetration which promotes the growth of herbaceous ground cover (Diemer 1986; Diemer 1992a; Aresco and Guyer 1999; Berish and Medica 2014). Anthropogenic structures can also act as barriers to gopher tortoise movements. Metcalf et al. (2023) reported avoidance of roads and human structures (i.e., buildings or fences) by gopher tortoises in a heavily urbanized area. Railways have also been shown to act as a barrier to gopher tortoise movement and directly influence individual health and survival. Rautsaw et al. (2017) reported a high number of encounters with deceased or dehydrated tortoises along railroads and only a few successful railway crossings. Anthropogenic structures such as roads and railways influence gopher tortoise behavior, but detailed descriptions of tortoise movements and behavior in response to these structures are lacking.

Gopher tortoise tracking

Our knowledge of gopher tortoise movements is primarily based on the use of very high frequency (i.e., VHF) radiotelemetry. However, VHF transmitters provide limited location data on individual movements (Bauder et al. 2015). Radiotelemetry data for gopher tortoises primarily consists of burrow locations because tortoises retreat into burrows when approached (McRae et al. 1981; Zimmerman et al. 1994; Nussear and Tuberville 2014). Therefore, even frequent VHF tracking does not provide detailed movement data for gopher tortoises. The utilization of GPS loggers can provide more frequent high resolution location acquisitions for wildlife than VHF transmitters. However, GPS loggers can be expensive (Scobie et al. 2014; Forin-Wiart et al. 2015; Peaden et al. 2017; Foley and Sillero-Zubiri 2019; Kauth et al. 2020; Stemle et al. 2022; Hromada et al. 2023). Recently, researchers have tested low-cost (i.e., <$100) GPS loggers to track gopher tortoise movements. Paden and Andrews (2020) were the first to report modification methodology and application of low-cost GPS loggers on gopher tortoises. Stemle et al. (2022) utilized low-cost loggers to examine movements of juvenile gopher tortoises and determined that they had larger home ranges than reported using VHF telemetry. The use of low-cost commercially available GPS data loggers has the potential to enable researchers to discern more detailed wildlife movement patterns and responses to anthropogenic barriers.

The goal of my research was to examine fine scale habitat requirements influencing gopher tortoise burrowing and movement patterns in longleaf pine ecosystems. In Chapter 1, I provide a review of pertinent literature. In Chapter 2, I assess the effect of soil texture (i.e., proportion of sand, silt, and clay particles) on burrow structure and temperature, and identify habitat variables important to gopher tortoise burrow site selection in longleaf pine forests within two different ecoregions in Georgia. In Chapter 3, I compare home range size, and the degree of home range overlap (i.e., area of a tortoises' home range used by other individuals) of tracked tortoises confined within a fenced area to that of an unfenced area. In the latter, I used low-cost GPS loggers to assess fine scale movement patterns. In Chapter 4, I summarize the conclusions and management recommendations of this study.

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CHAPTER 2

THE INFLUENCE OF SOIL TEXTURE AND VEGETATION STRUCTURE ON GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) BURROW CHARACTERISTICS AND BURROW SITE SELECTION[1]

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Abstract – The gopher tortoise (*Gopherus polyphemus*) is a keystone fossorial species that has experienced severe range-wide population declines due to habitat loss, degradation, and fragmentation. Gopher tortoises excavate extensive burrows that provide refuge from extreme temperatures, fire, and predation. Habitat characteristics, specifically soil and vegetation structure, greatly influence burrow structure and placement, but few studies have incorporated fine scale soil texture in burrow site selection models. In addition, few studies report specific estimates for soil texture and vegetation cover conducive to gopher tortoise burrowing. Our objectives were to assess the effects of soil texture on burrow temperature and structure and to examine fine-scale burrow site selection in longleaf pine (*Pinus palustris*) forests of southwestern Georgia. Our study was conducted at two study areas that differed in soil characteristics and land use history. Forest cover at Ichauway was primarily second growth longleaf pine forest characterized by karst topography with loamy sand soils whereas Greenwood was primarily old-growth longleaf forest consisting of iron rich clay soils. We assessed the effect soil texture on burrow structure and temperature for 80 burrows across our two study sites. Burrow length and depth decreased with increasing percent clay. However, we report similar temperatures across burrows suggesting that soil texture affected depth required for burrows to reach stable temperatures. At Ichauway, gopher tortoises selected burrow sites with higher percentages of sand, lower canopy and midstory cover, and more herbaceous ground cover at burrows than at non-burrow sites. We found no difference between habitat characteristics of burrow and non-burrow sites at Greenwood Plantation suggesting the habitat was more homogeneous than at Ichauway. Our results suggest that land use history influence in addition to vegetation and soil characteristics should be considered when assessing gopher tortoise burrow site selection.

Introduction

The gopher tortoise (*Gopherus polyphemus*) is one of six tortoise species found in North America and the only species in the southeastern United States (Bramble and Hutchinson 2014). Gopher tortoises occur in temperate to subtropical climates from Louisiana, east to South Carolina and south throughout Florida (Auffenberg and Franz 1982; Bramble and Hutchinson 2014). They are found in upland habitats including longleaf pine (*Pinus palustris*) savannas, sandhills, xeric oak hammocks (*Quercus* spp.), scrub, and pine flatwoods (Auffenberg and Franz 1982; Kaczor and Hartnett 1990; Nussear and Tuberville 2014). The gopher tortoise is a keystone fossorial species that influences vegetation structure through burrow excavation (Kinlaw and Grasmueck 2012). Burrows provide refuge from extreme temperatures, predators, and fire for gopher tortoises as well as over 360 commensal species (McRae et al. 1981; Alexy et al. 2003; Pike et al 2013; Goodman et al. 2018). Declines in gopher tortoise populations cause a substantial reduction in the number of burrows across the landscape which could lead to declines in biodiversity.

Gopher tortoise burrows consist of a half-moon shaped entrance, a long descending tunnel, and a mound of soil outside the entrance (i.e., apron). Burrow structure varies greatly depending on tortoise age class and soil type. Hatchling and juvenile burrows tend to have a greater angle of descent compared to burrows of subadults and adults (Doonan and Stout 1994). Hallinan (1923) found that angle of burrow descent varied across adult burrows as well, ranging from 15 – 30° within one study area. Burrow length can vary from 1 – 6 m depending on soil type, moisture, and depth (Hallinan 1923; Ultsch and Anderson 1986; Doonan and Stout 1994; Whitfield et al. 2022). Burrows in deep (i.e., vertical depth from surface to water table) well-drained sandy soils tend to be longer, deeper (i.e., vertical depth from the surface to burrow end), and more complex compared to those found in clayey soils (Hallinan 1923; Auffenberg and Franz 1982; Ultsch and Anderson 1986; Doonan and Stout 1994; Smith et al. 2005; Whitfield et al. 2022).

Several tortoise species, including the gopher tortoise use burrows for maintaining a stable body temperature (Spotila et al. 2014). Temperatures inside the burrow vary with season and latitude. Burrows have cooler daytime and warmer nighttime temperatures (25 – 27°C in summer and 12 - 17°C in winter) compared to ambient air temperatures (Douglass and Layne 1978; DeGregorio et al. 2012; Pike and Mitchell 2013; Harris et al. 2015). Temperature close to the burrow opening can fluctuate considerably depending on season, weather, and time of day (Douglass and Layne 1978; Pike and Mitchell 2013). As the burrow descends, temperature begins to stabilize and fluctuates less than 2°C at ≥ 3 m inside the burrow (Douglass and Layne 1978; DeGregorio et al. 2012; Pike and Mitchell 2013). Although past research has examined the structure (i.e., length and depth) and environment of gopher tortoise burrows, the role of soil characteristics (i.e., soil texture) on burrow structure and temperature has not been described.

Soil texture (relative proportions of sand, silt, and clay particles; Sun et al. 2004) can affect characteristics such as water retention (i.e., permeability) and aeration. Clay and sand particles possess widely different properties that influence drainage and insulating properties. Clay, fine-grained particles less than 2 μm in diameter (Dixon 1991; Kumari and Mohan 2021), have a crystalline structure that allows retention of water and plasticity (i.e., the ability to be molded) (Grim 1962; Mana et al. 2017; Kumari and Mohan 2021). In contrast, sand is composed of particles ranging from 0.05 mm to 2.0 mm (USDA definition) and lacks the structure found in clay particles, which allows for large pore spaces between particles. Large pore spaces allow for high water permeability and air flow (Brady 1984). The proportion and distribution of different particles influences soil characteristics. Soils dominated by clay particles are characterized by low permeability, high plasticity when saturated, and become hardened and compacted when dried. In contrast, sandy soils have high permeability and lack plasticity.

Differing characteristics between soil texture particles could influence gopher tortoise burrow excavation. For instance, the crystalline structure between clay particles can cause soils to cohere making burrow excavation more difficult, especially when dry. However, coherence could also make burrows more resistant to collapse (i.e., higher longevity) compared to burrows in sandy soils (Goodman et al. 2018). In addition, the lack of pore space and decreased air flow between clay particles imparts insulating properties that may allow burrows to reach stable temperatures more quickly (i.e., at shallower depths) in clayey soils compared to those in sandy soils (Brady 1984; Day 1992; Ikari and Kopf 2011). Overall, understanding the effect of soil texture on burrow structure and temperature could provide valuable information on gopher tortoise burrow site selection.

Previous studies have identified important habitat characteristics influencing burrow site selection by gopher tortoises, primarily soil and vegetation characteristics. Gopher tortoises are most abundant in areas with well-drained sandy soils, low canopy cover (30 – 60%), and abundant herbaceous ground cover (28 – 49.27%; Auffenberg and Franz 1982; Aresco and Guyer 1999; Boglioli et al. 2000, McIntyre et al. 2019). However, gopher tortoises are also found in habitat types with different habitat characteristics, such as less well drained soils, although often at lower densities (Castellón et al. 2012). Parts of southern Florida have extensive mesic flatwoods with poorly drained soils and scrub communities which have well drained soils but lack abundant herbaceous ground cover, however both support low-density gopher tortoise populations (Auffenberg and Franz 1982; Castellón et al 2020).

Most studies have identified characteristics of tortoise habitat at broad scales (i.e., state-wide, or regional; Auffenberg and Franz 1982; Aresco and Guyer 1999; Boglioli et al. 2000, McIntyre et al. 2019). Few have examined habitat characteristics at fine scales (i.e., at burrows). The spatial scale at which data is collected influences patterns observed in burrow site selection. For example, Catano et al. (2014) examined habitat metrics associated with gopher tortoise burrows in longleaf pine forests at spatial scales from 1 – 707 m^2 and found that increasing canopy cover within 10 m of a burrow was the best predictor of burrow abandonment. Castellón et al. (2020) found that microtopographic differences influenced burrow site selection of tortoises in mesic flatwoods and scrub communities with burrows more commonly found in areas where elevation was slightly higher than mean elevation. Although these studies provide valuable information regarding site selection, more fine-scale information is needed regarding soil textures conducive to gopher tortoise burrowing as they are found in a range of habitats that vary in soil characteristics.

Previous research has relied on the national Soil Survey Geographic Database (SSURGO; Natural Resources Conservation Service) to obtain soil texture classifications at burrows (Lau and Dodd 2015; Lavallin 2018). However, soil sampling conducted for this database is collected at coarse spatial scales (i.e., state or county level) and may not provide fine scale variation in soil texture. Studies using this database also report ranges of soil particles (e.g., sandy loam soils vary from 50 – 70% sand; Buol et al. 2011) rather than precise values for sand, silt, and clay (Lau and Dodd 2015; Lavallin 2018). Solis et al. (2022) conducted soil texture analysis to examine burrow placement of thirteen-line ground squirrel (*Ictidomys tridecemlineatus*) and determined that burrow site selection varied widely by site with variation in soil texture.

Collectively, these studies suggest the need to examine tortoise burrow site selection using vegetation and soil characteristics collected at finer scales.

In this study we examined fine scale habitat characteristics that influenced burrow structure and site selection at two sites in southwestern Georgia that differed in soil and vegetation characteristics. Our objectives were to 1) assess the effect of soil texture (i.e., proportion of sand and clay particles) on burrow structure and temperature, and 2) identify the effects of soil texture and vegetation structure on gopher tortoise burrow site selection. We hypothesized that burrows in soils with a higher percent of clay particles (i.e., clayey soils) would be shorter and shallower compared to burrows in sandy soils and that burrow temperature would not vary with soil texture due to the insulating properties of clay soils. Secondly, we hypothesized that gopher tortoise burrow sites would have higher percentages of sand in the soil, lower percent canopy cover, and higher percent of ground cover forage species (i.e., grasses forbs, and legumes) than random non-burrow locations.

Methods

Description of the Study Area

Our study was conducted at two sites in the Coastal Plain of southwestern Georgia that differed in soil and vegetation characteristics (Figure 2.1). The first site was located at Ichauway, which is the research site of the Jones Center in Baker County. Ichauway is an 11,796 ha property with mature second-growth longleaf pine (*Pinus palustris*) forest with native ground cover, mixed pine-hardwood forests, isolated wetlands and wildlife food plots. Ichauway lies within the Dougherty Plain ecoregion, which is characterized by karst topography and loam to sandy loam Ultisols (Edwards et al. 2013). Ichauway is managed with prescribed fire on a 1–3-year rotation. For this study we selected two 49 ha sampling areas (hereafter, GGC and GGX) known to have tortoise populations. Our two sampling areas were dominated by Wagram, Norfolk, Troup and Albany soil series which consists of very deep loam to loamy sand soils.

The second site was Greenwood Plantation in Thomas County, Georgia (Figure 2.1). Greenwood is a 1,730 ha property located in the Red Hills ecoregion with old growth and second growth longleaf pine forests interspersed with floodplain forests, seepage bogs, and wildlife food plots (Edwards et al. 2013). Uplands in the Red Hills consist of well-drained loamy soils with iron-rich clay layers within one meter of the soil surface and topography consists of rolling hills sculpted by surface drainage which can form floodplain forests and shrub bogs (Edwards et al. 2013). Upland forests at Greenwood are dominated by native ground cover in the understory. Uplands are managed with annual prescribed fire during the dormant season. The Georgia Department of Natural Resources (GaDNR) monitored the gopher tortoise population at Greenwood in 2019 (M. Elliott, Georgia DNR, personal Communication). We selected two sampling areas at Greenwood that differed in soil characteristics, including a 23 ha area with sandhill soils (hereafter, Plateau or PL) and a 28 ha area with clayey soils (hereafter, Old Growth or OG). Soils in OG consist of Norfolk (loamy sand) and Faceville (sandy loam) soil series while the PL is comprised solely of Lakeland (sand) soil series (National Resources Conservation Service (NRCS) Web Soil Survey, accessed 2022).

Burrow Structure and Temperature

We used previous burrow location data for Ichauway and Greenwood to randomly select 20 burrows at each sampling area (n = 80), excluding collapsed burrows. We refer to GGC, GGX, OG, and PL as sampling areas to distinguish them from our study sites (i.e., Ichauway and Greenwood). We measured burrow length, and angle of descent (hereafter, AOD) of burrows using a burrow camera (Environmental Management Systems, Canton, Georgia, USA). We marked the camera and hose in 5 cm increments to measure the length from the burrow opening to the back of the burrow. If a tortoise was present in a burrow, we recorded length as close to the end of the burrow as possible. The AOD of burrows was obtained using a digital protractor attached to a meter stick. Angle measurements were taken 50 cm inside the burrow to avoid bias caused by soil erosion at the burrow entrance (Doonan and Stout 1994). We took three readings from the protractor with the meter stick resting on the bottom of the burrow and used the average as the AOD for each burrow.

We calculated burrow depth for all sampled burrows using the Law of Sines (Eq.1). In this case, we measured burrow length, which was the hypotenuse, and AOD, which was the opposite angle (Figure 2.2). The angle between the surface and the end of the burrow was assumed to be 90° (Eq. 2).

$$a = b\left(\frac{\sin a}{\sin b}\right) \tag{Eq.1}$$

$$X = Length\frac{sinAOD}{sin90} \tag{Eq. 2}$$

We measured summer temperature within and outside burrows over a 7-day period between 13 August to 15 September 2022 using iButton temperature data loggers (-40°C - + 85°C capability; Thermochron iButton® DS12912G, Embedded Data Systems, Lawrenceburg, Kentucky, USA). One logger was placed at the end of each burrow using methodology described by Hengstebeck and Romagosa (2021). A second logger was placed on the apron of soil outside the burrow opening to monitor surface temperature. Loggers were programmed to collect temperature readings once/hour over the 7-day period. We calculated the average summer temperature for the 7-day sampling period. Two loggers were expelled by tortoises during data collection and were excluded from analyses.

Habitat Sampling

Soil sampling and texture classification

We collected soil samples at the same 20 burrows (i.e., burrow points) at each sampling area described in the previous section and at 20 random points where no burrow was present within 3 m of the point (i.e., non-burrow points). To avoid impacting burrows, we collected soil samples 3 m north and south of each designated point (i.e., burrow and non-burrow) for a total of two sampling locations/point. We kept the north and south soil samples separate to capture potential fine scale variation. We used a standard soil auger (American Management Systems (AMS, American Falls, Idaho) with quick connect extensions and mud bucket attachment to collect soil samples. Soil was emptied from auger bucket onto a tarp and arranged by sampling layer based on depth from the surface. The targeted maximum sample depth was 200 cm, which represents the average depth of gopher tortoise burrows (Smith et al. 2005). For each sampling location, we separated soil into six segments (0-25, 25-50, 50-75, 75-100, 100-150, and 150-200) and then homogenized the soil within each segment. We collected soil field characteristics of each segment, which included hand texture, moist color (Munsell scheme), structure, and consistency (Buol et al. 2011). After collecting field characteristics, we homogenized soil into 0 – 100 cm and 100 – 200 cm sections and placed soil samples into two quart-sized bags (i.e., 2 soil samples collected for each sampling location; and 4 samples per burrow or non-burrow point) This process was conducted for both north and south sampling locations (i.e., twice at each burrow and non-burrow point).

Soil samples were air dried for one month before processing. We used a 2 mm sieve (8” Brass/Stainless Sieve No. 270, Gilson Company, Inc., Lewis Center, Ohio, USA) to remove large particles (i.e., rock fragments and vegetation), and used 50 g of each sieved sample for particle size analyses. We used 5% sodium hexametaphosphate (GFS Chemicals, Powell, Ohio, USA) as a dispersing agent (hereafter, HMP). We mixed 100 mL of HMP with soil samples and allowed them to sit overnight (~16 hours; Ashworth et al. 2001). Samples were then rinsed into a metal electric mixer cup using DI water and mixed for 5 min using a commercial drink mixer (Single Spindle Drink Mixer, Hamilton Beach, Glen Allen, Virginia, USA) to agitate soil particles with the dispersing solution (Ashworth et al. 2001). We used the bouyoucos-hydrometer methodology (Gee and Bauder 1986) to determine percent sand, silt, and clay (i.e., soil texture) in each sample. Hydrometer readings were taken at 0.5 min, 1 min, 3 min, 90 min, 120 min, and 1440 min (D. Markewitz, University of Georgia, personal communication). We calculated blank (i.e., mixture of 100 mL HMP and 900 mL of deionized water) and temperature corrected proportions of sand, silt, and clay in each soil sample using equations derived by Gee and Bauder (1986). We averaged percent sand, silt, and clay of soil samples collected at sample points (i.e., burrow or non-burrow).

Vegetation

We examined vegetation characteristics at the same burrow and non-burrow points selected for particle size analysis to assess gopher tortoise burrow site selection at Ichauway and Greenwood (n = 20 burrows and 20 non-burrows per sampling area). Midstory and ground cover were estimated using the quadrat method (Higgins et al. 2012). We placed 4 quadrats 3 m away from our points (one in each cardinal direction) to avoid the influence of burrow excavation (i.e., burrow apron). We used quadrats of 3 x 3 m and 50 x 50 cm to visually estimate percent midstory and ground cover, respectively (Figure 2.3). Ground cover was classified into seven functional groups including grasses, forbs, legumes, ferns, subshrub trees (i.e., vines and woody-stemmed plants <100 cm), and bare ground. Estimates of percent cover were averaged across the four sampling quadrats to create one value for each vegetation parameter at each burrow and non-burrow point.

We used ArcMap 10.8.1 (ESRI, Redlands, California, USA) and aerial imagery with 1 m spatial resolution (National Agriculture Imagery Program [NAIP], 2021) to estimate percent canopy cover around the previously selected burrow and non-burrow points within each of the four sampling areas. We created 3 m buffers around all sampling points using the *Buffer Analysis* tool in ArcMap 10.8.1. We then clipped NAIP aerial imagery to the sampling areas using the *Clip Data Management* tool. Next, we classified approximately 10 training sites per sampling area. Training sites ranged in size from 50 – 800 1 m^2 pixels to differentiate between two cover types, no canopy (i.e., bare ground, ground cover, midstory [measured in quadrats], roads, and shadows) or canopy (i.e., hardwood and pine) using the *Draw Polygon* function found within the *Image Classification* tool. We created a classified raster file containing the two class types using the *Maximum Likelihood Classification Analyst* tool. Finally, we used the *Tabulate Area Spatial Analyst* tool to quantify the number of pixels of each cover type within the buffers. We estimated percent canopy cover as the percent of all pixels classified as canopy within each buffer.

Data analysis

All burrow structure and burrow site selection analyses were performed in program R (R Core Team 2023). We used percent clay as the soil metric for assessing the effects of soil texture on burrow structure and environment because we were specifically interested in how the properties of clay particles affect soil insulation (Hendricks 1942; Day 1992; Ikari and Kopf 2011). Soil texture data (i.e., percent sand and clay) was log-transformed to meet normality assumptions. We assessed the effect of percent clay on burrow temperature, AOD, length, and depth using linear regressions in package *stats*. We used a significance value of $p < 0.05$.

We analyzed gopher tortoise burrow site selection data from Ichauway and Greenwood separately because they occur in different ecoregions that vary in soil and vegetation characteristics. We used generalized linear models (GLM) with binomial distribution (burrow = 1, non-burrow = 0) to compare habitat characteristics at burrow and non-burrow points using package *lme4* in program R. Data was log-transformed as needed to meet normality assumptions. We fit models using explanatory variables including percent sand, canopy cover (CC), midstory cover (MC), ground cover (GC), grass, forb, legume, fern, subshrub tree, and bare ground (bare). We used percent sand as our soil parameter in burrow site selection models as gopher tortoises are more abundant in sandy soils, suggesting a preference for soils with higher percentages of sand (Auffenburg and Franz 1982; Aresco and Guyer 1999; Boglioli et al. 2000; Jones and Dorr 2004; Baskaran et al. 2006). We used a Pearson's correlation test in package *stats* to determine if any variables were strongly correlated ($|r| > 0.7$); however, none of the variables were strongly correlated ($|r| = 0.018 – 0.49$).

We created a set of 5 candidate models to examine burrow site selection at Ichauway and Greenwood (same models were used for both study sites; Table 2.1). We used Akaike Information Criterion for small sample size (AICc) for model selection (Burnham and Anderson 2004). If we had competing top models (i.e., within 2 AICc units) we conducted model averaging to calculate new β estimates, standard error, *z*-score, and *p*-values for variables in our top competing models.

Results

We found no difference in burrow temperature ($\beta = 0.11$, $R^2 = 0.017$, $F_{1,76} = 1.32$, $p = 0.26$) or AOD ($\beta = -0.01$, $R^2 = 5.0\text{e-}04$, $F_{1,76} = 0.038$, $p = 0.85$) with increasing percent clay in soils (Figure 2.4). However, burrow length ($\beta = -7.8$, $R^2 = 0.39$, $F_{1,76} = 48.5$, $p = 1.0\text{e-}09$) and depth ($\beta = -2.9$, $R^2 = 0.34$, $F_{1,76} = 39.3$, $p = 2.01\text{e-}08$) decreased with increasing percent clay. (Figure 2.4).

Of the 5 candidate models, only 1 model was supported by the data (Table 2.2) at Ichauway. Burrow site selection was influenced by percent sand, percent canopy cover, percent midstory, and total percent ground cover. Burrows had significantly higher proportion of sand ($p = 0.029$), lower percent canopy ($p = 0.0023$), higher percent ground cover ($p = 0.0041$) compared to sites without burrows (Table 2.3). Midstory cover estimates did not differ between burrow and non-burrows ($p = 0.65$). At Greenwood, there were 2 top competing models for burrow site selection containing the variables percent canopy cover, percent midstory cover, total percent ground cover, and percent sand (Table 2.4); however, none of the beta estimates were significant in the averaged model ($p > 0.05$; Table 2.5).

Discussion

Our results support our hypotheses regarding the effect of soil texture on gopher tortoise burrow structure and temperature. Burrows were shorter, declining from 650 to 250 cm as clay increased from 2 to 20%, and shallower, decreasing from 200 to 75 cm depth with the same 2 to 20% increase in clay. The relationship between burrow depth with soil texture may be related to closer proximity of clay soils to the water table relative to sandy soils. Clay soils are primarily formed through the physical disaggregation of rock and chemical decomposition of minerals leading to the formation of new clay minerals (Grim 1962; Mana et al. 2017). This process can cause changes in soil thickness, specifically causing clay rich soils to become shallower as minerals are leached out and arranged into sheets as they encounter barriers in the soil (Grim 1962; Buol et al. 2011; Mana et al. 2017). Therefore, depth and length of tortoise burrows are limited by depth to the water table because of the potential for flooding within their burrows.

Clay soils also have high water retention (Grim 1962; Mana et al. 2017; Kumari and Mohan 2021) which along with the depth to water table, increases the potential and duration of flooding. Tortoises have been observed using partially or fully flooded burrows (Means 1982; Ultsch and Anderson 1986), but they generally avoid submerging themselves and instead utilize space above the water or relocate to unflooded burrows (Ultsch 2006; Castellón et al. 2020).

In addition to low permeability, clayey soils have insulating properties caused by the lack of pore spaces conducive to air flow. We report similar temperatures across all burrows although burrows were shorter and shallower in clayey soils compared to sandy soils, suggesting that the insulating properties of clay allow burrows to reach stable temperatures closer to the surface. Alternatively, Ultsch and Anderson (1986) hypothesized that burrows were shorter in clayey soils due to increased levels of carbon dioxide, creating hypoxic and hypercarbic microenvironments. They hypothesized that burrows may be shorter in clayey soils as a result of decreased gas diffusion, reasoning that shorter burrows would allow gases to escape through the opening of the burrow. However, soil texture directly influences diffusion properties of soil based on the abundance and distribution of pore spaces. Soils with a high abundance of clay particles have less pore space between individual particles due to their crystalline structure thus, limiting the ability for gas to diffuse out of the burrow through the soil. Burrows may be shorter and shallower to facilitate the release of gases through the opening however, changes in soil texture may be the primary mechanism driving changes in burrow structure. Overall, soil texture greatly influences burrow structure and future research should continue to examine factors influencing variation in burrow structure and temperature.

Similar to previous studies (Boglioli et al. 2000; Jones and Door 2004; Catano et al. 2014; Kowal et al. 2014; Lau and Dodd 2015, McIntyre et al. 2019) we found that gopher tortoises at Ichauway selected burrow sites with high ground cover, low midstory, and low canopy cover. Contrary to our hypothesis, burrow site selection was influenced by total ground cover rather than individual functional groups within the ground cover. Our rationale for incorporating functional groups in our models was based on previous research that documented gopher tortoises preferentially feed on certain plant groups (i.e., grasses, forbs, and legumes; MacDonald and Mushinsky 1988; Birkhead et al. 2005). However, our results suggest that tortoises can attain adequate forage throughout the Ichauway sampling areas. Frequent prescribed fire (i.e., 1–3 year rotation) is used as a conservation tool to maintain the diverse herbaceous understory of longleaf pine forests at Ichauway, suggesting that tortoise forage species may be abundant the understory (Kirkman and Jack 2018). Our midstory cover (Table S2.2) estimates were lower than previously reported estimates (< 30% Boglioli et al. 2000; ~ 12.23% McIntyre et al. 2019), however, midstory did not appear to differ between burrows and non-burrows. The lack of difference in midstory cover between point types is likely caused by management practices employed at Ichauway (i.e., frequent prescribed fire) which limits the amount of midstory cover. Canopy cover estimates at our burrow sites (30%) were broadly comparable to those reported for other studies (30% Boglioli et al. 2000; ≤ 60% Jones and Door 2004; ≤ 40% Catano et al. 2014; 61.47 ± 14.42% McIntyre et al. 2019). Moreover, our canopy cover estimates derived using NAIP imagery were similar to other studies using remote sensing to estimate vegetation cover (Catano et al. 2014; Kowal et al. 2014), supporting our methodology for estimating canopy cover. High resolution NAIP imagery is widely available and updated frequently (every 2-3 years) allowing researchers to obtain canopy cover estimates more quickly than traditional methods.

Burrow site selection at Ichauway was also influenced by soil texture (i.e., percent sand). We designed our soil sampling to capture soil texture variation in close proximity to tortoise burrows and were able to capture variation in soil texture among burrows and non-burrows. Thus, we can provide specific values for clay and sand particles conducive to gopher tortoise burrowing (Table S2.3). Gopher tortoise burrows at Ichauway averaged 81% sand and 9% clay at burrows. Meanwhile, non-burrows points averaged 73% sand and 15% clay. The discrepancy in soil texture between burrows and non-burrows at Ichauway suggests that within site variation in soil texture influenced burrow site selection as tortoises demonstrated a preference for soils with higher percentages of sand, although sand particles appeared to be more abundant overall.

The apparent lack of burrow site selection by gopher tortoises at Greenwood may be influenced by the site's land use history. In contrast to Ichauway, which consists primarily of second-growth longleaf pine forests, Greenwood is dominated by old-growth longleaf pine forests that are burned annually during the dormant season. Consistency in management may have created a more homogeneous forest structure than typically seen in other forested areas (i.e., second growth) occupied by gopher tortoises. Old growth longleaf pine forests are characterized not only by large trees, but also by open patches with regenerating longleaf pine, and few intermediate sized trees (Noel et al. 1998). Death of old large longleaf pine trees creates open areas where sunlight reaches the understory and promotes regeneration of longleaf pine trees. Tortoise burrows are often located in these areas because tortoises require sunlight for basking, egg incubation, and dense herbaceous ground cover for foraging activities (Auffenberg and Franz 1982; Aresco and Guyer 1999). The abundance of these open patches may contribute to homogeneity of old growth longleaf pine forests, which may have obscured preference in burrow site selection. The model results may also be explained, in part, by our study design. We selected sampling areas with known tortoise burrows (GaDNR unpublished data) that broadly differed in soil texture (NRCS Web Soil Survey). However, the two Greenwood study areas (OG and PL) represented only 15% of the area known to support gopher tortoise populations (GaDNR unpublished data) and may not have been representative of the tortoise habitat across the entire site. Future research should further examine the effect of these parameters on burrow structure and site selection especially for areas with a more homogeneous habitat structure (e.g., old growth longleaf forests). Burrow site selection for gopher tortoises has been extensively studied; however, the incorporation of both fine scale field sampling and remote sensing may create more detailed site-specific patterns that can help inform land management practices.

Management Implications

The results of our research support the contention that gopher tortoises prefer areas with lower clay content, low canopy cover, low midstory cover, and high total percent ground cover. Managers should set goals for maintaining less than 30% canopy cover and greater than 65% ground cover to create areas conducive for gopher tortoise burrowing. Soil texture can vary within sites and land management practices should focus on maintaining cover estimates in areas with soil averaging 80% sand but can vary from 60 – 100% sand.

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Table 2.1. Logistic regression candidate models for examining factors influencing gopher tortoise (*Gopherus polyphemus*) burrow site selection in longleaf pine (*Pinus palustris*) forests at the Jones Center at Ichauway, Baker County, Georgia and Greenwood Plantation, Thomas County, Georgia. Model parameters include percent sand, canopy cover (CC), midstory cover (MC), ground cover (GC), and individual functional groups (i.e., grass, forb, fern, legume, subshrub tree, and bare ground).

Model #	**Model Parameters**
1	Sand
2	CC + MC + GC
3	CC + MC + Grass + Forb + Legume + Fern + Subshrub tree + Bare
4	Sand + CC + MC + GC
5	Sand + CC + MC + Grass + Forb + Legume + Fern + Subshrub tree + Bare

Table 2.2. Logistic regression results for examining gopher tortoise (*Gopherus polyphemus*) burrow site selection in longleaf pine (*Pinus palustris*) forests at Ichauway, Baker County, Georgia in the summer of 2022.

Model	**K**	**AIC*c***	**ΔAIC*c***	***w***	**Cum. *w***	**LL**
4	5	90.13	0	0.84	0.84	-39.66
2	4	93.54	3.42	0.15	0.994	-42.5
5	10	101.32	11.19	0.003	0.997	-39.06
3	9	101.93	11.8	0.002	0.999	-40.68
1	2	104.19	14.07	0.001	1.0	-50.02

Table 2.3. Coefficients (β), standard error (SE), z-score (z) and p-values (p) for the top model examining gopher tortoise *(Gopherus polyphemus*) burrow site selection in longleaf pine (*Pinus palustris*) forests at the Jones Center at Ichauway, Baker County, Georgia.

Parameter	**β**	***SE***	***z***	***p***
Sand	0.060	0.027	2.18	0.029
Canopy cover	-0.023	0.007	-3.04	0.0023
Midstory cover	-0.012	0.29	-0.45	0.65
Ground cover	0.05	0.017	2.87	0.0041

Table 2.4. Logistic regression results for gopher tortoise (*Gopherus polypheums*) burrow site selection in longleaf pine (*Pinus palustris*) forests at Greenwood Plantation, Thomas County, Georgia.

Model	**K**	**AIC*c***	**ΔAIC*c***	***w***	**Cum. *w***	**LL**
1	2	112.29	0	0.61	0.61	-54.06
2	4	113.84	1.55	0.28	0.89	-52.64
4	5	116.07	3.78	0.092	0.98	-52.62
3	8	119.48	7.19	0.017	0.99	-50.7
5	9	121.53	9.24	0.006	1.0	-50.44

Table 2.5. Averaged model coefficients (β), standard error (SE), z-score (z) and p-values (p) for the top models examining gopher tortoise (*Gopherus polyphemus*) burrow site selection in longleaf pine (*Pinus palustris*) forests at Greenwood Plantation, Thomas County, Georgia.

Parameter	**β**	***SE***	***z***	***p***
Sand	-0.00062	0.016	0.04	0.97
Canopy cover	-0.00024	0.0019	0.13	0.89
Midstory cover	-0.005	0.0047	0.10	0.92
Ground cover	0.00065	0.0045	0.14	0.89

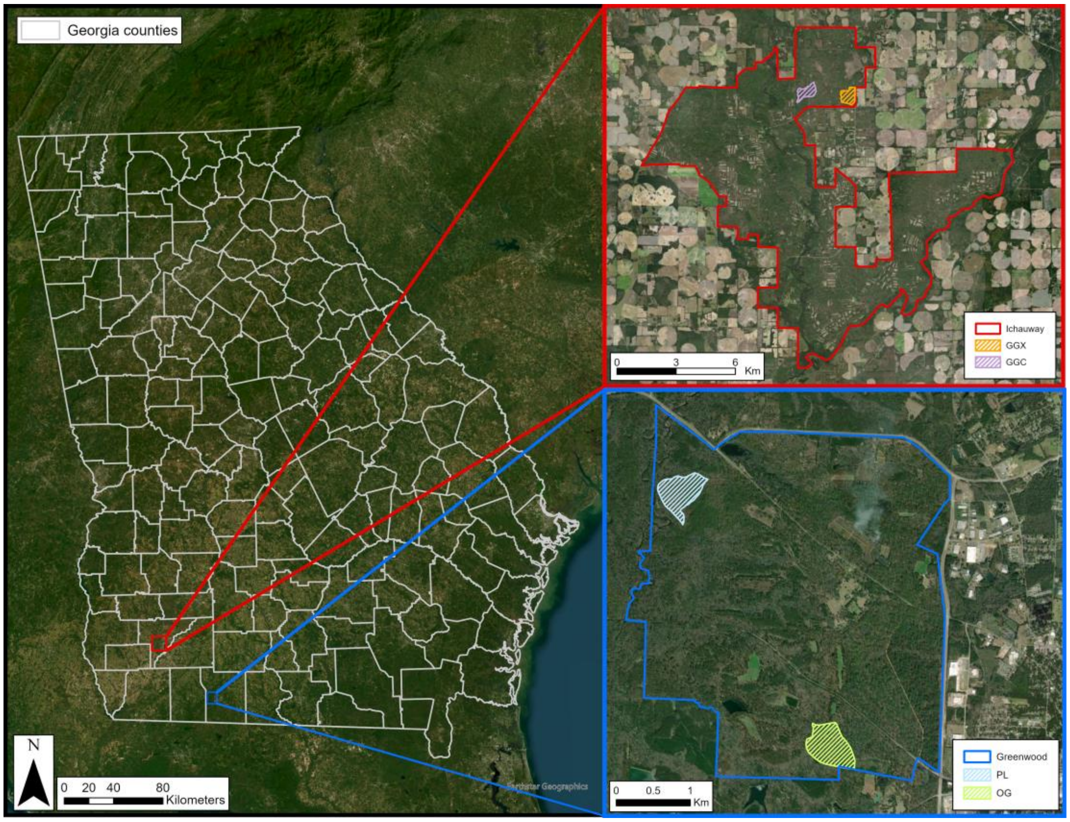

Figure 2.1. Study area map. Left panel depicts the counties within the state of Georgia. The top right panel (red) indicates the two second-growth longleaf pine (*Pinus palustris*) forest sampling areas at the Jones Center at Ichauway located in Baker County, Georgia. The bottom right panel (blue) indicates the two old growth longleaf pine forest sampling areas at the Greenwood Plantation study plots located in Thomas County, Georgia.

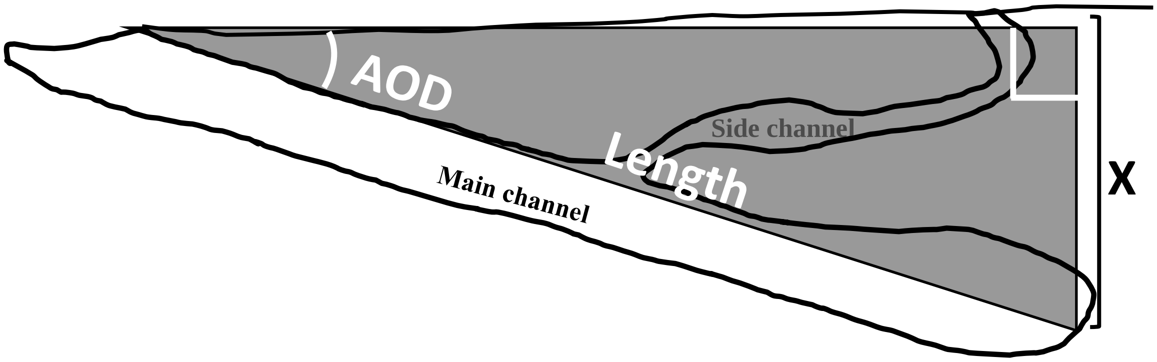

Figure 2.2. Schematic for gopher tortoise (*Gopherus polyphemus*) burrow structure measurements and calculations. Burrow length and angle of descent (i.e., AOD) were measured while depth (i.e., X) were estimated using the Law of Sines.

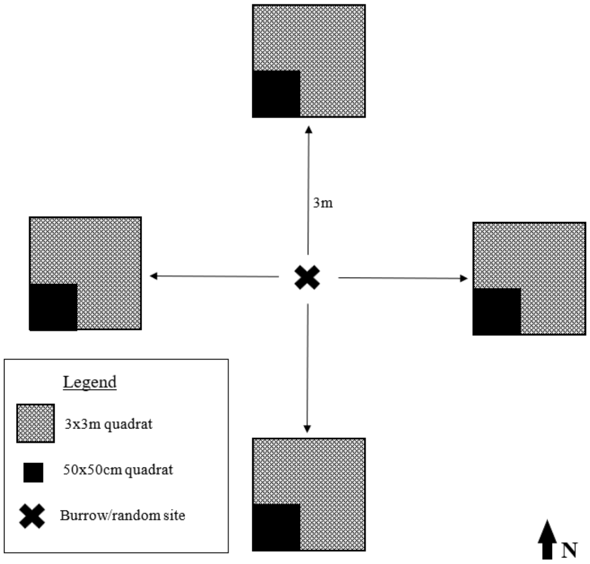

Figure 2.3. Quadrat vegetation sampling design for collecting midstory cover (3 x 3 m quadrat) and ground cover (50 x 50 cm quadrat) estimates around gopher tortoise (*Gopherus polyphemus*) burrows and non-burrow sampling points at the Jones Center at Ichauway, Baker County, GA and Greenwood Plantation, Thomas County, GA. Midstory and ground cover were optically estimated.

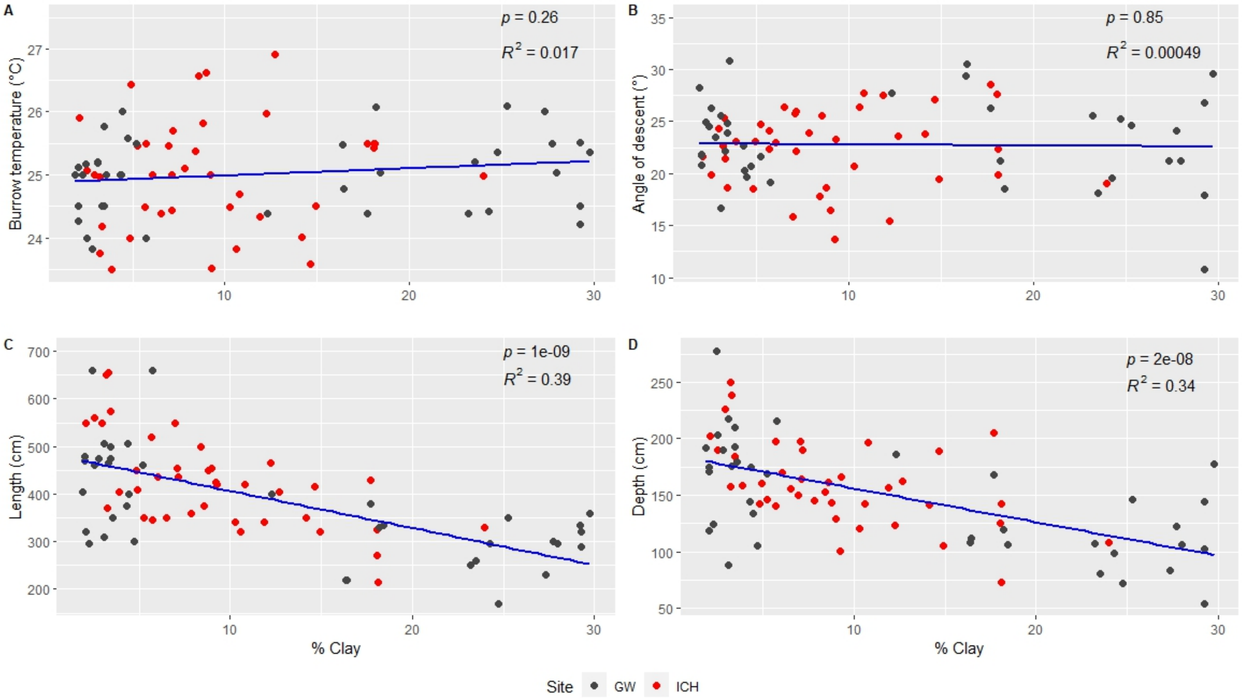

Figure 2.4. Relationship between percent clay in soils and gopher tortoise (*Gopherus polyphemus*) burrow temperature (A) angle of descent, (B) length, (C) and depth (D) at the Jones Center at Ichauway (Baker County, Georgia) and Greenwood (Thomas County, Georgia), 2021 – 2022. Only burrow length and depth are significant regressions.

Appendix S2.1

Table S2.1. Internal burrow temperature, tunnel length, and vertical depth from the surface of gopher tortoise (*Gopherus polyphemus*) burrows at the Jones Center at Ichauway in Baker County, GA and the Greenwood Plantation in Thomas County, GA. Temp = burrow temperature, AOD = angle of descent, SD = standard deviation.

Ichauway	**Temp ± SD (°C)**	**AOD ± SD (°)**	**Length ± SD (cm)**	**Depth ± SD (cm)**
GGC	24.8 ± 0.8	23.1 ± 3.6	406.5 ± 84.8	157.1 ± 27.1
GGX	25.2 ± 0.93	21.8 ± 3.8	442.5 ± 107.4	163.5 ± 45.9
Greenwood	**Temp ± SD (°C)**	**AOD ± SD (°)**	**Length ± SD (cm)**	**Depth ± SD (cm)**
OG	25.1 ± 0.62	23.2 ± 5.1	296.7 ± 61.8	116.4 ± 36.0
PL	25.0 ± 0.60	23.0 ± 3.3	443.5 ± 103.1	172.8 ± 44.3

Table S2.2. Canopy and ground cover estimates for burrows and non-burrows at sampling areas at Ichauway in Baker County, GA and the Greenwood Plantation in Thomas County, GA. CC = canopy cover, MC = midstory cover, GC = ground cover, B = burrows, NB = non-burrows, SD = standard deviation.

Ichauway	**CC ± SD (%)**		**MC ± SD (%)**		**GC ± SD (%)**	
	B	*NB*	*B*	*NB*	*B*	*NB*
GGC	41.7 ± 36.1	59.7 ± 34.9	11.2 ± 10.9	12.05 ± 13.8	70.0 ± 13.0	55.2 ± 20.7
GGX	18.7 ± 30.1	60.4 ± 37.1	6.6 ± 7.3	7.2 ± 6.6	55.6 ± 15.1	39.4 ± 22.2
Greenwood	**CC ± SD (%)**		**MC ± SD (%)**		**GC ± SD (%)**	
	B	*NB*	*B*	*NB*	*B*	*NB*
OG	24.5 ± 31.1	28.4 ± 34.1	8.3 ± 5.8	14.8 ± 18.9	74.1 ± 17.4	75.1 ± 15.1
PL	22.8 ± 28.4	30.9 ± 39.4	9.2 ± 9.6	5.5 ± 4.8	68.6 ± 16.3	76.1 ± 13.5

Table S2.3. Estimates of percent sand and clay at burrows and non-burrows for sampling areas at Ichauway in Baker County, GA and the Greenwood Plantation in Thomas County, GA. SD = standard deviation.

Ichauway	**Sand ± SD (%)**		**Clay ± SD (%)**	
	Burrows	*Non-burrows*	*Burrows*	*Non-burrows*
GGC	80.73 ± 9.1	68.5 ± 14.1	9.3 ± 4.7	19.7 ± 10.3
GGX	82.7 ± 8.2	78.1 ± 11.1	8.6 ± 5.9	10.6 ± 6.3
Greenwood	**Sand ± SD (%)**		**Clay ± SD (%)**	
	Burrows	*Non-burrows*	*Burrows*	*Non-burrows*
OG	65.5 ± 7.4	66.9 ± 5.7	23.6 ± 5.4	23.7 ± 3.7
PL	89.6 ± 8.1	89.6 ± 7.3	3.3 ± 1.0	3.1 ± 0.06

CHAPTER 3

EFFECTS OF LONG-TERM FENCING ON GOPHER TORTOISE HOME RANGE SIZE AND OVERLAP[2]

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[2] Susen, M.C., L.L. Smith, and S.B. Castleberry. To be submitted to *Southeastern Naturalist*.

Abstract – Urbanization has caused habitat loss and fragmentation through the creation of anthropogenic features that can act as barriers to wildlife movement. Anthropogenic features, such as roads and roadside fencing, have been shown to alter tortoise movement. Our goal was to assess the effect of long-term fencing on *Gopherus polyphemus* (Gopher tortoise) movement patterns by comparing home range size and degree of overlap. We utilized modified low-cost GPS loggers to monitor movement of adult Gopher tortoises in a fenced predator exclusion plot and unfenced control plot at the Jones Center Ichauway, Baker County, Georgia. We used adaptive local convex hulls (a-LoCoH) to create utilization distributions for adult tortoises for a 30-day period during the active season. Our results suggest that fencing influences Gopher tortoise movement patterns. Home ranges of Gopher tortoises overlapped more in the fenced population than in the unfenced population, but home range size did not differ between populations. The use of low-cost GPS loggers allowed us to collect more frequent data per individual and to describe differences in behavior likely caused by fence presence.

Introduction

Urbanization has resulted in habitat loss and fragmentation through the creation of barriers to animal movements in the form of roads, railways, and other infrastructure. Habitat fragmentation alters wildlife behavior and isolates populations by reducing connectivity (Fahrig 2002; Fahrig 2017). Many tortoise species have been greatly affected by the loss of habitat connectivity and presence of anthropogenic structures, such as roads and roadside fencing. For example, *Gopherus agassizii* (Desert tortoise) are often struck and killed by motor vehicles (Forman and Alexander 1998; Peaden et al. 2017). The use of roadside fencing has been implemented to reduce tortoise mortality from motor vehicles, but these anthropogenic features alter tortoise movement patterns (Fusari 1982; Peaden et al. 2017; Ruby et al. 1994). Deviations from natural movement patterns in the presence of barriers include changes in behavior (i.e., pacing), distance traveled, and home range size (Fusari 1982; Hromada et al. 2023; Peaden et al. 2017). These behavior changes can affect tortoise survival as individuals are exposed to extreme temperatures for longer periods of time (Hromada et al. 2023; Peaden et al. 2017).

Gopherus polyphemus (Gopher tortoise) is another North American tortoise species facing threats caused by urbanization. Few studies have examined the effect of anthropogenic structures on Gopher tortoise movements, primarily focusing on roads, railways, and buildings. The presence of roads elongate movements by acting as a movement corridor to more suitable habitat (i.e., 0.6 – 2.6 km; McRae et al. 1981). Gopher tortoises may select roadsides because of the low canopy cover and increased sunlight penetration which promotes the growth of herbaceous ground cover suitable for foraging (Aresco and Guyer 1999; Berish and Medica 2014; Diemer 1986; Diemer 1992a). Anthropogenic structures also can act as barriers to Gopher tortoise movements. Metcalf et al. (2023) reported avoidance of roads and human structures (i.e., buildings or fences) by individuals in a heavily urbanized area. Railways have also been shown to act as a barrier to Gopher tortoise movement and directly influence individual health and survival. Rautsaw et al. (2017) reported a high number of encounters with deceased or dehydrated tortoises and only a few successful railway crossings. Anthropogenic structures influence gopher tortoise behavior, but more research is needed to discern specific patterns of response to these structures.

Previous research examining gopher tortoise movement relied on traditional radio telemetry (i.e., Very High Frequency, VHF). More recently, the utilization of GPS loggers has been shown to provide more frequent location acquisitions of wildlife species, which allows researchers to discern detailed movement patterns (Foley and Sillero-Zubiri 2019; Forin-Wiart et al. 2015; Hromada et al. 2023; Kauth et al. 2020; Peaden et al. 2017; Scobie et al. 2014; Stemle et al. 2022). GPS loggers are effective at discerning the influence of anthropogenic structures on wildlife behavior. For example, Scobie et al. (2014) found that *Athene cunicularia hypugaea* (Western burrowing owl) increased avoidance of roads with increasing vehicle speeds. Hromada et al. (2020) reported that Desert tortoises moved along anthropogenic barriers (i.e., road fencing) but avoided roads. Paden and Andrews (2020) were the first to report methodology for modification and use of low-cost GPS loggers on gopher tortoises. Paden (2018) examined the effects of translocation on Gopher tortoise movement using modified GPS loggers and reported longer movements and larger home ranges for translocated tortoises than resident tortoises. Stemle et al. (2022) utilized low-cost loggers to examine movements of juvenile Gopher tortoises and determined that they had 6.6-fold larger home ranges than previously reported. Clearly, the use of low-cost commercially available GPS data loggers has the potential to allow researchers to discern more detailed wildlife movement patterns than traditional VHF telemetry.

The goal of our study was to assess the effects of an anthropogenic barrier (i.e., long-term fencing) on adult Gopher tortoise movements using modified commercially available low-cost GPS data loggers. Our objectives were to 1) compare home range size of tortoises within a long-term fenced plot to tortoises in an unfenced plot and 2) compare the amount of home range overlap (i.e., area within a home range used by other individuals) for tortoises within a long-term fenced plot to tortoises in an unfenced plot. We hypothesized that tortoises in the fenced plot would have larger home ranges and higher degree of home range overlap compared to those in the unfenced plot. We also predicted that male tortoises would have larger home ranges compared to females due to mate seeking behavior (Diemer 1992b; Eubanks et al. 2003; McRae et al. 1981).

Methods

Description of the Study Area

Our study took place at Ichauway, the research site of the Jones Center in Baker County, Georgia (Figure 3.1). Ichauway is an 11,796 ha property with mature second-growth longleaf pine (*Pinus palustris*) forest with native ground cover, mixed pine-hardwood forests, isolated wetlands and wildlife food plots. Ichauway lies within the Dougherty Plain ecoregion which is characterized by karst topography and loam to sandy loam Ultisol soils (Edwards et al. 2013). The site is managed with prescribed fire on a 1–3-year rotation. Research for this project was conducted in a long-term predator exclusion plot (49 ha; hereafter, exclosure) and an unfenced control plot (49 ha; hereafter, control) that were established in 2003. The exclosure, which was designed to exclude mesocarnivores consisted of a 1.1-m high mesh fence (10.2 x 5.1-cm mesh) with exterior electrical wires running along the bottom, middle, and top of the fence (Conner et al. 2010). The exclosure fence restricted Gopher tortoise movements within the plot, while tortoise movements at the control were not constrained.

Tortoise trapping

Trapping occurred from 26 May to 17 June 2022. We targeted Gopher tortoise burrows ≥ 25 cm in carapace length (McRae et al. 1981) to ensure we would capture adult tortoises large enough to carry tracking equipment. We scoped burrows (Susen et al. 2023) to determine occupancy and placed tomahawk live traps (108SS Tomahawk Live Trap®, Hazelhurst, Wisconsin, USA) at the entrance of occupied burrows. Traps were shaded with burlap and checked twice a day (~08:00 h and ~15:00 h) to prevent tortoises from overheating. All trapped tortoises were brought to the laboratory for processing. Only tortoises weighing more than 3,000 g were fitted with tracking equipment. We used the same protocol to re-capture tracked individuals in October 2022 to retrieve loggers. All trapped tortoises were soaked in a tepid water bath for ~10 minutes to prevent dehydration and were returned to their burrow of capture.

Tracker modification and application

We modified i-gotU GT120B GNSS (Mobile Action®) data loggers to monitor Gopher tortoise movement using methodology developed by Paden and Andrews (2020). The differences between our methodology and Paden and Andrews (2020) were changes in battery type and epoxy brand used to attach tracking equipment to tortoises. We used flat 3.7V 2200mAh rechargeable lithium-polymer batteries rather than the cylindrical lithium-ion batteries (Figure 3.2). We used NuMetal epoxy putty ($23/lb. at the time of study, KBS Coatings®, Valparaiso, Indiana) to reduce modification costs. Tracking equipment was adhered to the carapace directly behind the head (Figure 3.2) to avoid interference with nesting and breeding activities (Paden and Andrews 2020). The total weight of the tracking equipment and epoxy putty averaged 113 g and was < 5% of an individual tortoise's total body mass. Tortoises were tracked from May to October 2022. Loggers were programmed to collect locations every 30 minutes from 08:00 – 20:00 EST. We used VHF radio transmitters (BD-2, BD-2N, SI-2 and SI-2T, Holohil Systems, Carp Ontario, Canada) to relocate individuals to remove tracking equipment at the end of the study. All tracking equipment and epoxy was removed from individuals at the conclusion of this study.

We conducted a stationary test of the GPS units to determine location error (i.e., distance between a known location and a GPS acquired position; Morris and Conner 2017). For this test, one unit was placed in a field with no canopy cover and programed to collect GPS locations every 30 minutes for 7 consecutive days. Coordinates of the known position were collected using a Juniper Archer 3 with attached Geode GNSS Receiver (Juniper Systems®, Logan, Utah, USA) with sub-meter accuracy. We used the *Point Distance tool* in ArcGIS Pro 3.1.3 (ESRI, Redlands, California, USA) to calculate distance between all GPS acquired positions and our known location (Paden and Andrews 2020). Average location error was 35 m and ranged from 1 – 191 m.

Data Analysis

We used Mobile Action® software to download data from all retrieved GPS loggers. We excluded locations acquired within the first 48 hours for all tracked individuals to allow tortoises to adjust from disturbance caused by trapping and equipment attachment activities. We used package *AMT* in program R (Core Team 2023) to exclude extreme outliers by calculating step length between GPS locations. GPS locations were excluded if step length exceeded 100 m within a 30-minute sampling period because it is unlikely that a Gopher tortoise could move this distance in a short time frame. For tortoises in the exclosure we eliminated GPS locations recorded as outside the fence due to logger location error, as tortoise movement was confined to the plot.

We calculated both 100% and 95% minimum convex polygon (hereafter, MCP) for direct comparison to other studies and used 95% adaptive local convex hull (hereafter, a-LoCoH) to construct a utilization distribution for individual tortoises (Getz et al. 2007) using the *AMT* package in R. We used Wilcoxon rank sum non-parametric tests for all home range size comparisons between males and females regardless of treatment (i.e., all males versus all females), within plots (i.e., males versus females in the same plot type), and across plots (i.e., males versus males and females versus females in differing plot types). A Wilcoxon rank sum test was also used to compare home range size between control and exclosure tortoises regardless of sex.

We calculated home range overlap (i.e., amount of area within a tortoises' a-LoCoH home range used by other tortoises) for all tracked tortoises in ArcGIS Pro 3.1.3. We used the *Intersect* tool to identify areas where home ranges overlapped with other tracked tortoises and used the *Merge* tool to create a single polygon representing the total area of home range overlap specific to each tracked tortoise. We calculated percent home range overlap for each tortoise by dividing the amount of area shared with all other tracked tortoises by the total home range area specific to each tracked tortoise (e.g., 0.7 ha overlap/1.1 ha home range = 63.6% overlap). We used a Wilcoxon rank sum non-parametric tests to for the same comparisons made for home range size. We used a significance value of $p < 0.05$ for all statistical tests.

Results

We deployed tracking equipment on a total of 36 adult tortoises (18 per plot type) and tracked movement from June to October 2022. We tracked 9 males and 9 females at the control and 10 males and 8 females at the exclosure. The median operational period for our GPS units was 38 days. Therefore, to maximize the number of individuals used in analyses, we selected a 30-consecutive day tracking period that occurred during the tortoise activity season between 31 May through 21 July 2022 for estimating home range. We retrieved 34 of 36 trackers at the end of the study period. Of the two loggers not recovered, one had detached from the tortoise after deployment, and we were unable to relocate the second tortoise due to VHF transmitter failure. Of the retrieved loggers, six experienced operational errors and did not record any data for the tracking period. The remaining 28 data loggers successfully recorded from 5 – 250 days.

Sixteen of the 28 tracked tortoises met the 30-day minimum tracking requirement, 9 individuals at the control (3 males and 6 females) and 7 at the exclosure (4 males and 3 females). Mean 100% and 95% MCP home range sizes at the control were 4.12 ± 0.71 (SE) ha and 1.98 ± 0.36 (SE) ha, respectively, and 2.47 ± 0.28 (SE) ha and 1.19 ± 0.15 (SE) ha at the exclosure, respectively (Table 3.1). Mean a-LoCoH home range size was 1.29 ± 0.14 (SE) ha at the control and 0.97 ± 0.11 (SE) ha at the exclosure (Table 3.1). Mean a-LoCoH home range size was 1.3 ± 0.42 (SE) ha for males and 1.0 ± 0.32 (SE) ha for females. We found no differences between male and female home range size within ($p = 0.17$ for control; $p = 0.40$ for exclosure) or across ($p = 0.114$ males; $p = 0.95$ females) plots. Similarly, we found no difference in a-LoCoH home range size between all tortoises in the control and exclosure regardless of sex (Figure 3.3; $p = 0.071$).

Home ranges of 13 tortoises overlapped with at least one other individual, 8 at the control (Figure 3.4) and 5 at the exclosure (Figure 3.5). Percent home range overlap ranged from 3 – 89 % for the control and 44 – 99% for the exclosure (Table 3.2). We found no differences in percent home range overlap between sexes within ($p = 0.55$ for control; $p = 1.0$ for exclosure) or across

(p = 0.20 males; p = 0.26 females) plots. Percent home range overlap was greater in the exclosure than in the control regardless of sex (Figure 3.6; p = 0.016).

Discussion

We found that home ranges of adult Gopher tortoises overlapped more in a fenced population than in an unfenced population, but that home range size did not differ between populations. It appears that in the short-term, fencing altered tortoise behavior. Gopher tortoises within the exclosure were geographically constrained, and individuals appeared to share more space than unconstrained individuals in the control. Little is known about the carrying capacity of tortoise habitat, but there may be a threshold beyond which increased home range overlap affects forage availability (Ashton and Ashton 2008; McRae et al. 1981). Interestingly, one control tortoise (Figure 3.4. tortoise 4318A) appeared to use a nearby road as a movement corridor (Berish and Medica 2014; Diemer 1992a; McRae et al. 1981) to disperse. The ability to disperse increases foraging opportunities and limits the potential for overlapping home ranges.

Changes in the amount of home range overlap may also disrupt the social structure within Gopher tortoise populations. Social networks within populations are comprised of several non-random subgroups (i.e., cliques) that share geographic space but do not interact socially with each other (Guyer et al. 2014). Individuals within a clique will travel further distances to interact with members of the same clique while avoiding members of other cliques (Guyer et al. 2014; Johnson et al. 2009). The social structure within the exclosure may have been disrupted when tortoises were geographically constrained, forcing interactions between individuals that may have been avoided before.

The lack of differences in home range size between sexes and plots was likely the result of our short GPS data acquisition period. Due to limitation of the GPS trackers, home range size analysis only included 30 days of data occurring from June into early July and likely excluded long movements associated with nesting (late spring; Berish and Medica 2014; Diemer 1992a; McRae et al. 1981; Smith 1995) and breeding (late summer to early fall; Berish and Medica 2014; Douglass 1990). The exclusion of these extended movements could be masking the total effect of fencing on home range size as we likely only captured movements associated with foraging activities, which typically occur within 30 m of the burrow (Berish and Medica 2014; McRae et al. 1981; Smith 1995). Therefore, it appears that 30 days is an insufficient amount of time to capture the true effects of fencing on home range size of both males and females.

Another factor that may have influenced Gopher tortoise movement patterns in this study was the lack of mesocarnivores in the exclosure. However, it seems unlikely that the lower predation risk in the exclosure influenced our results because we targeted adult Gopher tortoises. Adult Gopher tortoises have fully calcified shells and have few predators, unlike subadults or juveniles (Mushinsky 2014). Alternatively, Cherry et al. (2016) presented evidence of altered plant communities within long-term predator exclusion plots and suggested that prescribed fire and predator exclusion influenced ground cover composition. Resulting changes in vegetation composition within the exclosure could have altered available forage species for tortoises. We did not measure forage availability in our study; however, if forage was limited in the exclosure, we might have expected tortoises to have larger home ranges than in the control, which was not the case.

We found that the presence of an anthropogenic barrier influenced Gopher tortoise movement behavior through increased home range overlap. Although our results may have been confounded by small sample size, GPS transmitter failure, and low precision, as well as a lack of replication (i.e., one control and one exclosure), we were able to collect more data per individual than with traditional VHF telemetry. For example, we were able to acquire an average of 544 locations per individual in a 30-day tracking period while VHF location acquisition occurring twice a week (Castellón et al. 2018) would only acquire 8 locations per individual. We were also able to describe differences in behavior likely caused by fence presence. Ever increasing urbanization and land conversion results in increased exposure and interaction between Gopher tortoises and anthropogenic structures resulting in behavioral changes associated with movement patterns. Future research should examine long-term effects of anthropogenic structures on Gopher tortoise home range size and social interactions.

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Table 3.1. Thirty-day active season home range size (i.e., 100 and 95% minimum convex polygon [MCP] and 95% adaptive local convex hull [a-LoCoH]) home range size (i.e., hectares) for 16 tracked *Gopherus polyphemus* (Gopher tortoise) in an unfenced control plot and fenced mesopredator exclosure plot at Ichauway, Baker County, Georgia in 2022.

Unfenced control

Tortoise id	**Sex**	**100% MCP (ha)**	**95% MCP (ha)**	**95% a-LoCoH (ha)**
1153A	M	4.56	1.81	1.22
4318A	M	5.08	3.96	1.93
4329A	M	4.73	2.51	1.73
290A	F	1.66	0.97	0.76
4293A	F	2.70	1.42	1.22
4317A	F	8.56	1.58	1.30
4321A	F	2.33	1.03	0.82
4323A	F	4.92	3.45	1.66
501A	F	2.58	1.13	0.97
Average		*4.12*	*1.98*	*1.29*

Fenced exclosure

Tortoise id	**Sex**	**100% MCP (ha)**	**95% MCP (ha)**	**95% a-LoCoH (ha)**
1079A	M	3.57	1.94	1.48
4294A	M	3.26	1.37	1.17
4324A	M	2.66	1.43	1.17
4325A	M	1.70	0.80	0.68

4319A	F	1.79	0.83	0.73
4322A	F	1.82	0.90	0.72
4330A	F	2.51	1.07	0.88
Average		*2.47*	*1.98*	*0.97*

Table 3.2. Thirty-day active season home range (i.e., 95% adaptive local convex hull) size (i.e., hectares) and percent home range overlap for 16 tracked *Gopherus polyphemus* (Gopher tortoise) in an unfenced control plot and fenced mesopredator exclosure plot at Ichauway, Baker County, GA in 2022.

Unfenced Control

Tortoise id	**Sex**	**#Individuals overlapping**	**Home range (ha)**	**% Overlap**
1153A	M	3	1.22	58.45
4318A	M	1	1.93	2.82
4329A	M	3	1.73	17.29
290A	F	2	0.76	59.31
4293A	F	0	1.22	0.00
4317A	F	3	1.30	40.32
4321A	F	3	0.82	89.17
4323A	F	3	1.66	52.00
501A	F	2	0.97	21.58
Average			*1.29*	*37.90*

Fenced Exclosure

Tortoise id	**Sex**	**#Individuals overlapping**	**95% a-LoCoH (ha)**	**% Overlap**
1079A	M	0	1.48	0.00
4294A	M	0	1.17	0.00
4324A	M	4	1.17	72.67
4325A	M	4	0.68	91.44

4319A	F	4	0.73	41.33
4322A	F	4	0.72	99.62
4330A	F	4	0.88	77.15
Average			*0.97*	*76.44*

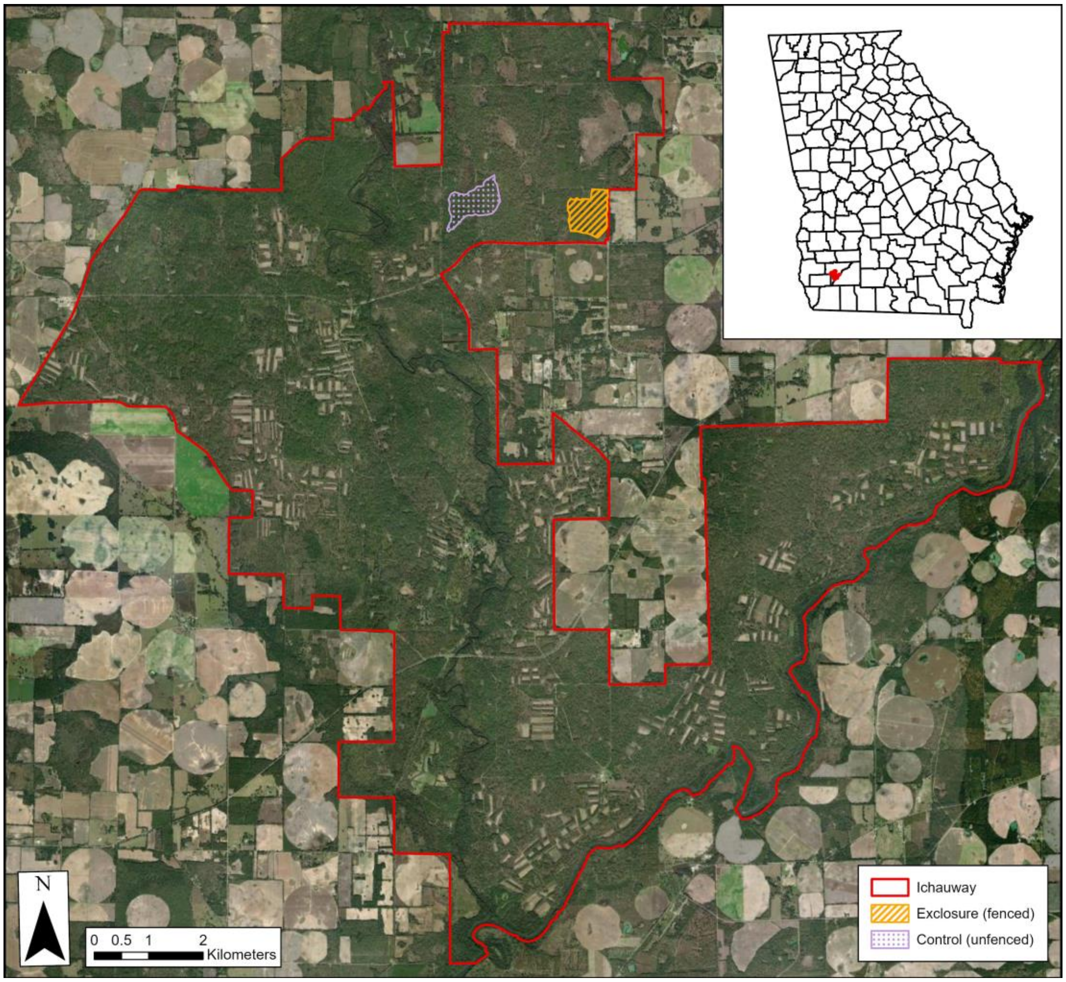

Figure 3.1. Study area map. Included is an outline of the study area, Jones Center at Ichauway located in Baker County, Georgia. Study plots for examining gopher tortoise active season movement patterns in an unfenced control plot (purple) and fenced mesopredator exclosure plot.

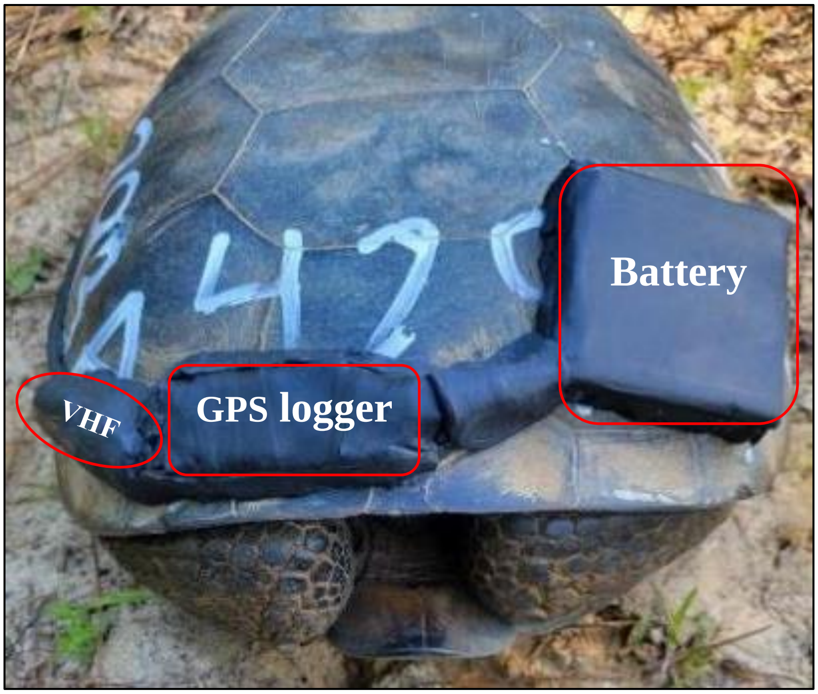

Figure 3.2. Tracking equipment (i.e., low-cost GPS logger and Very High Frequency radio transmitter) attached to an adult *Gopherus polyphemus* (Gopher tortoise) in the summer 2022 at the Jones Center at Ichauway, Baker County, Georgia.

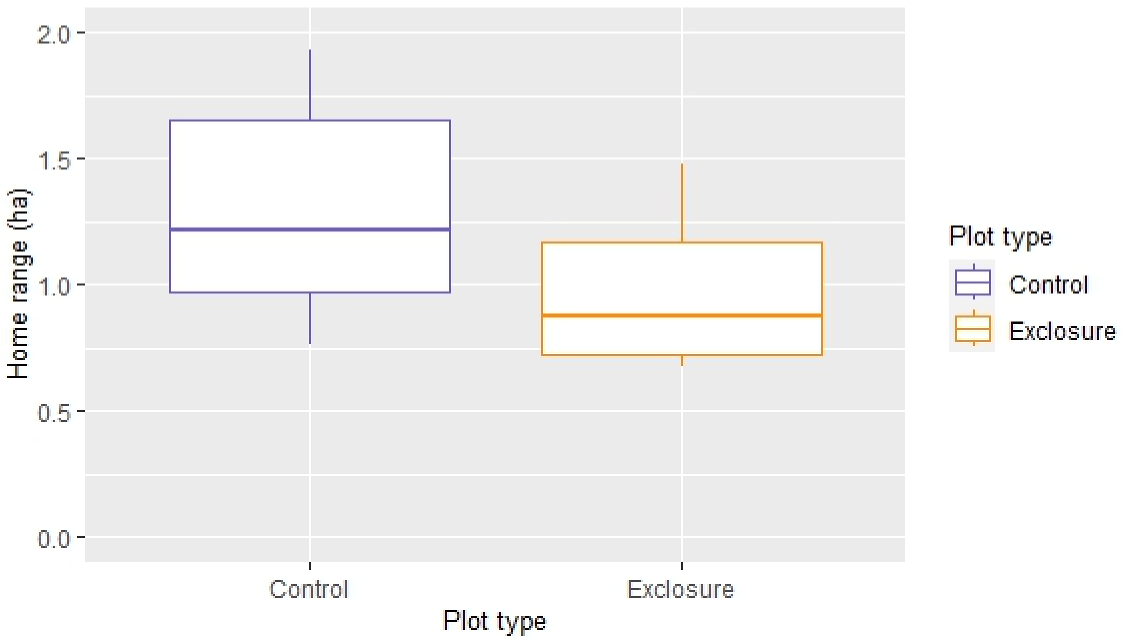

Figure 3.3. Mean thirty-day 95% adaptive local convex hull home range sizes (ha) for tracked *Gopherus polyphemus* (Gopher tortoise) in an unfenced control plot (n = 9) and a fenced mesopredator exclosure (n = 7) plot at the Jones Center at Ichauway, Baker County, Georgia in the summer of 2022.

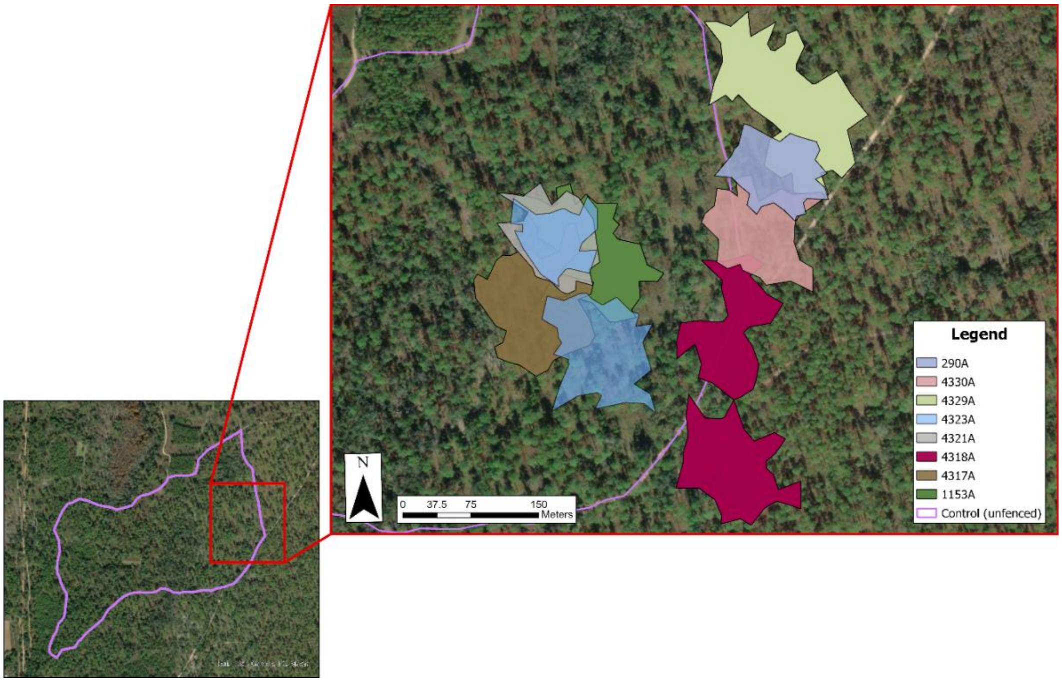

Figure 3.4. Thirty-day 95% adaptive local convex hull home ranges for tracked *Gopherus polyphemus* (Gopher tortoise) within a 49 ha unfenced control plot (n = 8) at the Jones Center at Ichauway, Baker County, Georgia in the summer of 2022. Only tortoises with overlapping home ranges are represented.

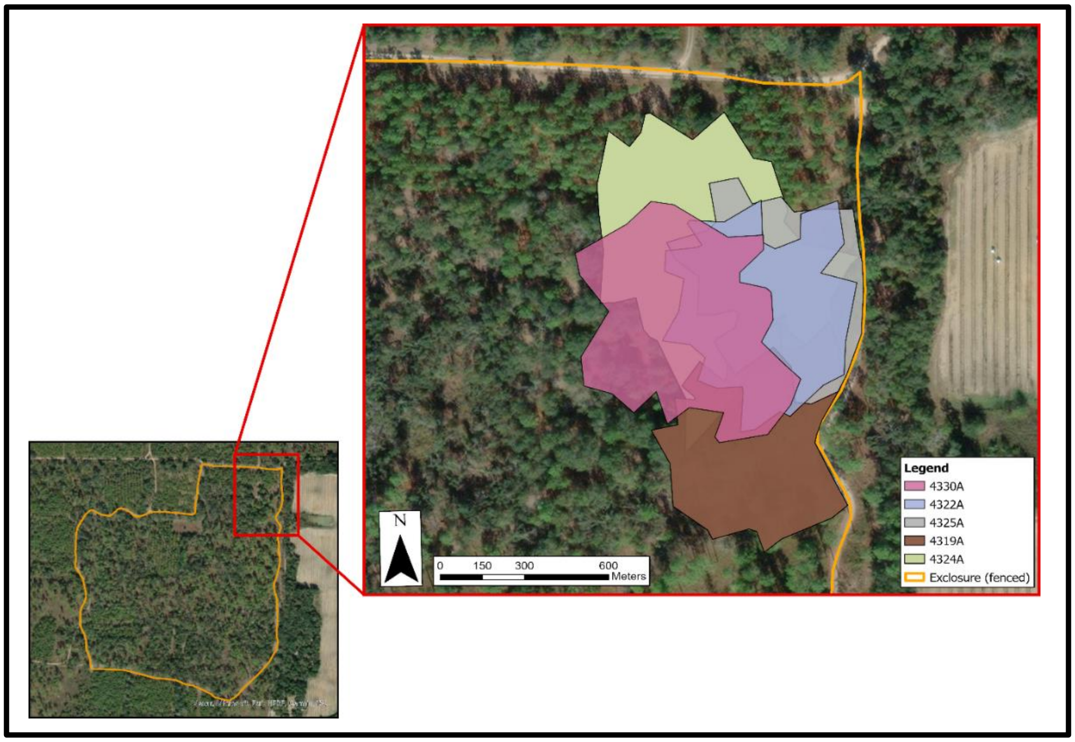

Figure 3.5. Thirty-day 95% adaptive local convex hull home ranges for tracked *Gopherus polyphemus* (Gopher tortoise) within a 49 ha fenced mesopredator exclosure plot (n = 5) at the Jones Center at Ichauway, Baker County, Georgia in the summer of 2022. Only tortoises with overlapping home ranges are represented.

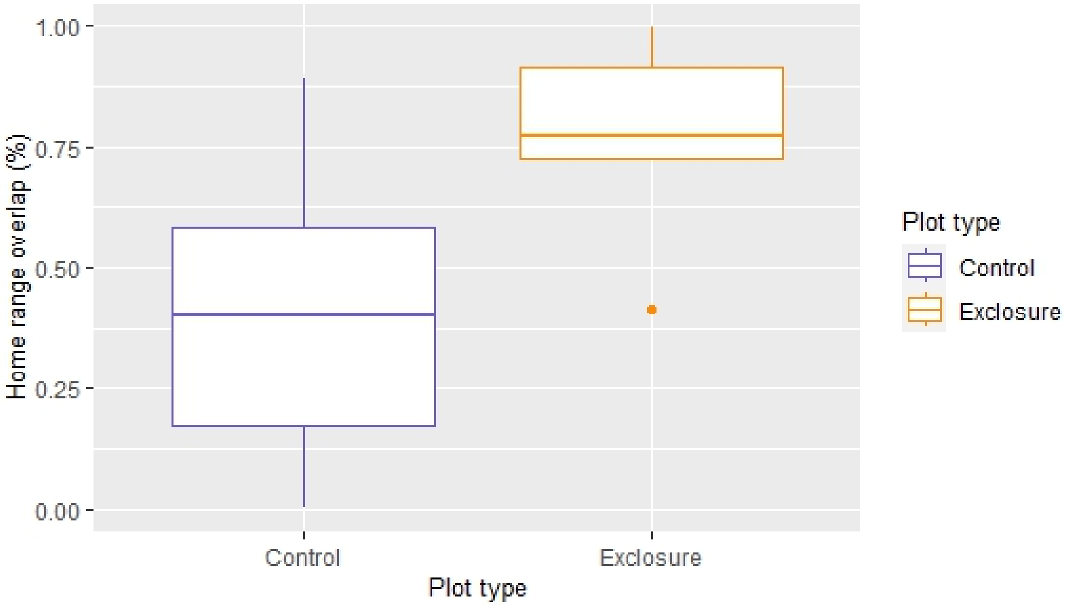

Figure 3.6. Mean thirty-day percent overlap of 95% adaptive local convex hull home ranges for *Gopherus polyphemus* (Gopher tortoise) in an unfenced control plot (n = 9) and a fenced mesopredator exclosure plot (n = 7) at the Jones Center Ichauway, Baker County, Georgia in the summer of 2022.

CHAPTER 4

CONCLUSION

The gopher tortoise has experienced range-wide population declines due to habitat loss and fragmentation (Landers and Speake 1980; Auffenberg and Franz 1982; Diemer 1992a). The species is state and federally listed across its range and research to address goals for habitat management and restoration are needed. Therefore, the goals of my study were to explore the relationship between habitat structure and gopher tortoise populations at a fine scale and to describe behavioral changes (i.e., movement) in the presence of one common type of anthropogenic structure. My specific objectives were to 1) assess the effects of soil texture on burrow structure, 2) examine fine-scale burrow site selection, and 3) investigate the effects of fencing on gopher tortoise movement.

I examined burrow characteristics and site selection at two sites in southwest Georgia. The first study site was located at the Jones Center at Ichauway in Baker County, GA. Ichauway is found in the Dougherty Plain ecoregion, which is characterized by karst topography with loam to sandy loam Ultisol soils (Edwards et al. 2013). My second study site, Greenwood Plantation in Thomas County, GA is located in the Red Hills ecoregion, which has well-drained, iron-rich loamy soils. In addition, Ichauway consists of second-growth longleaf pine forests while Greenwood is dominated by old growth longleaf pine forests. Both sites are managed with frequent prescribed fire.

My investigation into the effects of soil texture (i.e., relative proportion of sand, silt, and clay particles in soil) on burrow structure revealed that soil texture significantly influenced burrow structure. Burrow length and depth decreased with increasing percent clay, creating shorter and shallower burrows in clayey soils. However, burrow temperature did not vary with percent clay, suggesting that the insulating properties of clay may influence depth required to reach stable temperatures. These shorter and shallower burrows are suitable for thermoregulation purposes but studies reporting lower densities of tortoises in clay rich soils suggest that tortoises may not prefer this soil type (Auffenberg and Franz 1982; Jones and Dorr 2004).

At Ichauway I found that gopher tortoise burrows occurred at sites with a higher percentage of sand in the soil, lower canopy and midstory cover, and more abundant ground cover compared to sites without burrows. Burrow site selection was also influenced by total ground cover rather than individual functional groups that included forage and non-forage species, suggesting that preferences for forage species did not drive burrow site selection at Ichauway. Vegetation cover (i.e., canopy, midstory, and ground) estimates were comparable to those reported for other studies (Boglioli et al. 2000; Jones and Door 2004; Catano et al. 2014; McIntyre et al. 2019) which corroborates previous research stating that gopher tortoises prefer areas with lower canopy and midstory cover, and high ground cover. I found no difference between habitat characteristics of burrows and non-burrows at our second site, Greenwood Plantation, suggesting that vegetation characteristics were more homogeneous than at Ichauway perhaps due to differences in management and land use history at the two sites. Overall, my results support the contention that in heterogeneous habitats, gopher tortoises prefer areas with sandy soils, low canopy and midstory cover, and high herbaceous ground cover. However, the lack of burrow site selection at Greenwood demonstrates that land use history may be an important factor influencing burrow site selection.

I found that the presence of a fence influenced gopher tortoise movement patterns specifically, home ranges of adult gopher tortoises overlapped more in a fenced population than an unfenced population, but average home range size did not differ. In addition, there was no difference in home range size or degree of overlap between males and females in either the fenced or unfenced population contrary to previous studies that reported larger home ranges for male tortoises (Douglass and Layne 1978; McRae et al. 1981; Diemer et al. 1992b; Smith et. al 1995; Eubanks et al. 2002; Eubanks et al. 2003; Castellón et al. 2018). Increased home range overlap in my study is likely due to the constraint of the fence, whereas the short duration of my study likely masked differences in home range size between the sexes. Home range size analysis was limited to 30 days and did not include periods of increased activity, such as nesting (late spring; McRae et al. 1981; Diemer 1992a; Smith 1995; Berish and Medica 2014) or breeding (late summer to early fall; Douglass 1990; Berish and Medica 2014). The exclusion of these extended movements could be masking the actual effect of the fence on gopher tortoise home range size (McRae et al. 1981; Smith 1995; Berish and Medica 2014).

My study confirmed the influence of within site habitat variation on burrow site selection and provides data on habitat conditions including soil texture and vegetation structure conducive to gopher tortoise burrowing that can be used to inform management decisions. Additionally, I demonstrated the effects of a fence on gopher tortoise movements that could present potential risks to tortoise populations. Future research should continue to explore gopher tortoise burrow site selection studies, by incorporating fine scale soil and vegetation characteristics for populations throughout their entire range. I advocate the use of low-cost GPS loggers but recognize there are obstacles (e.g., location error or short GPS acquisition period) to overcome when applying these units to fossorial species. Research should prioritize investigating the impact of fences on behaviors throughout annual reproductive cycles to more comprehensively understand shifts in behavior.

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