Impact of Microhabitat Selection on Burrow Distribution of Nine-Banded Armadillos and Gopher Tortoises in a Pine Plantation

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ABSTRACT

Nine-banded armadillos and gopher tortoises cohabit pine forests in the southeastern United States but may compete for burrowing locations. This may be problematic because gopher tortoises are a declining species. To examine coexistence, a microhabitat selection study was carried out at Moody Air Force Base near Valdosta, Georgia. In addition, preference of habitat parameters was compared between burrow categories, such as armadillo burrow types based on location and gopher tortoise burrow types based on age of occupant. Eighty-six burrows were randomly selected and a discriminant analyses was used to identify parameters that differentiate the locations of both species' burrows from each other and from random sites (N = 250). Armadillo burrows (N = 40) were found in areas with higher vegetation density, greater canopy cover, steeper slopes and thicker ground cover than gopher tortoise burrows (N = 46). Steeper slopes, low visibility and farther distance from edges separated armadillo burrows from random sites. Armadillo prefer to build burrows on berms that have steeper slopes, higher vegetation density, higher ground cover, less sunlight and lower elevation than off berm burrows. In addition to the microhabitat study, I determined the detectability of different types of burrows by comparing burrow surveys conducted prior to and after a prescribed burn. Gopher tortoise juvenile and hatchling burrows and those of armadillos off berm had low detectability during the pre-burn survey. Adult gopher tortoise burrows had higher visibility than other burrow categories. This is the first study to provide evidence that synoptic armadillos and gopher tortoises prefer to build burrows in different microhabitats. This spatial niche partitioning was probably related to their physiology. Competition may be occurring because of the presence of coopted burrows and might suggest a complex or mixed mechanism to explain coexistence.

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Chapter I

INTRODUCTION

Different species can occur in a habitat at the same time (referred to as syntopic species) but their distribution patterns may not be the same. Species may prefer certain areas depending on the features habitats possess (Johnson, 1980). This immediate occupied space is known as a microhabitat (Morris, 1979; 1987). When different species inhabit the same area, both species are using available resources (Birch, 1957; Klomp, 1961) and different interactions can occur between them such as competition, parasitism or mutualism. Competition is where both species are acquiring a limited resource at the expense of the other species. Different species have been found to compete over food (Minot, 1981; Rothhaupt, 1988) and space (Schoener, 1983).

Even though competition may occur between syntopic species, they can coexist in a habitat via niche partitioning. Niche partitioning occurs when species segregate themselves in relation to when, where or what they utilize from the habitat (MacArthur & Levins, 1967; Rosenzweig, 1981). In many cases, species avoid competition by shifting their niche. There is also the possibility of niche partitioning without competition when species are specialized to use particular resources such that they do not need to compete for them (Lack, 1940; Harper, Clatworthy, McNaughton, & Sagar, 1961). This could be the result of behavioral and physiological factors of the two species rather than competition (Denton & Beebee, 1994). In addition two species can coexist if the habitat has empty niche space (Rohde, 2005; 2008) which refers to the idea that niche is considered as the character of an environment such that it has a certain capacity to sustain a limited number of species. Coexistence is possible between species until the niche is filled. Also, a habitat could be spatially heterogeneous at a small spatial scale (Monamy & Fox, 1999) and organisms could segregate at this microhabitat level by selecting different microsites resulting in coexistence. This could further be aided through character displacement where closely related species have evolved in such a way that they are able to utilize different resources and have diverged from each other (Brown & Wilson, 1956).

Pioneering studies done on coexistence mechanisms come from the study of diversity of fish in coral reefs where high intensity of competition occurs for living space (Smith & Tyler, 1973). Coexisting species of coral-dwelling gobies (genus *Gobiodon*) that are similar in habitat preferences and competitive abilities have been found to compete for access to vacant habitat space (Munday, 2004). Other syntopic coral reef fish and gobies (Munday, 2001) compete for limited resources and coexist via resource partitioning (Clarke, 1992).

Terrestrial organisms also compete for limited space. Neighboring plants utilize the same resources such as sunlight, minerals and nutrients, as well as physical space in soil (reviewed by Grime, 2006). Because vertebrates have the ability to move, spatial coexistence is a trade-off between resources used and resources available (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). In other words organisms select the habitat that maximizes their reproductive success and reduces the energetic cost of resource acquisition (Pianka, 1994). Examples of spatial competition involve tree holes for woodpeckers (Kappes & Harris, 1995), caves for salamanders (Culver, 1975) and burrows for pika (*Ochotona curzoniae)* and zokors *(Eospalax fontanierii)* (Zhang, Fan, Wang, & Jling, 1998; Zong, Xia, & Sun, 1986).

In the case of primary excavators (i.e., those who construct their own burrows) (Kinlaw, 2006a), there could be competition for space which is a relatively fixed resource (Sebens, 1982). Nevertheless, spatial coexistence has occurred between competing burrowing species. Such is the case for wolf spiders (Lycosidae) (Carrel, 2003) and rodents (Schröpfer & Klenner-Fringes, 1991). Animals can also inhabit and modify burrows dug by primary excavators and these individuals are known as secondary burrow modifiers (Kinlaw, 2006a), such as burrowing owls (*Athene cunicularia*) who use burrows constructed by black-tailed prairie dogs (*Cynomys ludovicianus*) (Desmond, Savidge, & Eskridge, 2000). An example of two syntopic primary excavator species distributed in the southeastern United States is the nine-banded armadillo (*Dasypus novemcinctus*, here after referred to as armadillo) and the gopher tortoise *(Gopherus polyphemus)*. Burrows are an important resource for both of these species (Kinlaw, 2006b) because, like all burrows, they provide protection against predators (Laundre, 1989; Reichman & Smith, 1990), fire (Burns, Flath, & Clark, 1989) and extreme climatic conditions (Pike & Mitchell, 2013).

The typical habitat of gopher tortoises (i.e., long-leaf pine forest, sandhill and mixed pine forest) is also utilized by armadillos and thus, competitive interactions between these species are possible (Kinlaw, 2006b). Competition for food is probably not an issue because gopher tortoises are herbivorous (Garner & Landers, 1981) and armadillos feed on insects and other invertebrates (reviewed in Loughry & McDonough, 2013). Some physical altercations between the two species have been recorded (Dziadzio, Smith, Chandler, & Castleberry, 2016; Galbreath, 1982). Armadillos have been observed using gopher tortoise burrows (Guyer & Hermann, 1997) and depredating their eggs (Douglass & Winegarner, 1977; Drennen, Cooley, & Devore, 1989; Smith, Steen, Conner, & Rutledge, 2013). Positioning of armadillo and gopher tortoise burrows may reflect this negative relationship; however, previous information suggests that burrowing processes for each species were independent (Anderson, Mixon, McDonough, Lee, & Lockhart, 2016) such that variables influencing each species' burrow placement may be different. If so, the distribution pattern of burrows could be the result of spatial niche partitioning between the species. If not, this might suggest that the distribution of burrows could also be explained in terms of empty niche space (Rohde, 2005; 2008). In other words, different species can co-occur if there is plenty of vacant space not utilized by either group. If this occurs, then available resources in the study area are enough to sustain both species and they can coexist until the niche space is filled.

Although both species utilize the same habitat, their requirements at the microhabitat level may differ. Different factors like soil type, canopy cover and slope of ground may influence whether an animal chooses to dig a burrow in a particular location. Also, considering that gopher tortoises are poikilotherms and armadillos endotherms, the degree of temperature modulation inside a burrow could play a role in burrow placement. Specific microhabitat features selected could explain how burrows are co-distributed within an area.

For my thesis, I examined if microhabitat site selection by two synoptic burrowing species, nine-banded armadillos and gopher tortoises, could explain coexistence. I also documented temperature modulation of two types of burrows to see if temperature regime also plays a role in burrow placement.

In addition to microhabitat site selection, I also examined the question of detectability of burrows during population surveys. The standardized survey technique used for gopher tortoise burrows is line transect distance sampling (LTDS) (Buckland, Anderson, Burnham, Laake, Borchers, & Thomas, 2001). LTDS relies on seeing burrows (Smith, Elliott, Linehan, Jensen, & Stober, 2009), which can be influenced by many factors such as burrow size and amount of vegetation present. Small burrows in thick vegetation could result in being overlooked and thus, the number of young tortoises being underestimated in an area (Howze & Smith, 2018; Paden, Andrew, Candal, & Renner, 2017). Detectability of armadillo burrows is also probably affected by heavy vegetation (Paden et al., 2017). Prescribed burning is one tool that might increase detection of burrows because it clears vegetation and exposes hidden burrows. In my study, I determined whether there is a difference in detectability of both gopher tortoise and armadillo burrows due to age of occupant or location, respectively. This was accomplished by completely surveying habitat for burrows before and after a prescribed burn. Understanding the detectability of different types of burrows may help in the management of hatchling and/or juvenile gopher tortoises that might have a high probability of being underreported.

This study focused on answering the following research questions:

1. What microhabitat parameters, if any, explain the differences in distribution patterns of burrow placement observed between armadillos and gopher tortoises?

2. Are there differences in the placement of burrows of gopher tortoises of different ages? For instance, do juveniles differ from adults in the positioning of burrows?
3. Are there differences in the placement of armadillo burrows relative to random sites and on features, such as berms?
4. Is there a difference in the detectability of armadillo and gopher tortoise burrows? Does detectability differ between burrows of different age groups of gopher tortoises and does detection differ with location for armadillo burrows?

Chapter II

LITERATURE REVIEW

This study focused on microhabitat variables that potentially allow the coexistence of two syntopic burrowing vertebrates. Therefore, in this literature review I first discuss microhabitat selection and related coexistence theories. Because my two study organisms, the nine-banded armadillo and gopher tortoise, are both burrowing, I will summarize information on burrowing ecology and studies pertaining to syntopic burrowing species. Lastly, the life histories of nine-banded armadillos and gopher tortoises will be covered as well as observed interactions between these species.

Microhabitat selection and coexistence theories

The natural environment where organisms live is not uniform, especially at a microhabitat level. A microhabitat is a small-scale physical requirement or ambient condition of an immediate area such as vegetation cover (Moura, Caparelli, Freitas, & Vieira, 2005). It can also include physical variables like soil, light intensity, humidity, temperature and air circulation (Huggett, 2004), as well as chemical variables such as nutrients, minerals, moisture and pH that can influence an organism's allocation of time and energy within its home range (Morris, 1987). Microhabitat also includes biotic factors such as availability of food and presence or absence of predators, parasites and/or diseases (Falkenberg & Clarke, 1998; Rosenzweig, 1981; Weinstein, Buck, & Young, 2018). Examples of different microhabitats in a forested community could be located within the trees themselves, along woodland edges, on elevated areas, within depressions and in proximity to fallen logs or decaying wood (Kuuluvainen & Laiho, 2004; Michel & Winter, 2009).

In a particular location where syntopic species with similar habitat requirements are present, each species is expected to occupy its own microhabitat or spatial niche (Hutchinson, 1957; 1959) to limit competition between them. Each species has a particular spatial distribution pattern (i.e., random, clumped or uniform) that is the result of responses of individuals to exogenous and endogenous processes (Fortin & Dale, 2005). An exogenous process is determined by factors related to environmental heterogeneity such as slope or elevation while an endogenous process involves interactions with conspecifics or other species like competition, predation and mutualism (Bascompte, 2009; Legendre & Fortin, 1989; Van Dam, 2009; Yitbarek, Vandermeer, & Allen, 2011). Because different spatial patterns are associated with microhabitat parameters such as food sources, shelter, climatic conditions and competition with other species; knowledge of patterns of habitat use help in understanding the underlying mechanism for spatial distribution and abundance (Hodara & Busch, 2010; Mohammadi, 2010; Stapp, 1997).

Different species can use the same resource in the same habitat resulting in niche overlap that may lead to interspecific competition for the limited resources (Pianka, 1994). Interspecific competition can exist in two forms; one form is exploitative competition where one species is more efficient in exploiting resources than competitors (they do not interact directly). The other is interference competition where a less efficient species may get displaced due to direct physical confrontation from a specialized competitor (Case & Gilpin, 1974). In some cases, coexistence is possible but the niches of the two species shift.

Mechanisms for coexistence can be explained through niche theory. Depending upon different life history strategies of species and their responses toward resources, some form of niche partitioning can occur (Chesson, 2000). This can happen by classical resource partitioning where species primarily do not share their principal resources and segregate (MacArthur & Levins, 1967; Rosenzweig, 1981) or secondarily, when species overlap in their preferences for primary resources while showing partitioning with respect to less important ones (Gurd, 2008; Rosenzweig & Abramsky, 1986). Temporal and spatial niche partitioning might be occurring as well. According to temporal niche partitioning, the times of utilization of resources differ (Armstrong & McGehee, 1980; Chesson, 1985). Spatial niche partitioning refers to different locations of where the resource is utilized (Chesson, 1985; May & Hassell, 1981).

A spatial niche can be formed in a homogenous or heterogeneous environment. In a homogeneous environment, it results from species exploiting different resources but the degree of exploitation depends on the life histories of species rather than the habitat attributes. It is an individual’s or a species’ character rather than the environment which allows them to partition (Chesson, 2000). For example, different wading birds utilize different areas relative to the waterline based on specific adaptations for aquatic browsing, filter-feeding and grazing (Kear, 2005). Due to evolved differences in a particular character, species exploit specific resources in the habitat enabling them to coexist. Spatial niches formed in heterogeneous environments are the response of species to environmental attributes (Chesson & Huntly, 1997). Species may compete for a limiting resource but the degree to which each species responds is affected by resource limitations depending on different attributes like elevation, temperature and humidity. For example, 11 species of *Anolis* lizard species (which were similar in morphology) were able to coexist because they utilize different elevations, amount of sunlight and moisture levels within a habitat (Williams, 1983).

Spatial heterogeneity of resources also explains a possible mechanism for species coexistence. Spatial heterogeneity in a habitat can result in competing species having a different response to a common competitive environment (Chesson, 2000). Thus, a spatially heterogeneous environment can have different patches, distribution of resources, environmental conditions and species composition (Fahrig & Merriam, 1994) that vary spatiotemporally. This may depend on the observation scale and/or habitat type under which the study is conducted (Wiens, 2000). One such study showed a complex relationship between habitat heterogeneity and species coexistence, resource partitioning and competition among syntopic populations in swamp rats *(Rattus lutreolus)* and long-tailed mice *(Pseudomys higginsi)* in wet sclerophyllous forest (Monamy & Fox, 1999). Male and female swamp rats were found to select open and dense canopy cover habitat, respectively, and, during breeding season, more long-tailed mice were found in open canopy cover areas (Monamy & Fox, 1999).

Sometimes niche partitioning can occur but without a change in niche breadth. In this case, species are specialized to use certain microhabitats more than others. Partitioning could be the result of physiological, psychological or behavioral differences between the species found in same habitat (Lack, 1940).

Niche partitioning may not be the only mechanism allowing two species to coexist. The vacant or empty niche concept could also explain coexistence (Rohde, 2008). It is opposite of the classical niche concept, suggesting that "niche" is a property of the environment rather than a species. A vacant niche contains resources that are not used by any species but have the potential to be utilized (Cornell, 1999; Tilman & Lehman, 2001). In such a situation, species may coexist without competition at a particular time because not all available resources are being used by existing species (Rohde, 2005). Further, coexistence occurs now but as the niche becomes more occupied, there will be more competition.

Burrowing ecology

Different animals have evolved to take advantage of different refuges within their environment (Reichman & Smith, 1990) to avoid predation or temperature extremes (Laundre, 1989). Examples of these refuges are caves (Howarth, 1980), hollow trees or above ground leaf nests (Pérez, 1992; Reichman & Smith, 1990), cavities among rocks (Pérez, 1992) and underground burrows (Ruffer, 1965). Underground burrows can take many shapes and are the result of different excavation techniques. Burrowing can be the result of combined actions such as trampling, wallowing and digging that excavates or moves soil, enabling animals to live underground (Shiemer, 1903).

Burrowing animals can be divided into two groups, fossorial and semi-fossorial. Fossorial animals spend most of their time living and foraging underground (e.g. moles). For these organisms, the energy acquired due to foraging underground exceeds the energy expended for burrowing. They have evolved efficient modes of burrow construction and display adaptive features like reduction of hind-limbs, eyes and external ears (Heffner & Heffner, 1990). These features can be seen in both of the fossorial armadillo species, the greater fairy armadillo (*Calyptophractus retusus*, reviewed in Smith & Owen, 2017) and the pink fairy armadillo (*Chlamyphorus truncatus*, reviewed in Cei, 1967).

Unlike fossorial species, semi-fossorial animals do not spend all their time underground. While they construct burrows for shelter and nesting (Seymour & Ackerman, 1980), they forage and search for mates above ground. Nine-banded armadillos and gopher tortoises are both examples of semi-fossorial animals. Some semi-fossorial burrows with same volume as fossorial burrows are less complex (White, 2005) and may require more energy to construct (White, Matthews, & Seymour, 2006). This is because semi-fossorial animals may not have adaptations that would reduce energy expenditure for burrowing. Some animals do not expend energy to construct burrows but just use those constructed by others. For example, the six-lined racerunner (*Aspidoscelis sexlineatus)* and northern bobwhite quail *(Colinus virginianus)* utilize gopher tortoise burrows (Cox, Inkley, & Kautz, 1987).

Signs of burrowing adaptations in vertebrates were first recorded in fossils from the Carboniferous period (Olsen & Bolles, 1975). In mammals burrowing evolved independently numerous times in different mammalian orders such as Marsupialia, Insectivora and Rodentia (Anderson & Jones, 1984). In addition early fossils of xenarthrans (a superorder that includes Cingulata and Pilosa) show burrowing adaptations present in the middle Paleocene (61.6-59.2 mya) (Avilla, Abrantes, & Bergqvist, 2004). Generally, mammalian digging adaptations include sturdy forelimbs with well-developed claws and a skeletomuscular system adapted to produce active transmission of powerful forces required for digging (Reichman & Smith, 1990). Likewise, a compact and cylindrical body shape in mammals facilitates burrowing. Extant armadillos and many extinct xenarthrans displayed fossorial adaptations in early and mid-Miocene (23-15 mya) (Vizcaíno, Bargo, Kay, & Milne, 2006). For example in armadillos, the olecranon process of the ulna extends beyond the juncture with the humerus which magnifies the force exerted by muscles of the upper limbs and back (Miles, 1941). Cingulates vary in extent of their burrowing lifestyles (fossorial, burrowing and/or digging, and no digging adaptations; reviewed in Nowak, 1999). They are effective diggers and burrowers that lost arboreal adaptations present in the xenarthran common ancestor (Gaudin & Croft, 2015).

For a species, the decision to dig burrows in a space might be influenced by microhabitat variables such as sloped surfaces for nine-banded armadillos (Zimmerman, 1990), food patches for pygmy rabbits (*Brachylagus idahoensis)* (Gahr, 1993) and vegetative cover for Columbian ground squirrels (*Spermophilus columbianus)* (Young, 1990). Depending on the species, burrows can have different functions. For example, Norway rats *(Rattus norvegicus)* have different burrows for residence, food storage and refuge to escape predators (Steiniger, 1952). *Gopherus dasyurus* has a few complex burrows that have four to five openings and a nest chamber used by females and/or litters. They also have simple burrows with two to three openings but without a nest (Shenbrot, Krasnov, & Khokhlova, 1997). Armadillos utilize a number of different physical spaces underground such as shelter (Z. J. Butler, pers. comm.), nesting and feeding burrows (i.e., food probes in Zimmerman, 1990).

Two burrowing species can cohabit the same area. Most studies done on syntopic burrowing species suggest that spatial niche partitioning promotes coexistence. In the case of two wolf spider species (*Geolycosa xera archboldi* and *G. hubbeli*), *G. xera archboldi* was found in xeric habitat (sand pine scrub with rosemary), whereas *G. hubbelli* was abundant in mesic habitat with an open canopy (Carrel, 2003). Another example involves syntopic rodents, where a bipedal jerboa, *Jaculus jaculus,* used a small portion of overall resources available. They were less dependent on their burrows and were frequently in search of new food patches. Whereas the quadrupedal *Gerbillus gerbillus* stayed close to burrows and utilized most of the food resources around them (Schröpfer & Klenner-Fringes, 1991).

Another example of two syntopic burrowing species is the armadillo and gopher tortoise found in the southeastern United States. For both species, burrows are important resources (Kinlaw, 2006b). While they coexist, the mechanism for this coexistence is not fully understood. So, this study is focused on understanding the mechanism for the placement of burrows of armadillos and gopher tortoises in a common habitat.

Life history of nine-banded armadillos

The nine-banded armadillo migrated into Georgia and Florida from Mexico within the last 150 years (Davis & Schmidly, 1994; Humphrey, 1974; Stevenson & Crawford, 1974; Taulman & Robbins, 2014). In North America, armadillos were first recorded in the lower Rio Grande Valley of Texas around 1849 (Audubon & Bachman, 1854). Soon, they began to spread north and east and their expansion was facilitated by roadways built by European colonists (Taulman & Robbins, 2014). Armadillos crossed the Mississippi River in the early 1940s (Humphrey, 1974) and continued moving eastward. In the 1920s there were several releases of captive armadillos in south central Florida creating a divided distribution. The Florida population subsequently expanded its range into Georgia (Humphrey, 1974; Stevenson & Crawford, 1974) and up the Atlantic coast through South Carolina to southeastern North Carolina (Taulman & Robbins, 2014). The Florida and Texas populations have now merged, resulting in the continuous distribution of the species throughout the southern United States (Taulman & Robbins, 2014).

Armadillos are asocial, nocturnal mammals with poor eyesight (McBee & Baker, 1982). Their estimated life span is around 15-17 years (C. M. McDonough, pers. comm.) although a captive individual lived 24 years (S. McPhee, pers. comm.). Males reach sexual maturity (production of viable sperm) at 1 year of age (McCusker, 1977) but may not have mating opportunities until older. Females are mature at about 18 months (McDonough, 1997; Peppler, Hossler, & Stone, 1986). They produce identical quadruplets (i.e., four genetically identical young; Prodohl, Loughry, McDonough, Nelson, & Avise, 1996). This type of reproduction is referred to as polyembryony (Newman & Patterson, 1910). Breeding is seasonal (McDonough, DeLaney, Quoc Le, Blackmore, & Loughry, 2000) with the majority of mating occurring in June and July in the United States. This species has delayed implantation, meaning they breed during the summer; the fertilized egg goes into stasis after a few divisions and implants in uterus in November (Enders, 1966). This process allows the birth of young to occur in spring with presumably increased food resources. Young emerge from burrows in early summer.

Armadillo diets consist of small invertebrates such as insects (mostly adults and larvae of beetles and ants as well as termites), occasionally fruit, small vertebrates and vertebrate eggs (Loughry & McDonough, 2013). Armadillos are preyed upon by different vertebrates like American alligator *(Alligator mississippiensis)* (McNease & Joanen, 1977; Shoop & Ruckdeschel, 1990), large felids (Carr, 1982; Kalmbach, 1943; Maehr, Belden, Land, & Wilkins, 1990), canids (Best, Hoditschek, & Thomas, 1981; Layne, 1976; Schrecengost, Kilgo, Mallard, Ray, & Miller, 2008) and black bear (*Ursus americanus)* (Bushnell, 1952; Stratman & Pelton, 1999). They frequently die following collisions with motor vehicles (Inbar & Mayer, 1999).

Armadillos are highly adaptable mammals and are found in hardwood forests and riparian areas across their range but are not as numerous in mature pine forest and agricultural fields (Gammons, Mengak, & Conner, 2009; McDonough et al., 2000). They have also been recorded inhabiting open prairie (Platt, Rainwater, & Brewer, 2004), grassland (Zimmerman, 1982) and scrubland (Gammons et al., 2009) but these are not their preferred areas. Male and female armadillos do not differ in general habitat selection, nor do they change habitats in different seasons (McDonough et al., 2000, Gammons et al., 2009).

Within a habitat, armadillos have distinct home ranges (Breece & Dusi, 1985; Clark, 1951; Fitch, Goodrum & Newman, 1952; Galbreath, 1980; Jacobs, 1979; Layne & Glover 1977; McDonough, 1994). Breeding males expand their home ranges during the mating season in Texas (McDonough, 1994) and home ranges of both males and females have been found to contract during winter on a coastal island in Georgia (Bond, Nelson, & Warren, 2000). Females have overlapping home ranges with males (Bond et al., 2000; Breece & Dusi, 1985; Clark, 1951; Fitch et al., 1952; Gammons et al., 2009; Herbst &

Redford, 1991; Jacobs, 1979; Layne & Glover, 1977; McDonough, 1994; Schell, 1994; Smith, 1992; Suttkus & Jones, 1999; Zimmerman, 1982).

Previously, researchers have anecdotally mentioned armadillo burrows being placed under thick, thorny brush (Taber, 1945) and fallen trees, next to tree roots and stumps and along sloped surfaces (Sawyer, Brinkman, Walker, Covington, & Stienstraw, 2012) but preference studies (comparison with random sites) were not performed. A few researchers have suggested that armadillos dig burrows in loamy and sandy soils with abundant canopy cover (Arteaga & Venticinque, 2008; Humphrey, 1974) but they also did not perform preference studies. Likewise, anecdotal reports suggest they avoid marshy areas of excess water (Davis & Schmidly, 1994) and may place burrows in areas with abundant insects which is related to rainfall and seasons (Wirtz, Austin, & Dekle, 1985). They may also build burrows throughout their home range but have been found in the Amazon to use areas located at lower elevations in the forest (Arteaga & Venticinque, 2008).

Adult armadillos use multiple burrows (Taber, 1945; Taylor, 1946); one to four burrows in one study (Bond et al., 2000) and up to 20 in another (C. M. McDonough, pers. comm.). They may stay in one burrow for a series of days before moving to another and this switching of burrows is greater in summer than winter (Bond et al., 2000). Burrow diameter can vary according to habitat type (Zimmerman, 1990) and geographical region (McDonough et al., 2000; Platt et al., 2004) as burrow width is related to diameter of their body. Burrows can be classified as shelter, nest or feeding. Shelter burrows are deeper and are devoid of nest materials; nest burrows are filled with pine straw or leaves. Feeding burrows are associated with probing for food and typically have a length ≤ 30 cm (Zimmerman, 1990). An armadillo's poor capability to generate heat (McNab, 1980) may play an important role in their decision to build a nest inside a burrow. Even though a burrow packed with nest material may limit oxygen levels, armadillos have the ability to survive in low oxygen environments (Johansen, 1961).

Two studies have found that compass orientation of burrow entrances was independent of direction (Platt et al., 2004; Zimmerman, 1990). Other parameters within the environment have been found to be linked to burrow placement. Different parameters like canopy cover, vegetation, elevation, slope of terrain and sunlight have been suggested as important for burrow placement (Arteaga & Venticinque, 2008).

While commensal usage of burrows has been well documented in species such as the gopher tortoise, researchers have only recently started to census other species that cohabit armadillo burrows. In the southeastern U.S. armadillo burrows provide refuge to different animals like Atlantic ghost crabs (*Ocypode quadrata)*, southern toads *(Anaxyrus terrestris),* eastern diamondback rattlesnakes *(Crotalus adamanteus),* coachwhips *(Coluber flagellum)*, eastern towhees *(Pipilo erythrophthalmus),* hispid cotton rats *(Sigmodon hispidus)* and opossums *(Didelphis virginiana)* (Butler & Coleman, 2018). There are also records of utilization of burrows by invasive species like Burmese python (*Python molurus)* (Metzger, 2013) and Tegu (Klug, Reed, Mazzotti, McEachern, & Vinci, 2015).

Life history of gopher tortoises

Gopher tortoises are native to the southeastern United States (Auffenberg & Franz, 1982) with populations in Georgia, Florida, southern South Carolina, Alabama, Mississippi and southeastern Louisiana (Diemer, 1992). They are protected throughout their range and are listed as vulnerable on the International Union for Conservation of Nature red list of vulnerable species (IUCN, 2019). They have state status as a threatened species within Georgia and Florida while in South Carolina, gopher tortoises have state endangered species status (US fish and wildlife service, 2018). Tortoise populations in western Alabama, Mississippi and Louisiana are federally listed as threatened under the US Endangered Species Act. The eastern population is currently a candidate for federal listing as threatened.

Gopher tortoises are found in various habitat types that include longleaf pine forests, pine flatwoods, scrub woodlands, mixed hardwood pine forests, coastal grasslands and dry prairies. Within these habitats, gopher tortoises are likely to be found in open canopy woodlands with abundant herbaceous cover and anthropogenic habitats including pastures and clear cuts (Auffenberg & Franz, 1982; Baskaran, Dale, Efroymson, & Birkhead, 2006; Breininger, Schmalzer, & Hinkle, 1994).

An adult gopher tortoise burrow varies in length depending on soil type but can be as long as 4.5 m and 2 m deep (Diemer, 1989). Their burrows may` be located along edges such as fire-lanes or roads because such places provide breaks in dense canopy cover (Layne, 1989; McCoy & Mushinsky, 1991; McRae, Landers, & Garner, 1981) and have fewer predators (Baskaran et al., 2006; Kowal, Schmolke, Kanagaraj, & Bruggeman, 2014; Stewart, Austin, & Bourne, 1993). Gopher tortoises dig burrows in well-drained sandy soils (Baskaran et. al., 2006; Jones & Dorr, 2004). Areas are typically more xeric and exhibit greater fire frequencies that stimulate pyric plant communities that benefit tortoises (Ashton & Ashton, 2008; Kaczor & Hartnett, 1990; Yager, Heise, Epperson, & Hinderliter, 2007). Gopher tortoises avoid burrowing in wetlands and soils with heavy clay content (Kushlan & Mazzotti, 1984).

Gopher tortoises have been referred to as ecosystem engineers because of their burrow construction. Their burrows provide shelter for more than 360 species (Lips, 1991). Southern cricket frog *(Acris gryllus dorsalis),* eastern indigo snake *(Drymarchon couperi)*, gopher frog *(Lithobates capito)*, southeastern five-lined skink *(Eumeces inexpectatus),* Florida mouse *(Podomy floridanus)* and Florida pine snake *(Pituophis melanoleucus mugitus)* are examples of commensal vertebrates that live within gopher tortoise burrows (Kent & Snell, 1994). As they play critical role (provide resources) in the ecosystem and help to maintain local diversity, gopher tortoises also are considered a keystone species (Eisenberg, 1983).

Estimation of age in gopher tortoises is generally based on carapace length and morphology (Auffenberg & Iverson, 1979; Landers, McRae, & Garner, 1982; Wilson, 1991). In southwestern Georgia, a hatchling (< 1 year old) carapace length measures 43-55 mm. Hatchlings range in width from 32.0-51.8 mm in Florida (Smith, 1995) and 46.4 ± 0.5 mm in southeast Georgia (Dziadzio, 2015). The juvenile stage (1-4 year old) has a length of 50-120 mm. Subadult carapaces are 120-230 mm long, representing 5-10 years of growth. Adults measure > 230 mm in carapace length (Doonan & Stout, 1994; Landers et al., 1982) and a female reached a maximum size of 387 mm in south Florida (Timmerman & Roberts, 1994). Burrow width is strongly correlated to the carapace length of the resident tortoise (Alford, 1980; Hansen, 1963; Martin & Layne, 1987; Wilson, Mushinsky, & McCoy, 1991). While these measurements can be used to assign an age classification to a burrow occupant, the variation in size at maturity described above and variation in burrow occupancy can confound size estimates of breeding populations based on carapace length across sites (Smith, Breininger, & Larson, 1997).

Geographic variation and differences in habitat structure, soil types or current forestry practices are related to variation in population structure and reproductive success of gopher tortoises (Aresco & Guyer, 1999; Smith et al., 1997). In Georgia life span is estimated to be about 60 years or longer (Landers et al., 1982), reaching maturity at 9-21 years (Landers et al., 1982, Mushinsky, Wilson, & McCoy, 1994). In north Florida and Georgia, adults have been observed in courtship from April to June, to lay eggs from May to June and to produce hatchlings in August and September (Moore, Strattan, & Szabo, 2009). They lay a single annual clutch of five to nine eggs (Diemer & Moore, 1994) in the aprons of burrows (mounds of dirt formed during construction) or in other open sandy areas.

In Georgia female and male adults use four and seven burrows, respectively, on average within a given year, while juveniles use one to two burrows (McRae et al., 1981). Even though juvenile gopher tortoises use several burrows, they spend more than 70% of their time in their primary burrow (Wilson, Mushinsky, & McCoy, 1994).

Home range of gopher tortoise can vary in size from 0.04 to 2.24 ha (Eubanks, Hollister, Guyer, & Michener, 2002). Juvenile home range is about 40 m^2 to 0.25 ha in a north Florida population (Diemer, 1992). Home-range size and movements of gopher tortoises may expand depending on habitat quality (Diemer, 1992; Mushinsky & McCoy, 1994), resources and density (Eubanks et al., 2002; Smith, 1995). Home range decreases with an increase in amount of herbaceous ground cover (Auffenberg & Iverson, 1979; Mushinsky & Gibson, 1991).

Gopher tortoises are diurnal (Mushinsky, McCoy, Berish, Ashton, & Wilson, 2006; Tuberville, Clark, Buhlmann, & Gibbons, 2005) but in summer they have been reported to move after sunset for a few hours and males have been recorded visiting female burrows after midnight (J. M. Lockhart, pers. comm.). Daily activity for adults forms a unimodal pattern in spring but a bimodal pattern during summer with peaks in late morning and late afternoon (McRae et al., 1981). In contrast juveniles are active mid-day in summer, using urination and salivation to avoid heat stress (Douglass & Layne, 1978; Rose & Judd, 1975), and do not form a bimodal pattern (Wilson, Clark, Buhlmann, & Gibbons, 1994).

Juveniles are only above ground to feed and disperse (Berry & Turner, 1986; Douglass & Layne, 1978). Their activity pattern is influenced by predator activity and thermoregulation (Wilson et al., 1994). Juveniles are found in thicker ground vegetation than hatchlings. They are also found under structures such as logs, fallen tree limbs, and stumps (Aresco, 1999). It is reported that juveniles are even cryptic in open areas and use shrubby areas for protection from predators (Beyer, 1993; Wilson, 1991).

Hatchling recruitment rate of gopher tortoises is presumed to be low in many populations (Butler & Hull, 1996; Congdon, Dunham, & van Loben Sels, 1993; Epperson & Heise, 2003; Heppell, 1998; Smith, 1997; Smith et al., 2009). Besides building their own burrows, hatchling gopher tortoises may use adult burrows (Smith, 1992) or holes and shallow depressions under thick vegetation (Butler & Hull, 1996; Guyer & Hermann, 1997; Pike, 2006; Smith et al., 1997). Both low recruitment and use of alternative shelters may be why hatchlings are recorded low in the population surveys (Smith et al., 2009).

Interactions between armadillos and gopher tortoises

Range expansion of armadillos from Texas and Florida into Georgia brought them in contact with gopher tortoises, a native inhabitant. Due to releases of captive armadillos, the first co-occurrence between these species occurred in Florida (Kinlaw, 2006b). Based on their life histories, potential competition for space exists. Armadillos might affect gopher tortoise demographics, but their presence does not seem to exclude gopher tortoises. There are a few instances reported where armadillo have negatively affected gopher tortoises. Armadillos have been found to occupy gopher tortoise burrows (Guyer & Hermann, 1997). Usurping of gopher tortoise burrows by armadillos has also been observed in my study site. Armadillos also depredate gopher tortoise eggs (Douglass & Winegarner, 1977; Smith et al., 2013) and were attracted to remnants of eggs as well as invertebrates present in depredated nests (Drennen et al., 1989). This attraction to depredated nests or eggs may be dependent on a high density of gopher tortoise nests (Degroote, Ober, McDonough, & Mizell III, 2013).

There also have been cases of aggressive interactions between gopher tortoises and armadillos (Dziadzio et al., 2016). During gopher tortoise nesting season (June and July), females were found to be aggressive toward armadillos, suggesting that females were guarding their nests. Also, the reverse has been reported, that is, armadillos have been aggressive towards gopher tortoises when confined together (Galbreath, 1982). When aggression or interference toward each other is observed, local displacement in the environment can occur. This evidence suggests a possibility that there could be competitive interactions between the two species. Burrow placement could reflect these interactions. Also, presence of coopted burrows in this study site (personal observation) implies armadillos use gopher tortoise burrows for nesting and/or shelter. Although the two species’ burrow distributions have been found to be independent of one other (Anderson et al., 2016), identifying microhabitat preferences, if any, and comparing between the two species will enable me to determine if coexistence occurs because of niche partitioning or if these species are specialized to use certain parameters available in the environment. This will also enable me to understand if these organisms are in some stage that supports the empty niche concept.

Chapter III

MATERIALS AND METHODS

Study Area

This study took place on Moody Air Force Base in Lowndes County, 14 km northeast of Valdosta, Georgia (around 30^{0}58’42” N and 83^{0}11’08” W). The specific study site covered 13.52 ha adjacent to the base’s main airstrip (Figure 1, 2). The site was dominated by planted loblolly pine *(Pinus taeda*) with mixed species of hardwoods. Ground cover included blackberry *(Rubus sp.)* and *Smilax* sp. with grasses and shrubs. Current vegetation communities in the study site were the result of land changes that occurred in 1980-1981. Important events in the study site included the establishment of the pine stand in 1980, the removal of every third row of trees in 1998 and the clearcutting of the western portion of the study area in 2015. Prescribed burns have been carried out in 2001, 2003, 2006, 2014, 2015 and 2017 (Moody Air Force Base records, G. W. Lee, pers. comm.).

The specific site was composed of 77.6% (10.53 ha) woodland and 22.4% (2.99 ha) grassland (measured using ArcGIS area calculator). The open grassland was the result of the 2015 clear cut and recently has been seeded with longleaf pine (*Pinus palustris*). In addition to the disturbances already mentioned, the site contained woodpiles and five berms. Berms, which total 0.06 ha, are mounds of dirt about 1 m high and were created when the area was windrowed in 1979 (Figure 2b). Two types of soil were found in the study site. Stilson loamy sand was more prominent at 64.1% while Tifton urban land complex made up 35.9% (USDA, 2017).

For both armadillos and gopher tortoises, burrows were a prominent factor indicating their presence. Stratified sampling was used to survey burrows in the entire plot during September 2016–January 2017. Strata were based on the rows of planted pines and each row was searched intensely for burrows. In the clear cut area, the ground was searched thoroughly by delineating parallel strips of land with flags. The berms were usually within a pine row and were checked on either side and on top for burrows. In January 2017 the study site was burned and afterward, was resurveyed in Febraury–May 2017 for any additional burrows using the same survey technique.

Burrows

Burrows were individually identified by a unique number on a metal tag, usually placed on the right-hand side as you face the burrow entrance. The coordinates for each burrow were recorded with a scientific grade GPS (Trimble Geoexplorer 6000 series). At least 100 fixes were taken per location and then averaged. For burrows located close together (within 2 m), 200 fixes were taken to improve accuracy. In addition, prominent physical features in the vicinity were noted such as whether the burrow was on a berm, within a woodpile, or under a fallen log, stump or tree root. Presence of these features help to construct, establish and protect burrows.

Determining burrow type (armadillo or gopher tortoise) was based on entrance shape. Armadillo burrows have a circular opening (Kinlaw 2006b; McDonough et al., 2000) and were further classified into regular or feeding burrows. If burrow length was ≤

25 cm, then they were considered feeding burrows; this is slightly different from Zimmerman (1990) who consider feeding burrows to be < 30 cm.

Gopher tortoise burrows have a half-moon shape (Auffenberg & Franz, 1982) with a prominent mound of sand or "apron" around the burrow entrance (Cox et al., 1987). Burrow entrance size reflects the size of the carapace of the resident tortoise because carapace length is correlated to burrow width (Doonan & Stout, 1994). I classified burrows with a width < 55 mm as hatchling, 55-220 mm as juvenile/subadult and > 220 mm as adult based on information of age classes from Doonan & Stout (1994).

Burrows with a distinct gopher tortoise entrance but packed with nesting material with an opening the shape of an armadillo burrow were considered "coopted". At times, coopted burrows will revert back to gopher tortoise burrows if nesting material is removed and fresh signs of gopher tortoise activity are found. Even though history of burrow interchange between the two species is interesting, these burrows were not included in the analysis of microhabitat selection.

Activity status

All burrows were classified as active or inactive (Auffenburg & Franz, 1982). If an animal was seen in the entrance or there was evidence of recent activity (such as excavated soil, tracks or scat), the burrow was considered active. An inactive classification was given if the entrance was intact and clear of major obstructions but lacked signs of recent activity. Burrows were considered abandoned if they were obstructed or collapsed and not in usable form. It was not always possible to determine whether a burrow was definitely active or inactive, so I recorded these burrows as questionable.

Microhabitat selection

Using a random number table, 40 armadillo burrows were selected by location such that 20 burrows each were on and off the berms. Similarly, 46 gopher tortoise burrows were chosen such that I selected 20 burrows each for adult and juvenile/subadult age classes. Only 6 hatchling burrows were present and used during microhabitat data collection period. So, in total, I took measurements for 86 burrows (Figure 3). To compare burrow sites with non-burrow locations, 250 random points (Figure 4) within the study area were generated using the “spatstat” package (Baddeley, Rubak, & Turner, 2019) in R version 3.5.1 (R core team, 2018). I took the same measurements (see below) for random points as I did for the 86 burrow locations.

Based on a review of the literature, parameters chosen for microhabitat analysis were characterized as either burrow or habitat parameters. Burrow parameters were variables that helped to identify the occupant of the burrow or were not an element of the habitat. I compared intrinsic burrow parameters such as height, width, ratio of height and width and tunnel angle between armadillos and gopher tortoises. I included whether an armadillo burrow had a nest or not as another burrow parameter when comparing burrows on and off berm.

Burrow height and width are important in identifying armadillo burrows (Medri, Mourão, & Rodrigues, 2006) and determining the potential age of occupant for gopher tortoise burrows (Landers et al., 1982). Maximum height and width at the entrance were measured to the nearest 0.1 cm using calipers. I also calculated the ratio of burrow height to width in order to identify armadillo and gopher tortoise burrows because of the different profiles of burrow entrances.

Tunnel angle within the burrow was found to differ between the two species in previous studies and so could aid in differentiating between the two types of burrows. Gopher tortoise tunnel angle has been reported to be 29° (Hansen, 1963) and 33.5° for armadillos (Sawyer et al., 2012). Tunnel angle (to the nearest 0.1 degree) was measured 10 cm inside the burrow entrance using the Clinometer application for a smart phone "smarttoolfactory".

Compass orientation of the entrance may be affected by human disturbances on an active military base. Man-made environmental noise, such as sound vibrations from planes taking off and landing, might affect an animal's behavior. Entrances being built in a particular compass direction could indicate a possible effect. Because the study site lies directly east of the main airfield, if sound vibrations do affect orientation, then I expected the entrance of burrows to be oriented away from the airfield in an easterly direction. Likewise, if winter climatic conditions are unfavorable to organisms, in order to minimize wind coming from a northerly direction, burrows should show a southern orientation. I determined the compass direction facing outward from each entrance using the iPhone Compass application.

Armadillos use burrows for thermoregulation (McNab, 1980). Nest material can help insulate burrow from cold air. So, to determine whether a burrow had nest material (i.e., nest burrow) or not (i.e., shelter burrow), a borescope (Provision PV 64-960 96", 10.5 mm obedient shaft Provision 960) was used.

To test whether habitat parameters (see Table 3) may influence the placement of burrows, I recorded the following environmental parameters; slope (inclination of ground), amount of sunlight, canopy cover, total above ground vegetation density, ground visibility near the entrance, amount of temperature modulation, distance to edges and elevation. I also measured these features for the 250 random points without burrows.

Slope at ground level was measured using the same application as for tunnel angle. These two measurements differ as tunnel angle was taken inside the burrow and slope of ground was measured outside, directly above the entrance. For armadillo burrows off berm, a straight pole was placed over the burrow, spanning the distance from the point above the entrance to ground in front. A smart phone was placed on this pole and slope was recorded. Because of the variation in slope of terrain around armadillo burrows on berms, two measurements were recorded, and the average calculated. The first measurement was taken on the ground directly above the burrow entrance. Because the mound of dirt from the construction of the burrow may affect the slope in front, the other measurement taken was along the side of the mound, avoiding the raised portion. For random points, the smart phone was placed on the surface of the ground.

Sunlight is important for gopher tortoises for basking, foraging and incubating eggs. Also, a decrease in canopy cover may be associated with an increase in herbaceous vegetation, an essential food source for gopher tortoises (Auffenberg & Franz, 1982; Mushinsky et al., 1994) and a factor in burrow placement (Auffenberg & Franz, 1982; Mushinsky et al., 1994; Rostal & Jones, 2002). The amount of sunlight in the vicinity of a burrow was measured with a lux meter on sunny days in five locations; four measurements were taken at 2.5 m from entrance at each of the four compass directions and one directly in front of the burrow. These five measurements were then averaged. Similar to sunlight, percent canopy cover was recorded in the same five locations using a densitometer. Values were averaged for each burrow and at each random point.

LiDAR vegetation data for the study site were obtained from Moody Air Force Base officials and above ground vegetation density was calculated in ArcGIS. The "spatstat" package in R was used to extract total vegetation density for burrows and random points.

The amount of vegetation around the entrance of a burrow affects its visibility. Thus, visibility could be an index for ground cover. Visibility was measured using a checkered board (43 x 31 cm) of alternating black and white squares (each color had 66 squares measuring 2.5 cm^2). The board was placed at the opening of the burrow. At 3 m, in front of the entrance, the number of black blocks visible was recorded. The visibility percentage was determined by dividing the number by 66. For example, if 33 black blocks were visible, the visibility percentage would be 50% (33/66 = 50%).

I recorded visibility measurements at 4 and 16 months post burn. Vegetation after a burn is sparse but over time ground cover quickly becomes established and ground visibility is expected to decrease. To see if this occurred, I compared the visibility recorded at the two time periods.

Anthropogenic disturbances such as military exercises (Kowal et al., 2014) can impact placement of burrows (Lau & Dodd, 2013). To determine if human disturbances had an effect on burrow placement, I measured the shortest distance (in meters) from the burrow to the nearest hard edge (paved or gravel roads, firebreak or study site boundary, see Figure 2b.) using the NN join function in QGIS Desktop 3.2.3.

To compare temperature across the two burrow types and to measure differences between temperatures within and outside burrows (temperature modulation), I used Thermocron iButtons. I attached iButtons to 1 m long flexible metallic tubing using zip ties. I maneuvered the tubing inside the burrow as far down as possible (maximum 1 m). I then measured how far the tubing was in the burrow and placed a second iButton with tubing the same distance on the ground surface in the direction of the burrow's tunnel. 1-Wire® software was used to import the temperature data from iButtons. Temperature was taken every 5 minutes for 72 hours and averaged over 1-hr blocks. In order to compare and help control for environmental and temporal variation, one burrow of each type was measured during the same 72-hr period. Data were taken during winter (December 2017-January 2018) and summer (July-August 2018) seasons and analyzed separately for 12-hr periods of day (6:00 am-17:00 pm) and night (18:00 pm-5:00 am). I compared the temperature difference to see how the animals' burrows modulate temperature during summer and winter.

I prepared a digital elevation model (DEM) for the study area using Google Earth Pro and QGIS desktop (Figure 5). Elevation of the study area varied only 6 m, ranging between 63-69 m. The grassland region on the west side ranged from 66-69 m and woodland 63-67m while berms ranged 63-66 m. I derived elevation for burrows and random points using the model.

I recorded if support structures such as a fallen log, tree (live or dead) stump or woodpile were found in the random sites. It was compared with burrow support structure associated with burrows.

Detectability of burrows

Burrows identified after the burn that were not previously recorded could be newly constructed, previously missed or ones that lost their metal tag. To eliminate accidental resampling of previously tagged burrows, those newly detected after the burn that were near previously recorded burrows were cross-checked during 2018 to confirm that they were a new burrow. That is, all burrows close in proximity were checked in the field to make sure there were actually two burrows and not one. Detection in the pre-burn survey would be the number of burrows observed in first survey divided by the total number observed after the second survey. To determine if different age classes of gopher tortoise burrows or locations of armadillo burrows were more visible during the first survey than others, detectability was calculated for all the types of burrows.

Data Analysis

Shapiro-Wilk test was used to test the normality of variables. The non-parametric Mann-Whitney test was used to compare burrow parameters (height, width and tunnel angle) between burrows on berm and off berm. Unpaired *t*-tests were used to compare means of variables between armadillo and gopher tortoise burrows and between armadillo burrows on and off berms.

To compare variables among gopher tortoise burrows of different age classes, I used one-way ANOVA. If the result was significant, I ran Tukey's *post-hoc* tests to see where significant differences lie. Comparison of temperature between day and night, burrow type, and for inside versus outside the burrows was tested with two-way ANOVAs. This test was also used to compare visibility between armadillo and gopher tortoise burrows for four months and sixteen months after the prescribed burn. Hatchling burrows were low in number, so they were removed from this analysis. Visibility data used in all previous analyses were from 16 months following the prescribed burn.

For gopher tortoise burrow orientation, I used a modified version of Rayleigh's test to determine if circular uniformity can be rejected in favor of the alternative hypothesis of unimodal pattern with a specified mean direction, that is, east (away from the airfield) and south (in the direction of increased sunlight). Because the orientation of armadillo burrows appeared to be multimodal, I used Kuiper's test of circular uniformity (instead of Rayleigh's test). Tests were carried out in R using "circStats" package (Lund & Agostinelli, 2018).

The variables (see Table 3) used in the microhabitat analysis could be highly correlated with each other and could affect the outcome, so a multicollinearity analysis was done. Because the value of variation inflation factor (VIF) was less than 2 and tolerance was less than 0.2 for all the variables, they were used in the analysis (Table 4). A principal component analysis was performed in R 3.5.1 on non-categorical variables to see how much of the variation between species could be explained by each variable. The "factoextra" package (Kassambara & Mundt, 2018) in R was used to create the biplot for the principal components analysis. I performed linear discriminant analysis using XLSTAT to evaluate which microhabitat variables were most influential in differentiating different groups. Linear discriminant analysis was performed for the following comparisons: 1) between armadillo burrows off berm, gopher tortoise burrows and random off berm sites; 2) between adult and juvenile gopher tortoise burrows and random off berm sites (because the sample size of hatchling burrows was less than the variables used in the discriminant analysis, it was not included); and 3) between armadillo burrows on and off berm from random sites on and off berm.

Chi-squared goodness-of-fit tests were used to compare the frequency of physical features such as logs and stumps that were associated with armadillo and gopher tortoise burrow entrances. In the analysis of support structures, I removed two features, presence of large roots and presence of a woodpile, because at random sites, I did not record any woodpiles and underground roots were not visible. I added frequencies of fallen logs and stumps together to analyze the use of support structures for burrow construction. For the analysis of these burrow support structures with random sites, Fisher exact tests were conducted. Again, to determine if differences in detectability of armadillo and gopher tortoise burrows exist, I used Chi-squared goodness-of-fit tests. If observed frequencies differed from expected, Pearson's standard residuals were used to determine which frequencies contributed to the difference. I used a significance level (α) of 5% for all statistical tests. QGIS desktop 3.2.3 was used in mapping the study area.

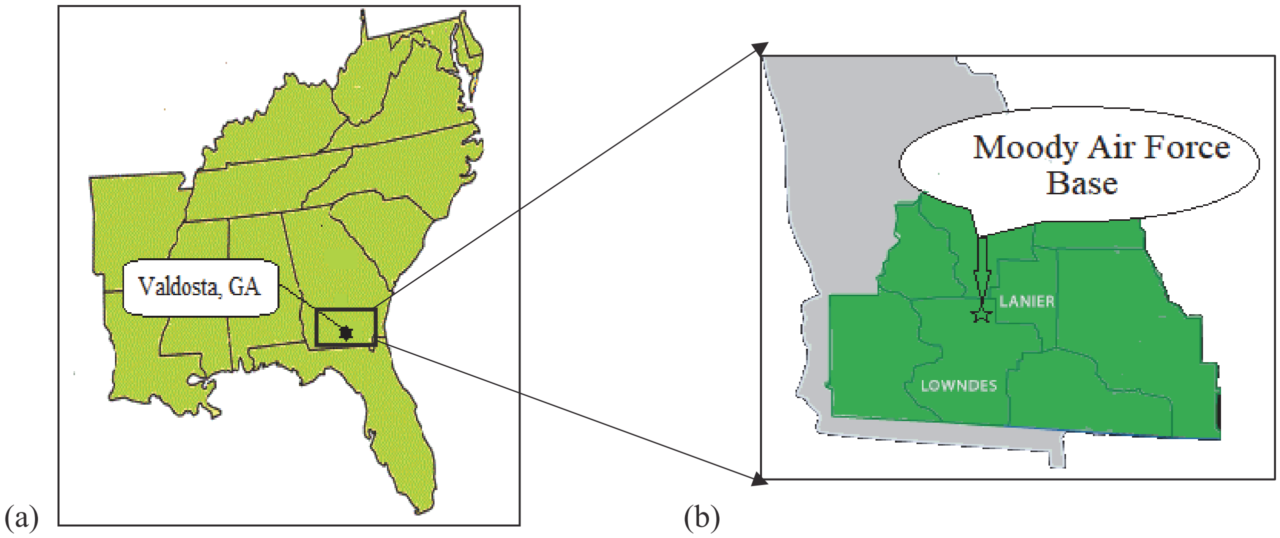
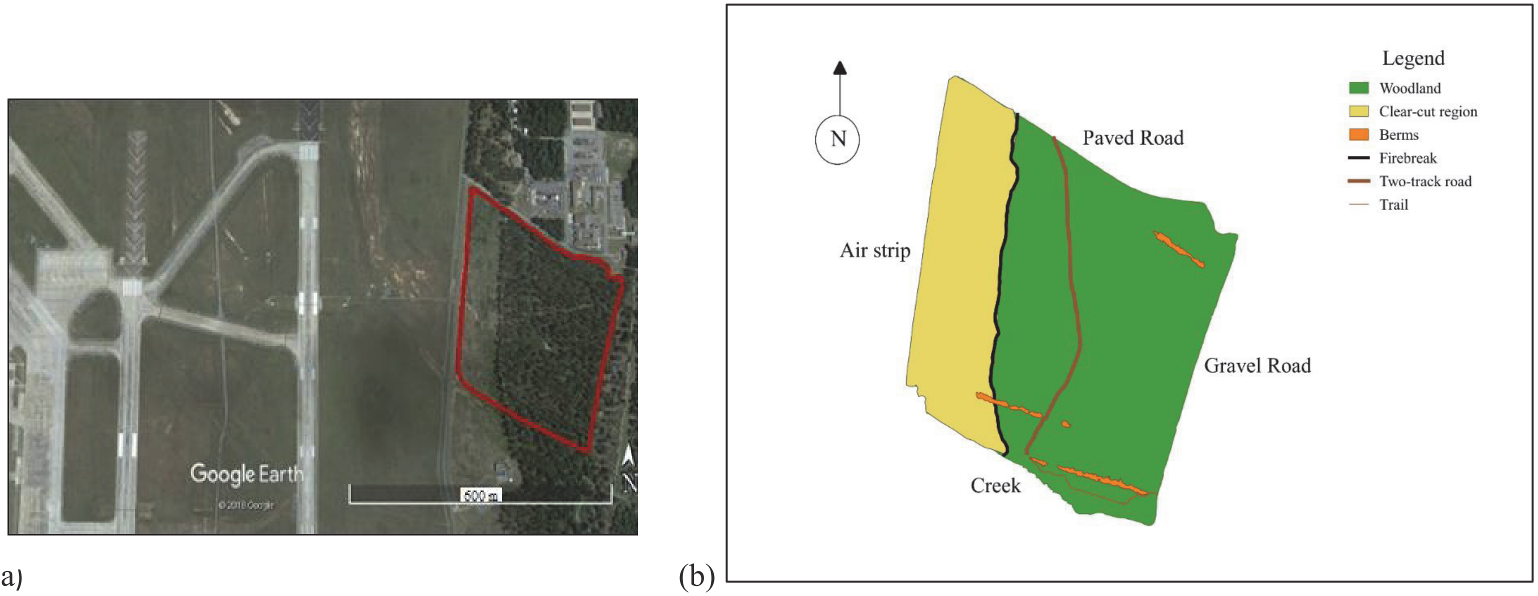


Figure 1. (a) Map of southeastern United States with Valdosta, GA indicated. (b) Enlarged map of a portion of southern Georgia in green showing Moody Air Force Base in Lowndes and Lanier counties.



(a)

(b)

Figure 2. (a) Aerial view of portion of Moody Air Force Base near Valdosta, GA that includes 13.52 ha study site (red outline) and adjacent air strip. (b) Enlarged view of the study site with habitat features. Characteristics of edges are given and compass direction indicated in upper left-hand corner.

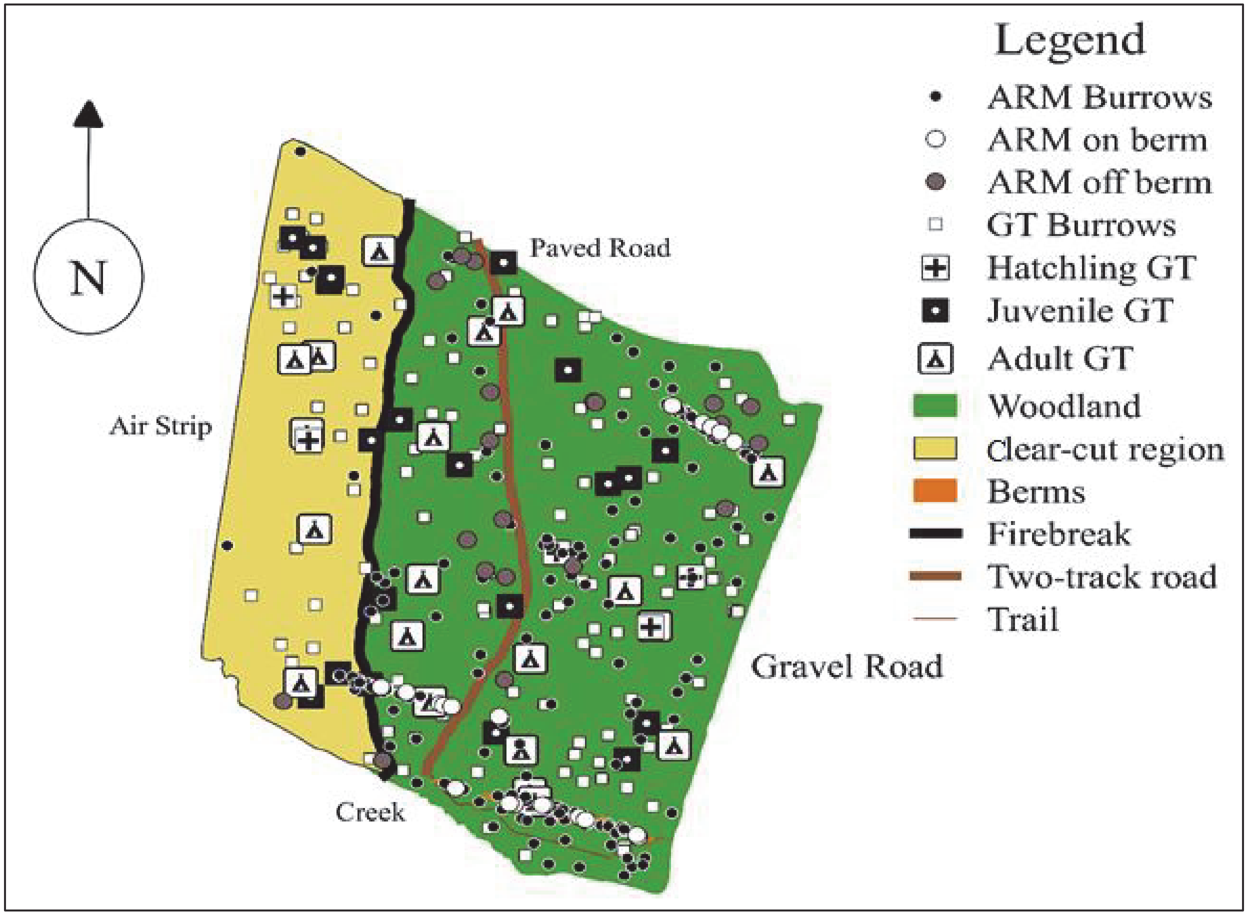


Figure 3. Distribution of 40 randomly chosen armadillo (ARM) burrows [on berm (N = 20) and off berm (N = 20)] and 46 randomly selected gopher tortoise (GT) burrows separated into age classes [hatchling (N = 6), juvenile (N = 20) and adult (N = 20)] used in microhabitat analysis. Habitat features are shown in study site at Moody Air Force Base. Characteristics of edges are given and compass direction indicated in upper left-hand corner.

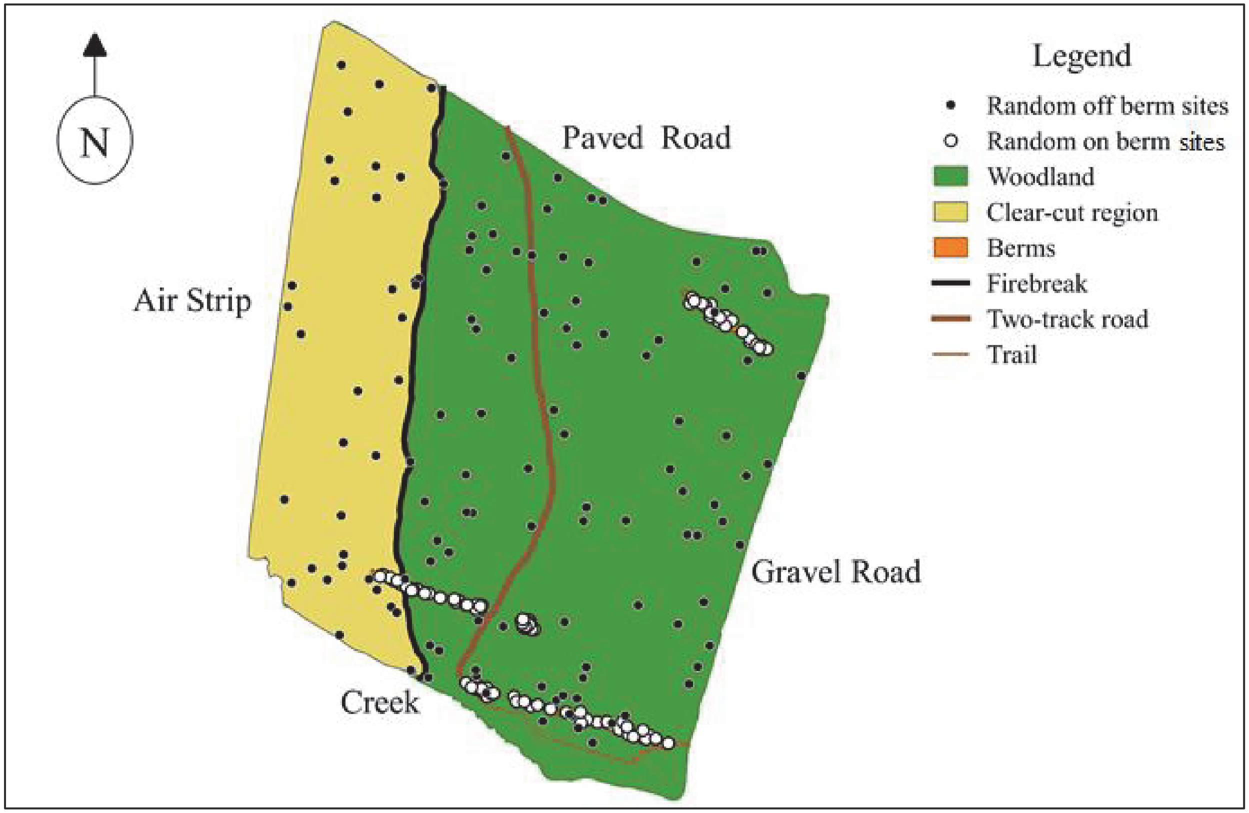


Figure 4. Distribution of 250 random points (125 on berm and 125 off berm) and habitat features in study site at Moody Air Force Base. Characteristics of edges are given and compass direction indicated in upper left-hand corner.

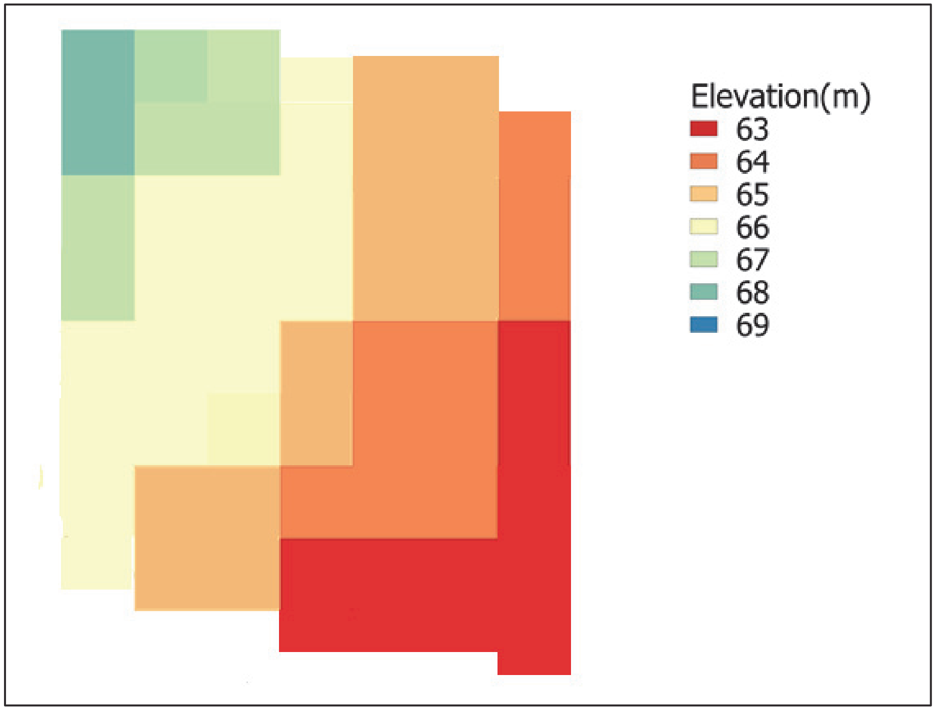


Figure 5. Digital elevation model (elevation above mean sea level) for the study site on Moody Air Force Base.

Chapter IV

RESULTS

I have sub-divided the results into various sections. In the first part, I describe the burrows of the two species. I then present results on habitat parameters that influence placement of armadillo and gopher tortoise burrows. This section is followed by whether parameters differ for armadillo burrows on and off berm and whether habitat features associated with burrow placement differ between age classes of gopher tortoises. Temperature data (i.e., maximum temperature differences inside and outside of burrows in summer and winter) were compared between burrow types. In the final section, I address findings regarding detectability of different age classes of gopher tortoise burrows or locations of armadillo burrows during the pre-burn survey.

General burrow information

I recorded 404 individual burrows (242 armadillo and 162 gopher tortoise) after two complete surveys conducted from September 2016 to May 2017 (Figure 3, Table 1). In addition I recorded the locations of other artifacts (structures other than burrows) constructed by these two species; 28 coopted (CPDT) burrows and 50 above-ground armadillo nests. While these structures were documented, such data were not formally included in the statistical analysis.

Armadillo burrows

Armadillo burrow intensity (= density) for the entire plot was 17.90 burrows/ha. On berm intensity was very high, 2133.33 burrows/ha (128 burrows/0.06 ha), while intensity off berms was lower: 8.47 burrows/ha (114 burrows/13.46 ha). There was also a dramatic difference in armadillo burrow intensity between the clear-cut region at 3.68 burrows/ha (11 burrows/2.99 ha) and the woodland at 21.94 burrows/ha (231 burrows/10.53 ha).

I compared the morphology of burrows on and off berm because the intensity of burrows was so much higher on berm. Armadillo burrows did not differ in height (on berm, median = 11.85; off berm, median = 13.85; Mann-Whitney U-test, $U = 170.50$, $p = 0.21$, Table 2) and width (on berm, median = 17.55; off berm, median = 17.50; Mann-Whitney U-test, $U = 194.5$ $p = 0.44$, Table 2). The ratio of height to width did not differ for burrows on versus off berms ($t = 0.71$, df = 38, $p = 0.24$, Table 2). Unlike burrow dimensions, tunnel angle was significantly steeper for burrows on berms (median = 33) than those found off berms (median = 38; Mann-Whitney U test, $U = 80$, $p = 0.0005$, Table 2).

Gopher tortoise burrows

Gopher tortoise burrows had an overall intensity of 11.98 burrows/ha. When age class of occupant was considered, intensity of hatchling burrows across the entire study site was lowest at 0.67 burrows/ha, then juvenile burrows at 3.99 burrows/ha and finally adult burrow intensity was 7.25 burrows/ha. Gopher tortoise burrow intensity was not substantially higher in the clear-cut area (14.04 burrows/ha, 42 burrows/2.99 ha) than in woodland (11.40 burrows/ha, 120 burrows/10.53 ha).

Because burrow width was used to define the age classes of gopher tortoise burrow occupants, the following comparisons only included ratio of height to width and tunnel angle. The ratio of height to width differed between the different age groups, with juveniles having the highest ratio followed by adults and then hatchlings (One-way ANOVA, $F = 4.26$, df = 2, 45, $p = 0.02$, Table 2). When tested *post hoc*, adults and juveniles differed (Tukey test; $q = 4.60$, df = 43, $p = 0.006$) but not the ratios of hatchlings and juveniles (Tukey test; $q = 3.12$, df = 43, $p = 0.08$) or those of adults and hatchlings (Tukey test; $q = 0.46$, df = 43, $p = 0.94$). Different age classes did not vary in their tunnel angle either (One-way ANOVA, $F = 0.64$, df = 2, 45, $p = 0.53$, Table 2).

When comparing armadillo burrows to those of gopher tortoises, I found average height of armadillo burrows was greater than that of gopher tortoise burrows ($t = 2.54$, df = 84, $p = 0.01$, Table 2), while average width did not differ between the two species ($t = 0.61$, df = 84, $p = 0.27$, Table 2). The average ratio of height to width of armadillo burrows (0.75) was significantly greater, reflecting a more oval shape, than that calculated for gopher tortoises (0.56) ($t = 4.25$, df = 84, $p < 0.0001$, Table 2). When tunnel angle was compared, armadillos had steeper angles ($t = 5.98$, df = 84, $p < 0.0001$, Table 2).

Burrow activity

The presence of burrows indicates the presence of animals, but not all burrows were active at the same time. I used all the burrows from the survey when considering their activity status. When the two species were considered separately, 58.68% of armadillo burrows and 50% of gopher tortoise burrows were inactive, whereas 32.64% and 33.33% of armadillo and gopher tortoise burrows, respectively, were active (Table 1). When I used percentages for active, inactive and questionable armadillo burrows (Table 1) to calculate expected values to compare to gopher tortoise burrow type frequencies, questionable burrows for gopher tortoise were almost double that of armadillo burrows ($\chi^2 = 14.19$, df = 2, $p = 0.0008$).

Compass orientation

Gopher tortoise burrows were not oriented in an easterly direction, away from the airfield (modified Rayleigh test: $z = -0.09$, N = 46, $p = 0.81$, Appendix A). However, gopher tortoise burrow entrances were oriented towards the south (R: $z = 0.26$, N = 46, $p = 0.005$, Figure 6(a), Appendix A). When age classes were tested separately, adult gopher tortoise burrows faced south (R: z = 0.35, N = 20, $p = 0.01$, Figure 6(b), Appendix A) whereas the null hypothesis of circular uniformity could not be rejected for juveniles (R: $z = 0.17$, N = 20, $p = 0.13$) or hatchlings (R: $z = 0.22$, N = 6, $p = 0.23$).

The null hypothesis of circular uniformity could not be rejected for orientation of armadillo burrows (Kuiper's test, V = 1.15, N = 20, $p > 0.05$, Figure 7(a, b), Appendix A). However, armadillo burrows on berms exhibited an antipodal pattern, reflecting the fact that most berms ran from east to west such that burrows were located on either the north or south side of the berm (Figure 7(c), Appendix A).

Placement of armadillo and gopher tortoise burrows

Principal component analysis was performed on 86 randomly selected burrows (armadillo and gopher tortoise burrows) to see what variation could be explained by each variable (See Table 3). A total of 44.72% of the variation was explained by principal components PC 1 (31.92%) and 2 (12.80%) (Figure 8, Table 5). PC 1 included habitat variables associated with shade and vegetation that separated armadillo and gopher tortoise burrows and PC2 grouped temperature difference in summer season, edge distance and visibility. I found armadillo burrows were associated with thicker total vegetation density, increased canopy cover, steeper slope, lower elevation and less sunlight penetration than gopher tortoise burrows. In addition, armadillo burrows were found where the temperature difference (modulation) in summer was less and visibility was lower (thick ground cover) than at gopher tortoise burrows (Figure 8, Table 3).

Comparison of random sites with burrows sites

When habitat parameters were compared among armadillo off-berm burrows, gopher tortoise burrows and random sites, the first and second discriminant functions accounted for 89.67% and 10.33% of the variation in discriminating these groups (Figure 9; Table 6). The first discriminant function nearly separated gopher tortoise burrows from armadillo burrows and the second discriminant function was important in separating burrow locations from random sites (Figure 9). Some overlap exists between random sites and burrow sites, which is supported by the fact that the second discriminant function only explained 10.33% of variation. The primary predictors that best discriminate armadillo burrows from those of gopher tortoises were greater amount of canopy cover, thicker total vegetation density and lower visibility at ground level (thicker ground cover) (Table 6). The primary predictors that best separate burrow locations from random sites were steeper slopes at ground level, farther edge distances and lower visibility at burrow sites (Tables 3, 6).

Burrow support structures

I found 50% of gopher tortoise burrows were associated with a type of burrow support structure where 30% of these burrows were associated with large roots. Likewise, 32.5% of armadillo burrows were found with roots and stumps but only 10.4% of the random sites were associated with support features (Table 7). I compared the association of support structures (large roots, fallen logs, stumps, woodpiles) between armadillo and gopher tortoise burrows. Armadillos and gopher tortoises did not differ in the proportion of burrows associated with each of the following support structures; roots ($\chi^2 = 2.85$, df = 1, $p = 0.09$), stumps ($\chi^2 = 0.78$, df = 1, $p = 0.37$) or logs ($\chi^2 = 0.45$, df = 1, $p = 0.50$). When support structures were compared with random sites (N = 125), the association of support structures at random sites and gopher tortoise burrows did not differ ($\chi^2 = 3.13$, df = 1, $p = 0.07$). I compared all 250 random sites with all armadillo burrows to determine if armadillos prefer support structures. Armadillo burrows also were found associated with support structures (Fisher's exact test, $p = 0.01$).

Influence of habitat parameters on the placement of different age classes of gopher tortoise burrows

I compared habitat parameters among adult and juvenile burrows and those of the 125 random sites off berm using linear discriminant analysis. The first discriminant function accounted for 84.30%, separating gopher tortoise burrows from random sites, even though some burrow overlap with random sites could be seen. The second discriminant function separated gopher tortoise adult and juvenile burrows (Figure 10) and accounted for 15.70% of the discrimination (Table 8). The primary predictors that best discriminated gopher tortoise burrow sites from random sites were less canopy cover, steeper slope at ground level and farther edge distances (Figure 10; Tables 3, 8). Higher visibility at ground level (low ground cover) was the dominant variable that separated adult from juvenile/hatchling burrow sites (Tables 3, 8).

I also compared associated burrow support structures between random sites and burrows of different age classes of tortoises. Burrow support structures had no influence on placement of hatchling (Fisher's exact test, $p = 0.38$) or juvenile burrows (Fisher's exact test, $p = 0.66$), but adult burrows were more associated with these structures (Fisher's exact test, $p = 0.01$).

In terms of visibility at ground level, adult gopher tortoise burrows were more visible, that is, found in areas with less vegetation compared to burrows of juveniles and hatchlings (One-way ANOVA, $F = 3.51$, df = 2, 43, $p = 0.04$, Table 3). When analyzed *post hoc*, adult burrow visibility was higher than juvenile burrows (Tukey test; $q = 3.73$, df = 43, $p = 0.03$). Visibility did not differ between adult and hatchling burrows (Tukey test; $q = 1.63$, df = 43, $p = 0.49$) or between hatchling and juvenile burrows (Tukey test; $q = 0.90$, df = 43, $p = 0.80$).

Influence of habitat parameters on the placement of armadillo burrows on and off berms

I conducted a linear discriminant analysis to compare habitat parameters between armadillo burrows on (N =20) and off (N = 20) berm and random sites on (N = 125) and off (N = 125) berm. The first, second and third discriminant functions accounted for 92.477%, 7.19% and 0.327% of the separation respectively, however, the third discriminant function was not statistically significant (Table 9). The first discriminant function separated off berm random sites from on berm random sites (Figure 11). All the variables except edge distance were predictors that discriminated these two sites. A steeper slope on berm had the highest contribution in the separation. In addition to steeper slope; higher total vegetation density, greater amount of canopy cover, lower sunlight penetration (all related) and lower elevation best defined the habitat quality of on berm random sites compared to off berm random sites (Tables 3, 9).

The second discriminate function separated armadillo burrows on and off berm (Figure 11). More canopy cover and higher visibility (low ground cover) differentiated on berm burrows from those off berm (Tables 3, 9). I also found that armadillo burrows on berms did not differ from random points on berms. However, armadillo burrows off berm had greater canopy cover (Wilks' $\lambda = 0.938$, $F = 9.40$, df = 1, 143, $p = 0.003$) and lower visibility at ground level (Wilks' $\lambda = 0.931$, $F = 10.673$, df = 1, 143, $p = 0.001$) than the random sites off berm.

Because all the berms in study area were found near edges of the study site, not unexpectedly, it was found that armadillo burrows on berms were closer to edges than burrows off berms ($t = 3.024$, df = 38, $p = 0.002$, Table 3). Elevation was lower ($t = 3.59$, df = 38, $p = 0.00048$, Table 3) and slope steeper ($t = -7.69$, df = 38, $p < 0.0001$, Table 3) on berm than off. Total vegetation density was higher ($t = 2.24$, df = 38, $p = 0.01$, Table 3) and sunlight penetration was lower ($t = 1.42$, df = 38, $p = 0.01$, Table 3) on berms as well. Visibility at ground level ($t = 0.92$, df = 38, $p = 0.18$, Table 3) and canopy cover ($t = 1.072$, df = 38, $p = 0.15$, Table 3) did not differ between on and off berm armadillo burrows.

Effect of fire on burrow visibility

Ground visibility (index of ground cover) did not differ between on and off berm armadillo burrows (two-way ANOVA, $F = 1.43$, df = 1, 40, $p = 0.23$). But when visibility between 4 months and 16 months post burn were compared, visibility decreased over the time period (two-way ANOVA, $F = 11.29$, df = 1,40, $p = 0.001$, Table 10). Visibility was different for the two age groups: it increased (by 6.67%) for adult gopher tortoises, whereas it decreased for juvenile burrows (by 4.47%) (two-way ANOVA, $F = 9.49$, df =

1, 40, $p = 0.002$) but did not vary significantly over the time lapsed (two-way ANOVA, $F = 0.024$, df = 1, 40, $p = 0.88$, Table 10). In other words, the variation of visibility was different for the age groups, but it didn't change over time of data collection.

Temperature modulation

Gopher tortoise and armadillo burrows modulate temperature. Gopher tortoise burrows have higher modulation than armadillo burrows during winter (Table 11). During winter, all burrows were warmer than surface temperature as expected. The mean temperature difference was smaller for armadillo burrows and had a lower difference of temperature compared to gopher tortoise burrows ($t = 4.54$, df = 1, 143, $p < 0.0001$, Figure 12; Table 11). In summer, even though both burrows were cooler than the surface, gopher tortoise burrows were warmer, with greater range of temperature difference than armadillo burrows (Figure 13; Table 11). Gopher tortoise burrows had higher modulation of temperature than armadillo burrows in summer ($t = 1.66$, df = 1, 142, $p = 0.008$).

Detectability of burrows

A total of 203 armadillo and 111 gopher tortoise burrows (314 total) were recorded during the pre-burn survey (September 2016-Janaury 2017). An additional 90 (39 armadillo and 51 gopher tortoise) burrows were recorded during the post-burn period (Feb- May 2017) (Figures 14, 15). The overall increase in percentage of burrows during post burn was 22.27%. Armadillo burrow percentage increased 16.11% while gopher tortoise increased 31.48%. Considering each gopher tortoise age class, juvenile and hatchling burrows were the least detectable during the pre-burn survey (Table 12).

More armadillo burrows were found off berm during post-burn than expected based on pre-burn proportions ($\chi^2 = 11.04$, df = 1, $p = 0.0009$). Therefore, the detectability of armadillo burrows was lower off berms during pre-burn survey compared to on berms (Table 12).

Detectability was lower for juvenile burrows during the pre-burn survey ($\chi^2 = 126.97$, df = 2, $p < 0.0001$, Table 12) than other age classes. The standard residual's mean value for juvenile burrows was higher (4.36) than expected (Table 12).

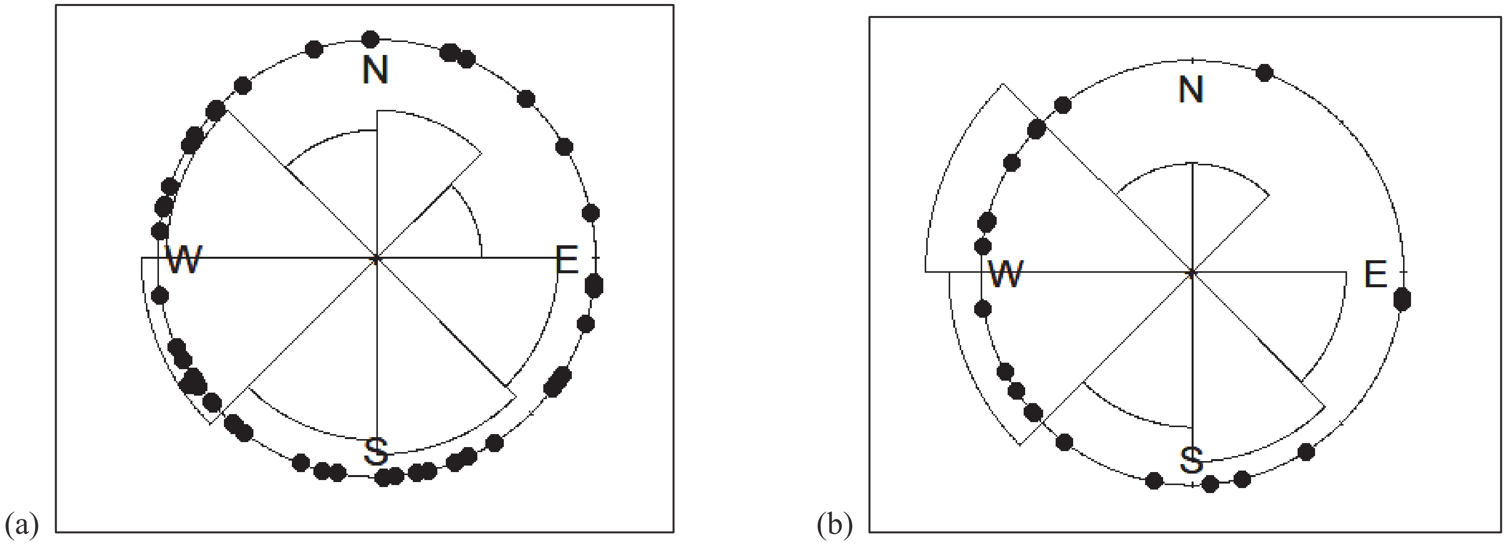


Figure 6. Rose diagrams of compass orientation of gopher tortoise (GT) burrows in study site at Moody Air Force Base. Size of pie is relative to burrow frequency in that 45 degree block. (a) Orientation of 46 gopher tortoise (GT) burrows. (b) Orientation of 20 adult GT burrows only.

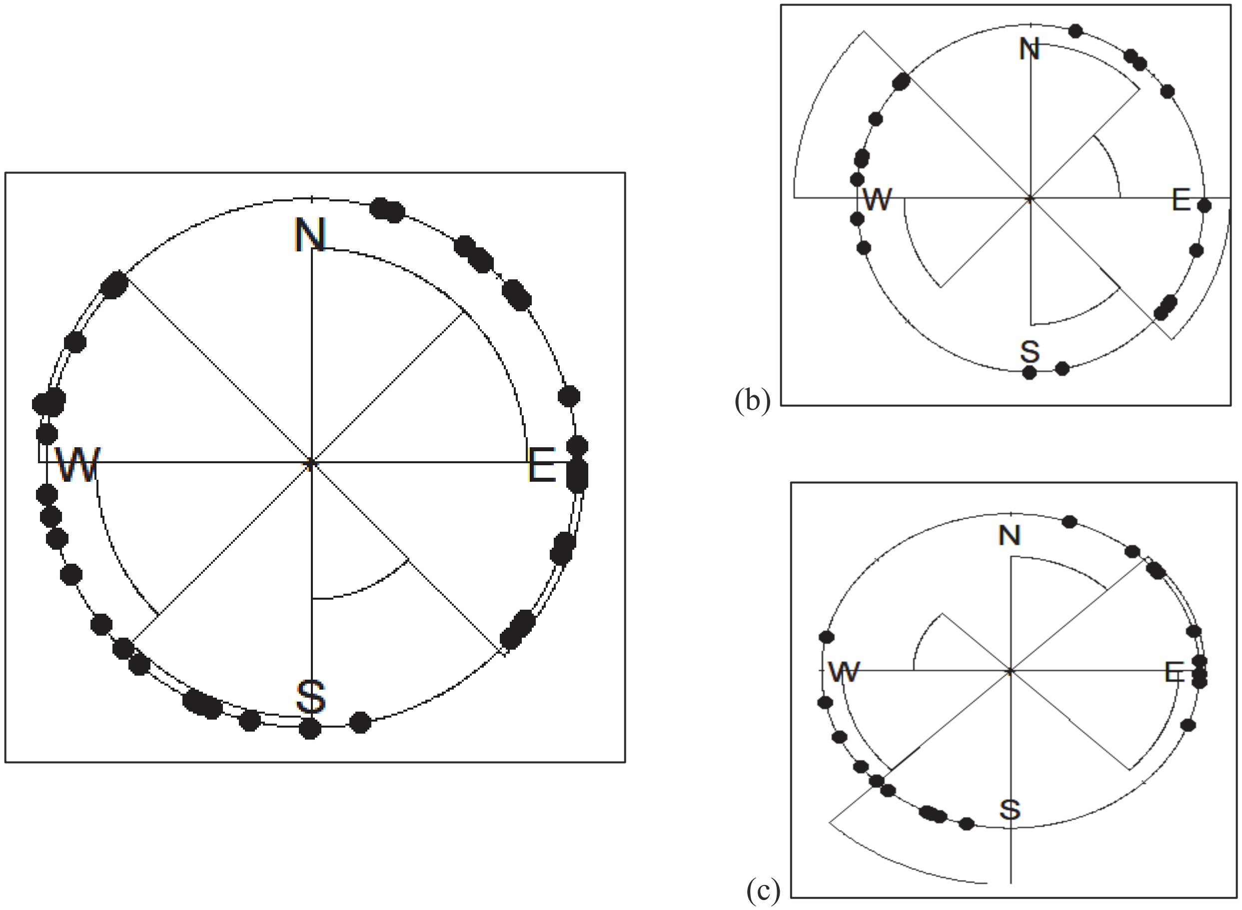


Figure 7. Rose diagram for compass orientation of armadillo (ARM) burrows in the study site at Moody Air Force Base. Size of pie is relative to burrow frequency in that 45 degree block. Compass orientation of (a) all 40 ARM burrows, (b) 20 ARM burrows off berm and (c) 20 ARM burrows on berm.

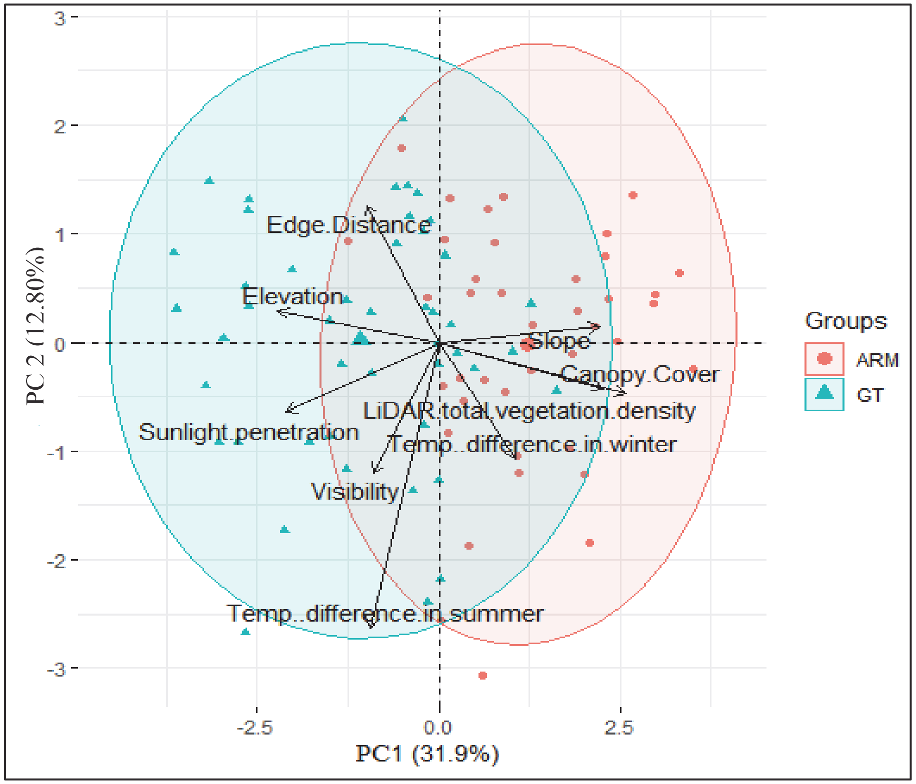


Figure 8. Principal components analysis (PCA) biplot considering nine variables for 86 armadillo and gopher tortoise burrows at Moody Air Force Base used in the burrow microhabitat analysis. Loadings for each principal component are provided in parentheses.

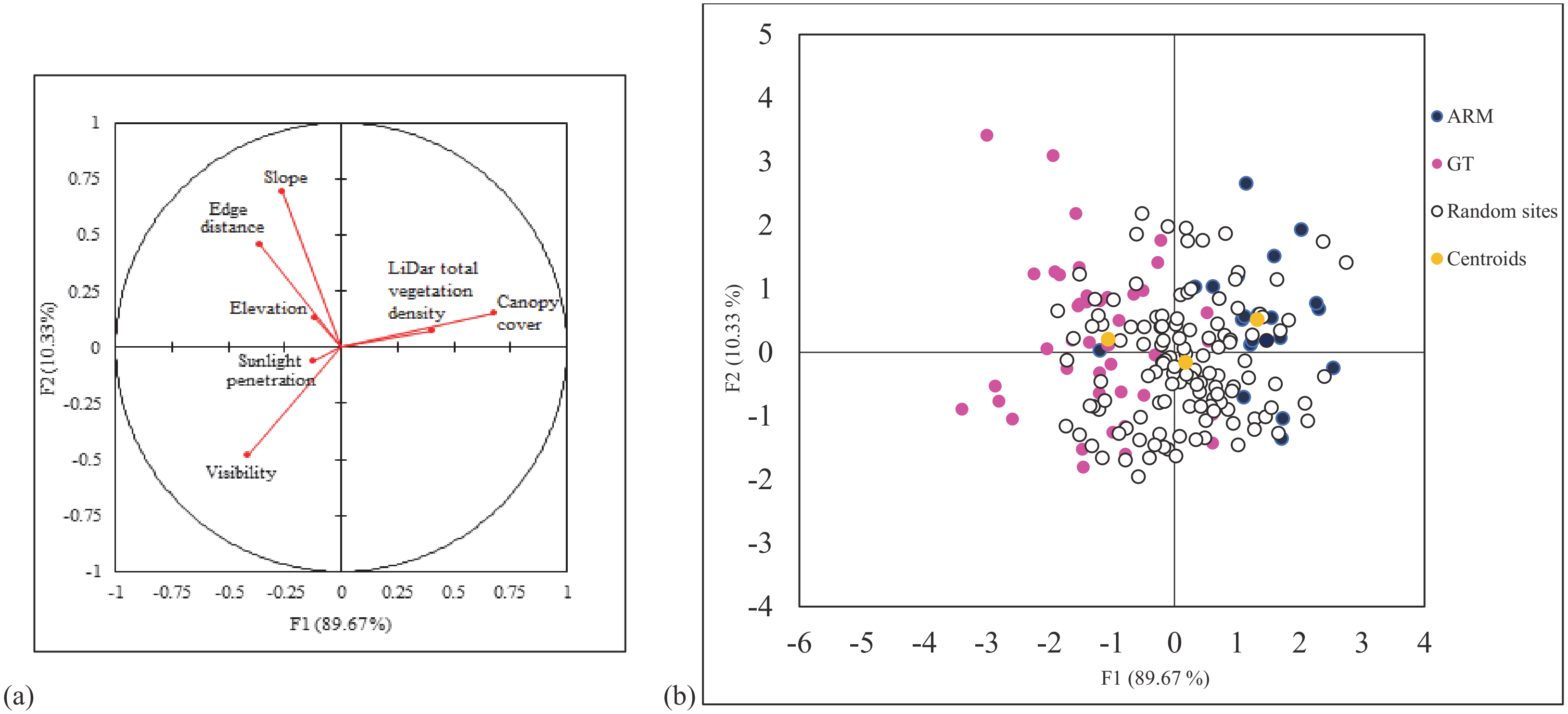


Figure 9. Linear discriminant analysis for armadillo burrows (ARM), gopher tortoise burrows (GT), and 125 random sites within the study area at Moody Air Force Base. (a) Habitat variables associated with the first (F1) and second (F2) discriminant functions. (b) Groups discriminated; F1 separated ARM and GT burrows and F2 burrow sites and random sites. Centroids are averages of each group.

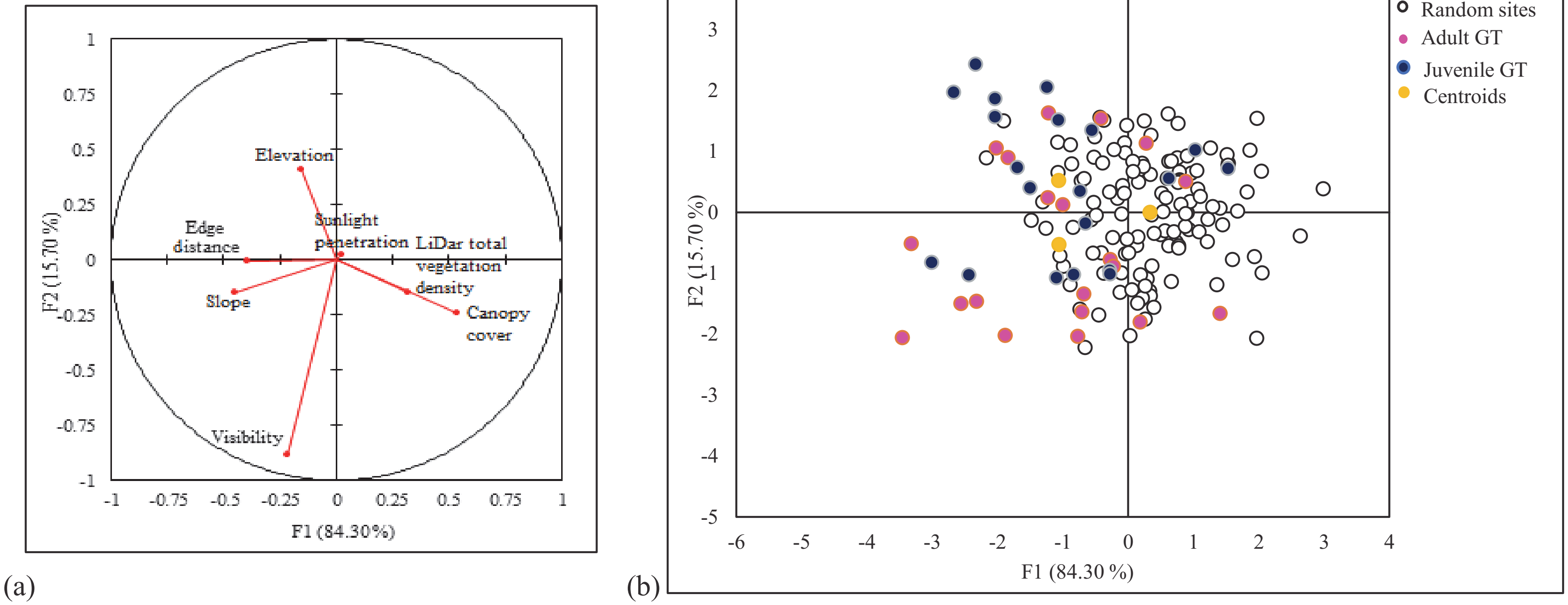


Figure 10. Linear discriminant analysis for juvenile and adult gopher tortoise (GT) burrows and 125 random sites within the study area at Moody Air Force Base. (a) Habitat variables associated with the first (F1) and second (F2) discriminant functions. (b) Groups discriminated; F1 separated random sites from GT burrow sites and F2 separated juvenile and adult GT burrows. Centroids are averages of each group.

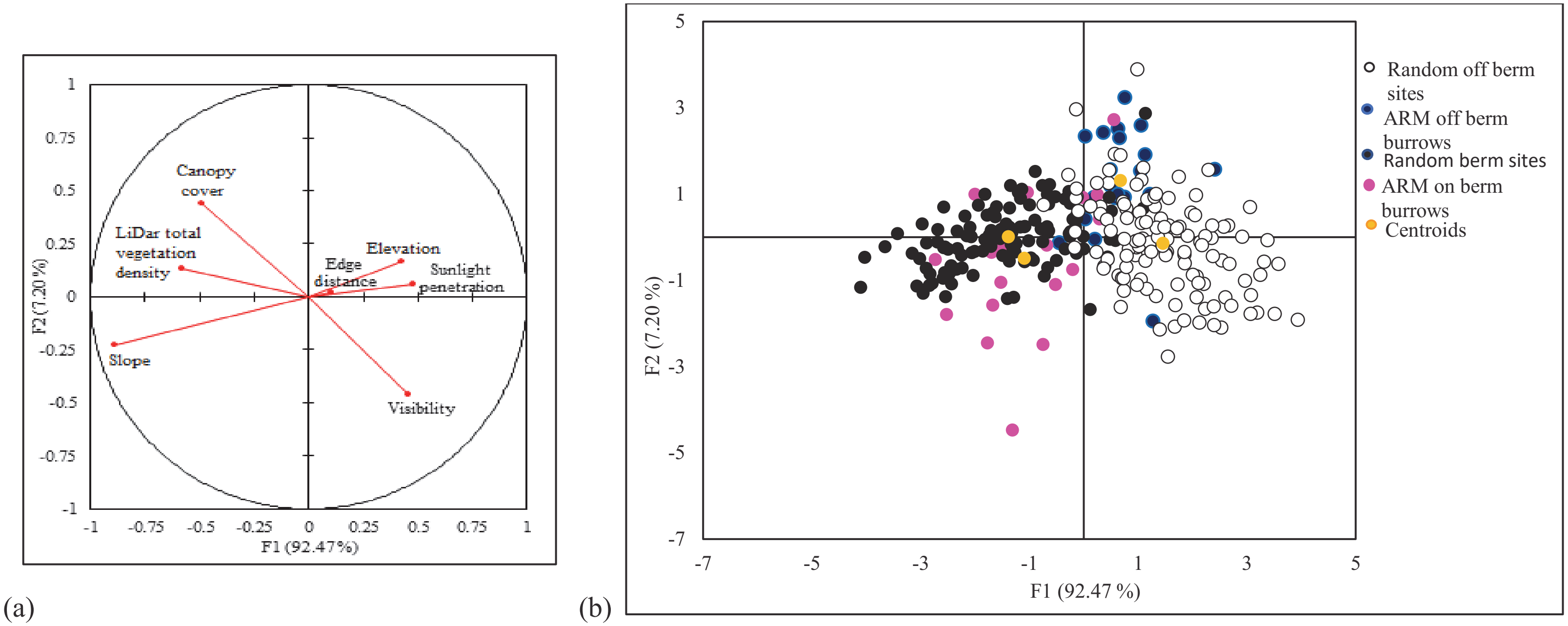


Figure 11. Linear discriminant analysis for armadillo (ARM) burrows on and off berms and for 250 random sites on and off berms within the study site at Moody Air Force Base. (a) Habitat variables associated with the first (F1) and second (F2) discriminant functions. (b) Groups discriminated; F1 separated random berm sites from random off berm sites and F2 separated ARM burrows on berms from burrows off berms. Centroids are averages of each group.

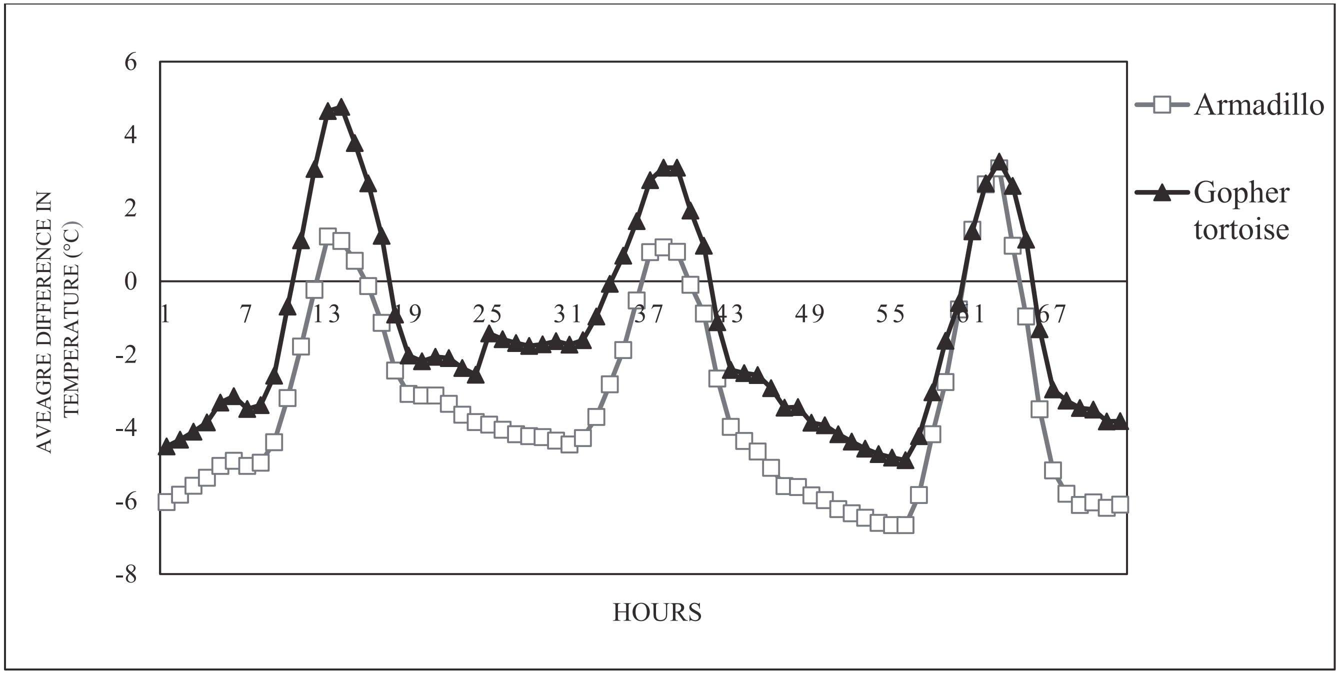


Figure 12. Average winter temperature difference calculated by subtracting temperatures inside from outside of randomly chosen armadillo (N = 40) and gopher tortoise burrows (N = 46) for 72 consecutive hours at Moody Air Force Base. Hour 1 starts at midnight.

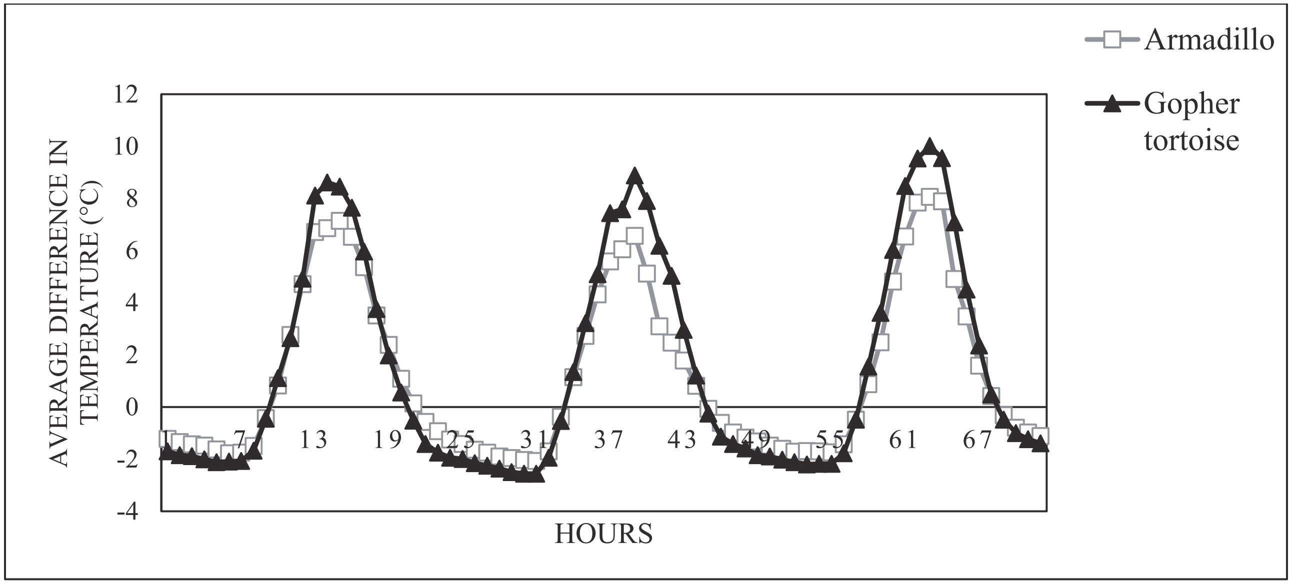


Figure 13. Average summer temperature difference calculated by subtracting inside temperature from outside of randomly chosen armadillo burrows (N = 40) and gopher tortoise burrows (N = 46) for 72 consecutive hours at Moody Air Force Base. Hour 1 starts at midnight.

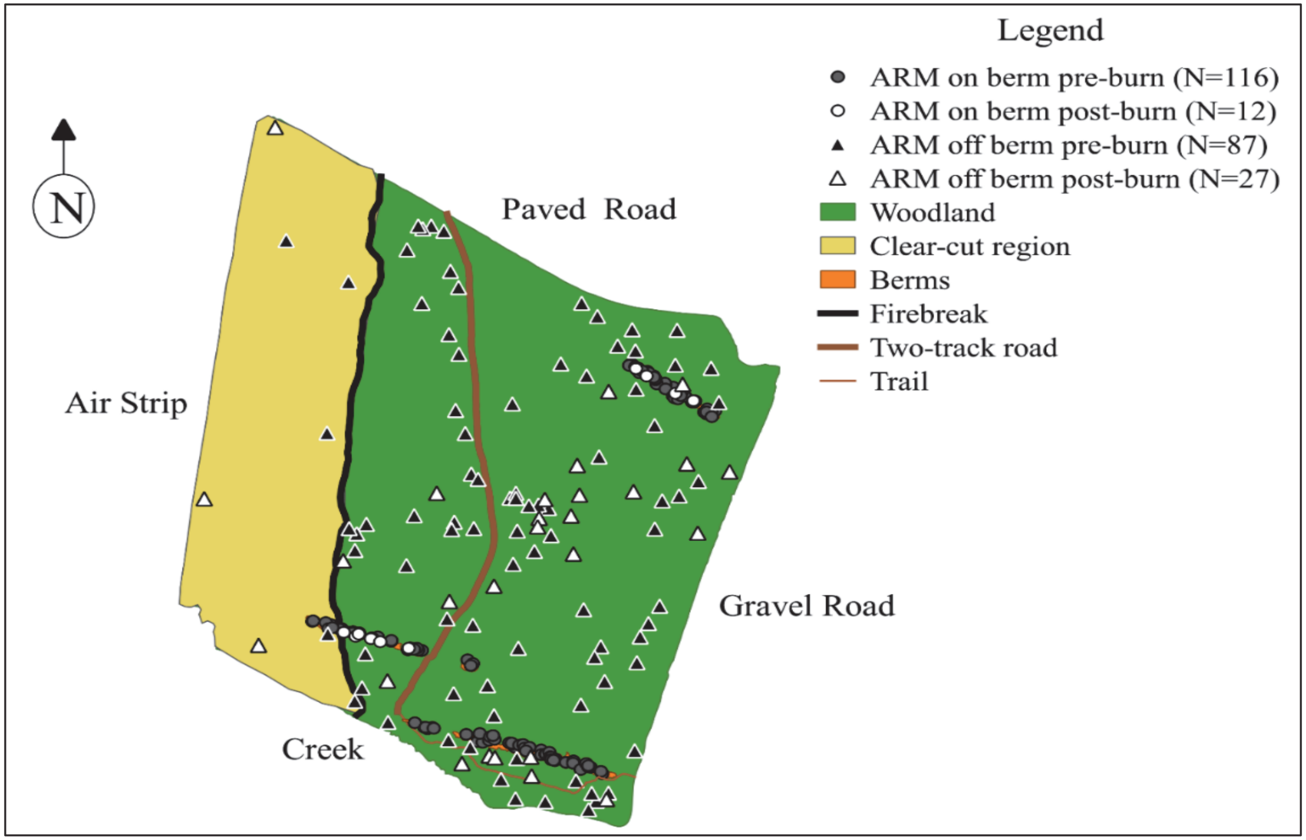


Figure 14. Distribution of armadillo burrows (ARM) on and off the berms during two time periods; pre-burn (Sept 2016-Jan 2017) and post-burn (Feb-May 2017) in the study site at Moody Air Force Base. Post-burn burrows are ones that were either built since initial sampling or not detected during the pre-burn survey. Habitat features and characteristics of edges in the study site are given and compass direction is indicated in upper left-hand corner.

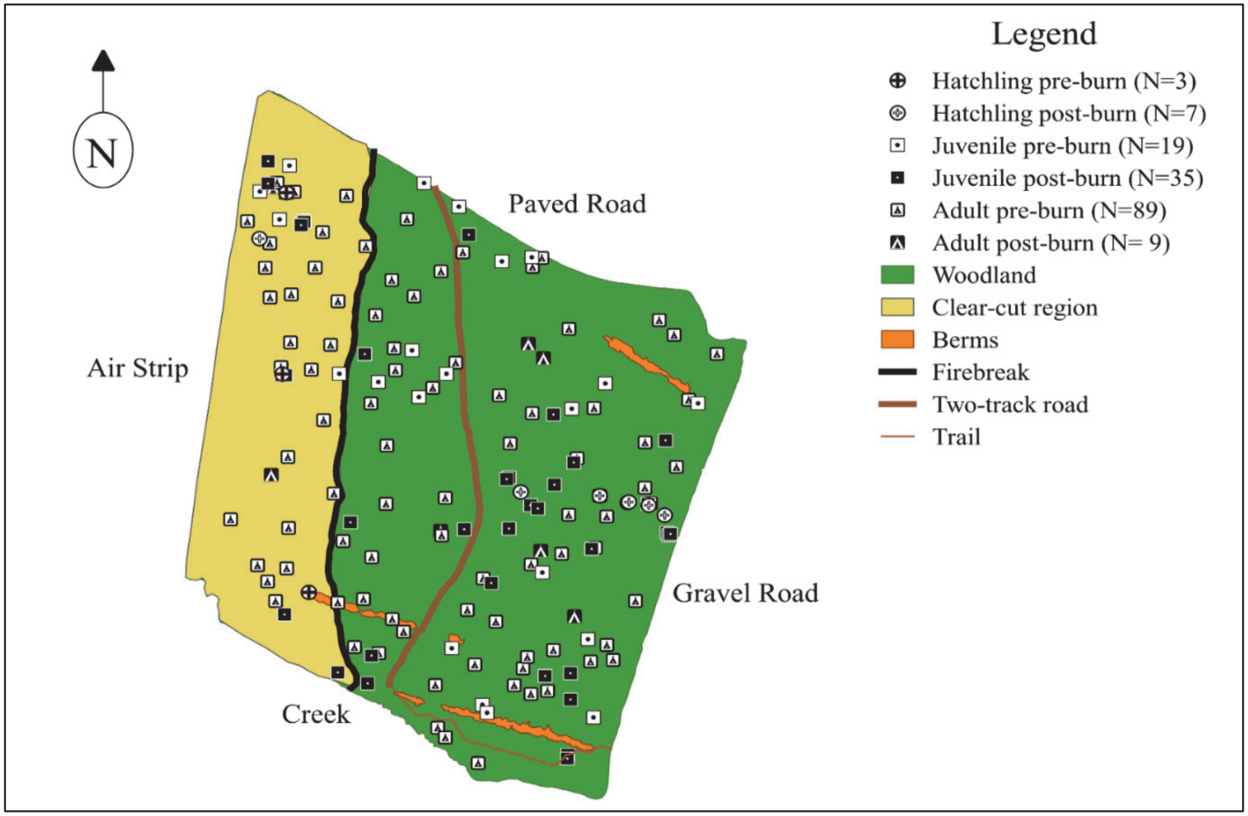


Figure 15. Distribution of the different age classes of gopher tortoise (GT) burrows identified prior to (Sept 2016-Jan 2017) and after the prescribed burn (Feb- May 2017) in the study site at Moody Air Force Base. Post-burn burrows were either constructed after or not detected during the pre-burn survey. Habitat features and characteristics of edges of the study site are shown and compass direction is indicated in upper left-hand corner.

Table 1. Comparison of frequencies of activity status of all armadillo (*Dasypus novemcinctus*) and gopher tortoise (*Gopherus polyphemus*) burrows in a 13.52 ha study site located on Moody Air Force Base in southern Georgia. Percentages are shown in parentheses.

Burrow type	Active	Inactive	Questionable	Total
Armadillo	79 (32.64)	142 (58.68)	21 (8.68)	242 (59.90)
Gopher tortoise	54 (33.33)	81 (50.00)	27 (16.67)	162 (40.10)
Total	133	223	48	404

Table 2. Measurements of burrow parameters for randomly chosen armadillo burrows by location and gopher tortoise burrows by age class in a 13.52 ha study site located on Moody Air Force Base in southern Georgia. Values for burrow parameters (discussed in methods section) are mean ± standard deviations. Measurement for ratio is given by height (ht) /width (wd). Units are found in parentheses after the parameter.

Burrow Type	Classification based on		Height (cm)	Width (cm)	Ratio (ht/wd)	Tunnel Angle (°)
Armadillo		On Berm (N = 20)	13.35 ± 3.25	17.85 ± 4.27	0 .78 ± 0.21	41.5 ± 5.56
(N = 40)	Location	Off Berm (N = 20)	13.27 ± 5.12	18.01 ± 4.71	0.73 ± 0.18	33.8 ± 4.39
		Average	13.31 ± 4.62	17.92 ± 4.38	0.75 ± 0.20	37.67 ±5.56
Gopher		Hatchling (N = 6)	2.55 ± 1.41	5.23 ± 0.22	0.49 ± 0.27	27.83 ± 10.37
Tortoise	Age class	Juvenile (N = 20)	7.23 ± 3.37	10.96 ± 4.75	0.67 ± 0.16	29.5 ± 4.69
(N = 46)		Adult (N = 20)	15.88 ± 2.73	31.53 ± 4.95	0.53 ± 0.16	29.00 ± 3.54
		Average	10.27± 4.28	19.79 ± 11.89	0.56 ± 0.21	29.00 ± 3.79

Table 3. Measurements of habitat parameters for 40 randomly chosen armadillo (on berm and off berm) and 46 gopher tortoise (hatchling, juvenile and adult) burrows and 250 total random sites (on berm and off berm) in a 13.52 ha study site located on Moody Air Force Base in southern Georgia. Values for habitat parameters (discussed in methods section) are mean ± standard deviations. Units are in parentheses after variables.

Burrow Type	Classification Based on	Sites	Average Slope (°)	Average Canopy Cover (%)	Average Total Vegetation Density (%)	Average Visibility (%)	Average Sunlight Penetration (lx)	Average Edge Distance (m)	Average Elevation (m)
Armadillo	Location	On Berm (N = 20)	33.24 ± 13.60	60.25 ± 17.14	78.81 ± 6.27	24.32 ± 30.76	45577.60 ± 25389.32	18.94 ± 15.28	63.95 ± 0.86
		Off Berm (N = 20)	8.40 ± 4.82	54.40 ± 17.34	71.69 ± 12.33	16.74 ± 24.53	64139.70 ± 22935.30	21.72 ± 20.49	65.05 ± 1.02
		Average	20.82 ± 16.11	57.23 ± 17.26	75.25 ± 10.54	20.53 ± 26.10	54858.65 ± 25664.40	20.34 ± 13.26	64.50 ± 1.11
Gopher Tortoise	Age Class	Hatchling (N = 6)	8.33 ± 4.95	21.67 ± 16.50	56.96 ± 26.54	42.68 ± 24.94	98390.00 ± 26626.07	37.11 ± 11.23	65.17 ± 1.94
		Juvenile (N = 20)	9.96 ± 8.27	16.10 ± 18.35	56.11 ± 18.10	32.73 ± 32.52	69136.25 ± 23860.13	30.63 ± 15.18	65.70 ± 1.45
		Adult (N = 20)	10.87 ± 8.31	23.45 ± 18.09	58.83 ± 17.22	60.61 ± 36.24	68490.00 ± 29782.09	30.40 ± 15.66	65.10 ± 1.48
		Average	10.21 ± 7.83	20.00 ± 17.41	57.40 ± 18.33	45.34 ± 35.29	72770.98 ± 29095.74	31.38 ± 17.66	65.39 ± 1.52
Random sites	Location	On berm (N = 125)	36.59 ± 19.71	61.46 ± 15.59	78.36 ± 6.57	17.04 ± 16.24	45202.88 ± 26416.2	19.89 ± 14.62	64.31 ± 0.84
		Off berm (N = 125)	7.20 ± 4.84	38.66 ± 30.68	64.16 ± 17.29	38.51 ± 30.68	69632.80 ± 31845.52	22.35 ± 16.88	65.14 ± 1.40

Table 4. Multicollinearity test for the variables used in the microhabitat analysis of armadillo and gopher tortoise burrows and random sites in a 13.52 ha study site located on Moody Air Force Base in southern Georgia. Units are found in parentheses after the parameter.

Variables	Tolerance	Variation inflation factor (VIF)
Slope (°)	0.97	1.02
Canopy Cover (%)	0.50	2.00
LiDAR Total Vegetation Density (%)	0.84	1.18
Visibility (%)	0.97	1.02
Sunlight Penetration (lx)	0.56	1.77
Edge Distance (m)	0.98	1.01
Elevation (m)	0.73	1.37

Table 5. Principal Components Analysis based on habitat parameters (shown in Table 3) with eigen values, variation (%) and Principle components (PCs) for 86 randomly chosen armadillo and gopher tortoise burrows used in the microhabitat analysis at Moody Air Force Base. Values in bold are considered significant. Units are in parentheses after variables.

Variables	PC1	PC 2	PC 3	PC4
Eigenvalue	2.87	1.15	1.08	1.04
Variation (%)	31.90	12.82	11.94	11.59
Slope (°)	**0.69**	-0.05	0.05	0.36
Canopy Cover (%)	**0.71**	0.13	-0.03	-0.32
LiDAR Total Vegetation Density (%)	**0.80**	0.15	-0.11	-0.04
Visibility (%)	-0.28	**0.37**	0.53	0.62
Sunlight penetration (lx)	**-0.65**	0.20	-0.35	-0.003
Edge Distance (m)	-0.31	**-0.39**	-0.39	0.488
Elevation (m)	**-0.69**	-0.09	-0.13	-0.27
Temperature difference in winter (°C)	-0.33	-0.33	0.70	-0.30
Temperature difference in summer (°C)	-0.29	**0.81**	-0.05	-0.12

Table 6. Discriminant function analysis showing discriminant loadings and significance level of predictor variables contributing to the discriminant function for 125 random sites and armadillo and gopher tortoise burrows used in microhabitat analysis in study site at Moody Air Force Base. F1 and F2 are the first and second discriminant functions. Values in bold are considered significant. Units are in parentheses after variables.

Variables	F1	F2	Lambda	$F_{(2, 188)}$	p-value
Eigenvalue	0.48	0.06			
Discrimination (%)	89.67	10.33			
Slope (°)	-0.26	**0.69**	0.95	4.73	0.010
Canopy Cover (%)	**0.68**	0.15	0.85	16.84	< 0.0001
LiDAR Total Vegetation Density (%)	**0.40**	0.07	0.95	5.24	0.006
Visibility (%)	**-0.42**	**-0.48**	0.93	6.89	0.001
Sunlight Penetration (lx)	-0.12	-0.06	0.10	0.49	0.61
Edge Distance (m)	-0.36	**0.46**	0.95	5.20	0.006
Elevation (m)	-0.12	0.13	0.10	0.51	0.60

Table 7. Frequency of support structure associated with burrows and random sites in a 13.52 ha study site located on Moody Air Force Base in southern Georgia. Numbers in parentheses represent sample size.

	Support structure				
Location (N)	Root	Log	Stump	Woodpile	No features
Armadillo burrows (40)	6	2	7	1	24
On berm (20)	1	0	1	0	18
Off berm (20)	5	2	6	1	6
Gopher tortoise burrows (46)	14	4	5	0	23
Hatchling (6)	0	0	1	0	5
Juvenile (20)	4	1	1	0	14
Adult (20)	10	3	3	0	4
Random points (250)	0	8	18	0	224
Random points (On berm) (125)	0	5	11	0	109
Random points (Off berm) (125)	0	3	7	0	115

Table 8. Discriminant function analysis showing discriminant loadings and significance level of predictor variables contributing to the discriminant function for 125 random sites and juvenile and adult gopher tortoise burrows in microhabitat analysis in study site at Moody Air Force Base. F1 and F2 are the first and second discriminant functions. Values in bold are considered significant. Units are in parentheses after variables.

Variables	F1	F2	Lambda	$F_{(2,168)}$	p-value
Eigen value	0.33	0.06			
Discrimination (%)	84.68	15.32			
Slope (°)	**-0.46**	-0.12	0.95	4.75	0.010
Canopy Cover (%)	**0.56**	-0.35	0.92	7.82	0.001
LiDAR Total Vegetation Density (%)	0.33	-0.23	0.97	2.57	0.080
Visibility (%)	-0.27	**-0.86**	0.94	5.24	0.006
Sunlight penetration (lx)	-0.08	0.29	0.99	0.50	0.605
Edge Distance (m)	**-0.46**	0.19	0.95	4.81	0.009
Elevation (m)	-0.13	0.39	0.99	1.07	0.344

Table 9. Discriminant function analysis showing discriminant loadings and significance level of predictor variables contributing to the discriminant function for 250 random sites (on and off berm) and armadillo on and off berm burrows used in microhabitat analysis in study site at Moody Air Force Base. F1, F2 and F3 are the first, second and third discriminant functions. Values in bold are considered significant. Units are in parentheses after variables.

Variables	F1	F2	F3	Lambda	$F_{(3, 286)}$	p-value
Eigen value	1.89	0.15	0.01			
Discrimination (%)	92.47	7.20	0.33			
Slope (°)	**-0.89**	-0.23	0.38	0.48	104.26	< 0.0001
Canopy Cover (%)	**-0.49**	**0.44**	-0.07	0.82	20.90	< 0.0001
LiDAR Total Vegetation Density (%)	**-0.58**	0.13	-0.63	0.77	28.16	< 0.0001
Visibility (%)	**0.46**	**-0.46**	0.05	0.84	18.57	< 0.0001
Sunlight Penetration (lx)	**0.48**	0.06	0.14	0.85	16.78	< 0.0001
Edge Distance (m)	0.100	0.02	0.22	0.99	0.66	0.58
Elevation (m)	**0.43**	0.17	0.54	0.88	13.61	< 0.0001

Table 10. Visibility (%) at ground level for armadillo burrow types (on berm and off berm) and gopher tortoise burrow types (hatchling, juvenile and adult) at two points in time after the prescribed burn held in late January of 2017.

Burrow Type		% Visibility 4 months after burn	% Visibility 16 months after burn
Armadillo	On Berm (20)	43.11	24.32
	Off Berm (20)	36.86	16.74
	Total	39.98	20.53
Gopher tortoise	Hatchling (6)	48.48	42.68
	Juvenile (20)	37.20	32.73
	Adult (20)	53.86	60.61
	Total	46.51	45.34

Table 11. Temperature difference between inside and outside of randomly selected armadillo burrows (N = 46) and gopher tortoise burrows (N = 40). Average temperature difference (X ± SD °), average maximum temperature difference (T_{max}), minimum difference in temperature (T_{min}) and average range ($T_{max} - T_{min}$) recorded during cold (winter) and hot (summer) seasons for 72 consecutive hours at Moody Air Force Base are given.

Season	Variables	Armadillo	Gopher tortoise
Cold (winter)	X ± SD (°)	3.37 ± 2.58	1.40 ± 2.63
	T_{max} (°)	6.66	4.72
	T_{min} (°)	-3.08	-4.76
	$T_{max} - T_{min}$ (°)	9.74	9.48
Hot (summer)	X ± SD (°)	1.22 ± 3.18	1.51 ± 4.05
	T_{max} (°)	8.07	10.01
	T_{min} (°)	-2.06	-2.56
	$T_{max} - T_{min}$ (°)	10.13	12.57

Table 12. Armadillo (*Dasypus novemcinctus*) and gopher tortoise (*Gopherus polyphemus*) burrows recorded during pre-burn survey (September 2016 - January 2017) and additional burrows found post-burn (February – May 2017) on a 13.52 ha study site at Moody Air Force Base. Values were used to determine pre-burn detectability [pre-burn/(pre-burn + post-burn)].

Burrow Type	Classification based on		Pre-burn	Pre-burn Detectability (%)	Post-burn
Armadillo		On berm	116	90.63	12
	Location	Off berm	87	76.32	27
Gopher Tortoise		Hatchling	3	30.00	7
	Age Class	Juvenile	19	35.19	35
		Adult	89	90.82	9

Chapter V

DISCUSSION

The placement of armadillo and gopher tortoises burrows at Moody Air Force Base in south central Georgia suggests microhabitat niche partitioning. This is the first study to conduct a habitat preference study for a syntopic population of these two burrowing species. Other studies have considered gopher tortoise burrow placement (Aresco, 1999; Aresco & Guyer, 1999; Baskaran et al., 2006; Boglioli, Michener, & Guyer, 2000; Hermann, Guyer, Waddle, & Nelms, 2002; Kowal et al., 2014; Mitchell, 2005; Rostal & Jones, 2002) but did not consider armadillo burrow placement. Previous armadillo burrow studies either were not in an area where gopher tortoises co-occur (Platt et al., 2004) and/or only anecdotally mentioned habitat features associated with burrows and did not measure the overall environment to document how placement differed from the environment as it is presented to the organism (Platt et al., 2004; Sawyer et al., 2012; but see Arteaga & Venticinque (2008) for elevation preference). By incorporating random point analysis, this study advances the understanding of how armadillos select burrow locations by demonstrating a difference between microhabitat variables between burrow locations and random sites. It also provides insight on the mechanism of coexistence between armadillo and gopher tortoise burrows.

Placement of armadillo and gopher tortoise burrows

This is the first comprehensive preference study using multiple microhabitat features to determine burrow placement for armadillos. They chose cooler areas with microhabitat features that affected temperature (i.e., denser vegetation as measured by LiDAR, more canopy cover, and lower amount of sunlight) leading to cooler burrow temperatures in summer. Armadillos preferred to build burrows in denser vegetation, which is similar to research in the Amazon that found more active burrows in extended primary forest cover (Arteaga & Venticinque, 2012).

Armadillos in the United States inhabit areas with subtropical and temperate climates (Layne & Glover, 1985). This suggests a physiological reason. Armadillos are poor thermal regulators with low basal metabolic rates and body temperature (Boily, 2002; Johansen, 1961; McNab, 1980) so they might prefer shady areas with more stable temperatures and humid conditions that would help maintain metabolic rates within burrows. Thus, in subtropical climates, such as South Georgia, they might moderate ambient heat by burrowing in cool, shady places. This is the opposite of gopher tortoises. As ectotherms, they have specific thermoregulatory needs and so ambient temperatures would be a fundamental factor determining habitat quality (Webb, Shine, & Pringle, 2005; Andersson, Krockenberger, & Schwarzkopf, 2010). Gopher tortoise chose open canopy areas that provide sunlight to the forest floor; a finding that is consistent with the results of previous studies (Aresco & Guyer, 1999; Baskaran et al., 2006, Boglioli et al., 2000; Rostal & Jones, 2002; Hermann et al., 2002; Mitchell, 2005). This species needs sunlight to maintain its body temperature and to successfully incubate eggs (Mushinsky et al., 1994; Rostal & Jones, 2002) so burrowing in open areas with more sunlight would provide thermoregulatory benefits to the animal (Wilson et al., 1994). More sunlight at ground level may increase the amount of time that tortoises' operative environmental temperature is met, increasing time for normal daily activity patterns (Rostal & Jones, 2002). In addition, areas with more sunlight could facilitate growth of herbaceous vegetation on which they forage (Auffenberg & Franz, 1982; Mushinsky et al., 1994; Rostal & Jones, 2002).

The greater temperature fluctuation differences in gopher tortoise burrows compared to armadillo burrows probably can be explained in terms of where the burrows were placed. Areas with a higher vegetation cover may have lower temperatures and be less dry (Kapos, Wandelli, Camargo, & Granade, 1997). Armadillo body temperature may fluctuate somewhat with the armadillo's environment (McNab, 1980). In order to keep their temperature at an optimum level, armadillos modify their daily activities so that they are active only during the warm afternoons of cold winter days and cooler late afternoons and nights of summer (Kalmbach, 1943; Layne & Glover, 1985; McDonough & Loughry, 1997). As previously mentioned, armadillos are inefficient homeotherms and they use burrows to avoid heat load during high ambient summer temperatures, possibly preventing evaporative water loss and energy expenditure (McNab, 1980). However, gopher tortoises are active during summer and inactive in winter spending most of their time in burrows (McRae et al., 1981) which provide a thermally distinct microhabitat that protects them from lethally high ambient temperature (Pike & Mitchell, 2013). Gopher tortoises also regulate their body temperature, activity and metabolism with respect to the environment (Anderson, 2001). In extreme climatic conditions, burrows act as a thermal refuge for these species, that is, cooler in summer and warmer in winter (Anderson, 2001).

The placement of armadillo burrows in dense, thorny vegetation may protect occupants from predation by limiting visual exposure (Brown, Kotler, Smith, & Wirtz, 1988; Kotler, Brown, & Hasson, 1991). Also, if attempting to flee a predator, the likelihood of a successful capture is decreased if the predator has to move through thick and/or thorny brush. While armadillo burrows in thick vegetation has been anecdotally observed (Taber, 1945) it was not confirmed statistically.

Higher visibility for gopher tortoise burrows may be due to excavating the burrow and constructing the characteristic apron. In addition, because of their dietary habits, they clear vegetation from areas around the entrances of their burrows increasing their visibility. Other studies also found high visibility at ground level for gopher tortoise burrows (Edwards, Jones, Evans, Roberts, & Londo, 2009; Roastal & Jones, 2001).

Not surprisingly, visibility at ground level changed with time since prescribed burn. I expected a decrease in visibility from four to sixteen months post burn due to an increase in vegetation density. However, at adult gopher tortoise burrows, visibility at ground level actually increased during the one-year period. This was probably due to adult gopher tortoise activity of clearing vegetation around their burrows. For all other burrow categories, visibility at ground level decreased, as expected. The decrease in visibility at juvenile and hatchling gopher tortoise burrows was not as much as at armadillo burrows. The herbaceous dietary habits of juveniles and hatchlings (MacDonald & Mushinsky, 1988) could have reduced the ground cover near their burrows as well. The lower visibility at armadillo burrows may reflect the vegetative growth of woody cover, vines and shrubs during that time (Yager et al., 2007). Prescribed burning can affect the soil (Neary, Ryan, & DeBano, 2005), decomposition of dead organic matter and nutrient recycling (Oslon, 1963; Stoszek, 1988) that create opportunities for new plants to become established (Turner, Romme, Gardner, &

Hargrove, 1997). The prescribed burn at this location took place in late January. Previously, winter burns have resulted in an increase in the number and density of hardwood stems (Brose & Van Lear, 1999; Langdon, 1981) because oaks were protected from surface fires and sprouted post-burn (Brose & Van Lear, 1999).

This study site had a comparatively high density of armadillo burrows (Table 13). Its overall armadillo burrow density (17.90 burrows/ha) is the second highest reported. The highest, 27 burrows/ha, being recorded in a subtropical habitat dominated by pine forest and savannah in Belize (Platt et al., 2004). This could be due to the subtropical/tropical climate that might support armadillos at a high density. Higher food availability, easier soils to forage and build burrows, access to water and thick vegetation for predator protection also could be important factors influencing armadillo abundance (Fitch et al., 1952; McDonough et al., 2000). Burrow intensity within the clear-cut area in the present study was comparable to other grassland densities reported in the literature (Table 13). It is important to note that the man-made berms found in this pine plantation had an extremely high concentration of burrows, around forty-eight times higher than any previously published (2133.33 burrows/ha, Table 13). What effect berms have on the armadillo population and on gopher tortoise biology is unknown. If managers are interested in reducing armadillo populations, one action to take might be to eliminate or avoid the construction of berms.

Gopher tortoise burrows were farther from edges than armadillo burrows and random sites. Other studies have found tortoises close to edges (Baskaran et al., 2006; Eubanks et al., 2002). Before the clear-cut on the western side of the study area, there was an edge effect, but now it seems there is no effect of edge on gopher tortoise burrows

(Anderson, Mixon, McDonough, Lee, & Lockhart, 2017). It is possible that the clear-cut may have increased sunlight penetration on the western side, or that not enough time has passed since the clear-cut for an edge effect to develop. The inclusion of the creek as an edge also could have affected results, as the creek might not functionally serve as an edge than permits light through to the forest floor. The creek only flowed intermittently, but it could have been an important source of water for armadillos, when available. Four out of five berms happen to be near the creek so, this factor could also explain why armadillo burrows are closer to edges.

Both species' burrow sites were found where the immediate ground had steeper slopes than random points. Ridges in soil could provide a point to start burrow construction and the sloping may limit pooling water from running into the burrow after heavy rainfall. Also, higher ground may allow gopher tortoises to tolerate extremely shallow water tables (Castellon, Anderson, Rothermel, & Beck, 2019 in review). Kowal et al. (2014) found low slope with other variables (sandy soils, high elevation, farther distance to waterbodies and paved road) are preferred by gopher tortoise.

The result of preference of slope for armadillo burrows confirms previous anecdotal reports of armadillos burrowing on slopes (Sawyer et al., 2012; Zimmerman, 1990; Table 13) where preference testing was not done. Arteaga & Venticinque (2008) did attempt to measure slope of the environment by dividing the study site into different declination classes and found the highest armadillo burrow density in the steeper slope classes. My measurements were on a smaller spatial scale, which may shed light on the specific ground level factors influencing choice in the placement of burrows. The propensity to dig burrows into a steep slope could be to reduce the energetic cost of construction because the optimum angle for burrow construction to minimize energy costs is perpendicular to the surface (Polis, Myers, & Quinlan, 1986). As a caveat, it is not clear whether armadillos and/or gopher tortoises chose areas with steeper slopes off berm or if the steeper slope compared to random points was due to modifications made during burrow construction.

While elevation explained part of the variation between armadillo and gopher tortoise placement of burrows, it was probably correlated with berm location or other attributes rather than a single defining factor. That said, another study did find a higher density of armadillo burrows at lower elevation (Arteaga & Venticinque, 2008). Even though the clear-cut region is at higher elevation compared to other places in study area, elevation alone was not the only significant factor. A similar result was found by Castellon et al. (2019 in review) who found that elevation was confounded by the effects of microtopography (effect of small-scale topographic variation and depth to groundwater on burrows distribution). Depth to groundwater was not considered in this study. In this study gopher tortoise burrow placement was more related to open canopy than elevation.

Gopher tortoises and armadillos may purposefully choose to use support structures to construct burrows but it depends on the availability of these structures in the habitat. Another study did find that one third of gopher tortoise burrows were associated with support structures although roots were not included as a feature (Aresco, 1999). Support structures (logs, stumps) associated with juvenile gopher tortoise burrows supported them and protected the animals from predators (Aresco, 1999). Other studies (Clark, 1951; Fitch et al., 1952; Platt et al., 2004) anecdotally suggest that such features are associated with armadillo burrows. The use of support structure (roots, logs, stumps) by armadillos could save energy when building, improve the integrity of the burrow after it is built (Clark, 1951; Fitch et al., 1952) and protect occupants from predators as well (Platt et al., 2004).

Based on the selection of microhabitat features in the environment, spatial niche partitioning between these two species is occurring. However, this may not be due strictly to competition but a specialization that may be a consequence of each species' physiology that necessitates the use of completely different microhabitats in the environment. That is, armadillos are endotherms with low basal metabolic rates and low body temperature and also are poor thermoregulators (Boily, 2002; Johansen, 1961; McNab, 1980). Gopher tortoise are ectotherms who need sunlight to regulate body temperature (Auffenberg & Franz, 1982; Mushinsky et al., 1994; Rostal & Jones, 2002; Wilson et al., 1994).

This may not be the only mechanism currently working because the presence of coopted burrows hint at some kind of competition between armadillos and gopher tortoises. Armadillo could be using coopted burrows as opportunistic shelters because using previously built burrows is energetically less expensive than building their own. While it is not clear why armadillo use or usurp gopher tortoise burrows, these burrows represent a widening of the niche for armadillos as they are able to adapt to different microhabitats. This is counterintuitive because presence of a similar species with overlap in resource use would normally narrow a niche. In addition, I did not find evidence that either species was placing burrows randomly in the environment (i.e., their burrow placement differed from random sites). This suggested that the empty niche concept (Rohde, 2005; 2008) was not viable for the placement of burrows, at least off berm.

Comparison of placement of different age classes of gopher tortoise burrows

Juvenile burrows were placed in areas with thicker ground vegetation which might protect them from predators. This was similar to findings from other studies (Beyer, 1993; Wilson, 1991). Surprisingly, I found hatchling burrows were more visible than juveniles. This could be due to hatchlings burrowing near adult burrows that were more visible or it could be a coincidence because of the small sample size (N = 6).

More adult burrows were associated with larger roots, providing structural support to burrow entrances. While adult burrows were found with support structures more than juveniles, this was opposite Aresco's (1999) observations that juvenile tortoises build burrows under structures such as logs, fallen tree limbs, and stumps more than adults. More work needs to be done to determine what habitat features might be important to facilitate juvenile burrowing in order to potentially increase recruitment into a population.

Comparison of placement of armadillo burrows on and off berm

Berms had an extremely high density of armadillo burrows. Berms were found to have even denser vegetation, more canopy cover and less sunlight than other areas in the study site. Given these were microhabitats that armadillos preferred, this is not surprising. Berms, because of their construction (raised surfaces created off the surrounding ground), have steeper slopes than off berm. The tunnel angle on berm was steeper than off berm (Table 2). This also suggested it was easier to dig burrows on berm than off berm. Berms (all but one) lie in the southern portion of the study site that has lower elevation; therefore, elevation was about a meter lower for burrows on berm compared to off berm.

Armadillo burrows were generally more concealed (i.e., placed in areas of dense ground vegetation), but visibility of armadillo burrows was greater on than off berms. Higher visibility of burrows on berms could be due to: a) the large number of burrows concentrated in such a small area, b) heavily travelled animal trails that crisscross the berms, c) vegetation taking longer to return after a burn on the berms compared to off, or d) potentially higher visibility of berms on heavily sloped surfaces (as compared to relatively flat ground).

On the berms, microhabitat features of armadillo burrows had similar values to random points on berms, which suggest armadillos randomly choose burrow locations there. Another possibility is that berms are very uniform in distribution of microhabitat features. Armadillos seem to be filling the niche on the berms randomly which supports empty niche concept as armadillo burrows are randomly placed irrespective of habitat parameters.

Burrow morphometrics

The ratio of height to width of armadillo burrows (0.75) was similar to previous studies (Layne, 1976; McDonough et al., 2000; Platt et al., 2004; Sawyer et al., 2012) with the exception of one in Oklahoma where circular entrances (ratio 0.9) were recorded (Zimmerman, 1990). Burrow dimensions can vary according to habitat (McDonough et al., 2000; Zimmerman, 1990) and geographical location (McDonough et al., 2000, Platt et al., 2004; Table 13). In this site, unsurprisingly, dimensions of burrows on berms were similar to those off berms because armadillos have multiple burrows within a habitat (Bond et al., 2000; Gammons, 2006; McDonough et al., 2000). Burrow entrance dimensions are closely correlated with body size (McDonough et al., 2000), so similarly sized burrow entrances also suggest the same or similarly sized occupants. This might also explain why the mean height and width of armadillo burrows in this study site were smaller than those recorded from other studies (Table 13). The average weight of adult armadillo in this study site (3.82 kg, N = 12) was less than those found in nearby north Florida (4.11 kg, N = 201) and other sites (reviewed in Loughry & McDonough, 1998).

The only burrow morphometric that differed between on berm and off berm was tunnel angle. Tunnel angle was higher on berm but it is hard to assess the reason. Armadillo burrows on berms initially point downward (perpendicular to the sloped surface) but then rise upward into the berm, so steeper tunnel angle on berms might affect air flow or reduce wet conditions.

Similar to armadillo burrows, ratio of height to width of gopher tortoise burrows (0.53) in my study site falls within the range of other studies (Doonan, 1986; Hansen, 1963). The higher ratio of height to width of juvenile burrows compared to adult burrows suggest a slightly more circular opening. Thus, these burrows also may be misidentified as armadillo burrows except for their smaller size. This difference in burrow dimension may reflect a pattern in development where height of the juvenile body grows more than length, but as animals age, the length catches up (Diemer, 1986). This difference between adult and juvenile burrow dimensions ratio has not been reported before and more data from other studies are needed to confirm this difference.

Compass orientation

There was no detectable effect of the airstrip on the orientation of both types of burrows. Tortoises were expected to orient their burrows to allow sunlight to shine directly inside burrows (Morafka, Adest, Aguirre, & Recht, 1981) because of thermal characteristics (McCoy, Mushinsky, & Wilson, 1993). In my study site, gopher tortoises did show a preference for the southwestern direction. This could result from thermal flux that comes from the southern and western directions (Boes, 1981). Also, it has been noted previously (McCoy et al., 1993) that shaded tortoise burrows were oriented southerly and westerly to a greater extent than burrows not shaded. When I tested orientation among different gopher tortoise age classes, only adult burrows preferentially faced southwest. This is different from a few studies that report no evidence of directionality for gopher tortoise burrows preference (Diemer, 1987; Doonan, 1986; Hansen, 1963). Preference has been shown in a particular direction when topographic relief such as ridges may have led tortoises to orient their burrows (Diemer, 1992; Doonan, 1986; McCoy et al., 1993). Individuals also may concentrate their burrows along the edges of firebreaks and roads because such places provide breaks in the dense canopy cover (Layne, 1989; McCoy & Mushinsky, 1991; McRae et al., 1981) and thus, may lead to orientation in a particular direction.

Armadillo burrows were expected to be oriented south to modify burrow temperature or east to minimize sound disturbance. However, armadillos did not show preference for any particular direction which was similar to previous studies (Platt et al., 2004; Sawyer et al., 2012; Zimmerman, 1990). One explanation could be that burrows are protected by thick ground vegetation which blocks wind and possibly noise. Studies of other armadillo species however did find that burrows oriented to minimize exposure to winds (Abba, Sauthier, & Vizcaíno 2005; González, Soutullo, & Altuna, 2001). Although I could not reject the null hypothesis of circular uniformity for armadillo burrows on berms, there was a clear antipodal pattern due to the orientation of the berms, which may violate a basic assumption of most tests of uniformity. Failure to reject the null hypothesis of circular uniformity for off berm burrows was similar to the findings of Sawyer et al. (2012), who contends that orientation may impact burrow direction weakly but microhabitat variables such as slope are more important.

Detectability of burrows

Habitat structure can affect whether burrows are visible to people (detectable) during surveys to estimate population size. Thick vegetation or leaf litter can obscure entrances and aprons which can result in underestimating population size (Howze & Smith, 2018). Smaller juvenile and hatchling burrows have a higher probability of going undetected along with armadillo burrows that are often found in areas of low visibility. In the study site, prescribed burning removed close to two years of vegetation and debris and revealed additional burrows that were undetected during a complete survey finished less than a month prior. The increase in frequency of burrows detected after a burn was also recorded by others (Howze & Smith, 2018; Paden et al., 2017).

Visibility was higher on berm, so detection would be expected to be higher. Another reason on berm burrows were more detectable could be due to observer bias. Because berms had a greater intensity of armadillo burrows, I may have been more vigilant in sampling on berm during the pre-burn survey. When I only considered adult gopher tortoise burrows and compare them with armadillo burrows, I found armadillo burrows were less detectable than gopher tortoise burrows which may be due to armadillo preference for areas with low visibility, a finding that supports the results of Paden et al. (2017).

The higher detectability of adult gopher tortoise burrows than other age classes during a pre-burn survey has also been found in another study (Howze & Smith, 2018). Adult burrows were more obvious in the environment because the entrances and the surrounding aprons were large and found in more visible habitat, whereas such differences may be less stark following a burn.

My work supports Howze & Smith (2018), who observed juvenile and hatchling gopher tortoise burrows having low detectability. This observation has now been found with two different sampling methods, LTDS (Howze & Smith, 2018) and complete sampling (this study). Low detection of juvenile and hatchling burrows during pre-burn surveys is most likely due to those burrows having higher probability of being covered by thick ground vegetation or woody debris (Pike, 2006). Losing 33% of hatchling burrows from post burn to data collection in four months supports others who found that hatchling burrows have a lower chance of persisting in the environment (Guyer & Hermann, 1997; Smith et al., 1997; Smith et al., 2009). In addition, hatchlings may be underrepresented in the habitat because they may not burrow but take shelter in shallow depressions under vegetation (Pike, 2006) which may go undetected.

Detecting hatchling burrows to estimate population size and recruitment is important because hatchling survivorship and recruitment rate are low regardless (Ballou, 2013; Butler & Hull, 1996; Congdon et al., 1993; Epperson & Heise, 2003; Heppell, 1998; Smith, 1997; Smith et al., 2009). Low juvenile and hatchling burrow detection can affect management strategies for gopher tortoise populations because lower burrow observations lead to assumptions of lower recruitment of juveniles and hatchlings into the population (Howze & Smith, 2018).

Detectability is affected by the thickness of vegetation, so prescribed fire could be a conservation tool to improve estimates of younger age classes in a population that might otherwise be underestimated. Life history traits of gopher tortoises include late maturity and low survival when young which suggest they might be slow to respond demographically to conventional habitat management. Moreover, decline in population size and habitat quality are big challenges to conserving this vulnerable species (Tuberville et al., 2005). More accurate estimates of juvenile and hatchling burrows should improve population size estimates. Knowing the detectability would allow managers to adjust recruitment rates of a population, enabling better predictions of population growth or decline.

Conclusions

Microhabitat partitioning between nine-banded armadillos and gopher tortoises allows coexistence of both species in same habitat but it is not clear if it is via competition or specialization. Physiology of both species suggest specialization for their optimal habitat, but coopted burrows may indicate some degree of competition. Armadillos are abundant on berms as the habitat quality fulfills their specific habitat requirements like steeper terrain, overall denser total vegetation, and less direct sunlight. When armadillos placed burrows off berm, they again chose areas with higher total vegetation density, more canopy cover and areas with less visibility (thick ground cover). Gopher tortoises chose areas with open canopy that provided enough sunlight for this ectothermic species to bask and raise its body temperature. Juveniles and hatchlings dug burrows in thicker vegetation at ground level than adults, perhaps to avoid predators.

This study has important management implications. Because armadillos like to construct burrows on man-made disturbances like berms, these structures should be eliminated if possible. Likewise, if canopy cover is opened, it would be favorable to gopher tortoises.

This study has focused on the microhabitat selection of two syntopic burrowing species, the armadillo and gopher tortoise. Further study could be carried out to find out why armadillo usurp the gopher tortoise burrows when their microhabitat requirements are different. It would be interesting to identify more coopted burrows and record their microhabitat parameters to include in the analysis and see how they relate (either separate or overlap) with armadillo burrows' requirements. There is also a chance that coopted burrows are related to burrow density because relatively few coopted burrows were recorded in an additional survey at the Lake Louise Field Station (which is also in Lowndes County), whereas about 20% of the burrows were coopted in my study site. Also, armadillos were constructing a large number of burrows on berms but I did not investigate how these burrows are being utilized. Armadillo burrows on berms were filled with nest material during winter but in summer they were cleared. A study could be carried out to determine how armadillo are using on and off berm burrows, and if they were switching burrows during different seasons.

Table 13. Comparison of armadillo habitat, burrow density and burrow morphometrics across study sites. Entries are organized in descending order of density of burrows (burrows/ha; * burrows/quadrate). Abbreviations ht = height, dia= diameter and ta= tunnel angle (⁰).

Studies	Location	Habitat	Density	Slope (°)	ht (cm)	dia (cm)	Ratio	ta
This study	Georgia	On berm	2133.33	33.24	13.35	17.85	0 .78	41.5
Platt et al. 2004	Belize	Pine forest	27.00		13.90	18.50	0.75	
This study	Georgia	Pine forest with mixed hardwoods	22.29		13.27	18.01	0.73	33.8
Arteaga and Venticinque (2012, 2008)	Amazon	Primary continuous forest	2.78-14.8	25.2-32.3				
McDonough et al. 2000	Brazil	Forest	6.90		14.30	18.12	0.78	
Platt et al. 2004	Belize	Savannah	5.80		13.30	19.00	0.70	
Sawyer et al. 2012	Alabama	Pine forest	5.70	24.60	20.40	25.70	0.79	33.5
McDonough et al. 2000	Brazil	Disturbed	4.40		12.21	15.99	0.76	
This study	Georgia	Clearcut (grassland)	3.34					
McDonough et al. 2000	Florida	Wetland	3.30		15.02	19.38	0.77	
McDonough et al. 2000	Brazil	Swamp	2.90		14.28	17.90	0.79	
McDonough et al. 2000	Florida	Hammock	2.70		15.38	19.00	0.80	

McDonough et al. 2000	Brazil	Grassland	2.10		11.74	15.33	0.76	
Zimmerman 1990	Oklahoma	Bottomland riparian, brushland and upland	1.74	16	19.80	21.90	0.90	29
McDonough et al. 2000	Florida	Upland pine	1.70		15.79	21.03	0.75	
Taylor 1946	Texas	Live oak savannah	0.61					
Taylor 1946	Texas	Live oak shin oak grassland	0.52					
McDonough et al. 2000	Florida	Field	0.30		15.33	20.50	0.76	
Layne 1976	Florida				15.33	20.00	0.77	
Kinlaw 2006	Florida	Pine forest	1.85 *					
		Oak hammock	0.71*					
		Sand pine	0.65*					
		Oak scrub	0.45*					

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APPENDIX: A

Compass orientation grouped in 45 degrees (°) blocks for 86 armadillo and gopher tortoise burrows chosen at randomly for microhabitat analyses. Armadillo burrow types are grouped by location, either on (N=20) or off a berm (N=20). Gopher tortoise burrows are grouped by age class Hatchling (N = 6), Juvenile (N = 20) and Adult (N = 20). Burrows were located in the study site at Moody Air Force Base.

Orientation	Grouped degrees (°)	On berm	Off berm	Hatchling	Juvenile	Adult
North	316-360	1	1	0	2	1
Northeast	0-45	3	3	1	1	0
East	46-90	5	2	0	2	2
Southeast	91-135	0	3	0	3	1
South	136-180	4	2	1	5	3
Southwest	181-225	6	0	2	5	6
West	226-270	0	4	0	0	2