Habitat Use and Activity Patterns of the Gopher Tortoise (*Gopherus polyphemus*) Inhabiting Military Test Ranges and Forested Sandhills at Eglin Air Force Base, Florida

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Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Master of Science
In
Fisheries and Wildlife

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13 September 2019
Blacksburg, Virginia

Keywords: Burrow, habitat, herbaceous, juvenile, longleaf pine, ruderal, selection, vegetation

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ABSTRACT (academic)

Eglin Air Force Base (Eglin) in the Florida panhandle provides extensive forested Gopher Tortoise habitat. However, many of Eglin's tortoises reside on treeless, disturbed testing and training ranges (test ranges). Due to the apparent significance of test ranges as Gopher Tortoise habitat on Eglin, it was important to identify site characteristics that influenced their use by tortoises as well as differences among sites that might explain observed variability in burrow densities. The primary goals of this thesis were to identify how vegetation characteristics and burrow site selection differed between forested and test range vegetation types, and if there was a relationship between vegetation characteristics and differences in burrow densities among sites. I conducted vegetation surveys at 19 tortoise occupied sites (seven forested and 12 test ranges), with an emphasis on herbaceous groundcover (primary tortoise forage). Secondly, I distributed a questionnaire to natural resource personnel at other military installations throughout the southeast to identify common management practices used to maintain similar testing and training areas. Finally, I explored differences in juvenile tortoise surface activity between forested sites and test ranges, as surface activity may affect survival and recruitment. Test range herbaceous communities were diverse and shared similarities with forested understories, but were also unique in many ways. Differences in burrow densities did not appear to be related to variation in vegetation among sites, but differences in burrow site-selection and juvenile activity patterns between test range and forested vegetation types suggested a difference in how tortoises use these habitats.

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ABSTRACT (public)

The Gopher Tortoise is an important component of a number of upland ecological

communities throughout the southeastern U.S., but populations have experienced

significant declines over the past century, largely in conjunction with the loss of longleaf

pine (*Pinus palustris*) forests. Military installations have preserved large tracts of longleaf

pine, often while implementing prescribed fires that mimic natural lightning-ignited fires

(frequent low intensity fire is a necessary component of longleaf pine communities),

which in turn has provided refuges for many imperiled longleaf associates, including the

Gopher Tortoise. Eglin Air Force Base in the western Florida panhandle presents a

unique situation in which large tracts of longleaf pine sandhill (suitable Gopher Tortoise

habitat) are available, but tortoise sub-populations on base are small, and many tortoises

currently inhabit treeless military testing and training ranges (test ranges) rather than

typical forested sandhill. My objectives were therefore to identify factors that may have

been influencing use of test ranges as habitat by gopher tortoises and that might explain

observed differences in burrow densities among sites. In Chapter 1, I compared

vegetation structure, composition, and burrow site selection among sites and between

forested and test range vegetation types. I also attempted to identify relationships

between vegetation characteristics and variation in burrow densities (a proxy for

abundance within a given area) among sites. In Chapter 2, I distributed a questionnaire to

other military installations throughout the southeast to identify common management

techniques used to maintain testing and training areas at other tortoise-occupied military

installations, as these techniques likely affect their suitability as tortoise habitat. In Chapter 3, I compared surface activity patterns of juvenile Gopher Tortoises between forested and test range vegetation types, as surface activity in these vulnerable, but important size classes may affect survival rates. I found that test ranges generally had greater herbaceous vegetation cover than forested sites (greater forage availability), were highly species diverse in terms of groundcover plants, and had herbaceous communities that shared a number of common sandhill plant species with forested sites, but also were unique in a number of ways. I also found that adult tortoises (burrow site selection) and juvenile tortoises (surface activity) may have exhibited different behaviors in novel test range vegetation types compared to individuals inhabiting more natural longleaf pine sandhill on base. However, I did not find strong evidence that current vegetation structure or composition was related to observed differences in burrow densities among sites and that other factors might have played a greater role in structuring Eglin's remnant tortoise sub-populations.

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Preface

The Gopher Tortoise

       The gopher tortoise (*Gopherus polyphemus*) is a large, long-lived terrestrial turtle adapted to fire-maintained xeric habitats, particularly longleaf pine (*Pinus palustris*) communities, of the southeastern U.S. (Auffenberg & Franz 1982, Diemer 1986). Currently, longleaf pine ecosystems are critically imperiled, with remnant tracts confined to fragmented, often degraded stands totaling roughly 2% of their historic distribution, which once included much of the Atlantic and Gulf Coastal Plains (Noss 1989, Means 1996).

       Consequently, gopher tortoises have experienced dramatic range-wide declines and widespread population fragmentation over the past century (Auffenberg & Franz 1982, Diemer 1989, Wilson et al. 1997). The gopher tortoise's current range extends from southeastern South Carolina into peninsular Florida and west into eastern Louisiana (Gopher Tortoise Council 2013). Due to significant population declines, the gopher tortoise was federally listed as threatened in the western part of its range (Alabama west of the Tombigbee and Mobile Rivers, Mississippi, and Louisiana) in 1987 (USFWS 2011, Gopher Tortoise Council 2013). The eastern population has recently been proposed as a candidate for federal listing and gopher tortoises are listed as protected non-game species in eastern Alabama, and state threatened in Georgia, Florida, and South Carolina (Gopher Tortoise Council 2013).

       Gopher tortoises excavate extensive burrows known to provide shelter to a wide array of vertebrate and invertebrate commensal species (Jackson & Milstrey 1989, Alexy et al. 2003). The effects of this burrowing activity within longleaf pine and other xeric upland communities of the southeastern coastal plain are thought to help facilitate high plant and animal species richness associated with these assemblages (Landers & Speake 1980, Jackson & Milstrey 1989). Population declines have therefore been cause for concern as the gopher tortoise is considered a

keystone species within many xeric habitats (Eisenberg 1983, Jackson & Milstrey 1989). The burrow maintains a consistent thermal environment that provides the tortoise, as well as its commensals, with shelter from extreme temperatures and frequent fires (Pike & Mitchell 2013). Burrows can provide refuge as well as foraging and breeding opportunities for over 300 known vertebrate and invertebrate commensal species, including multiple threatened and endangered species, many of which may be highly dependent on the presence of burrows on the landscape (Jackson & Milstrey 1989, Alexy et al. 2003). Certain commensals such as the gopher frog (*Lithobates capito*), Florida mouse (*Podomys floridanus*), the federally threatened eastern indigo snake (*Drymarchon couperi*), and multiple invertebrates are considered gopher tortoise burrow obligates (Landers & Speake 1980, Eisenberg 1983, Alexy et al. 2003, Roznik & Johnson 2009). These species may not be able to persist in the absence of tortoises and their burrows.

Further, gopher tortoises move large volumes of soil while excavating burrows over the course of a lifetime, create extensive tunnels that may persist for years depending on soil composition, and potentially influence local floral assemblages through digging and seed dispersal (Kaczor & Hartnett 1990, Kinlaw & Grasmueck 2012, but see Birkhead et al. 2005). The gopher tortoise therefore meets the criteria proposed by Jones et al. (1994) of an ecosystem engineer (Kinlaw & Grasmueck 2012). It is likely that disturbances created by tortoise burrowing activity promote environmental heterogeneity and, in doing so, facilitate biodiversity through the creation of new available niche space (Landers & Speake 1980, Eisenberg 1983, Catano & Stout 2015).

Gopher tortoises are primarily herbivorous, feeding on leafy vegetation as well as seeds, fruits and occasionally non-plant matter including insects, bone, and charcoal (Garner & Landers 1981, MacDonald & Mushinsky 1988). Adult gopher tortoises are generalist foragers but may

demonstrate selective feeding habits when preferred foods (i.e. protein- & nitrogen-rich taxa) are available. There is some evidence to suggest juvenile tortoises may be more selective than adults (Garner & Landers 1981, MacDonald & Mushinsky 1988, Mushinsky et al. 2003). Grasses typically are the most readily available forage and make up the bulk of the gopher tortoises' diet but tend to be consumed in equal or lower proportions to what is available (Garner & Landers 1981, MacDonald & Mushinsky 1988). Many forbs, when present, are selected at a higher rate than what is proportionally available (Garner & Landers 1981). Additionally, legumes and other nutritious forbs appear to form an important component of juvenile tortoise diets (Garner & Landers 1981, MacDonald & Mushinsky 1988).

Eglin Air Force Base and Current Gopher Tortoise Status on Site

Eglin Air Force Base is located in the western Florida panhandle, encompassing parts of Okaloosa, Santa Rosa and Walton Counties. Containing roughly 187,000 ha of actively managed longleaf pine forests, much of which is upland sandhill (Provencher et al. 2003), Eglin represents some of the largest remaining contiguous tracts of potential gopher tortoise habitat in the region (USFWS 2011). However, prior to recent decades, much of Eglin's longleaf pine habitat was degraded (Dale & Beyeler 2001, Litt et al. 2001, Provencher et al. 2001), primarily due to fire-suppression. Canopy closure and hardwood encroachment presumably relegated gopher tortoises to disturbed areas where tree canopy cover remained sparse and may have contributed to population declines, though historic population sizes on Eglin and population trends are not known (Sutter et al. 2001). In addition to shifts in habitat condition, current distribution of tortoises on Eglin may also partly reflect past harvest by people for food, which was historically intense in the Florida panhandle (Auffenberg & Franz 1982, Diemer 1986) and may still occur to some extent on Eglin (Jeremy Preston, Jackson Guard Eglin AFB Natural Resources Division, personal communication).

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Despite large expanses of seemingly high-quality habitat that now exist on Eglin due to improved management, gopher tortoise burrow densities remain low in extant sub-populations across base (Sutter et al. 2001), many of which are found on open testing and training ranges (test ranges) and in other human-disturbed/ruderal areas, often in isolation from one another. Furthermore, initial assessments suggested there were considerable differences in vegetation characteristics, burrow densities, and recruitment potential among sites where tortoises currently occur. Occupancy surveys recently conducted on Eglin detected burrows or tortoises at only 53 of 507 surveyed sites, with low occupancy probability (<15%) beyond 60 m from previously documented burrows (Gorman et al. 2015). Considering adult burrows are conspicuous features on the landscape (> 90% detection rates on Eglin for adult burrows), these findings suggested that the vast majority of Eglin sandhill was potentially unoccupied by gopher tortoises despite what appeared to be an abundance of suitable habitat. Furthermore, long-term monitoring suggested tortoise densities within many sub-populations have remained low (and may be declining) and it was unknown whether tortoises inhabiting test range peripheries used adjacent forested areas (Haas et al. 2016).

Eglin's tortoise-occupied test ranges are often expansive (the largest exceeds 4,000 ha), treeless areas that can serve multiple purposes such as live-fire training exercise areas, landing zones, and bombing range impact buffers. The open condition found on test ranges is achieved through some combination of mechanical treatments (mowing, roller chopping in the past) as well as prescribed or incidental fire and herbicide. In addition to generally lacking trees, test ranges are typically free of tall shrubs and initial assessments suggested at least some test ranges appeared to have a high diversity of native longleaf sandhill plants while others seemed to

contain an abundance of weedy, early successional species and/or non-native erosion control species.

Canopy openness and frequent low-intensity fire are largely responsible for high herbaceous species richness and abundance in longleaf pine forests under natural disturbance regimens (Provencher et al. 2001). Test ranges that have not experienced heavy soil disturbance or been seeded with non-native erosion control species were therefore expected to potentially exhibit comparable levels of herbaceous diversity to well-managed forested sites, without the canopy or mid-story. Alternatively, an abundance of woody shrubs may indicate a lack of disturbance, particularly the absence of frequent fire (Reinhart and Menges 2004), while heavy, frequent soil disturbance resulting from mechanical treatments such as roller-drum chopping may promote encroachment and eventual dominance of weedy species (Rickey et al. 2007, Menges & Gordon 2010).

State-listed species may be afforded protection by the U.S. Air Force on installations when conservation efforts are not in conflict with military mission goals (U.S. Air Force 2004, USFWS 2011). The presence of tortoises on test ranges may therefore interfere with mission objectives under certain circumstances. Additionally, the ability to operate on tortoise-occupied test ranges could be further impeded should gopher tortoises receive federal protection in the eastern portion of the range, which includes Eglin. Due to the ecological importance of gopher tortoises within healthy upland communities throughout much of the southeast, Eglin natural resources staff recognize the base's significance as a provider of contiguous tracts of potential high-quality habitat. Given that the eastern population of the gopher tortoise is a candidate for federal listing, a better understanding of why and how tortoises continue to use test ranges is of high priority. While preliminary assessments suggested considerable differences existed, we

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lacked a clear understanding of how variable test ranges were in terms of vegetation structure and composition, particularly in regards to herbaceous groundcover (i.e. primary gopher tortoise forage), or the extent to which groundcover on test ranges resembled the understory of gopher tortoise-occupied longleaf pine sandhill on Eglin. Further, it was unknown if/how those vegetation differences might correspond to observed differences in tortoise sub-population structures/densities across base.

Identifying factors that may have been influencing burrow site selection, population structure, and recruitment potential in these novel habitats was a crucial first step towards determining whether tortoises could persist on test ranges long-term. Additionally, these efforts were expected to generate some insight into management practices that would promote healthy tortoise populations while still maintaining the necessary conditions for military testing and training exercises. Therefore, as part of a Department of Defense (DoD) Legacy Resource Management Program project at Eglin, I attempted to assess vegetation structure and plant species composition, with an emphasis on herbaceous ground cover, on tortoise-occupied test ranges and within forested sandhills where tortoises occur (Chapter 1).

Management strategies used on test ranges promote conditions necessary for training and testing activities, namely open sightlines and short vegetation required for munitions scoring. When management regimens are prescribed, there is likely minimal consideration for the potential biotic impacts associated with different strategies. In addition to a better understanding of how and why tortoises use test ranges and similar disturbed areas, identifying common management practices used to maintain these sites and their potential effects on gopher tortoises will be beneficial to natural resource managers on military installations throughout the tortoise's range. I therefore developed a questionnaire that was distributed to test range/natural resource

personnel at multiple installations known to harbor gopher tortoises in an attempt to identify

these practices (Chapter 2). Information obtained via this survey, in conjunction with the work

described in Chapter 1, will be used to inform data-driven recommendations that could further

mitigate future conflicts between military training objectives and tortoise conservation goals.

The density of active and inactive juvenile and subadult burrows on the landscape (i.e.

juvenile recruitment potential) appeared to be highly variable among test ranges and forested

sites with populations large enough to reproduce (Goodman et al. 2018). Juvenile gopher

tortoises are highly susceptible to predation as well as dangers posed by extreme environmental

conditions. Vegetation structure may affect the time and effort required by juveniles to meet

nutritional and thermoregulatory demands. I therefore compared activity patterns (i.e. time spent

outside the burrow) of juvenile tortoises between structurally different vegetation types, test

ranges and forested sandhill (Chapter 3).

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Chapter 1

Habitat use of military test ranges and forested sandhills by Gopher Tortoises at Eglin Air Force Base, Florida

William M. Moore

Abstract

The gopher tortoise (*Gopherus polyphemus*) is a species of conservation concern throughout its range and is considered a keystone species within longleaf pine (*Pinus palustris*) communities. Eglin Air Force Base (Eglin) features some of the largest remaining contiguous tracts of potential tortoise habitat. However, many of Eglin's tortoise sub-populations are currently located on treeless military testing and training ranges (test ranges) and exist at low densities. Burrow densities within adult and juvenile (indicators of reproductive success) size-classes vary considerably among sites, both forested and test ranges, presumably due to differences in current and historical management strategies, mission use, and vegetation characteristics across base. To mitigate future conflicts between conservation goals and military training objectives, it is important to assess the value of test ranges to gopher tortoises and to understand why tortoises appear to select them over adjacent forested areas. Here, I conducted vegetation surveys with an emphasis on herbaceous ground cover composition at two scales: 1) site-wide and 2) burrow (use vs availability). My primary objectives were to determine how groundcover vegetation varied among sites and between forested and test range vegetation types, if differences in vegetation characteristics corresponded to differences in burrow densities among sites, if tortoises selected burrow locations in relation to presence and abundance of major vegetative cover classes, and if burrow site selection differed between vegetation types. Vegetation surveys were conducted from June-August at 11 sites (8 test ranges and 3 forested sites) in 2017 and 8 additional sites (4 test ranges and 4 forested sites) in 2018 (19 sites total).

Plant species richness, composition, and % cover estimates varied considerably among sites and between forested sites and test ranges. My results confirmed that test range herbaceous communities often shared some characteristics of forested sandhills, but were also unique in a number of ways. My results did not indicate a direct relationship between vegetation cover and burrow densities or activity patterns, suggesting other factors may have had a greater influence on current tortoise population structure. For example, nesting season mowing events in 2017 destroyed burrow aprons (likely destroying nests) and collapsed burrows at two sites with previously high densities of juvenile burrows. At the burrow-scale, I found some evidence that gopher tortoises may have been selecting burrow locations differently between forested sites and test ranges in relation to groundcover vegetation. While adequate herbaceous cover is important to gopher tortoises, it does not appear that current vegetation conditions alone explain variability in burrow densities observed among sites on Eglin.

Keywords: *Gopherus polyphemus*, habitat management, herbaceous, forage, ruderal

Introduction

Gopher tortoises prefer fire-maintained open canopy habitats with xeric soils, usually dominated by an overstory of longleaf pine (*Pinus palustris*), a sparse midstory consisting mainly of drought/fire tolerant oaks (*Quercus sp.*), and diverse herbaceous groundcover (Auffenberg & Franz 1982). Frequent low-intensity fires maintain the open structure and high herbaceous species richness and abundance under natural disturbance regimens within these habitats (Provencher et al. 2001, Walker and Silletti 2007, Oswalt et al. 2012). Canopy openness allows light to penetrate to ground level, promoting herbaceous plant growth (Means 1997, Provencher et al. 2001) which constitutes the bulk of the gopher tortoise's diet (Auffenberg & Franz 1982, Diemer 1986, MacDonald and Mushinsky 1988). Further, ample

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light penetration increases soil temperature, which in turn accelerates tortoise egg development in nests, and shortens incubation periods (Landers et al 1980).

Habitat characteristics may affect gopher tortoise movement patterns (McRae et al. 1981, McCoy et al. 2013), density, and colonization (Auffenberg & Franz 1982). For example, long-term monitoring of a population inhabiting pine plantations in northern Florida indicated considerable fluctuations in immigration, emigration, density (and possibly recruitment) that may have been at least partially attributed to shifting habitat conditions throughout the study period, particularly changes in tree canopy cover in response to clearcutting, thinning and replanting (Berish et al. 2012). Tuberville et al. (2014) suggested that habitat conditions resulting from different management histories at three study sites in Georgia and Alabama probably contributed to the dissimilarity in demographic structures and adult sizes among tortoise populations at those sites. Additionally, tortoises residing in areas with diverse and abundant herbaceous ground cover tend to have smaller home ranges and may travel shorter distances to forage than individuals inhabiting areas where such growth tends to be sparse (McRae et al. 1981, Diemer 1986, Innes 2009).

Habitat degradation, typically resulting from fire suppression, is one of the primary threats currently facing gopher tortoises (Auffenberg & Franz 1982, Diemer 1986). While prescribed burning is used as a surrogate for natural lightning-ignited fires with positive results, these efforts alone may not always adequately maintain the open structure of longleaf forests under historic disturbance regimens, particularly if there is an over-reliance on dormant-season burns that tend to be less effective at reducing hardwoods (Outcalt 2000, Outcalt & Brockaway 2010). In the absence of fire, hardwood encroachment begins to shade out the understory, limiting foraging and basking opportunities, and the habitat becomes increasingly unsuitable for

tortoises (Auffenberg & Franz 1982, Garner and Landers 1981, Diemer 1986). As tree canopy cover increases, avoidance of unfavorable patches may confine tortoises to forest openings and restrict movements (McCoy et al 2013). At some threshold, habitat quality declines to an extent that forces gopher tortoises to emigrate from an area entirely, often relegating them to highly disturbed open-canopy or treeless areas (Garner and Landers 1981, McRae et al. 1981, Auffenberg & Franz 1982, Diemer 1986). These sites may include military test ranges as well as powerline rights-of way, road edges, firebreaks, old fields and pastures, among other anthropogenic or ruderal areas.

Alternatively, lack of tree canopy associated with many disturbed areas may promote ideal conditions for thermoregulation, nest incubation, and, assuming adequate forage remains available, could potentially increase the appeal of these open vegetation types to tortoises (Auffenberg & Franz 1982). It is often assumed that tortoises use disturbed areas in response to poor or deteriorating habitat quality in surrounding forests. However, disturbed areas lacking canopy often harbor greater tortoise densities than adjacent forested patches of suitable quality (Auffenberg & Franz 1982, Lora Smith, Joseph W. Jones Ecological Research Center at Ichauway, personal communication). In some cases, areas cleared of trees may mimic conditions created by large-scale natural disturbances such as intense storms or fire (Auffenberg & Franz 1982, Breininger et al. 1994, Rautsaw et al. 2018). Further, juveniles may have faster growth rates in some disturbed habitats compared to more natural forested sites (Landers et al. 1982, Godley 1989). The value, or lack thereof, associated with these human-altered vegetation types and their ability to serve as population sources or sinks may be frequently overlooked in the literature (though see Hathaway 2012, Harris 2014, Rautsaw et al. 2018).

Longleaf pine forests are generally managed through some combination of fire, chemical, and mechanical treatments, often with the goal of promoting favorable wildlife habitat (e.g. improving/maintaining habitat for game species and/or species of conservation concern, restoration of degraded habitat). However, most disturbed areas tend to be abandoned clearings or are maintained in an open state without consideration for their habitat value. Management practices used to maintain both forested and disturbed areas may have positive, negative, or neutral impacts on gopher tortoises. For example, Menges and Gordon (2010) reviewed multiple studies on the use of various combinations of mechanical treatments, herbicide, and fire to manage an array of pyrogenic systems in Florida and concluded that prescribed burning, in general, best achieved desired habitat conditions, though other practices could be used to augment the effectiveness of fire.

It is important to note, however, that fire alone may not improve conditions rapidly enough to observe a response by tortoises over short time intervals, particularly in degraded sites. Yager et al. (2007) for example, did not observe significant improvement in herbaceous cover or an obvious response by tortoises to the application of dormant and growing season burning in degraded forest adjacent to disturbed areas occupied by tortoises at Camp Shelby, Mississippi. While mechanical treatments may be a preferred short-term solution to removal of woody vegetation, particularly larger hardwoods and shrubs, there is some concern regarding the collapse of burrows caused by heavy equipment (Diemer & Moler 1982, Diemer 1992, Epperson 1997). Additionally, many plant species in pyrogenic systems require fire for seed production and germination (Walker & Silletti 2007) and the herbaceous diversity and abundance seen in well-maintained longleaf communities may not be achievable with mechanical treatments alone (Provencher et al. 2001, Reinhart & Menges 2004).

Currently, mowing is the most widely used practice to keep test range vegetation short, though other strategies, including fire, are used to various degrees as well (K.C. Jones, Virginia Tech staff based at Eglin AFB, unpublished management histories). The frequency and type of management appear to vary considerably depending on mission requirements, and past and present management practices have shaped the current vegetation characteristics found on Eglin's test ranges. Forested sites on base are currently managed primarily through the application of prescribed fire, though they may have received other mechanical and chemical treatments in the past (particularly for heavily degraded sites). However, fire return intervals can be highly variable depending on access, priority, and weather conditions, among other factors. Many of the forested sites on Eglin where tortoises still occur reflect this variability in burn regimens, as herbaceous cover, midstory, and canopy can differ significantly among sites, with some areas demonstrating clear signs of fire-suppression while others feature open conditions and extensive groundcover.

Burrow surveys of tortoise-occupied test ranges and forested sites on Eglin indicated tortoise densities varied widely among sites (Goodman et al. 2018). Certain test ranges had some of the highest densities of active and inactive tortoise burrows of any resident sub-populations currently on base (Goodman et al. 2018, C.A. Haas, Virginia Tech, unpublished data). High densities are not necessarily indicators of habitat quality (Van Horne 1983) and it is unclear whether gopher tortoises are using these areas out of necessity or intentionally selecting them. Further, if gopher tortoises are using test ranges simply because they lack an overstory, these vegetation types could be acting as population sinks if tortoises fail to reproduce or recruit.

However, at least some test ranges at Eglin contain relatively high densities of juvenile-sized burrows, suggesting that under certain circumstances, test ranges may be providing high-

quality habitat that promotes reproduction and possibly increases recruitment potential.

Abundant and diverse herbaceous cover is a necessary component of the gopher tortoise's diet, and forage quality and composition may be especially important to nesting females and juveniles because of their direct effects on egg, clutch, and hatchling size, as well as juvenile growth rates (Landers et al. 1980, Mushinsky 2014). Further, forage availability and composition likely influence foraging time and effort (Diemer 1986, Hathaway 2012).

The goals of this study therefore, were to: a) Determine how vegetation composition, particularly herbaceous groundcover, and structure varies among sites and between test ranges and forested sandhills on Eglin Air Force Base. b) Determine if variation in vegetation characteristics corresponds to differences in burrow densities and tortoise activity patterns among sites and, if possible, determine how different management practices on test ranges influence vegetation composition and structure. c) Identify if and how vegetation cover and composition may be influencing burrow site selection within gopher tortoise-occupied test ranges and forested sites (use vs. availability).

Materials and Methods

Study Site Selection, Burrow Surveys, and Camera Trapping

Two-observer line-transect surveys (see Gorman et al. 2015) were conducted using Jackson Guard's (Eglin's Natural Resource Branch) gopher tortoise burrow observation database. Surveys were conducted in spring/summer of 2016 and fall/spring of 2017-2018 to locate burrows at sites likely to have at least 10 burrows within a 10-ha survey area (see Table 1.1 for site list, survey area sizes, and burrow density estimates). In some low-density sites, survey areas were expanded until at least 10 active or inactive burrows (see below for definition) were located (though the 10-burrow minimum was relaxed beginning in the fall of 2017), resulting in survey area sizes between 10 ha – 19.7 ha. These survey area boundaries were used

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for all site-wide vegetation measurements while 10 burrows within each survey area were selected for inclusion in burrow-scale (use vs availability) vegetation measurements. Burrow density estimates obtained through these surveys (Table 1.1) were used in analyses exploring relationships between vegetation variables and burrow densities. Burrow width, measured ~ 50 cm from mouth of the burrow, is strongly correlated with the carapace length of the resident tortoise and provides a good approximation of size and age class (Doonan & Stout 2004). Initial density estimates (all active and inactive burrows/ha) were categorized by size-class as follows: total burrow densities (all size classes combined), adult burrow (≥230 mm in width, Iverson 1980) densities, total juvenile and subadult burrow (all burrows < 230 mm) densities, sub-adult burrow (131 mm – 230 mm) densities, and juvenile burrow (≤130 mm) densities. At the burrow-scale, I combined subadult and adult size classes into a single category (see burrow-scale vegetation surveys below) but the burrow density categories above were included as response variables for multiple regression analyses exploring possible relationships between burrow densities and vegetation variables at the site-wide scale.

I used tortoise activity data acquired through a separate camera trapping study (Goodman et al. 2018, C.A. Haas, Virginia Tech, unpublished data) in analyses exploring the relationships between vegetation variables and activity patterns. Activity was separated into two categories defined as follows: average exit duration- total amount of time spent on the surface (i.e. the timespan between a tortoise exiting and reentering its burrow) and average excursion duration-total amount of time spent away from the burrow (i.e. the timespan between a tortoise exiting and returning to the camera frame). Excursions were assumed to have primarily represented foraging bouts, though tortoises may have left the immediate vicinity of the burrow for a number of other reasons as well. Exit duration and excursion duration were calculated using mean

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durations of individual camera-trapped tortoises within each site to generate site-wide averages. Site-wide exit and excursion durations were used as response variables in regression analyses.

During the initial burrow surveys, burrows were categorized as active, inactive or abandoned, as described in Smith et al. (2009). Active burrows had obvious signs of recent use, including tracks, slides, scat, and tended to be clear of most debris/litter. Inactive burrows were not necessarily unoccupied but lacked obvious signs of recent use and may have had some litter/debris accumulating in the entrance. A burrow was considered abandoned when it had not been recently used by a tortoise, generally had considerable debris and litter accumulating in the entrance, and/or was collapsed. Gopher tortoises may use multiple burrows simultaneously and will regularly re-occupy previously abandoned and inactive burrows. Therefore, when I revisited these burrows to conduct burrow-scale vegetation measurements, I reassessed activity status as tortoise presence can have a significant effect on the structure and composition of plant species in the burrow's vicinity (Kaczor and Hartnett 1990).

Current and historical management information obtained from Eglin's long-time Test Range Habitat Manager, and fire management and herbicide application records from the United States Air Force Wildland Fire Center and Jackson Guard Forestry Division on Eglin were used to develop a qualitative habitat management profile for each site (see Table 1.2). In total, vegetation surveys were conducted at 19 sites (7 forested sites and 12 test ranges) in the summers of 2017 and 2018 (see Figure 1.1 for site map).

Vegetation Surveys- Site Wide Scale

To assess site-wide (within study site boundaries) vegetation characteristics, surveys were conducted at three forested sites and six test range sites (n=9 sites) in 2017 and four additional sites in each vegetation type in 2018 (n=8 sites, n=17 sites total both years). Due to time constraints, only one or two survey areas were included for site-wide vegetation surveys on

test ranges with multiple disjunct burrow clusters (clusters that were not necessarily isolated, but were separated by ~0.5-1 km) in 2017, which is why B70C1 and C62N were not surveyed at this scale.

Within a survey area, I established three evenly spaced north-south oriented transects which divided the site into equal-width quarters (Figure 1.2). Along each transect, ten 1-m^2 plots (n=30 per site) were placed randomly within a range of distances from one another that averaged out to roughly the transect length when added together (i.e. for a 600 m transect, plots were placed randomly between 50-70 m from one another). Within each 1-m^2 plot, all plants were identified to the lowest taxonomic level possible (usually to species, though sometimes genus). If multiple similar-looking species were difficult to differentiate and were only identified to genus, that group was considered a single species in any estimates of species richness or diversity. For example, *Paspalum praecox and P. setaceum* were initially difficult to tell apart and formed a single category *Paspalum* spp*.,* which was treated as a single species, whereas *P. notatum* could be easily differentiated from the former two and was treated as a separate, unique species. Standard Daubenmire (1959) cover classes (1 = < 5 %, 2= 5-25 %, 3 = 25-50 %, 4 = 50-75%, 5 = 75-95%, 6 = > 95%, midpoints for each class were used in all analyses) were used to estimate percent cover (looking down from above, estimated total surface area encompassed within the plot) for each taxon as well as for bare ground, litter and lichen. All plants were also assigned to one of the following major vegetative ground cover classes: non-leguminous forbs (forbs), grasses and sedges (graminoids, families Poaceae and Cyperaceae respectively), leguminous-forbs (legumes, family Fabaceae), and non-vining woody plants (shrubs). Other cover class categories included cactus (prickly pear, *Opuntia humifusa)*, fern (bracken fern, *Pteridium aquilinum*), woody vines (vines, e.g. *Smilax sp.*), and yucca (Adam's needle, *Yucca filamentosa*),

though these groups generally were not major components of the vegetative cover for most sites and were not reported with site-wide estimates.

Additionally, I identified a suite of species that I felt were reliable indicators of past soil disturbance which formed an additional cover class category (disturbance species cover). Disturbance cover included non-native erosion control grasses: carpet grass (*Axonopus fissifolius*) and bahiagrass (*Paspalum notatum*), as well as common ruderal species: poor Joe (*Diodia teres*), rustweed (*Polypremum procumbens*), and woody goldenrod (*Chrysoma pauciflosculosa*) (Hunter 1972, Kirkman et al. 2013). I also included slender bluestem (*Schizachyrium tenerum*) in my list, which is not typically reported as a ruderal grass. However, this species was rare or absent in forested sites, was a dominant grass on some test ranges, and became dominant after treatment in sand pine (*Pinus clausa*) removal sites on Eglin (but was not a major groundcover component in forested reference sites) in a previous study by Provencher et al. (2000). Heavy past mechanical disturbance may have promoted the exposed, nutrient-poor soils on certain test ranges to which slender bluestem is well-adapted (Leithead et al. 1976, Walsh 1994).

For forested sites, basal area and point-intercept tree canopy cover estimates (Floyd & Anderson 1982) were taken at two randomly selected plots along each transect (n=6 total per site). Tree canopy cover-transect direction was determined using a random compass bearing with the vegetation plot serving as the midpoint. Percent tree canopy cover was then estimated as the number of points intercepting shrubs and trees taller than 1.5 m, measured every 1 m along a 20-m transect divided by the total number of points (x/20 per transect, n=120 points/site). Basal area in forested sites was estimated using an angle gauge (Jim-Gem® Cruz All, Basal Area Factor of 10) while standing in the center of two other randomly selected plots along each transect (n=6

measurements total/site). The number of 'in' trees (trees wide enough to be counted) was multiplied by 10 (basal area factor) for each measurement and the average of those six measurements was used to estimate site-wide basal area in ft^2/acre (0.23 m^2/ha).

Vegetation Surveys-Burrow Scale (Use vs. Availability)

Burrow scale vegetation surveys were conducted at the same three forested sites surveyed at the site-wide scale and two additional test ranges (B70C1 and C62N) in 2017 (n=11 sites total). All eight sites in 2018 were surveyed at both the site-wide and burrow scales. Ten burrows were selected from each site (except for B71 in 2018 due to restricted access which limited the availability to nine accessible burrows, n=111 burrows total in 2017 and n=79 burrows in 2018). Burrows were selected non-randomly to include a range of activity statuses and size-classes and to incorporate as much of the survey area as possible (burrow statuses and size classes were not equally distributed within each site as the total pool of burrows to choose from within most sites was typically limited). As was the case in the site-wide scale, all burrows ≤ 130 mm at the burrow scale were considered juveniles. In contrast to the site-wide scale, burrows > 130 mm were collectively considered 'adults' at this scale, however, it should be noted that this size range contains both individuals that have yet to reach reproductive size (and would normally be considered subadults), along with fully mature adults. I avoided using burrows that were within 30 m of one another whenever possible, as they would likely not have represented independent samples.

Using the aforementioned cover-class method, five 1-m^2 plots were randomly placed within a buffer (use, i.e. foraging) around each burrow with a radius of 30 m for adults and 8 m for juveniles. These buffers were based on typical maximum-foraging distances reported for adult (McRae et al. 1981) and juvenile (McRae et al. 1981, Diemer 1992, Figure 1.3) gopher tortoises. To determine if burrow site-selection was influenced by vegetation availability, I

randomly established five additional plots within a larger (available) buffer around each burrow

that was beyond the typical foraging area, but still hypothetically accessible to the tortoise

inhabiting the burrow. The buffer sizes were as follows: 60-85 m for adults and 16-30 m for

juveniles (Figure 1.3). These buffer sizes were equivalent in size to at least double the foraging

radius and ≤ to reported estimates for mean daily maximum distances traveled by adult (Eubanks

et al. 2003) and juvenile (Pike 2006) gopher tortoises, respectively.

At forested sites, the basal area and tree canopy cover methods described for the site-

wide scale were used for each burrow. However, within the smaller foraging buffer, three

transects were established with the midpoint of the center transect directly to the right of the

burrow apron (observer oriented with back turned to mouth of the burrow), running parallel with

the burrow's azimuth (Figure1.4). Transects were 20 m in length, spaced 15 m apart from one

another with points taken every 1 m along each transect (n=20 points/transect, 60 total) for

adults, and 10 m spaced 8 m apart with points taken every 0.5 m for juveniles. Within the larger

availability buffer, three additional transects were established at the first three randomly placed

vegetation plots. The direction of the transect was determined using a random compass bearing

and the vegetation plot again served as the midpoint. Basal area was also recorded at these three

plots, standing in the plot's center and estimates were averaged together to estimate basal area

within the entire availability buffer for that burrow.

Statistical Analyses-Site-wide Scale
Mean cover estimates for major cover classes and individual plant taxa were calculated as

the estimated total coverage divided by the number of plots per site. For forested sites, tree

canopy cover and basal area estimates were averaged to provide a site-wide estimate. Alpha

diversity, beta diversity, and total species richness were calculated for each site as metrics for

species richness and diversity (see Whitaker 1960 for original conceptual descriptions of these

terms). In this study, alpha diversity (α) referred to the average number of species per 1-m² plot within a site. Species richness (S) was the total number of species encountered per site. Beta diversity (β) was calculated as S/α-1 which provided a metric of relative variability among 1-m² plots. If α and S were identical, β=0, i.e. all plots contained the same species. The further β was from zero, the more heterogeneous a site was in terms of species within each plot.

Species diversity at the site-wide scale was explored further using Shannon Diversity (H', Shannon 1948) and the inverse of Simpson's Diversity (1-D, Simpson 1949) indices. Both indices are commonly used diversity metrics, place different emphases on dominant/rare species, and both were selected a priori to account for different aspects of diversity (Morris et al. 2014). The Shannon Index incorporated relative abundances for individual taxa (% cover estimates) and total species richness within a site to estimate diversity. For these estimates, greater values corresponded to increased evenness (similarity in abundances among species present within a site) and greater total species richness (i.e. greater the index value for a site, the more 'diverse' it was). Lower values indicated lower species richness and/or dominance of fewer, more abundant species within a site. Similarly, the inverse of Simpson's Index also estimated diversity based on the total number of species and their relative abundances; however, these values ranged between zero and one (the closer to one, the greater the diversity) and were interpreted as the likelihood that two randomly selected individuals within a site belonged to different species.

Major vegetative cover class estimates were averaged for each vegetation type (n=7 forested sites and n=10 test ranges). Two sample t-tests were then used to compare means for major cover classes and total species richness (S) between vegetation types. Comparisons (i.e. patterns and associations) of herbaceous communities among sites and between test ranges and forested sites at the site-wide scale were made using hierarchical cluster analysis and non-metric

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multidimensional scaling (NMDS), both of which provided different (but somewhat complementary) ways of analyzing and visualizing community data (Oksanen 2015). Percent cover estimates for herbaceous plant species were used to create a site-by-species abundance (cover) matrix. Hierarchical cluster analysis (average linkage method) was performed using Bray-Curtis dissimilarity measures (Bray & Curtis 1957) as the distance metric and results were visualized in a dendrogram to explore 'relatedness' among sites in terms of herbaceous community composition (Quinn & Keough 2002). In ecological studies, average linkage tends to be the most commonly used linkage method in hierarchical clustering and is recommended for many applications (Quinn & Keough 2002). Bray-Curtis coefficients have a number of properties that make this distance metric well-suited for multivariate analyses in ecological studies as well, particularly in that shared zero-values (i.e. shared absences of certain species which are common in community datasets) do not contribute to increased similarity between sites (Legendre & Legendre 1998, Oksanen 2015).

NMDS compared site-wide herbaceous communities based on species rank orders again using Bray-Curtis dissimilarities as the distance metric. NMDS has the benefit of making no assumptions regarding linear relationships among variables or normal data distributions and is thus a popular technique for analyses of vegetation community data (Noy-Meir 1974, Peet 1980, Oksanen 2015). NMDS is an iterative approach in which a number of random starts are used until similar solutions with minimized stress (similar to goodness of fit, i.e. how well rank order distances between observations are maintained in two-dimensional plotted space) are found (Oksanen 2015, Dexter et al. 2018). The maximum number of random starts was set to 100 but a solution was always reached within 20 iterations. Multiple ordinations were performed with an increasing number of dimensions (k). The final number of dimensions (k=4) chosen was selected

based on visual assessment of a scree plot (stress value upon reaching a solution plotted against increasing k) to determine a point at which stress was not substantially reduced by increasing the number of dimensions. Further, a solution with a stress value of <0.1 was set as an upper threshold, a value at which both the interpretation of points and overall ordination shape are generally considered appropriate (Dexter et al. 2018). A permutational multivariate analysis of variance (PERMANOVA) was performed to determine if there was a statistical difference in herbaceous communities between forested sites and test ranges based on Bray-Curtiss distances. Results were then visualized in two dimensions illustrating apparent overlap and dissimilarities between vegetation types based on herbaceous species associations.

Woody plants were excluded from cluster analysis and NMDS, as the focus was to compare herbaceous ground cover among sites and between forested sites and test ranges. Shrub cover tended to be much greater and more diverse in forested sites compared to test ranges, and likely would have obscured the similarities and differences in herbaceous composition between the two community types that I wished to detect. Certain species which were encountered infrequently (i.e. in a single plot) were assumed to be too rare for meaningful site or vegetation type associations and thus were also excluded from cluster and NMDS analyses.

Multiple regression was used to explore possible relationships between vegetation variables (predictors) and burrow densities within different size-classes (response). Predictor variables included vegetation type (forested or test range) and major cover class estimates (total combined herbaceous cover, shrub cover, and total disturbance species cover). Multiple regression was also used to determine if activity patterns (average exit & excursion duration, response) were related to the same vegetation variables mentioned above.

Statistical Analyses-Burrow Scale

Paired t-tests were used to determine if means of the major cover class estimates surrounding burrow sites (foraging/use buffers) differed from those of the surrounding available habitat (availability buffers) within forested sandhills and test ranges. Paired t-tests were also used to detect differences in tree canopy cover and basal area between foraging buffers and surrounding available habitat in forested sites. Alpha diversity, beta diversity, and species richness were again calculated for each site within both foraging and availability buffers using the burrow as the sampling unit rather than individual plots (e.g. α diversity would refer to species/burrow, estimated for both buffers).

Compositional analysis (Aebischer et al. 1993) was used to determine whether major cover classes at burrow sites (foraging/use buffers) differed from what was proportionally available in the larger paired availability buffers. Compositional analysis tested for significance of vegetative cover class selection via Wilks-lambda, generated a ranking matrix that placed cover classes in order of relative use, and indicated whether cover classes were used significantly more or less than one another via pair-wise comparisons.

All diversity and similarity indices, cluster analysis, and NMDS analysis were generated/conducted using package vegan (Oksanen et al. 2018) and compositional analyses were conducted using package adehabitatHS (Calenge 2006) in R-studio version 1.2.1335 (RStudio Team 2016). All other statistical tests were performed in JMP Pro 13.0.0 (SAS Institute Inc. 2016).

Results

Over the summers of 2017 and 2018, I sampled 2,405 vegetation plots across 19 sites and documented over 130 plant species. Rarely did I estimate percent cover for a given species to encompass greater than 10% of the vegetative groundcover within a site. Species accumulation

curves generally indicated the sampling effort was sufficient to detect the majority of common species present within a site at both scales (Fig. 1.5 & Fig. 1.6), though there appeared to be exceptions where increased sampling effort may have been necessary to accurately estimate species richness within certain sites (both forested and test range).

Site-wide Scale

Mean percent cover estimates for major cover classes varied considerably among sites within both forested and test range vegetation types (Appendix B). Among forested sites, tree canopy cover estimates ranged from 15.8% (Bull Creek) to 66.7% (Garnier Creek) and basal area estimates from 18.3 ft^2/acre (201E) to 68.3 ft^2/acre (Garnier Creek, Table 1.3).

Estimated species diversity was also highly variable among sites (Table 1.4). Test ranges featured both the highest and lowest estimated total species richness (S), which ranged from 34 total species (B70E) to 74 total species (C74). Alpha diversity estimates (α) ranged from 4.9 species per 1-m^2 plot (forested site Garnier Creek) to 18.1 species per plot (test range B75). Beta diversity (β) estimates suggested test range B75 was the most uniform site in terms of species composition among 1-m^2 plots (β =2.3), while forested site Garnier Creek, despite having the second lowest species richness among sites (S=38 total species), had the greatest amount of variability among plots (β=6.7). Shannon Index (H) values ranged from 2.4 (test range B70E) to 3.5 (forested site Rogue Creek and test ranges B75 & C74). Simpson's Index values ranged from 0.86 (test range B70E) to 0.95 (forested sites Bull Creek, Pine Log, & Rogue Creek and test ranges B75, C64, & C74).

I found the following differences in percent cover between forested sites (n=7) and test ranges (n=10, Table 1.5). All comparisons below are presented as estimated average % cover ± one standard error. Forested sites, on average, had less bare ground cover (18.1 ± 3.1 vs. 34.3 ± 5.6, DF=13.53, t=2.53, p=0.02), graminoid cover (23.6 ± 5.7 vs. 42.0 ± 2.7, DF=8.65, t=2.93,

p=0.02), and disturbance-prone species cover (2.7 ± 1.5 vs 18.0 ± 2.2, DF=14.49, t=5.69, p=<0.01) compared to test ranges. Forested sites tended to have greater leguminous forb (legume) cover (8.6 ± 1.8 vs 4.0 ± 0.7, DF=7.61, t= 2.43, p=0.04) and litter cover (50.5 ± 6.8 vs 21.0 ± 2.8, DF=8.00, t= 4.03, p=<0.01) than test ranges.

Cluster analysis comparisons of herbaceous community structures among sites indicated most test ranges generally had species compositions and abundances that were more similar to those found on other test ranges than to herbaceous understories in forested sites (Figure 1.7). Among all sites, forested sites Bull Creek and Middle Creek were most similar. Among test ranges, C52N, C62S, and C64 were most similar to one another followed by B71 and B75, then B70E and C72. All other sites exhibited increasingly dissimilar herbaceous communities and did not form particularly tight groups, with the forested site Garnier Creek being the least similar to all others. The larger cluster containing most test ranges and the cluster containing forested sites 201E, Bull Creek, Middle Creek, Turtle Creek, and test range C74 were more similar to one another than to the group containing Garnier Creek, Pine Log, and Rogue Creek, though the distances between smaller clusters within those groups tended to be relatively large.

NMDS (final stress value =0.08) indicated herbaceous communities in forested sites and on test ranges were somewhat distinct, with certain species demonstrating no affiliation for one vegetation type over the other while others appeared to be better represented in either forested sites or test ranges (Figure 1.8). Results of the PERMANOVA indicated that overall, herbaceous communities in forested sites were distinct from those found on test ranges ($F_{1,15}$=4.50, p<0.01). Visual assessment of the two-dimensional plot and 95% confidence intervals suggested forested site herbaceous communities were far more variable than those of test ranges, the latter of which generally concentrated in the lower left quadrant of the ordination space (<0.1 NMDS axis 1,

<0.1 NMDS axis 2). The primary disparities between forb communities in forested sites and on test ranges involved disturbance-prone species (e.g. poor Joe *Diodea teres*) that expectedly showed greater association with test ranges, and a number of infrequently encountered species, most of which appeared to show more affiliation with forested sites. The most obvious differences in graminoid species composition between forested sites and test ranges included two non-native erosion control species, carpet grass (*Axonopus fissifolius*) and bahiagrass (*Paspalum notatum*), which were exclusively found on test ranges, as well as a native species, slender bluestem (*Schizachyrium tenerum*), which was far more abundant on test ranges than in forested sites. Other bluestems (*Andropogon* spp.) and little bluestem (*Schizachyrium scoparium*), alternatively, demonstrated greater affiliation with forested sites.

Burrow Densities, Activity Patterns & Major Cover Classes
        Neither major vegetative cover classes nor vegetation type (forested vs test range) predicted burrow densities. Specifically, I found no relationship between vegetation measurements and total burrow densities ($F_{4,11}=0.73$, p=0.59, Table 1.6), adult burrow densities ($F_{4,11}=0.87$, p=0.51, Table 1.7), total juvenile burrow densities (juvenile+subadult, $F_{4,11}=0.69$, p=0.61, Table 1.8), subadult burrow densities ($F_{4,11}=0.82$, p=0.54, Table 1.9), or juvenile burrow densities ($F_{4,11}=0.78$, p=0.56, Table 1.10). Likewise, I found no evidence to indicate the same predictors (excluding disturbance cover) were significantly related to tortoise activity patterns. Mean exit duration ($F_{3,12}=2.33$, p=0.13, Table 1.11) and mean excursion duration ($F_{3,12}=0.68$, p=0.68, Table 1.12) were unrelated to vegetation variables measured at the site-wide scale.

Burrow Scale-Use vs. Availability -Differences between Burrow Sites and Paired Availability Buffers
        Mean percent cover estimates differed between burrow locations and paired availability buffers for certain cover classes in both vegetation types (Table 1.13). Within forested sites (n=70 burrows), burrow locations, on average, had greater graminoid cover (27.0 ± 2.1 vs. 20.8 ±

1.7, DF=69, t=5.56, p<0.01) and less litter cover (48.1 ± 1.9 vs. 56.2 ± 1.9, DF=69, t=5.05, p<0.01) than within paired availability buffers. For test ranges (n=120 burrows), burrow locations, on average, had greater legume (4.8 ± 0.3 vs. 4.0 ± 0.3, DF=119, t=2.39, p = 0.02) and shrub cover (15.1 ± 1.0 vs. 12.2 ± 0.9, DF=119, t=2.64, p=0.01), and less bare ground cover (34.3 ± 1.4 vs. 38.0 ± 1.4, DF=119, t=3.90, p < 0.01) compared to paired availability buffers.

Mean tree canopy cover and basal area estimates in all forested sites were roughly equal or lower at burrow locations compared to paired estimates within surrounding available habitat (Table 1.14). Canopy cover was significantly lower at burrow locations at Middle Creek (28.3 ± 2.6 vs. 39.5 ± 3.0, DF=9, t=2.81, p=0.02), Pine Log (30.0 ± 3.8 vs. 39.5 ± 5.0, DF=9, t=2.46, p=0.04), and Turtle Creek (31.7 ± 3.1 vs. 42.2 ± 3.5, DF=9, t=2.33, p=0.04). Basal area at burrow locations was significantly less in Garnier Creek (31.0 ± 7.5 vs. 50.0 ± 4.5, DF=9, t=2.31, p=0.05) and Rogue Creek (23.0 ± 3.4 vs. 38.0 ± 4.7, DF=9, t=3.50, p=<0.01).

As was the case at the site-wide scale, species diversity varied considerably among sites (Table 1.15). Total species richness estimates (S) ranged from 38 species (burrow locations, forested site Garnier Creek) to 87 species (availability buffers, test range C74). Alpha diversity estimates ranged from 12.7 species/burrow (burrow locations, Garnier Creek) to 39.7 species/burrow (availability buffers, C74). Beta diversity estimates ranged from β=0.8 (availability buffers, test range B75) to β=1.6 (availability buffers, forested site Middle Creek and burrow locations, test range B71).

Burrow Scale, Use vs, Availability- Cover Class Preferences

I found evidence that gopher tortoises were selecting burrow locations preferentially in relation to the presence of certain cover classes in both forested sites (Wilk's λ=0.42, p<0.01, Table 1.16) and on test ranges (Wilk's λ=0.42, p<0.01, Table 1.17). In forested sites, graminoids were selected over other cover classes and were significantly preferred over all

others except bare ground in pairwise comparisons. On test ranges, legume and shrub cover were ranked as the top two cover classes, though compositional analysis did not suggest a strong preference among the top five ranked cover classes in pairwise comparisons.

Discussion

Herbaceous groundcover on test ranges was often diverse and, to some extent, similar in composition to that of fire-maintained longleaf sandhill on Eglin. However, plant species diversity and species composition were highly variable among tortoise-occupied sites for both vegetation types and forage availability (i.e. total herbaceous cover) tended to be higher, on average, on test ranges compared to forested sites. In most cases, there did not appear to be an obvious relationship between current vegetation characteristics and burrow densities within tortoise-occupied sites. I found evidence that gopher tortoises were selecting burrow locations differently between test ranges and forested sites.

Site-wide Scale Comparisons between Forested Sandhills and Test Ranges

The higher graminoid and non-leguminous forb cover on test ranges compared to forested sites was not surprising due to the exposed conditions found on test ranges that promote herbaceous growth (Means 1997, Röttgermann 2000, Provencher et al. 2001). This tends to be the case in a number of open, human-disturbed vegetation communities frequently inhabited by tortoises in Florida (Auffenberg & Franz 1982). However, the average graminoid and forb cover estimates in forested sites were skewed lower by sites where midstory cover and canopy closure were more extensive, and the differences in total herbaceous cover may not be as pronounced between test ranges and forested sites with less hardwood encroachment. It is not entirely clear why legume cover was significantly higher in forested sites when overall non-leguminous forb cover was otherwise higher on test ranges; though, an ecological monitoring report for Eglin (Kindell & Johnson 2000) listed legumes as indicators of a lack of mechanical soil disturbance.

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Bush-hogs used to mow test ranges, while likely not as impactful on soil as roller-drum choppers, are heavy, compact soil in wheel ruts (the entire back end of the mowing deck is supported by a row of wheels), and churn soil by ripping woody vegetation from the ground (personal observation). The blades also sit inches from the ground and can cause additional soil disturbance when mowing on sloped topography (U. S. Air Force 2015). Soil disturbance resulting from mowing events and/or during site-preparation may therefore suppress legume growth on test ranges, at least for some species. Alternatively, fire records indicated that most test ranges burn far more frequently than typical longleaf sandhill (primarily due to frequent ignitions from testing and training activities, see Table 1.2). Test ranges also likely feature different fuel characteristics than those typically found in forested sites (e.g. greater cover of bunch grasses, abundant small pieces of coarse wood, and a lack of pine cones and needles) which affect fire ignitability, intensity, and behavior (Wenk et al. 2011, Dell et al. 2017). Wiggers et al. (2013) found that a suite of legume species had different germination rates in response to experimentally manipulated fuel types. Temperature-induced seed germination or mortality was attributed to variations in fuel characteristics (i.e. temperature and heat transference to soil while burning) and it was suggested that heterogeneity in fuel loads and types (particularly pine cones and small pieces of coarse wood) may affect fine-scale species distributions in longleaf pine ecosystems. Certain legume species may therefore be less adapted to potentially novel fire behavior on test ranges due to differing fuel characteristics/distributions, particularly if burns are sufficiently frequent and intense enough to cause seed mortality rather than germination. Frequent mowing could also exacerbate the relative impacts of fire if resulting soil disturbance displaces seeds outside of optimal germinating temperature ranges or within lethal limits.

Higher estimated bare ground cover on test ranges and litter in forested sites was somewhat expected, though these measurements are likely affected by the time since last fire or mowing event, season, and are expected to fluctuate considerably in both vegetation types. Higher shrub cover in forested sites was also expected, though may have been skewed by sites with dense midstories. Comparisons of shrub cover between vegetation types should also be interpreted with caution, as my sampling design was most suitable for measuring ground cover and ignored structural differences in woody vegetation height. Structurally, shrubs on test ranges tend to remain ≤ 1 m tall as frequent mowing inhibits their vertical growth, while all woody plants, regardless of size, were categorized as shrubs in forested sites (though any part of a shrub or tree exceeding ~ 1.5 m was excluded from cover estimates). The abundance of disturbance prone species on test ranges compared to forested sites was also not surprising considering the frequent mechanical disturbance that promotes such growth (Hobbs & Huenneke 1992, Rickey et al. 2007). Weedy/early successional species were poorly represented in forested sites and were mostly present in the two former pine-plantations, Garnier Creek and Pine Log. Total species richness (all cover classes) did not differ between forested sites and test ranges. In most sites, species richness was comparable to the estimated median number of species/400 m^2 (44 species) in what were considered forested reference plots on Eglin by Provencher et al. (2000), though my sites often exceeded these estimates (median = 53 species) probably due to much larger sampling areas.

Two forested sites (Bull Creek and Middle Creek) had the most similar herbaceous communities based on Bray-Curtis distances, and formed a distinct pair in the cluster analysis. Among the seven forested sites, they had the highest total estimated herbaceous cover, open canopies (1st and 3rd lowest canopy cover estimates respectively) and the lowest estimated shrub

cover. Open canopy and a lack of midstory may have contributed to diverse, but similar, herbaceous groundcover between these two sites. Excluding C61A and C74, test ranges generally had herbaceous communities that were relatively similar to one another. There was no obvious pattern among test ranges in relation to recent management (Table 2, number of mowing events ~ 2011-2017) or geographical proximity to one another. The other three forested sites (Garnier Creek, Pine Log, and Rogue Creek) formed another group that was dissimilar to all other sites, though they were also relatively distant from one another. Among forested sites, they were the three with the least amount of estimated total herbaceous cover, the highest estimated canopy cover, and the highest estimated basal area. Herbaceous communities in these sites may have featured assemblages of species that were more shade tolerant compared to forested sites with more open canopies and less midstory shrub cover.

NMDS results indicated forested and test range herbaceous communities, despite comparable total species richness, shared a number of species but were also somewhat distinct in composition from one another. A number of disturbance prone and erosion control species, as expected, were rarely (or never) encountered in forested sites and were highly associated with test ranges. Certain rare forbs that showed apparent associations with either forested sites or test ranges were encountered infrequently and/or at few sites throughout my sampling efforts, and it is difficult to discern from these data alone if these species' presence was indicative of an association with one vegetation type over the other. For example, two species that were primarily associated with forested sites, slender blazing star (*Liatris gracilis*) and narrowleaf silkgrass (*Pityopsis graminifolia*), were both only encountered in relatively high frequencies (7/30 & 13/30 plots respectively) at a single site, Rogue Creek. Otherwise, slender blazing star was encountered in seven plots within all other sites combined (though six of which occurred in three

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other forested sites) and narrowleaf silk grass was not documented at any other site. Similarly, soft greeneyes (*Berlandiera pumila*), a species associated with test ranges, was only encountered once among all other sites (in a single plot on test range C61A) outside of test range C64, where it occurred in 12/30 plots. These species may have been patchily distributed rather than more abundant in specific vegetation types.

Among common species, many showed no obvious association with either vegetation type while others were apparently better represented in either forested or test range sites based on these results. The presence and cover of a number of forbs and grasses, many of which were regularly encountered during my vegetation surveys on Eglin, have been reported in the literature as indicators of reference conditions (and/or a lack of recent soil disturbance) in longleaf communities. However, indicator species lists are often inconsistent and appear to vary regionally. For example, two forbs common on Eglin, Carolina wild petunia (*Ruellia carolinensis*) and sweet goldenrod (*Solidago odora*), have been reported as both indicators of reference conditions and past disturbance by different authors (Hedman et al. 2000, Kirkman et al, 2004, Ostertag & Robertson 2007, Kirkman et al. 2013). Both species were found in both vegetation types but the former demonstrated no obvious association with one over the other, while the latter was more highly associated with forested sites. Four other common forbs at Eglin, coastal plain dawnflower (*Stylisma patens*), scaleleaf aster (*Symphyotrichum adnatum*), eastern silver aster (*S. concolor*) and goat's rue (*Tephrosia virginiana*), were suggested to be indicators of undisturbed longleaf understory by Ostertag and Robertson (2007) in a study conducted in south Georgia and north Florida. In this study, I found the first three species were more highly associated with test ranges while goat's rue appeared to be more common in forested sites. Further, slender bluestem (*Schizachyrium tenerum*), a native grass that was

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considered a disturbance indicator in this study, was reported to be more abundant in reference conditions by both Kirkman et al. (2004) and Ostertag and Robertson (2007) in studies conducted in southwest Georgia. However, as previously stated, this species also readily colonized sand pine removal sites on Eglin while being relatively uncommon in reference plots (Provencher et al 2000).

It should be mentioned that while test ranges appeared to share some overlap in herbaceous community composition with forested sandhill on Eglin, species abundances/cover likely differ in ways that were difficult to quantify given the high species diversity in both vegetation types. Most common herbaceous plants were documented in both vegetation types but were highly variable in frequency of occurrence and cover estimates, though few species ever appeared to be dominant in any survey area. Given my limited sample sizes and large survey areas, among site and between vegetation type comparisons should be interpreted cautiously. A greater sampling effort at the site-wide scale may have revealed differences in abundances/cover for certain species, particularly for a number of small/low growing forbs that tended to be abundant but generally fell within the lowest cover category (<5%) in most plots. This may have been especially true for certain highly diverse sites (e.g. forested site Rogue Creek and test range C74) where I continued to encounter new species at relatively high rates towards the end of my sampling effort (i.e. species accumulation curves had yet to level off at 30 plots, see Fig. 1.5).

The effects of different forms of disturbance, as well as the range of biotic and abiotic conditions across sites, are interactive (Brudvig & Damschen 2011), further confounding the underlying factors that shape current vegetation communities on test ranges and, to a lesser extent, in forested sandhills. Many non-generalist native forbs and grasses may respond differently to varying edaphic/hydrological conditions and fire regimens (Peet & Allard 1993,

Rodgers & Provencher 1999, Smith et al. 2002). It is therefore difficult to determine a suite of species that represent true longleaf reference conditions across large geographic areas, as most assemblages may be regionally specific and not easily defined given considerable past human influence in most extant longleaf stands (Frost 1993, Rodgers & Provencher 1999, Kirkman et al. 2013). Further, it can take a considerable length of time before previously disturbed sites resemble reference conditions in longleaf sandhill (Provencher et al. 1996), and time since site-preparation and the available seed bank may be important factors determining current vegetative communities on test ranges. Other studies have indicated that plant communities that form after past anthropogenic disturbance are highly variable in the extent to which they resemble reference or undisturbed longleaf pine communities. Early successional species and native generalists may dominate these communities (e.g. Provencher et al. 2001). Alternatively, as I observed between test ranges and forested sites, some sites with significant past disturbance histories may share a number of similarities in community composition with undisturbed longleaf sites, though both assemblages may feature a number of unique species (e.g. Ostertag & Robertson 2007).

Both the combined effects of current disturbances (fire, mowing, and mission use), in conjunction with the available seedbank/dispersal ability of plant species in nearby forested areas post-clearing, affect the current herbaceous community structure on test ranges to some degree, though the relative contributions of each are unknown. Likewise, the extent to which test range herbaceous assemblages fall somewhere along a continuum between early-successional/ruderal community and intact longleaf sandhill understory is influenced by the above factors. However, most test ranges did harbor a wide array of common, native forbs and grasses that are typical groundcover associates of forested longleaf sandhill and, at a glance, include many species

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reported to be eaten by gopher tortoises in the literature (Garner & Landers 1981, MacDonald & Mushinsky 1988, Mushinsky et al. 2003).

Comments on Test Range Management

Test ranges are (typically) mowed annually, and sometimes more frequently as mission requirements dictate. Mowing can mimic some of the effects of prescribed fire (Ashton & Ashton 2008, Menges & Gordon 2010), but only limited management histories dating back to 2011 are available, making it difficult to draw conclusions regarding the role of mechanical treatments in shaping vegetation communities on test ranges (or their effects on tortoise densities). Some sites (e.g. C61A) were mowed less than once a year in that timeframe according to the provided records (though this seems dubious) while others (e.g. B70, B75) were mowed between two to five times annually. The lack of mowing records for C61A suggests not all mowing events were reported as this site is used as used as a jump zone for paratrooper exercises and the vegetation therefore needs to be kept consistently low to the ground. It was also unclear if test ranges were mowed in their entirety for each reported maintenance event. It seems probable that larger test ranges were mowed in blocks or in smaller areas prioritized for mission activity (i.e. it was unlikely the entire range could be mowed as frequently as reported) and it is unknown how often mowed areas included my survey plots except when direct observations were made. Two different sites on the same test range (B70E & B70C1) for example, differed considerably in species richness and a number of major vegetative cover class categories, but it is unclear whether those differences reflect heterogeneous management, differences in mission activity, and/or past disturbance, among other possible factors.

Burrow Densities, Activity Patterns, & Vegetation Cover & Composition

For most sites, I found no relationship between current tortoise burrow densities and vegetation variables expected to be indicators of habitat quality. Within forested sandhills at

Eglin where tortoises still occur, some stands had dense tree canopies and extensive midstories. Burrow densities were low and it is unlikely these areas can support tortoise populations without taking measures to restore groundcover and reduce tree canopy/midstory. The amount of tree canopy closure and lack of herbaceous cover within Garnier Creek in particular suggests there is little, if any suitable habitat remaining at this site. Burrow density within this site was low (0.9 per ha), and only a single burrow appeared active during vegetation surveys.

Both Rogue Creek and Turtle Creek have been surveyed for tortoises at least twice in the past seven years as part of a long-term monitoring study and both have experienced declines in active tortoise burrows between subsequent surveys (C.A. Haas, Virginia Tech, unpublished data). The likelihood of burrow abandonment increases with increasing tree canopy cover (Aresco & Guyer 1999, Catano et al. 2014) and the resident tortoises may be emigrating in response to the relatively dense shrub and tree canopy cover within these sites. Other possible causes for decline should not be ruled out however, as a recent habitat suitability index (HSI) developed for indicator species (including tortoises) inhabiting longleaf savanna in southwest Georgia predicted wider ranges of basal area, canopy cover, and herbaceous cover were suitable for most species compared to traditional habitat recommendations (GCPOLCC 2013, McIntyre et al. 2019). The mean suitable basal area and tree canopy cover conditions proposed by McIntyre et al. (2019) in their HSI for tortoises exceeded estimates I obtained for all tortoise-occupied forested sites on Eglin (though the methods used, soils, and vegetation communities differed between studies). Estimated herbaceous cover in my study for some forested sites fell below optimal conditions in the tortoise HSI, while other forested sites and almost all test ranges on Eglin met or exceeded desired mean herbaceous cover, though methods used to obtain vegetation cover estimates again differed between studies.

While general positive associations between herbaceous cover and burrow densities have been reported (Diemer 1986, Breininger et al. 1994, Innes 2009), I failed to detect a similar relationship between burrow densities within tortoise-occupied sites and combined graminoid and forb cover. Among the three forested sites with the highest total herbaceous cover, 201E and Bull Creek had comparatively high burrow densities. The third site, Middle Creek, had only a few active burrows despite what otherwise appeared to be suitable habitat. Among test ranges, B70E had the lowest estimated herbaceous cover, the lowest plant species richness, and the greatest amount of relative disturbance species cover of any site. This site in particular may have been degraded by extensive past mechanical disturbance which could partially explain its low burrow densities (0.9 burrows/ha) and lack of juvenile burrows.

Excluding B70E, estimated combined herbaceous cover tended to be high and forage availability (not necessarily quality) did not seem to be a limiting factor affecting tortoise densities. One of the most productive (i.e. sites with relatively high burrow densities, especially within younger age classes) test ranges on Eglin, C61A, is another previously surveyed site for which a recent follow up survey revealed an increase in burrow density as well as an expansion of area used (C.A. Haas, Virginia Tech, unpublished data, Vivian Porter, Virginia Tech staff based at Eglin AFB, personal communication). This site had relatively low estimated total herbaceous cover (~64%), forb (~21%), and legume (~1%) cover among test ranges, yet harbors one of the highest densities of juvenile and subadult burrows on Eglin. Further, it is worth noting that C61A is managed primarily through mowing (it has experienced one fire in the past decade and only four mowing events have been documented, though it has likely been mowed more frequently than reported) and is used mainly as a jump zone. This site may have been impacted comparatively little in relation to other tortoise-occupied test ranges over the past decade. Other

test ranges may have experienced declines in active burrow densities based on repeated visits (personal observation), though we currently lack long-term survey data to detect trends.

I anticipated the relative abundance of disturbance-prone plant species would serve as a proxy for past soil disturbance in the absence of detailed management histories, and that there would be a negative relationship between disturbance cover and burrow densities. This proved not to be the case, as the relative abundance of disturbance-prone species cover on test ranges demonstrated little relationship with burrow densities within any size class. Some test ranges with particularly abundant disturbance cover such as B70E and C52N did in fact have low burrow densities and few or no juvenile tortoise burrows. Alternatively, sites such as C74 had an abundance of disturbance prone species yet had high burrow densities compared to most other sites. It should be mentioned however, that much of the disturbance cover on C74 consisted of erosion control grasses and forbs planted near stream slopes and was not necessarily representative of vegetation in areas of the survey plot where most tortoise burrows occurred. C74 was also one of the most species-diverse sites, forested or test range, and the only test range considered more similar to forested sites in terms of herbaceous community structure according to my cluster analysis.

Additionally, I lacked evidence to suggest tortoise activity patterns were related to current vegetation characteristics in either vegetation type. However, this may have been mostly due to limitations of the available camera trapping data. The data used were collected to study commensal communities, not necessarily tortoise activity patterns, and only a limited number of tortoise-occupied burrows (i.e. active) were camera-trapped, even within higher-density sites. These data had to be pooled, often over different time spans, from a handful of individual tortoises for each site. Interpretation of activity patterns was therefore severely limited in scope.

Burrow-Scale Use vs Availability

Initially, my goal was to determine if tortoises selected burrow sites based on the presence of particular plant species; however, plant species assemblages in most sites were too diverse and variable to identify any meaningful patterns, should any exist, without a significantly increased sampling effort. Taxon-specific effects may have also been obscured by foraging and digging activities (Kaczor & Hartnett 1990). While I was unable to identify factors influencing burrow site selection at a finer scale, I did find evidence that broader differences in vegetation characteristics between forested sites and test ranges may have had an effect.

Estimated basal area and tree canopy cover were equal or higher on average, often significantly so, at unused locations than within foraging buffers around burrows in all forested sites, which was consistent with other studies (e.g. Mitchell 2005, Boglioli et al. 2000, Rostal & Jones 2002). Graminoid cover was significantly higher within foraging buffers and litter cover was significantly lower compared to unused locations in forested sites, likely due to generally more sun-exposed conditions and lack of a litter producing overstory associated with burrow locations. It is difficult to tease apart the relative effects of canopy openness and herbaceous plant cover on burrow site selection, as both are interconnected (Auffenberg & Franz 1982, Aresco & Guyer 1999, Provencher et al. 2001, Jones & Dorr 2004). However, a number of studies have suggested a positive relationship between herbaceous cover and burrow locations (Rostal & Jones 2002, Tuberville 1998, Innes 2009, McIntyre et al. 2019).

Results of the compositional analysis indicated graminoids were selected over all other vegetative cover classes, followed by bare ground, forbs, and legumes, though pairwise comparisons between the latter three categories were not significant. These results are generally supported based on what has been reported in the literature regarding gopher tortoise diets (see

Garner & Landers 1981, Macdonald & Mushinsky 1988); though these rankings should not be considered forage preferences.

On test ranges, legume and shrub cover were significantly higher within foraging buffers and bare ground cover was significantly lower compared to unused locations. On most test ranges, herbaceous cover is both abundant and uniformly distributed. Forage availability and basking opportunities on test ranges are likely not major factors limiting burrow site selection compared to some forested sites where suitable burrow locations are presumably more restricted, particularly for sites where midstory and canopy openings are less abundant. At the site-wide scale, legumes were more abundant in forested sites on average and gopher tortoises on test ranges may be more likely to select burrow locations based on legume availability, especially if other available forbs do not have the same nutritional value (Macdonald & Mushinsky 1988, Mushinsky et al. 2003, Hathaway 2012). Boglioli et al. (2000) suggested legumes were positively affected by tortoise activity near burrows (i.e. seed dispersal and digging activity) which contributed to a greater abundance of legumes at burrow locations (but see Birkhead et al. 2005). However, Tuberville et al. (2007) found legumes were more abundant at burrow locations than in surrounding habitat only under management prescriptions where forage availability was otherwise limited. Importantly, the difference in average legume cover between foraging and availability buffers in my study was less than one percent (with low variance), and so the difference may be more an artifact of a large sample size (n=120 total burrows) rather than a biologically meaningful result.

Likewise, the difference in shrub cover between buffers was less than three percent. Assuming gopher tortoises are in fact selecting burrow locations based on the presence of shrubs, it may be due to a general lack of cover and shade present on test ranges, though gopher tortoises

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also readily eat fruits and flowers of many understory shrubs when available (Garner & Landers 1981). Further, shrubs and other structures (e.g. coarse woody debris) may be particularly important cover sources for smaller size classes that are more vulnerable to predation, as completely exposed conditions could increase predation risk (Breininger et al. 1988, Ashton & Ashton 2008).

The results of the compositional analysis also indicated that legume and shrub cover were selected over other vegetative cover classes (ranked first and second respectively), though pairwise comparisons were not significant except for all but the least preferred classes, which included bare ground (considered the second most preferred cover class in forested sites). As with herbaceous cover, bare soil important for burrowing is abundant on test ranges and may not be a limiting resource within these sites.

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Table 1.1. Results of gopher tortoise burrow density surveys conducted during the spring/summer from 2016 to 2018 on Eglin Air Force Base, FL for all sites used in vegetation surveys (this study). Densities are reported as all active and inactive burrows/hectare (abandoned burrows were excluded) for different size classes. Size classes were defined as follows: Adult ($\geq$ 230 mm); subadult (>130 mm < 230 mm); and juvenile ($\leq$ 130 mm).

Vegetation Type	Year	Site	Survey Plot Size (ha)	Total Burrows/ha	Adult Burrows/ha	Subadult Burrows/ha	Juvenile Burrows/ha
Forested	2017	201E	9.9	1.7	0.5	0.7	0.5
		Pine Log	10.5	1.3	0.3	0.1	0.9
		Rogue Creek	12.4	1	0.4	0.4	0.2
	2018	Bull Creek	10	2.3	0.4	0	1.9
		Garnier Creek	10.4	0.9	0.7	0	0.2
		Middle Creek	14	0.7	0.4	0	0.3
		Turtle Creek	19.7	0.9	0.3	0.3	0.3
Test Range	2017	B70C1	11.8	0.6	0.3	0.3	0
		B70C2	12.1	0.8	0.5	0.3	0
		B70E	13.9	1.1	0.9	0.1	0.1
		C61A	10.4	4.3	0.5	1.7	2.1
		C62N	10	1	0.4	0	0.6
		C62S	10.4	1.7	0.6	0.1	1
		C64	16.5	0.4	0.1	0.2	0
		C72	10.6	1.4	0.4	0.6	0.4
	2018	B71	10.6	4.9	1.8	1.4	1.7
		B75	10.4	2.3	0.5	1.1	0.7
		C52N	11.9	0.8	0.3	0.3	0.2
		C74	10.4	4.9	0.8	1	3.1

Table 1.2. Management activity at study sites (dating back to ~ 2011) on Eglin Air Force Base, FL. For test ranges, it is unknown how often survey plots were mowed, as mowing events likely did not always include an entire test range (particularly for the largest ranges, e.g. B70), but were generally reported as range-wide events. Test range B70 is divided into different burn units and fires were reported separately for B70E and B70C survey areas. The records presented are the best available information for comparisons of relative disturbance/management among sites. Mowing events during the gopher tortoise nesting season occurred between May-October. Growing season fires occurred between April and September. Because mowing did not occur in forested sites, those columns are filled with 'not applicable' symbols (N/A).

Vegetation Type	Year	Site	Nesting Season Mowing	Total Mowing	Growing Season Fires	Total Fires
Forested	2017	201E	N/A	N/A	9	14
		Pine Log	N/A	N/A	5	9
		Rogue Creek	N/A	N/A	3	7
	2018	Bull Creek	N/A	N/A	1	5
		Garnier Creek	N/A	N/A	1	1
		Middle Creek	N/A	N/A	5	10
		Turtle Creek	N/A	N/A	1	4
Test Range	2017	B70C	11	34	16	55
		B70E	11	34	3	20
		C61A	1	4	0	1
		C62	3	7	6	33
		C64	5	6	5	16
		C72	9	18	39	111
	2018	B71	2	9	14	35
		B75	12	22	18	40
		C52N	5	13	15	40
		C74	0	6	15	40

Table 1.3. Site-wide scale percent tree canopy cover and basal area estimates within all forested sites surveyed on Eglin Air Force Base, FL.

Results are provided as means ± SE. Mean tree canopy cover and basal area estimates obtained from n=6 samples per site.

Year	n	Site	% Canopy Cover	BA (ft/acre)
2017	6	201E	20.8±9.0	18.3±6.0
		Pine Log	35.8±7.3	50.0±5.1
		Rogue Creek	35.6±4.7	56.7±9.6
2018	6	Bull Creek	15.8±5.2	25.0±5.6
		Garnier Creek	66.7±5.1	68.3±6.5
		Middle Creek	28.3±5.6	26.7±4.9
		Turtle Creek	35.0±6.5	23.3±6.7

Table 1.4. Site-wide scale plant species diversity indices for all sites surveyed on Eglin Air Force Base, FL.

Species richness (S) = Total species/site. Alpha (α) = Average species/plot. Beta (β) = S/ α -1, describes relative variability in species composition among plots within a site and increases in value with increasing dissimilarity among plots. Shannon-Weaver Indices (H) increase in value with increasing species diversity and evenness. Inverse Simpson's Indices ($1-D_s$) increase in value as the likelihood that two randomly selected individuals from the community are different species, i.e. the greater the value, the more even the site is in terms of species composition.

Vegetation Type	Year	Site	S	α	β	H	$1-D_s$
Forested	2017	201E	53	12	3.4	3.2	0.94
		Pine Log	48	8.2	4.8	3.2	0.95
		Rogue Creek	73	12.2	5	3.5	0.95
	2018	Bull Creek	64	15	3.3	3.4	0.95
		Garnier Creek	38	4.9	6.7	2.6	0.87
		Middle Creek	46	12.3	2.8	3.1	0.93
		Turtle Creek	59	11.7	4	3.2	0.93
Test Range	2017	B70C2	41	11.8	2.5	3	0.93
		B70E	34	6.5	4.3	2.4	0.86
		C61A	51	12	3.2	3.1	0.92
		C62S	48	11.5	3.2	3.2	0.94
		C64	58	14	3.1	3.4	0.95
		C72	50	10.9	3.6	3.2	0.94
	2018	B71	53	11	3.8	3	0.92
		B75	59	18.1	2.3	3.5	0.95
		C52N	55	13.3	3.1	3.1	0.93
		C74	74	12.1	5.1	3.5	0.95

Table 1.5. Site-wide scale two-sample T-test results comparing major vegetative cover class estimates and average species richness (S) between forested sites and test ranges on Eglin Air Force Base, FL.
Results are provided as means ± SE. Significant differences between forested sites and test ranges highlighted in bold (α=0.05). Cover classes are defined as follows: Bare = bare ground cover; Forb = non-leguminous forb cover; Graminoid= graminoid cover, i.e. grasses (Family Poaceae) & sedges (Family Cyperaceae); Legume = leguminous-forb cover (Family Fabaceae); Litter = non-living plant material cover, i.e. leaves & woody debris; Shrub = woody plant cover; & Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates).

Vegetation Type	Bare	Forb	Graminoid	Legume	Litter	Shrub	Disturbance	S
Forested (n=7)	18.1±3.1	20.9±5.6	23.6±5.7	**8.6±1.8**	**50.5±6.8**	25.8±4.2	2.7±1.5	54.4±4.5
Test Range (n=10)	**34.3±5.6**	28.4±2.9	**42.0±2.7**	4.0±0.7	21.0±2.8	16.0±1.9	**18.±2.2**	52.3±3.4
t	2.53	1.18	2.93	2.44	4.03	2.17	5.69	0.38
p	**0.02**	0.27	**0.02**	**0.04**	**<0.01**	0.06	**<0.01**	0.71

Table 1.6. Multiple regression ANOVA table and coefficients for total burrow density (all size classes combined) predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as: Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates); Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Total burrows /ha	Model	4	5.00	1.25	0.73	0.21	0.59
	Error	11	18.91	1.72			
	Total	15	23.92				

Predictor	Est.	SE	t	P
Intercept	1.37	2.16	0.64	0.54
Disturbance	0.02	0.06	0.26	0.80
Forage	0.01	0.02	0.67	0.52
Vegetation type	0.07	0.63	0.12	0.91
Shrub	-0.03	0.05	-0.74	0.47

Table 1.7. Multiple regression ANOVA table and coefficients for adult (≥230 mm) burrow density predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as: Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates); Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Adult burrows /ha	Model	4	0.15	0.04	0.87	0.24	0.51
	Error	11	0.48	0.04			
	Total	15	0.63				

Predictor	Est.	SE	t	P
Intercept	0.58	0.34	1.70	0.12
Disturbance	0.01	0.01	0.94	0.37
Forage	-0.01	0.01	-0.57	0.58
Vegetation type	0.04	0.10	0.40	0.70
Shrub	-0.01	0.01	-0.76	0.46

Table 1.8. Multiple regression ANOVA table and coefficients for total juvenile burrow density (juvenile + subadult) predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as: Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates); Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Total juvenile burrows /ha	Model	4	4.34	1.09	0.69	0.20	0.61
	Error	11	17.22	1.57			
	Total	15	21.56				

Predictor	Est.	SE	t	P
Intercept	0.87	2.06	0.42	0.68
Disturbance	0.01	0.06	0.08	0.94
Forage	0.01	0.02	0.78	0.45
Vegetation type	0.03	0.60	0.05	0.96
Shrub	-0.03	0.04	-0.68	0.51

Table 1.9. Multiple regression ANOVA table and coefficients for subadult (131-229 mm) burrow density predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as: Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates); Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	P
Subadult	Model	4	0.83	0.21	0.82	0.23	0.54
burrows /ha	Error	11	2.79	0.25			
	Total	15	3.62				

Predictor	Est.	SE	t	p
Intercept	0.42	0.83	0.51	0.62
Disturbance	-0.01	0.02	-0.48	0.64
Forage	0.01	0.01	0.37	0.72
Vegetation type	-0.25	0.24	-1.03	0.32
Shrub	-0.01	0.02	-0.16	0.87

Table 1.10. Multiple regression ANOVA table and coefficients for y= juvenile (≤ 130 mm) burrow density predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as: Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates); Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	P
Juvenile	Model	4	2.62	0.65	0.78	0.22	0.56
burrows /ha	Error	11	9.23	0.84			
	Total	15	11.85				

Predictor	Est.	SE	t	p
Intercept	0.41	1.51	0.27	0.79
Disturbance	0.02	0.05	0.40	0.70
Forage	0.01	0.01	0.93	0.37
Vegetation type	0.28	0.44	0.63	0.54
Shrub	-0.03	0.03	-0.87	0.40

Table 1.11. Multiple regression ANOVA table and coefficients for average exit duration (time spent outside burrow) predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as: Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Average exit	Model	3	186.77	62.23	2.33	0.37	0.13
	Error	12	320.67	26.72			
	Total	15	507.44				

Predictor	Est.	SE	t	P
Intercept	19.84	6.25	3.17	< 0.01
Forage	0.06	0.06	0.93	0.37
Vegetation type	4.21	1.63	2.59	**0.02***
Shrub	-0.12	0.18	-0.67	0.51

Table 1.12. Multiple regression ANOVA table and coefficients for average excursion duration (time spent away from burrow, presumably foraging) predicted by percent cover estimates for major vegetative cover classes.
Predictor variables are defined as follows: Forage= combined herbaceous cover (forbs and graminoids); Vegetation type= categorical, forested or test range; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Average excursion	Model	3	30.17	10.06	0.51	0.11	0.68
	Error	12	235.58	19.63			
	Total	15	265.75				

Predictor	Est.	SE	T	P
Intercept	16.64	5.36	3.11	< 0.01
Forage	-0.04	0.05	-0.70	0.50
Vegetation type	1.11	1.39	0.80	0.44
Shrub	-0.09	0.15	-0.58	0.58

Table 1.13. Burrow scale paired T-test results comparing cover classes between foraging/use (U) and availability (A) buffers within forested sites (n=70 burrows) and test ranges (n=120 burrows) on Eglin Air Force Base, FL.

Results are presented as means ± SE. Significant differences are highlighted in bold. Cover classes are defined as follows: Bare = bare ground cover; Forb = non-leguminous forb cover; Graminoid= graminoid cover, i.e. grasses (Family Poaceae) & sedges (Family Cyperaceae); Legume = leguminous-forb cover (Family Fabaceae); Litter = non-living plant material cover, i.e. leaves & woody debris; Shrub = woody plant cover; & Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates).

Vegetation Type	U/A	Bare	Forb	Graminoid	Legume	Litter	Shrub	Disturbance
Forested	U	18.9±1.1	22.4±1.9	**27.0±2.1**	9.3±0.8	48.1±1.9	25.0±2.0	3.3±0.7
(n=70)	A	17.4±1.2	20.2±1.7	20.8±1.7	8.2±0.6	**56.2±1.9**	24.4±1.6	3.2±0.7
	t	1.35	1.79	5.56	1.86	5.05	0.35	0.21
	p	0.18	0.08	**<0.01**	0.07	**<0.01**	0.72	0.83
Test Range	U	34.3±1.4	31.2±0.8	39.3±1.1	**4.8±0.3**	22.5±1.0	**15.1±1.0**	15.4±1.2
(n=120)	A	**38.0±1.4**	31.2±0.8	39.2±1.1	4.0±0.3	21.5±0.9	12.2±0.9	16.8±1.0
	t	3.90	0.01	0.02	2.39	1.42	2.64	1.35
	p	**<0.01**	0.99	0.98	**0.02**	0.16	**0.01**	0.18

Table 1.14. Burrow scale comparison of tree canopy cover and basal areas estimates between foraging, availability buffers among forested sites.

Burrow scale paired T-test results comparing canopy cover and basal area estimates within forested sites between foraging/use (U) and availability (A) buffers. Results are provided as means ± SE. Significant differences are highlighted in bold (α=0.05). Mean tree canopy cover and basal area estimates obtained from n=10 burrows (paired use/availability buffers) per site.

Year	n	Site	U/A	Canopy	BA(ft/acre)
2017	10 burrows	201E	U	21.3±3.7	9.0±3.8
			A	26.8±4.0	19.0±4.8
			t	1.23	1.50
			p	0.25	0.17
		Pine Log	U	30.0±3.8	35.0±6.7
			A	**39.5±5.0**	47.0±9.4
			t	2.46	1.02
			p	**0.04**	0.33
		Rogue Creek	U	22.3±3.4	23.0±3.4
			A	25.3±4.1	**38.0±4.7**
			t	0.47	3.50
			p	0.65	**<0.01**
2018	10 burrows	Bull Creek	U	20.3±4.4	25.0±4.8
			A	28.2±4.5	25.0±2.7
			t	1.41	0.00
			p	0.19	0.99
		Garnier Creek	U	55.2±5.9	31.0±7.5
			A	55.2±3.6	**50.0±4.5**
			t	0.00	2.31
			p	0.99	**0.05**
		Middle Creek	U	28.3±2.6	19.0±3.1
			A	**39.5±3.0**	25.0±3.4
			t	2.81	1.26
			p	**0.02**	0.24
		Turtle Creek	U	31.7±3.1	21.0±3.1
			A	**42.2±3.5**	28.0±4.2
			t	2.33	1.21
			p	**0.04**	0.26

Table 1.15. Burrow scale plant species diversity indices for all sites surveyed on Eglin Air Force Base, Florida within foraging/use (U) and availability (A) buffers.

Species richness (S) = Total species/site. Alpha (α) = Average species/burrow. Beta (β) = S/ α -1, describes relative variability in species composition among burrows within a site and increases in value with increasing dissimilarity among burrows.

Vegetation Type	Year	Site	U/A	S	α	β
Forested	2017	201E	U	73	30.8	1.4
			A	66	31.2	1.1
		Pine Log	U	69	29.8	1.3
			A	80	32.1	1.5
		Rogue Creek	U	63	26.4	1.4
			A	63	27.1	1.3
	2018	Bull Creek	U	77	37.2	1.1
			A	81	36.9	1.2
		Garnier Creek	U	38	12.7	2
			A	52	16.1	2.3
		Middle Creek	U	66	26.9	1.5
			A	83	31.4	1.6
		Turtle Creek	U	75	30.8	1.4
			A	69	29.8	1.3
Test Range	2017	B70C1	U	63	29.7	1.1
			A	57	27.0	1.1
		B70C2	U	55	25.2	1.2
			A	61	27.6	1.2
		B70E	U	56	24.6	1.3
			A	56	24.8	1.3
		C61A	U	67	31.4	1.1
			A	71	33.6	1.1
		C62N	U	80	34.9	1.3
			A	79	36	1.2
		C62S	U	67	28.8	1.3
			A	76	31.5	1.4
		C64	U	78	36.3	1.1
			A	80	35.7	1.2
		C72	U	81	36.9	1.2
			A	81	37	1.2

Table 1.15 Continued.

Vegetation Type	Year	Site	U/A	S	α	β
Test Range	2018	B71	U	66	25.4	1.6
			A	65	29.8	1.2
		B75	U	70	34.6	1
			A	65	35.9	0.8
		C52N	U	63	30.4	1.1
			A	59	30	1
		C74	U	73	35.1	1.1
			A	87	39.7	1.2

Table 1.16. Compositional analysis results ranking vegetative cover classes within all forested sites surveyed on Eglin Air Force Base, FL.
Analysis was performed using percent cover estimates for major cover classes within foraging/use buffers and availability buffers. Significant pairwise log-ratio differences (α=0.05) between cover classes are highlighted in bold. Log-ratio differences were used to rank cover classes from most preferred (1) to least preferred (8).

		Wilke's-λ	P		Vegetation Type:	**Forested**			
		0.4157	0.002		n=70	burrows			
		Use↓	Avail→						
Rank	Cover Class	Bare	Fern	Forb	Graminoid	Legume	Litter	Shrub	Vine
2	Bare		**2.10***	0.15	-0.11	0.15	**0.33***	0.21	**0.47***
8	Fern	**-2.10***		**-2.22***	**-2.26***	**-2.07***	**-1.85***	**-1.98***	**-1.56**
3	Forb	-0.15	**2.22***		-0.26	<0.01	0.18	0.07	0.34
1	Graminoid	0.11	**2.26***	**0.26***		**0.26***	**0.44***	**0.32***	**0.60***
4	Legume	-0.15	**2.07***	- <0.01	**-0.26***		0.18	0.06	0.34
6	Litter	**-0.33***	**1.85***	-0.18	**-0.44***	-0.18		-0.12	0.15
5	Shrub	-0.21	**1.98***	-0.07	**-0.32***	-0.06	0.12		0.26
7	Vine	**-0.47***	**1.56***	-0.34	**-0.56***	-0.33	-0.15	-0.26	

Table 1.17. Compositional analysis results ranking vegetative cover classes within all test range sites surveyed on Eglin Air Force Base, FL.
Analysis was performed using percent cover estimates for major cover classes within foraging/use buffers and availability buffers. Significant pairwise log-ratio differences (α=0.05) between cover classes are highlighted in bold. Log-ratio differences were used to rank cover classes from most preferred (1) to least preferred (7).

		Wilke's-λ	P		Vegetation Type:	**Test Range**		
		0.4151	0.002		n=120	burrows		
		Use↓	Avail→					
Rank	Cover Class	Bare	Forb	Graminoid	Legume	Litter	Shrub	Vine
6	Bare		**-0.13***	**-0.13***	**-0.28***	**-0.17***	-0.20	1.77
5	Forb	**0.13***		- <0.01	-0.14	-0.03	-0.08	**1.89***
4	Graminoid	**0.13***	<0.01		-0.14	-0.03	-0.07	**1.95***
1	Legume	**0.28***	0.14	0.14		0.11	0.06	**2.17***
3	Litter	**0.17***	0.04	0.03	-0.11		-0.04	**1.87***
2	Shrub	0.20	0.08	0.07	-0.05	0.04		**2.07***
7	Vine	**-1.77***	**-1.89***	**-1.95***	**-2.17***	**-1.87***	**-2.07***	
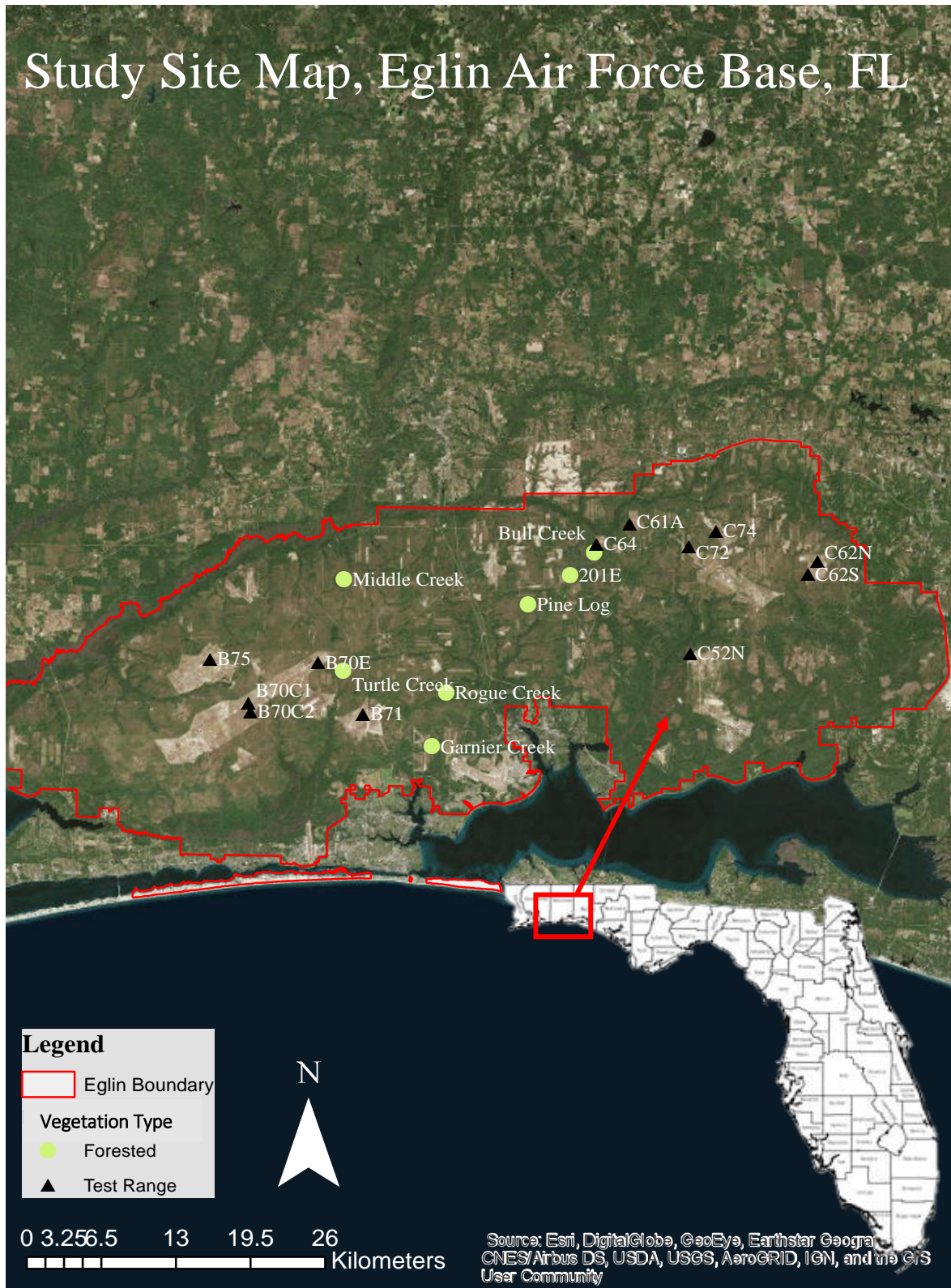
Figure 1.1. Study sites at Eglin Air Force Base Florida.
Forested sites are designated by green circles. Test ranges are designated by black triangles.
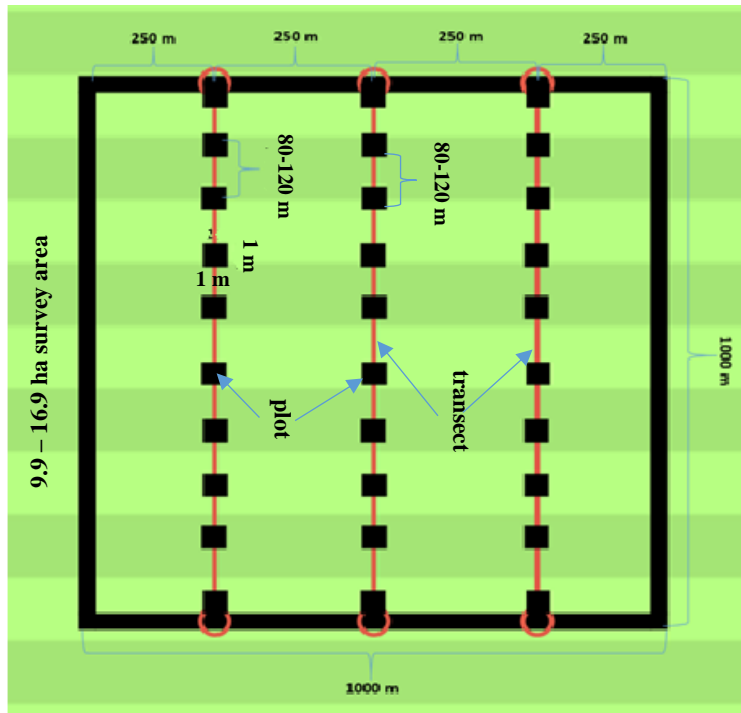
Figure 1.2. Site-wide scale vegetation sampling design.
Spacing of transects and plots and length of transects depended on overall size and shape of original survey area. Thirty 1 x 1 m plots were sampled per site along three evenly spaced, north-south running transects (10 plots per transect). All plants within plots were identified to genus or species and assigned a % cover estimate using standard Daubenmire classifications. Plots were spaced randomly within a range of distances that would roughly average out to the length of the transect when added together. In the hypothetical example shown, a 10 ha survey area forming a perfect 1000x1000 m square would have transects spaced 250 m apart, dividing the survey area into equal width quarters, and plots placed randomly between 80-120 m from one another along the transects so that the average distance between plots should be roughly 100 m.
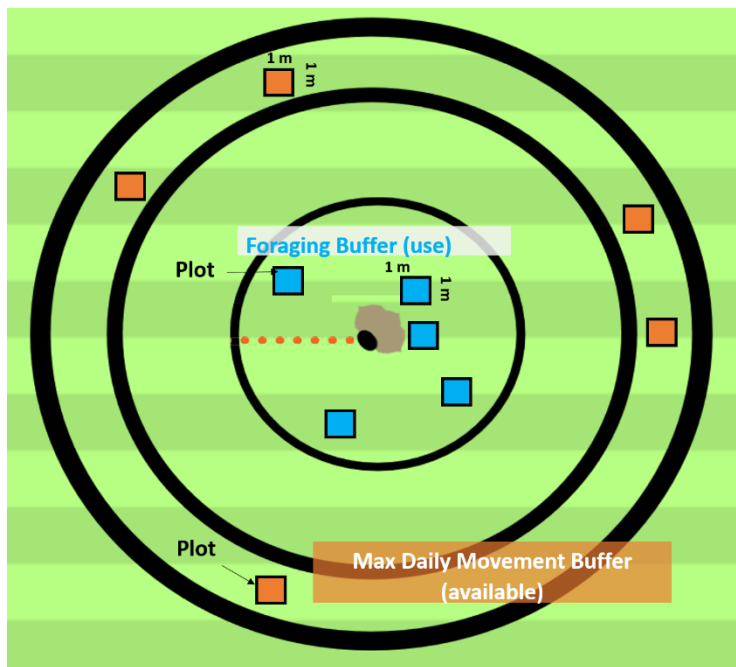
Figure 1.3. Burrow scale vegetation sampling design.
Five 1x1 m. plots were placed within 30-m radius for adults and 8 m for juveniles based on typical maximum foraging distances. All plants within plots were identified to genus or species and assigned a % cover estimate using standard Daubenmire classifications. The first plot was always placed within 1 m of the apron, with the remaining four randomly placed within the foraging/use buffer. The larger availability buffer was double the distance of the foraging buffer (60 m for adults, 16 m for juveniles) and up to 85 m for adults, and 32 m for juveniles, based on mean maximum daily movement estimates. Five additional plots were placed randomly within this buffer to represent habitat that was hypothetically accessible to the tortoise, but beyond typical foraging distances. Using two or more burrows within 30 m of one another was avoided whenever possible.

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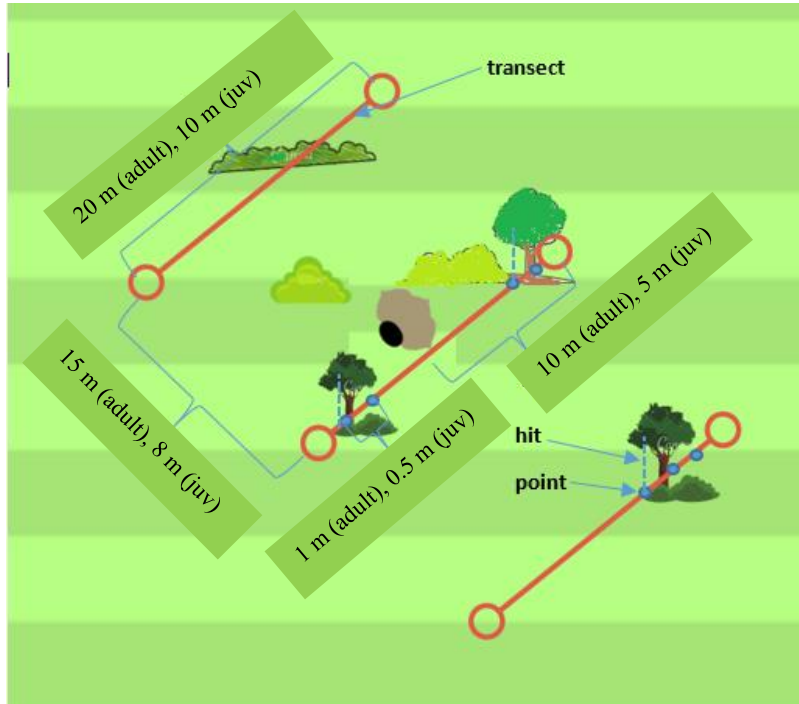
Figure 1.4. Burrow scale tree canopy cover estimate sampling design.
Within foraging buffer, three evenly spaced transects were oriented in the direction of the burrow's azimuth. Transects were 20 m for adults with a point taken every 1 m, or 10 m for juveniles with a point taken every 0.5 m totaling 20 points/transect. The burrow entrance served as a rough midpoint for each transect. In this hypothetical example, the far transect represents zero canopy cover, the middle transect has 4 points intersecting canopy, and the closest transect has 3 points intersecting canopy for a total of 7/60 sampling points intersecting canopy = 11.7% estimated canopy cover for this burrow. Three additional transects were established at the first three randomly placed vegetation plots within the availability buffer using random compass bearings to determine direction. The vegetation plot served as the midpoint. Again, the number of sampling points intersecting canopy out of 60 total would provide the canopy cover estimate within the availability buffer to be paired with that burrow.
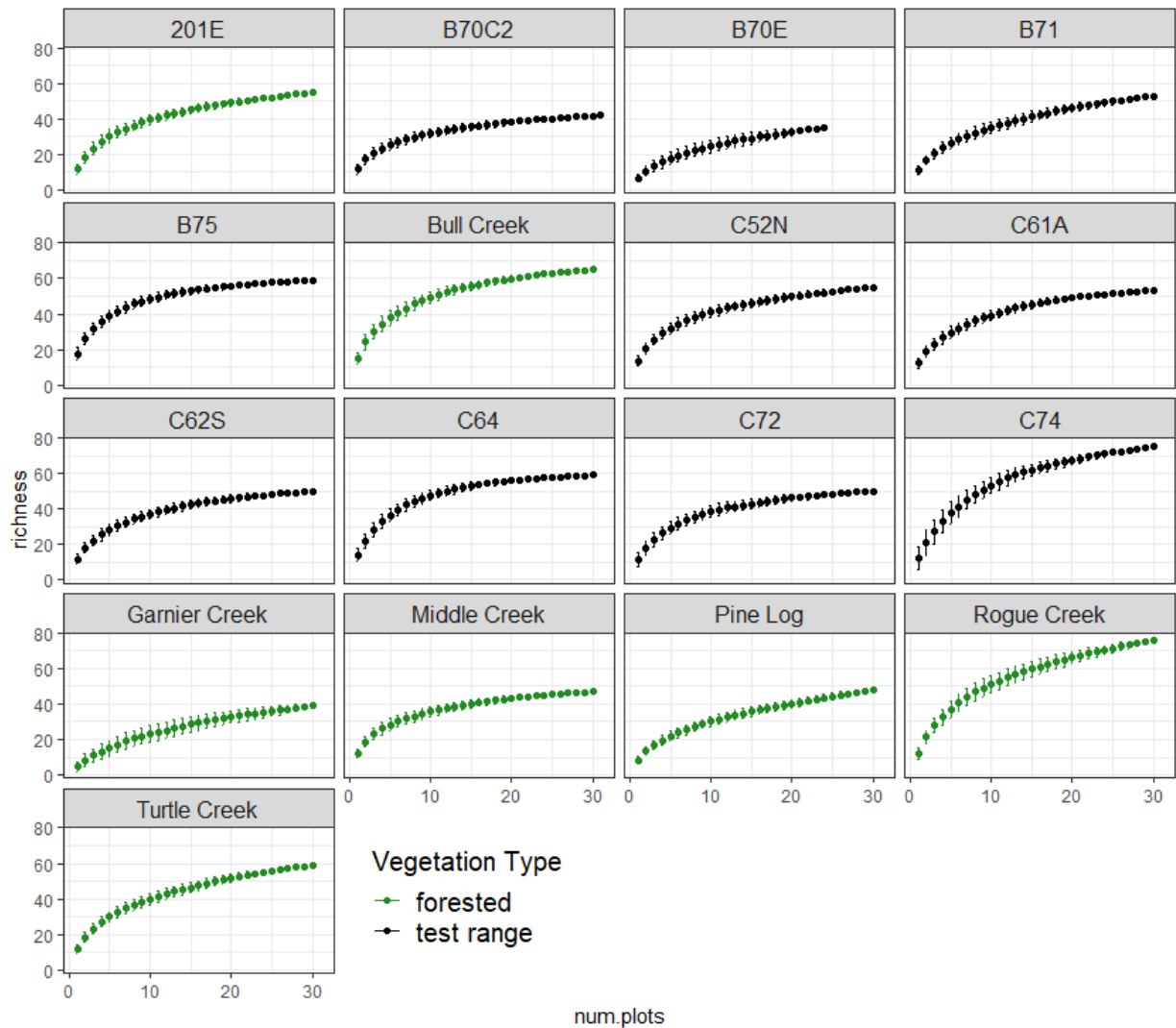
Figure 1.5. Site-Wide Scale Species Accumulation Curves.
Relationship between plant species richness (species detected) and sampling effort (number of plots/site) for all sites surveyed at site-wide scale. For most sites, 30 plots appeared to be sufficient in detecting most common species, as new species detection rates level off. However, new species were still being encountered at a high rate for certain sites (e.g. forested site Rogue Creek and test range C74) suggesting 30 plots may not have been sufficient to account for diversity found in all sites.
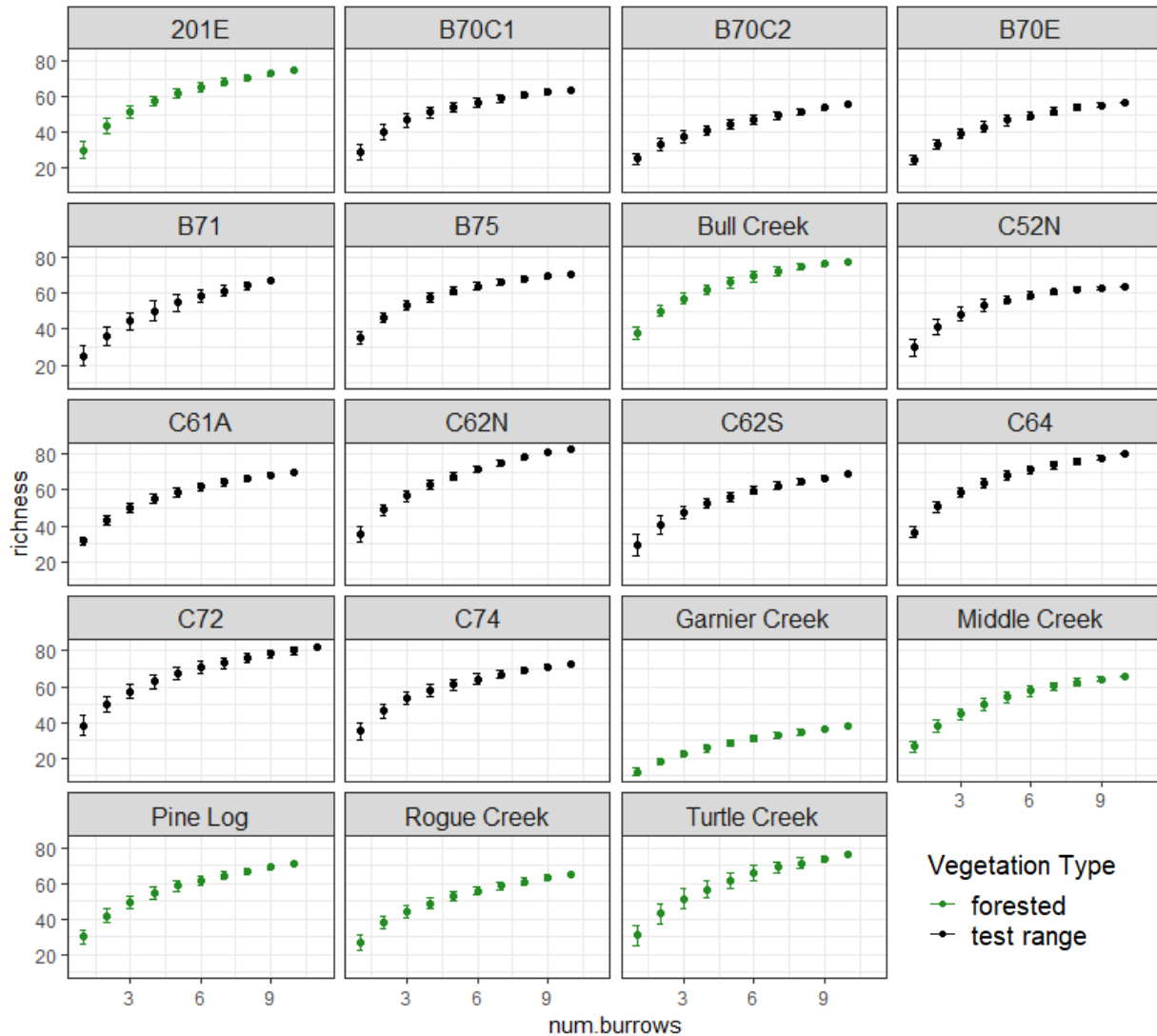
Figure 1.6. Burrow Scale Species Accumulation Curves (Foraging Buffers).
Relationship between plant species richness (species detected) and sampling effort (number of burrows/site) within foraging/use buffers for all sites surveyed at the burrow scale. For some sites, 10 burrows appeared to be sufficient in detecting most common species, as new species detection rates level off. However, new species were still being encountered at a high rate for certain sites (e.g. forested site Turtle Creek and test ranges C72 and C74) suggesting 10 burrows may not have been sufficient to account for diversity found in all sites.

Figure 1.7. Hierarchical Clustering of Sites Based on Estimated Herbaceous Community Structure. The dendrogram depicts relative similarities among sites based on presence and estimated percent cover for forb and graminoid species (excluding some rare species). Bray-Curtis dissimilarity indices among sites were used to generate the distance matrix. Distances (y-axis) range from 0 (complete community overlap) to 1 (no shared species). Forested sites are highlighted in green, test ranges are highlighted in black.
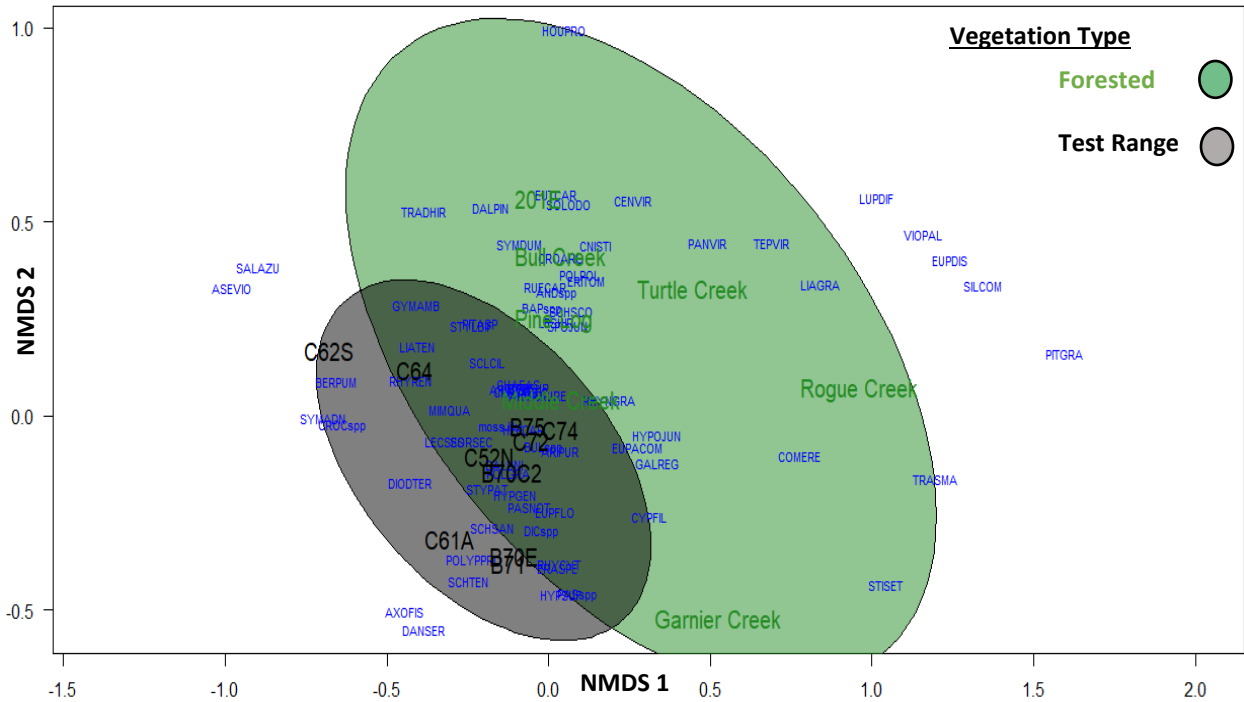
Figure 1.8. Non-Metric Multi-Dimensional Scaling (NMDS) Sites & Herbaceous Species.
Visual representation of overlap and dissimilarity in species composition and relative cover for
herbaceous plants between test ranges (black labels) and forested sties (green labels) at the site-wide
scale. Each code is a unique species identifier (blue labels). Ellipses represent 95% confidence intervals
for each vegetation type.

Chapter 2

Testing and Training Range Management Practices at Military Installations within the Range of the Gopher Tortoise

William M. Moore

Abstract

On Eglin Air Force Base in Florida, many gopher tortoises currently reside in expansive military testing and training areas (test ranges) that are maintained in an open state (i.e. vegetation kept short through some combination of mowing, roller-drum chopping, fire, chemical treatments). Burrow densities vary significantly among tortoise-occupied test ranges. Management practices, both past and present, may at least partially explain differences in burrow densities and vegetation characteristics we currently observe on Eglin. Therefore, a broader understanding of how these unique landscapes are managed on other tortoise-occupied installations could help mitigate future conflicts between military training objectives and gopher tortoise conservation goals. I developed a questionnaire that was distributed to natural resource personnel at gopher tortoise-occupied installations throughout the southeast to document common management practices used to maintain test ranges and other human altered habitats on Department of Defense (DoD) lands. In conjunction with habitat work conducted on Eglin (Chapter 1), this questionnaire was developed to better understand how testing and training ranges are managed, as the practices used will likely determine whether these habitats can support tortoise populations long-term. We received responses for eight DoD installations and outlying properties, all of which reported that gopher tortoises occupied testing and training ranges and suggested a wide array of management techniques were used to maintain these areas.

Keywords: *Gopherus polyphemus*, DoD, habitat management, mowing, ruderal

Introduction

Military installations can encompass large tracts of undeveloped land and often serve as valuable refuges for imperiled ecological communities, including longleaf pine ecosystems. Currently, the Department of Defense (DoD) manages nearly 30 million acres of land harboring over 300 threatened and endangered species nationwide, including the gopher tortoise (USFWS 2009). In the southeastern U.S., DoD lands have been instrumental in preserving the largest remaining tracts of contiguous longleaf pine forest (Frost 2007) with military installations currently holding roughly 18% of all remnant longleaf pine forests in the southeastern United States (USFWS 2011), including large expanses of potential and known gopher tortoise habitat. Eglin Air Force Base, for example, contains over 187,000 ha of land, of which 74% or more consists of longleaf pine sandhill habitat (Provencher et al. 2003). Live-fire exercises have historically aided in maintaining the integrity of pyrogenic systems on military lands by providing frequent ignition sources (Wilson et al. 1997) and more recent improvements in habitat management practices on DoD lands, including the implementation of prescribed fire, have benefited both longleaf pine communities and gopher tortoises occurring on military installations (USFWS 2011, USFWS 2016).

Currently, there are eighteen military installations on which gopher tortoises have been documented within the southeastern U.S. across four states: Alabama (1), Florida (12), Georgia (4) and Mississippi (1) (Wilson et al. 1997, USFWS 2013). Information regarding the status of gopher tortoise populations on DoD lands is fairly limited, usually consisting of confined-area survey results and, in some cases, extrapolated population estimates based on potential habitat availability. As of 2016, all Air Force, Army, Marine Corps, and Navy installations had up to date Integrated Natural Resource Management Plans (INRMPs) which included a wide variety of practices currently employed to benefit gopher tortoises and improve habitat (USFWS 2016).

Practices specifically identified as beneficial to tortoises currently employed on DoD lands included the following: prescribed fire, herbicide application, mid-story/hardwood removal, timber thinning, measures to avoid vehicular travel in close proximity to burrows, invasive vegetation control, translocation from unsuitable areas, designation of protected areas, research projects, population surveys, predator removal, public outreach, and wiregrass/native understory restoration (USFWS 2011, USFWS 2016).

Among tortoise-occupied installations, multiple properties reported gopher tortoises residing on test-ranges, airfield peripheries, or similar human-altered/ruderal areas maintained in an open state. Naval Air Station (NAS) Orlando in Florida reported the majority of its tortoises residing in abandoned agriculture fields and cleared meadows (USFWS 2016). NAS Jacksonville reported that past and present longleaf pine restoration efforts have attracted tortoises away from runway clear zones (USFWS 2016). Burrow surveys conducted at Kings Bay Naval Submarine Base in southeast Georgia by Tuberville et al. (2009) found the majority of active burrows, mostly belonging to adults with little evidence of recruitment, in ruderal areas. Similarly, tortoise burrows on NAS Whiting Field in the Florida panhandle were largely restricted to ruderal areas, presumably due to fire-suppression in surrounding forests (Davis and Russo 2007). Likewise, surveys of tortoise populations on Camp Shelby, Mississippi in 1995, 1999, and 2000 suggested tortoises mostly inhabited disturbed areas, documented a decline in total population size, and found an adult-skewed burrow size-class distribution, indicating poor recruitment (Epperson and Heise 2001). Additionally, Theodorakis (2008) provided evidence that training activities, in conjunction with vegetation structure on Camp Shelby, may have been influencing gene flow between gopher tortoise sub-populations on base.

Management strategies used to maintain test ranges, as well as the testing and training activities that occur in these areas, affect vegetation structure and composition and may directly or indirectly affect resident gopher tortoise populations (see Chapter 1 for description of potential impacts from various management practices). Further, expansive open areas with abundant grasses and forbs such as test ranges may attract gopher tortoises based on what has been observed at Eglin and elsewhere; however, it was unknown the extent to which tortoises used these sites at other installations or how test ranges and their management strategies varied among installations. My objectives therefore were to: a) Document whether gopher tortoises were known to use testing and training areas at other installations. b) Document common management practices used to maintain these sites (e.g. mechanical [mowing, roller-drum chopping], fire, chemical [herbicide]) and the variability in management regimens used among sites. c) Obtain similar information for other human-disturbed/ruderal vegetation types (e.g. power line rights-of-way, old fields, clear cuts) that are also commonly used by gopher tortoises.

Materials and Methods

I developed and distributed a questionnaire (Appendix D) with the assistance of Partners in Amphibian and Reptile Conservation (PARC) DoD coordinator, Chris Petersen. Twenty-seven DoD properties with confirmed tortoise populations as well as 15 potentially tortoise-occupied properties were identified across 28 installations within all six states in the gopher tortoise's range. Head natural resource personnel were contacted for each military branch who were asked to distribute the questionnaire down their chains of command to appropriate managers and installation biologists. The questionnaire had three primary goals: 1) identify management practices (mechanical, fire, chemical) and frequencies used to maintain the open conditions found on test ranges and similar areas. 2) Identify management practices used to maintain other open, ruderal/disturbed areas that tortoises frequently inhabit such as powerline rights-of-way

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and clearcuts. 3) Obtain any information available regarding presence of tortoises inhabiting these sites. All resource managers were encouraged to return surveys regardless of how many questions they were able to answer, as any response provided potentially useful information. Responses were presented in descriptive summaries and tables.

Results

I had seven total respondents representing eight installations and outlying properties (Table 2.1). One individual represented two installations and completed separate questionnaires for each. We considered these separate responses. For this chapter, I have focused primarily on responses to questions specific to testing/training areas and airfields (henceforth collectively referred to as test ranges).

Among respondents, all reported tortoises inhabiting human-altered vegetation types and seven of eight installations reported tortoises occupying test ranges. Management techniques used to suppress vegetation (Table 2.2) and mission activity (Table 2.3) in these areas were somewhat variable. All respondents reported that test ranges were maintained by mowing and seven of eight installations reported the use of herbicides as well. An additional five installations reported chainsawing/logging occurred on test ranges. Two installations reported the use of roller-drum chopping. Additionally, it was reported that test ranges on six installations were managed with prescribed fire to some extent and three reported that incidental fires (i.e. lightning-fires or fires ignited by training activities) were generally allowed to burn.

Four installations commented on the season of burn (open response), of which, two reported dormant season prescribed fires only. One reported growing season (March-October) fires and some supplemental winter burning for areas in need. One reported that potential tortoise habitats had received growing season (April-May) fires at least once since 2012 and dormant season fires in years prior.

Among the eight installations that responded, seven indicated that certain management practices were used on test ranges specifically to improve or maintain gopher tortoise habitat. Additionally, a number of other beneficial management activities used on tortoise-occupied test ranges (open response, described here in text but not listed in the table) were identified. Five respondents listed prescribed fire and one installation each listed midstory removal, mechanical clearing, timber harvest, and "RCW/Gopher Tortoise" as management practices implemented for the benefit of gopher tortoises.

Respondents indicated that test ranges were used for a wide variety of testing and training activities. Three reported tactical land vehicle use, two reported bivouacs, three reported live-fire/incendiary exercises, and one reported no training activities occurred. Additionally, five installations listed other activities/conditions (open response) which included military personnel and aircraft movement, runway clear zone, flight operations in cleared areas, minimal live-fire (blank cartridges), and airfield.

When asked to comment on variability in the frequency and timing of management practices used to maintain test ranges (open response), most respondents indicated that management strategies were highly variable over time and space. One installation reported that it did not have test ranges, though open areas occupied by tortoises were used periodically for land navigation exercises only. Another installation commented that management was variable and that most habitat was "overgrown/had not been managed properly for several years." A third installation mentioned attempts to reduce midstory vegetation on 600 acres/year across base, some of which included tortoise habitat, and a fourth indicated prescribed burning at 2-3 locations per year, weather permitting.

Discussion

We received responses from fewer than a third of the installations within the range of the gopher tortoise. Natural resource managers may be overburdened by reporting, may lack the requested information about range management practices, or may prioritize actual hands-on management work over reporting information. The responses received, while limited, do help place the practices used on Eglin Air Force Base in a broader context.

Seven of the eight respondents were aware of gopher tortoises residing in areas designated for testing and training activities, suggesting use of these habitats by tortoises may be somewhat widespread among military installations. Similar to Eglin, test ranges on the participating installations were maintained predominantly through mowing, though herbicide was apparently widely used elsewhere as well. Roller-drum chopping, which has been discontinued on Eglin due to recognition of adverse soil impacts (U.S. Air Force 2015), was apparently still in use at two of the responding installations. Six installations reported that prescribed or incidental fires occurred on test ranges but, of the four who elaborated on fire season and frequency in their open response answers, it was unclear whether those individuals were reporting generally for all tortoise-occupied sites across base or speaking specifically for testing and training areas. Based on these responses, fire may not be as widely integrated on test ranges at other installations compared to Eglin or this information is not widely known. Similarly, while seven participants indicated that management practices were employed to improve or maintain tortoise habitat, it was unclear whether or not they were specifically referencing test ranges (or if 'test ranges' may have included forested habitats where training activities occurred). Participants also reported a wide array of mission uses on test ranges at their respective installations that differed from many of the testing and training activities on Eglin's ranges. Only three of the eight participants indicated test ranges were used for live-

fire/incendiary exercises, which may explain why fire was not widely reported in these areas. In

contrast, most of Eglin's test ranges where tortoises occur are used for munitions testing. On

Eglin, test ranges receive frequent prescribed burns and testing and training activities provide an

ignition source for wildfires. In contrast, these areas on other installations were used for ground

maneuvers (bivouacs and ground vehicle use) or as airfields. Further, the use of

logging/chainsawing in other testing and training areas suggests participants may have again

been referring to forested areas where training occurs rather than sites cleared of trees. The

expansive, frequently burned, treeless test ranges found on Eglin requiring large buffers around

impact areas may therefore be absent among military installations that participated in this

questionnaire. However, similar areas at these installations may also have restricted access due to

unexploded ordinance, limiting the ability of natural resource personnel to assess tortoise

populations in some testing and training areas.

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Tables and Figures

Table 2.1. Branches and locations of installations that participated in our test range management questionnaire.

Installation	Branch	State
Fort Benning	Army	GA
Fort Stewart/Hunter Army Airfield	Army	GA
MacDill AFB	Air Force	FL
Marine Corps Logistics Base Albany	Marine Corps	GA
NAS Jacksonville/OLF Whitehouse/ Rodman Range	Navy	FL
NAS Pensacola/Bronson Field/Saufley Field	Navy	FL
Naval Submarine Base Kings Bay	Navy	GA
NAS Whiting Field	Navy	FL

Table 2.2. Management practices used to maintain test ranges at participating installations (n=8).

Management Practice	# of Installations	% Installations
Fire	6	75
Prescribed	6	75
Incidental	3	37.5
Herbicide	7	87.5
Mechanical	8	100
Chainsawing/Logging	5	62.5
Mowing/Bush-Hogging	8	100
Roller-Drum Chopping	2	25

Table 2.3. Reported mission activity occurring on test ranges at participating installations (n=8).

Mission Activity	# of Installations	% Installations
Bivouacs	2	25
Live-fire/Incendiary Exercises	3	37.5
None	3	37.5
Tactical Land Vehicle Use	3	37.5
Other (open response write-ins)	5	62.5
Airfield	1	12.5
Flight Ops. In Cleared Areas	1	12.5
Military Personnel & Aircraft Movement	1	12.5
Minimal Live-fire (Blanks)	1	12.5
Runway Clear Zone	1	12.5

Chapter 3

Activity patterns of juvenile Gopher Tortoises inhabiting forested sandhills and test ranges on Eglin Air Force Base, Florida

William M. Moore

Abstract

Juvenile recruitment is essential to the growth and stability of any population. Juvenile gopher tortoises are highly vulnerable to thermal stress and predation risk; however, in order to grow, they must emerge from burrows to feed. Due to these risks, juvenile gopher tortoises spend most of their time underground while rarely straying far from the burrow when on the surface. Juvenile gopher tortoise burrows are difficult to detect because of their small size and individuals in smaller size classes are thought to occur in low abundances even in high-quality habitat. Juveniles are therefore difficult to target for research and few studies have explored above ground activity patterns, particularly how activity may differ in structurally dissimilar vegetation types. My objective was to determine if surface activity patterns of juvenile tortoises differed between two structurally different vegetation types on Eglin Air Force Base, fire-maintained forested sandhills and human-altered military test ranges. I hypothesized that conditions affecting surface activity in juvenile tortoises (e.g. foraging opportunities and/or cover) would be directly tied to the relative risks associated with predation and/or heat stress. Surface activity in these vulnerable size classes may therefore indirectly affect survival rates. I placed trail cameras at burrow entrances to determine if activity patterns (i.e. length and frequency of surface activity bouts) for juvenile gopher tortoises differed between non-forested test ranges and forested sites on Eglin. Surface activity bouts were shorter in duration on test ranges but occurred more frequently compared to those of juvenile tortoises inhabiting forested sites. Though juvenile

tortoises on test ranges exhibited different activity patterns from those inhabiting forested sites, the reasons for these differences were not entirely clear.

Keywords: *Gopherus polyphemus*, basking, camera-monitoring, foraging, surface activity

Introduction

Among demographic parameters, juvenile survival and recruitment rates may have the largest effect on long-term population viability in gopher tortoises (Tuberville et al. 2009). Broadly, physiological constraints, energy demands, and predation pressures are greater for juvenile reptiles (McRae et al. 1981, Morafka et al. 2000, Mushinsky et al. 2003). Adult gopher tortoises have few natural predators; however, recruitment rates are thought to be low, largely resulting from high rates of nest and juvenile depredation (Landers et al. 1980, Alford 1980, Diemer 1986). Neonate gopher tortoises are approximately 40-55 mm at hatching and mature slowly (Landers et al. 1980, Wilson 1991). They may remain in particularly vulnerable juvenile size classes for up to ten years or more before carapace and plastron scutes begin to harden at roughly 110-120 mm carapace length (Landers et al. 1982, Wilson 1991). A wide variety of mammals (primarily meso-carnivores), birds (primarily raptors) and snakes, including many common burrow commensals, are confirmed predators of juvenile gopher tortoises (Douglas and Winegarner 1977, Landers et al. 1980, Wright 1982, Wilson 1991, Perez-Heydrich 2012).

Additionally, hatchling and juvenile survivorship may exhibit considerable spatial and temporal variation possibly as a result of differences in composition and relative abundances of predator assemblages, among other factors (Pike and Seigel 2006, Perez-Heydrich et al. 2012). Most annual survival estimates from radio-telemetry studies suggest mortality of young gopher tortoises (primarily due to predation), especially hatchling-sized individuals, tends to be high, with telemetry-based estimates ranging from 34-100% mortality within a year (Wilson 1991, Butler & Sowell 1996, Epperson and Heise 2003, Pike and Seigel 2006, Perez-Heydrich et al.

2012, Smith et al. 2013). The relatively low 34% mortality estimate resulted from a predator exclusion experiment conducted by Smith et al. (2013) in which ~ 40 ha plots surrounded by exclosures designed to keep out meso-carnivores (monitored from the start of the nesting period + 329 days after hatching for radio-tagged individuals) had significantly higher nest success (66.41 ± 9.65% vs. 34.93 ± 10.34%) and hatchling survivorship (74.4% vs. 37.5%) than unfenced plots.

Juvenile gopher tortoises tend to be highly reclusive and are rarely observed above ground (Wilson 1991, Butler et al. 1995). Predation and temperature-associated risks presumably constrain surface activity in juvenile gopher tortoises but the strategies used to balance thermoregulatory and nutritional demands against those risks are not well-understood (Congdon 1989, Mushinsky et al. 2003). Juvenile and hatchlings and their burrows tend to be difficult to detect on the landscape (Wilson 1991, Deimer 1992, Tuberville 2014), which, in addition to their comparative rarity, presents challenges when targeting juvenile tortoises for study (Wilson 1991, Morafka et al. 2000, Pike & Grosse 2006, Tuberville et al. 2014). Most studies have focused on survival (Wilson, 1991, Butler & Sowell 1996, Epperson & Heise 2003), home range/movements (Beyer 1993, Epperson & Heise 2003, Pike 2006), diet (Mushinsky et al. 2003), growth rates (Landers et al. 1982, Mushinsky et al. 1994, Aresco & Guyer 1999), or habitat preferences (Beyer 1993, Raymond 2007) in juvenile age classes. Above ground activity and movement in adult tortoises may be influenced by habitat characteristics (McRae et al. 1981, Auffenberg & Franz 1982, Mushinsky et al. 2003), but the relationship between habitat and surface activity patterns in juvenile tortoises has received little attention (but see Mushinsky et al. 2003, Pike 2006, Pike & Grosse 2006).

Wilson (1991) rarely documented juvenile tortoises above ground, and when they were observed on the surface, they were usually foraging. Pike and Grosse (2006) monitored the activity patterns of hatchling and juvenile gopher tortoises in coastal strand and scrub vegetation types in central Florida, finding they left their burrows infrequently and suggested there may have been behavioral differences between hatchling and larger juvenile size-classes. For both size-classes, activity was most frequently observed in the morning and decreased as the day went on, suggesting that juvenile tortoises may be under strict thermal constraints. Furthermore, Auffenberg & Weaver (1969) noted that captive juvenile gopher tortoises were especially susceptible to desiccation, suggesting prolonged periods spent outside of the relatively constant moisture and temperature of the burrow could be detrimental. Mushinsky et al. (2003) proposed that three non-mutually exclusive factors limited duration and distance traveled during observed juvenile tortoise foraging bouts in a central Florida sandhill: 1) Small tortoises may reach satiation quickly. 2) Thermal limitations minimize time juvenile tortoises can spend away from their burrows before risking hyperthermia. 3) High predation pressure selects for more cautious behavior in juvenile tortoises.

On Eglin, active juvenile burrows were located consistently at a handful of sites, both forested and test ranges, during one or both of my field seasons while no active juvenile burrows were found at others (personal observation). This was consistent with previous studies on Eglin that found densities of juvenile burrows were highly variable among sites (Haas et al. 2016). The structural differences in vegetation between test ranges and forested habitats could potentially cause differences in surface activity patterns within juvenile size classes. Risks associated with predation and heat stress for juvenile gopher tortoises are assumed to be directly related to above ground activity and the effort required to meet physiological demands via foraging and

thermoregulation. Knowledge of juvenile gopher tortoise behavior outside the burrow is limited, and, to my knowledge, few studies have explored activity patterns in smaller size classes, particularly within heavily human-altered vegetation types such as test ranges. The considerable amount of available herbaceous vegetation on test ranges (see chapter 1 of this study) may allow young tortoises to reach satiation quickly without travelling far from the burrow and therefore limit time spent on the surface. The exposed conditions on test ranges presumably decreases the time necessary for basking as well. Alternatively, the complete lack of any tree canopy or midstory on test ranges may limit available thermal refugia outside the burrow, and may limit foraging efficiency during periods of extremely high temperatures due to increased risk of hyperthermia and/or desiccation. Though growth rates are unknown for Eglin tortoises, other studies have found evidence that juvenile tortoises may reach adult sizes more quickly in some human altered/ruderal vegetation types compared to more natural forested areas (Landers et al. 1982, Godley 1989, Harris 2014), but the mechanisms behind accelerated growth in these habitats are speculative. The goals of this study, were therefore to: a) Determine if surface activity bouts differed in duration between forested sandhill sites and test ranges on Eglin Air Force Base. b) Determine if total daily surface activity and/or frequency of surface bouts differed between forested sites and test ranges. c) Determine if there was a relationship between activity patterns and major vegetative cover classes (Chapter 1).

Materials and Methods

Camera-monitored burrows included in this study were located in four ways: 1) Previously active and inactive burrows located during prior burrow density surveys (chapter 1) were revisited to assess current status or locate newly excavated burrows near old ones. 2) Juvenile burrows were encountered opportunistically while conducting other fieldwork. 3) Targeted searches were conducted near adult burrows as young tortoises that hatch from nests in

burrow aprons often excavate their first burrows within close proximity to the nest site and tend to disperse slowly/over short distances within their first years of life (Butler et al. 1995, Smith 1995, Pike 2006). 4) Camera data from a handful of active juvenile burrows collected for a separate commensal study were summarized for the purposes of this study.

Burrows under 130 mm in width (as described in chapter 1) were classified as juvenile burrows for this study, though they ranged in size from that of hatchlings/yearlings to tortoises that were at least a few years old (range 50 mm -130 mm). Twenty active juvenile burrows were located during the 2017 field season, 11 were located during the 2018 season, and an additional seven from the 2018 commensal study were also included (n=38 total).

Originally, I proposed a balanced design in which forested and test range sites were randomly paired during each monitoring session; however, juvenile burrows were only detected at a handful of sites, active burrows were difficult to locate, and were regularly abandoned (though sometimes re-occupied at a later date). Due to these limitations, camera monitoring was restricted to six sites in 2017 (two forested sites and four test ranges) and five sites in 2018 (two forested sites and three test ranges). One burrow from an additional forested site was also included from the commensal study in 2018.

The number of available burrows for camera monitoring fluctuated depending on abandonment of previously occupied burrows and discovery of new active burrows. The number of cameras deployed and number of sites monitored per session were therefore dependent on active burrow availabilities, and some burrows were monitored multiple times if they remained occupied during successive deployment sessions. For burrows that were monitored for multiple sessions, activity bout durations were averaged and reported as single estimates. I felt confident that the same tortoise used the same burrow in these instances, as burrow sharing among

conspecific juvenile gopher tortoises has rarely been observed (Pike 2004, Pike & Antworth 2005, Pike 2006, though see also Radzio et al. 2016 regarding burrow cohabitation and apparent competition).

Site-specific restrictions further limited the burrow availability for monitoring. Test range C61A, one of the sites with the largest number of active juvenile burrows known on Eglin, was sampled just once as permission to set cameras was only granted during Fourth of July weekend in 2017 when the range was not in use. Test ranges C62N and C62S were mowed in July of 2017, collapsing all previously known active burrows. No other juvenile burrows were located during the 2017 field season at those sites post-mowing, though additional active burrows were located in 2018 at C62S.

At juvenile burrows suspected to be active, trail cameras (Moultrie Cam model M-990i Gen 2) were mounted on metal stakes ~ 0.5-1 m from the burrow entrance so that the entire burrow and its apron were roughly centered within the camera frame and no vegetation was obscuring the burrow entrance. Cameras were programmed to take pictures at 10-second intervals between 08:00 and 18:00 (Central Daylight Time) when tortoises were expected to be most active. This time-frame included bimodal activity peaks observed in adult gopher tortoises by McRae et al. (1981), as well as unimodal primary periods of activity for juveniles described in Douglas & Layne (1978) and Wilson et al. (1994).

Typically 8-10 cameras were deployed during each monitoring session, spread between 3 to 4 sites (cameras were deployed between at least one forested site and one test range simultaneously each session) depending on the availability of active burrows. Cameras were usually deployed and rotated once a week. I conducted eight total camera monitoring sessions in 2017, seven of which occurred between 25 June and 17 August, and the eighth from 13-15

October. Three trapping sessions were conducted in 2018 that occurred between 6 July to 1 September. Data for the seven burrows from the commensal study were collected between 11 April to 14 August 2018. Generally, monitoring periods lasted roughly four days before the memory card was filled and/or batteries were drained, though were longer or shorter in a number of cases. Memory cards were collected each week and photos were reviewed to determine if burrows were active. All photos featuring tortoise activity were stored before the memory card was erased and re-deployed during the next monitoring session.

The time stamps displayed on each photo were used to determine when an individual exited or entered its burrow and exited or entered the camera frame. Average exit duration (average exit) for each tortoise was the mean duration of all its exits (the amount of time that individual spent on the surface with at least half of its carapace exposed, see Table 3.1 for terminology and definitions). Average excursion duration (average excursion) for each tortoise was the mean duration of all its forays away from the burrow (time between leaving the camera frame and returning to view). Exit durations included excursions whenever they occurred (i.e. for each excursion, a corresponding exit event included the length of time spent away from the burrow in addition to the time it spent in the camera frame = the total time spent outside the burrow). Juvenile gopher tortoises spend much of their time foraging when above ground (Wilson 1991, Mushinsky et al. 2003), thus, it was assumed that feeding was the primary motivation behind excursions in this study. However, on occasion, tortoises left the vicinity of their burrows for multiple hours. I assumed that these extended excursions were not representative of typical foraging behavior (i.e. the tortoise may have taken shelter elsewhere) and these events were not included in exit or excursion calculations. Average amount of time spent on the surface per day (average daily exit) was the total amount of time spent outside the

burrow each day averaged over the number of full camera-monitored days per session. Average amount of time spent away from the burrow per day (average daily excursion) was the total amount of time spent outside the burrow and out of camera view each day averaged over the number of full camera-monitored days per session. Partial days (i.e. days when the camera was set or removed/re-set) were excluded from this estimate for ease of calculation and because human presence probably affected behavior (tortoises often did not exit their burrows the first day cameras were set, even when set earlier in the morning). Similarly, average number of exits per day (exits per day) and average number of excursions per day (excursions per day) were calculated by totaling the number of exits and number of excursions per day for each individual and averaging them over the number of full camera-monitored days per session. I did not calculate average daily exit, average daily excursion, exits per day, or excursions per day for data collected from tortoises in the commensal study as different camera settings were used and the start and end dates for each monitoring session were unknown. Individual averages for each tortoise were then used to calculate averages for each vegetation type (forested and test range).

Temperature was expected to have an effect on juvenile tortoise activity so soil temperatures were taken at one or two burrow locations within each site per monitoring session using i-button temperature loggers buried ~ 3 cm beneath the surface near the burrow apron, recording temperatures each hour. In most cases, at least one i-button was used at each site per trapping session, and sometimes more depending how far apart burrows were if multiple burrows were trapped at a site during that session. The average, maximum, and minimum temperatures were recorded for the duration of each trapping session (8:00-18:00 h) starting when the tortoise first exited its burrow to the final time it re-entered its burrow prior to cameras being collected.

Site-wide vegetation cover estimates (chapter 1) were used to determine if surface activity duration or frequency were related to percent cover for major vegetative cover classes. A subset of juvenile burrows was included in both this study and the burrow-scale (use vs. availability) portion of chapter 1. I also tested to see if there was a relationship between major vegetative cover classes within 8-m foraging buffers around these burrows and activity duration/frequency of the resident tortoises.

Statistical Analyses

Total number of exits and excursions (exit and excursion frequencies) for all juvenile tortoises in this study were graphed according to time of day for each vegetation type and graphs were visually interpreted to determine possible daily activity peaks. Two sample t-tests were used to determine if average exit, average excursion, average daily exit, average daily excursion, exits per day, and excursions per day differed between forested sites and test ranges. Activity data for tortoises within each vegetation type were pooled as sample sizes were too limited to explore among-site differences. I used a linear regression to determine if activity patterns were associated with burrow width (as an index of tortoise size/age). I used multiple regression to determine if there was a relationship between vegetation cover estimates (site-wide and burrow-scales, data obtained from chapter 1) and activity patterns, though sample sizes were too small to assess relationships between vegetative cover class estimates and activity patterns in forested sites and test ranges separately. Bare ground cover, total herbaceous cover, litter cover, and shrub cover were selected as cover class variables that were most likely to affect surface activity and were included as predictors in all regressions.

Results

During the 2017 and 2018 field seasons, 38 active juvenile tortoise burrows were located, among four forested sites and six test ranges. Excluding the three mentioned below, 35 burrows

provided activity data, 15 of which were located in forested sites and 20 of which were located on test ranges. Burrows ranged in width from ~ 50 to 130 mm. Maximum (average maximum 36.6 C° in forested sites vs 39.5 C° on test ranges) and mean (average 28.8 C° in forested sites vs 30.6 C° on test ranges) soil temperatures on test ranges were slightly higher compared to forested sites. Minimum (average minimum 23.4 C° in forested sites vs 23.6 C° on test ranges) temperatures did not differ between habitat types.

Burrow abandonment occurred frequently and was occasionally documented on camera when the resident tortoise would exit its burrow and not return for the duration of the study period. Among the 38 active burrows, four remained occupied for multiple camera monitoring sessions and only a single 65 mm burrow in a forested site remained occupied for the duration of a field season (2017). In one case, a tortoise occupied a previously inactive 68 mm burrow on a test range sometime prior to 1 August 2017 where it remained until it left at 1015 on 8 August and did not return.

The three individuals listed below abandoned their burrows the day following camera placement. These tortoises may have been disturbed by my presence near the burrow while setting cameras and were therefore excluded from analyses. A tortoise occupying a <90 mm burrow in a forested site was observed on 1 July 2017. It left its burrow at 0957 and returned over three hours later at 1305. It then emerged and retreated a number of times before apparently abandoning the burrow sometime outside of the camera's operating hours that evening or the following morning. Similarly, a tortoise occupying a 62 mm burrow in a different forested site repeatedly exited and entered its burrow in surface bouts that lasted one to three minutes before it left its burrow permanently at 1318 on 6 July 2018. A third individual inhabiting a <90 mm burrow on a test range abandoned its burrow at 0910 on 1 July 2017 (it had not emerged prior to

abruptly departing that morning). The (presumably) same tortoise then attempted to enter an

occupied 60 mm burrow (also being monitored) located ~ 20 m from the original burrow at

0917, but was barred from entry by the resident individual. After it attempted to enter the burrow

several times while the resident tortoise obstructed the burrow mouth, the intruding individual

left the camera frame at 0920 and was not seen again. The remaining 35 camera-monitored

burrows were assumed to represent unique individual tortoises (i.e. it is unlikely that the same

tortoise was observed at multiple active burrows) based on differences in burrow sizes and

distances between camera-monitored burrows.

Camera data suggested that exit frequencies (i.e. how often tortoises emerged from their

burrows, not the duration of time spent on the surface, n=1080 exits) exhibited a more or less

unimodal distribution in both forested and test range habitats (Fig. 3.1). Peak exit frequencies

were similar between vegetation types as well. In both forested and test range habitats, exit

frequency increased between ~0800 and 0900, peaked between ~ 0900-1300, and tapered off

slowly later in the afternoon. Excursion frequencies (n=216 excursions) exhibited a more

bimodal distribution and were more dissimilar between forested sites and test ranges (Fig. 3.2).

In forested sites, excursions peaked in frequency prior to ~1100 and again after ~1500, with a

moderate lag in activity between ~1200 and 1400. Contrastingly, on test ranges there was a

moderate peak in excursion frequency between ~1000 and 1100, a slight lag around noon, and a

gradual increase from ~ 1300 to 1700 until tapering off prior to 1800.

I found evidence that juvenile tortoises inhabiting forested sites and test ranges exhibited

different surface activity patterns. All comparisons below are presented as estimated average

duration (minutes) or average number of exits/excursions, ± one standard error. On average,

juvenile tortoises inhabiting test ranges appeared to exit their burrows more frequently but for

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shorter amounts of time compared to individuals in forested sites (Table 3.2). Average exit duration was 7.7 min. longer for juvenile tortoises inhabiting forested sites than for those on test ranges (24.3 ± 2.1 min. vs. 16.6 ± 1.6 min., DF= 28.46, t=2.94, p=<0.01). Average excursion durations, were nearly identical to average exit durations within both forested sites and on test ranges (23.7 ± 3.3 min. vs. 16.7 ± 2.3 min., DF=26.88, p=0.09). The difference in average excursion duration between vegetation types (7.0 min. longer in forested sites) was nearly identical to the difference in average exit duration, but excursions tended to be more variable in length (forested exit duration CV=33.04 vs. excursion duration CV=53.38, test range exit duration CV =43.62 vs. excursion duration CV=62.71). Tortoises occupying test ranges exited their burrows an average of 3.2 times/day more compared to those in forested sites (8.3 ± 1.1 exits/day vs. 5.1 ± 0.7 exits/day, DF=22.69, t=2.54 p=0.02), and left the vicinity of their burrows twice as frequently (1.9 ± 0.2 excursions/day vs. 1.0 ± 0.1 excursions/day, DF=16.23, t=3.46, p= <0.01). Average daily exit and average daily excursion durations (i.e. total amount of time spent outside the burrow and away from the burrow, outside the camera frame per day, respectively) did not differ between forested and test range vegetation types.

I found no relationship between burrow width (and by proxy, tortoise size/age class) and average exit duration ($F_{1,20}$=0.75, p=0.40, $R^2 = 0.04$), average excursion duration ($F_{1,20}$=0.16, p=0.69, $R^2 < 0.01$), average daily exit duration ($F_{1,12}$=1.34, p=0.27, $R^2 = 0.10$), average daily excursion duration ($F_{1,12}$=0.03, p=0.87, $R^2 = <0.01$), exits per day ($F_{1,12}$=2.65, p=0.13, $R^2 = 0.18$), or excursions per day ($F_{1,12}$=0.1.64, p=0.22, $R^2 = 0.12$). However, sample sizes were small as widths for some burrows were visually estimated and those without exact width measurements were excluded from regressions.

I found a slight negative relationship between exits per day and site-wide habitat variables ($F_{4,20}$=3.55, p=0.02, $R^2 = 0.42$, Table 3.3), though litter cover (p=0.02) was the only significant predictor. Average exit duration ($F_{4,29} = 2.02$, p=0.12, $R^2 = 0.22$, average excursion duration ($F_{4,29}$=1.53, p=0.22, $R^2 = 0.17$), average daily exit duration ($F_{4,20}$=0.56, p=0.69, $R^2 = 0.11$), average daily excursion duration ($F_{4,20}$=0.70, p=0.60, $R^2 = 0.13$), and average number of excursions per day ($F_{4,20}$=2.61, p=0.07, $R^2 = 0.34$) were not related to site-wide vegetation cover estimates. Average exit duration was significantly related to burrow scale vegetative cover class estimates ($F_{4,10}$=8.05, p= <0.01, $R^2 = 0.76$, Table 3.4). Both total forage cover (p=0.01) and shrub cover (p=0.01) had a significant, positive relationship with average exit duration. Average excursion duration ($F_{4,10}$=2.30, p=0.13, $R^2 = 0.48$), average daily exit duration $F_{4,8}$=0.66, p=0.64, $R^2 = 0.25$), average daily excursion duration $F_{4,8}$=1.11, p=0.41, $R^2 = 0.36$), average number of exits per day ($F_{4,8}$=1.08, p=0.43, $R^2 = 0.35$), and average number of excursions per day ($F_{4,8}$=1.38, p=0.32, $R^2 = 0.41$) were not related to burrow-scale vegetation estimates.

Discussion

Trail camera monitoring revealed differences in juvenile tortoise surface activity between forested sites and non-forested test ranges. Specifically, I found that juvenile tortoises inhabiting Eglin's test ranges generally exited their burrows for considerably shorter amounts of time, but at higher frequencies than forest-dwelling juveniles, suggesting vegetation differences may have affected surface activity to some extent (though see alternative explanation below). Variability in excursion duration could have been due to a number of factors including local forage availability and vegetation structure (e.g. shrub cover/height), and/or individual variability in responses to perceived threats, among other possibilities, all of which could hypothetically extend or abbreviate foraging bouts. However, additional research is needed to quantify foraging activity versus other aboveground behaviors in structurally different vegetation types.

Further, on test ranges, juveniles averaged two excursions per day compared to one for those in forested sites. It should be noted however, that juveniles in both vegetation types often went multiple days without leaving their burrow aprons, appearing to only come to the surface to bask. Individuals left their burrows infrequently, but when they did, sometimes left multiple times in a single day. Caution should therefore be taken when interpreting these data as, similar to their average duration, excursions away from the burrow fluctuated widely from day to day in frequency and in total daily duration. Average daily exit and average daily excursion durations were similar between vegetation types, suggesting juvenile tortoises may have been using alternative basking/foraging strategies that required similar total effort.

Most juvenile burrows I located did not remain active for more than one monitoring session and once an individual left, the burrow usually was not reoccupied (aside from one exception), suggesting most burrows were permanently abandoned. In a telemetry study, Butler et al. (1995) found that nearly half of all burrow changes by juvenile tortoises occurred after transmitter battery replacement and I cannot discount the potential effects cameras and repeated visits to burrows might have had on behavior. However, I only documented a few abandonments on camera (see results) and most apparent abandonments occurred outside of camera monitoring sessions. Additionally, Pike (2006) found that hatchling sized tortoises tended to dig 1-3 burrows per month on average between May and September, indicating young gopher tortoises may be naturally inclined to change burrows frequently, particularly during the warmest months of the year.

I found juvenile tortoises in both vegetation types exhibited a unimodal exit frequency distribution, with peaks around mid-day hours that tapered off in the late afternoon, similar to the daily activity patterns for juveniles described by Douglas & Layne (1978). Excursion frequency

had a slightly bimodal distribution that was more comparable to summer (July-August) foraging bout distributions described for adult tortoises in southwest Georgia by McRae et al (1981). Most of my data were collected from June-August and high temperatures during the warmest months of the year, while not limiting general surface activity near the burrow entrance and apron, may have constrained foraging excursions to the cooler morning and late afternoon hours.

Few other studies have reported on surface activity in juvenile gopher tortoises directly and the following comparisons between those that have and my study should be interpreted with caution due to methodological differences. Mushinsky et al. (2003) made direct observations of foraging juveniles in a central Florida sandhill and found they spent an average of 19.4 ±10.3 min. on the surface while foraging, which fell roughly half-way between average excursion durations (reported above) for juvenile tortoises inhabiting forested sites and test ranges I documented on Eglin.

Pike and Grosse (2006), to my knowledge, presented the only other published data using remote camera monitoring on surface activity in juvenile gopher tortoises (other authors, e.g. Radzio et al. 2016, have used remote cameras to monitor social interactions, but did not explicitly record surface activity duration). The authors continuously monitored two hatchling-sized (46 and 49 mm carapace length, CL) tortoises for four and 11 days, and six juvenile tortoises (95 -121 mm CL) from 37-73 days at their burrows from June-October in central Florida coastal strand and scrub. In the central Florida study, hatchling and juveniles only emerged ~70% and ~ 32% of the days they were monitored, respectively. In contrast, despite the shorter daily camera monitoring window I used, Eglin tortoises in both habitat types generally emerged from their burrows at least once a day, though few individuals remained at their original burrows long enough to monitor them for more than three to eight days (one or two consecutive

monitoring sessions). Further, when they were active, hatchling tortoises spent over twice as much time (42.9 ± 9.4 min.) on the surface as juvenile tortoises (18.8 ± 2.0 min.) in the central Florida study. The average length of surface activity periods for juveniles in that study was similar to what I found within forested sites and on test ranges at Eglin (reported above). In contrast, the average length of surface activity for hatchlings reported by Pike and Grosse far exceeded average exit durations I documented in either vegetation type. Almost all burrows located in forested sites for my study were less than 100 mm in width while juvenile burrows on test ranges fell within a wider range of sizes (50 mm–130 mm). Though the central Florida study had a small sample size (particularly for hatchling tortoises), I could not discount the possibility that differences in surface activity patterns between vegetation types in my study may have been an artifact of the greater variability in juvenile sizes on test ranges rather than differences in vegetation structure. However, I did not find a strong relationship between burrow width (for burrows I had obtained measurements for, n = 22) and average exit duration, though larger juvenile size classes did, on average, have shorter exit durations. Smaller size classes (<90 mm) had much greater variability in average exit duration in my study. In contrast to average exit durations reported by Pike and Grosse, however, only two juvenile tortoises on Eglin in this study averaged ≥ 42 minutes per exit bout, regardless of size, and the majority did not exceed 30 minutes in average exit duration.

Gopher tortoises also inhabit a number of structurally different vegetation types throughout their range and may exhibit behavioral plasticity allowing them to adjust foraging and basking strategies accordingly under different environmental conditions (Douglas & Layne 1978, Radzio & O'Connor 2017), including somewhat novel conditions associated with human-altered landscapes. Juvenile size and vegetative differences, therefore, may not be mutually

exclusive explanations for the differences I observed in juvenile activity patterns between test ranges and forested habitats. Additionally both hatchling-size tortoises in the Pike and Grosse study spent significantly more time on the surface and emerged from their burrows less frequently than juvenile tortoises on Eglin, regardless of size or vegetation type, lending evidence to the possibility that surface activity may differ among structurally different vegetation types (i.e. coastal scrub vs. forested sandhill vs. test range).

I attempted to account for within and between site temperature differences (as temperature was expected to influence above ground behavior) using i-buttons buried ~ 3 cm below the soil near select burrow aprons. Logistical issues (limited logger availability per site, failing loggers, lost loggers etc.) limited the usefulness of the temperature data collected; though, I recognized the importance temperature plays in surface activity. In hindsight, a different sampling method and greater effort may have been necessary to capture the effects of structural differences between forested sites and test ranges on temperature at a microhabitat scale relevant to foraging juvenile tortoises. Ambient air temperatures were not expected to differ significantly among sites at any given time (localized weather events aside) due to their relatively close proximity to one another (~ ≤25 km).

Differences in vegetation structure, rather, may have contributed to fine-scale variation in temperatures at ground level that differed between vegetation types. For example, a general lack of tree canopy, mid-story, and other tall vegetation on test ranges could limit shade availability that otherwise might allow juvenile tortoises to move within a wider temperature gradient while foraging (Pike 2006, Halstead 2007). Additionally, taller woody vegetation may conceal young tortoises from predators and contribute to a greater sense of security while basking or foraging away from the burrow (Pike 2006). This may explain the positive relationship I found between

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shrub cover at the burrow scale and exit duration (sample sizes were too small to differentiate between forested sites and test ranges), though I did not detect an effect of shrub cover on excursion duration or excursions per day. Alternatively, increased shade may have required tortoises to bask longer when shrubs were abundant. A general absence of tall woody vegetation on test ranges may limit foraging durations during periods of high temperatures and/or through behavioral responses to threat perception, though consequently may also increase basking efficiency. Forested sites also generally had far more leaf litter, which juvenile tortoises are known to use for shelter, while test ranges had significantly more bare sand, which has a comparatively greater rate of heating on tortoise body temperature in direct sunlight than other substrates (Douglas & Layne 1978). I found a slight negative relationship between site-wide litter cover and exits per day, though it was unclear why this was the case as there was no noticeable effect of litter cover on exit or excursion duration, or on excursions per day. Though further work is needed, these structural differences may present more severe high-end temperature extremes at ground level on test ranges with fewer sheltering opportunities while outside the burrow, limiting the time a juvenile tortoise could remain surface active. Alternatively, these conditions also could decrease time needed for thermoregulation and increase digestion rates (Radzio & O'Connor 2017).

Lastly, test ranges generally had higher forage (graminoid and forb) availability than forested sites, though the differences between habitat types was less pronounced between test ranges and most forested sites where active juvenile burrows were detected. I found a positive relationship between burrow-scale forage availability and exit duration (possibly an increase in basking time in response to greater food intake), though I again did not detect a similar effect on excursion duration or excursions per day. Abundance and quality of forage available within close

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proximity to the burrow presumably affects the necessary effort required to meet nutritional demands (Orians & Pearson 1979, Mushinsky et al. 2003). Halstead (2007) suggested juvenile foraging paths indicated feeding to satiation was prioritized over avoidance of predators and environmental stressors. Similarly, Mushinsky et al. (2003) described a positive but asymptotic relationship between food plant availability along foraging paths and foraging effort throughout the summer. This curve was suggested to potentially represent a point of diminishing returns at which juvenile tortoises reached satiation and/or were approaching their thermal limit. If temperature was not a limiting factor and reaching satiation was prioritized, juveniles on test ranges may have been meeting forage requirements and/or optimal body temperatures quickly, allowing them to take advantage of abundant food resources by leaving their burrows more frequently.

Vegetation structure, forage availability/quality, size-class, temperature, and individual behavioral variability may all influence how immature gopher tortoises strategically balance growth and the risks associated with aboveground activity. Further, sample sizes were small and most data were collected during the warmest months of the year. Continued monitoring of juvenile tortoises on Eglin is necessary to better understand potential differences between vegetation types while also accounting for possible site-specific effects, seasonal shifts in activity patterns, and any behavioral differences among juvenile size-classes.

Juvenile gopher tortoises remain the subject of relatively few studies due to low detectability and presumably low abundances. However, as camera technology continues to advance, the ability to observe these cryptic size-classes with minimal intrusion can increase understanding of difficult to study, yet critically important life-stages. Future studies should address the relative effects the above factors and others have on surface activity in vulnerable

size-classes. Understanding whether differences in foraging and basking behavior exist among

size classes and/or among vegetation types will be valuable to conservation efforts, as

management strategies could be tailored to better address the needs of juveniles within a

population.

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Tables and Figures

Table 3.1. Terms and definitions used to describe juvenile tortoise activity patterns.
Averages were calculated for each juvenile tortoise (see exceptions for individuals camera monitored for separate Legacy commensal study below) and then averaged by vegetation type (forested or test range). Vegetation type averages for average exit and average excursion durations were calculated using individual estimates for all tortoises included in the study. Eight tortoises from a separate camera study on burrow commensal species were excluded in calculations of average daily exit and average daily excursion duration durations, exits per day, and excursions per day.

Term	Definition
Duration	
Average Exit	Mean duration of all exits in minutes during which tortoises came out of their burrows with at least half of their carapaces exposed
Average Excursion	Mean duration of all forays away from the burrow in minutes during which tortoises completely left the camera frame
Average Daily Exit	Total amount of time tortoises spent outside the burrow in minutes each calendar day averaged over the number of full camera trap days per trapping session
Average Daily Excursion	Total amount of time tortoises spent away from their burrows (i.e. outside the camera frame) in minutes each calendar day averaged over the number of full camera trap days per trapping session
Frequency	
Exits per Day	Total number of times tortoises exited their burrows each day averaged over the number of full camera trap days per trapping session
Excursions per Day	Total number of times tortoises forayed away from their burrows each day averaged over the number of full camera trap days per trapping session

Table 3.2. Two sample T-test results comparing average activity durations and frequencies between forested sites and test ranges for juvenile gopher tortoises.
Results are provided as means ± SE. Sample sizes (burrows used to calculate estimates) varied for different activity pattern estimates: Average exit and average excursion durations (n=15 tortoises in forested sites, n=20 tortoises on test ranges), average daily exit, average daily excursion durations, exits/day, and excursions/day (n=12 tortoises in forested sites, n=15 tortoises on test ranges).

Vegetation Type	Duration				Frequency	
	Avg. Exit	Avg. Excursion	Avg. Daily Exit	Avg. Daily Excursion	Exits/Day	Excursions/ Day
Forested	**24.3±2.1**	23.7±3.3	121.2±18.8	19.9±2.8	5.1±0.7	1.0±0.1
Test Range	16.6±1.6	16.7±2.3	124.0±12.5	22.8±2.6	**8.3±1.1**	**1.9±0.2**
t	2.94	1.74	0.13	0.77	2.54	3.46
p	**<0.01**	0.09	0.90	0.45	**0.02**	**<0.01**

Table 3.3. Multiple regression ANOVA table and coefficients for Exits per day predicted by site-wide scale percent cover estimates for major cover classes.
Cover estimates were obtained from site-wide vegetation surveys for 24 camera-monitored burrows. Predictor variables are defined as: Bare = exposed soil cover; Forage= combined herbaceous cover (forbs and graminoids); Litter = non-living plant material cover, i.e. leaves & woody debris; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Exits/Day	Model	4	155.43	38.86	3.55	0.42	**0.02**
	Error	19	218.74	10.94			
	Total	23	374.17				

Predictor	Est.	SE	t	P
Intercept	18.60	3.77	4.93	<.01
Bare	-0.06	0.09	-0.68	0.51
Forage	-0.07	0.04	-1.50	0.12
Litter	-0.17	0.07	-2.56	**0.02***
Shrub	-0.01	0.13	-0.07	0.95

Table 3.4. Multiple regression ANOVA table and coefficients for Average exit duration (time spent outside burrow) predicted by burrow scale percent cover estimates for major cover classes.
Cover estimates were obtained from vegetation surveys within 8-m foraging buffers for a subset of 15 juvenile tortoises. Predictor variables are defined as follows: Bare = exposed soil cover; Forage= combined herbaceous cover (forbs and graminoids); Litter = non-living plant material cover, i.e. leaves & woody debris; Shrub= woody plant cover.

Response		DF	SS	MS	F	R^2	p
Avg. Exit	Model	4	488.79	122.20	8.05	0.76	**<0.01**
	Error	10	151.71	15.17			
	Total	14	640.49				

Predictor	Est.	SE	t	p
Intercept	-8.03	5.14	-1.56	0.15
Bare	0.21	0.13	1.65	0.13
Forage	0.09	0.03	2.80	**0.02***
Litter	0.18	0.09	2.08	0.06
Shrub	0.58	0.16	3.54	**<0.01***
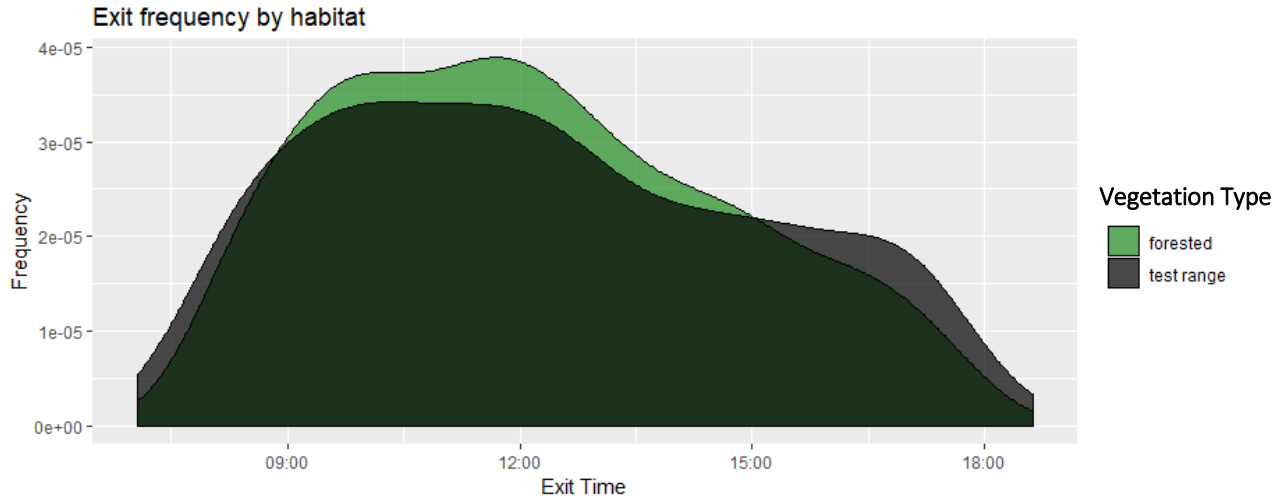
Figure 3.1. Exit frequencies of juvenile tortoises on Eglin AFB by time of day for forested sites (green) and test ranges (gray).
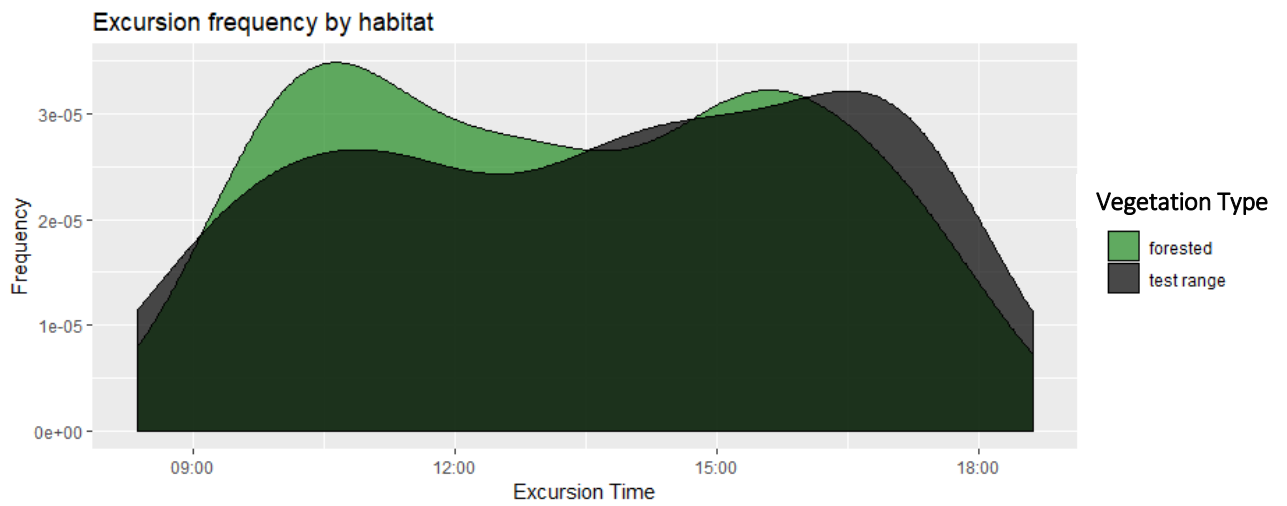
Figure 3.2. Excursion frequencies of juvenile tortoises on Eglin AFB by time of day for forested sites (green) and test ranges (gray).

Conclusions

Due to dwindling suitable habitat, military installations may play an increasingly important role in Gopher Tortoise conservation efforts by providing large tracts of contiguous, undeveloped land. Eglin Air Force Base in particular may serve as one of the most important refuges for Gopher Tortoises in the Florida panhandle going forward due to its size, current management practices, and availability of suitable habitat. In addition to typical longleaf sandhill habitat, Eglin has numerous, expansive test ranges, a number of which currently harbor tortoise populations and include some of the highest burrow densities on base. My primary goal for this thesis was to document the vegetation characteristics on test ranges that make them appealing to Gopher Tortoises, compare test ranges to forested sandhills where tortoises still occur on base, and identify possible explanations for differences in burrow densities among sites.

I found that test ranges had unique, but highly diverse, herbaceous communities compared to those found in forested sites where tortoises currently occur on Eglin and generally had greater herbaceous (forage) availability than forested sites, particularly in terms of graminoid cover. I also found evidence that adult tortoises may have been selecting burrow locations differently between forested sites and test ranges, favoring locations with greater graminoid and bare ground cover in the former, and more legume and shrub cover in the latter (chapter 1).

Results of the questionnaire indicated that gopher tortoises may regularly use cleared habitats designated for testing and training activities at other installations, though only a small subset of installations harboring gopher tortoises participated. However, it was also suggested that use of these habitats by tortoises, the management practices used to maintain them, and the testing and training activities that occur are variable from installation to installation. Responses indicated that the expansive, cleared areas used for munitions testing found on Eglin may be unique, at least among participating installations. Further, based on responses among

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participating installations, natural resource managers may lack data for population trends in testing and training areas and may only have cursory knowledge of the management practices used to maintain non-forested tortoise habitats (chapter 2).

Lastly, I found that juvenile tortoises exhibited different activity patterns in forested sites compared to structurally different test ranges. Juvenile tortoises inhabiting test ranges had surface bouts that were shorter in duration on average, but left their burrows more frequently compared to juveniles in forested vegetation types. These results suggested differences (e.g. structure, forage, threat perception etc.) between forested sites and test ranges may influence behavior in vulnerable juvenile size classes, though the exact mechanisms for these differences in surface activity were not clear (Chapter 3).

Alternative Explanations for the Current State of Eglin's Resident Gopher Tortoise Populations

I found little evidence to support my hypothesis that differences in burrow densities among most sites could largely be explained by current vegetation characteristics and I detected no obvious patterns between burrow densities and the vegetation variables measured. A number of possible alternative explanations and potential contributing factors are presented below and may be worth further exploration.

Forage Quality: Despite many similarities in herbaceous species assemblages among sites and between vegetation types, this study did not address the quality of forage in either test ranges or forested sandhills. On most test ranges and within some sandhills where tree canopy cover has remained relatively sparse, forage availability was high, but relative quality would be difficult to quantify considering the high species diversity and a general lack of dominant species. Adult gopher tortoises may be selective foragers depending on availability of certain plant taxa but their nutritional demands seem to be readily met by a wide variety of plants

(Diemer 1986, Macdonald & Mushinsky 1988). The high calcium, nitrogen, and protein content in certain legumes and other forbs appears to be important, particularly for egg development in nesting females and growth rates for juveniles (Macdonald & Mushinsky 1988, Mushinsky et al. 2003), and the relative abundance of nutritious forbs may be more critical to these demographic groups. While juvenile burrow densities can be high within a number of sites at Eglin, we lack any knowledge of growth rates within smaller size classes. Due to significant predation risk in juvenile gopher tortoises (Butler & Sowell 1996, Epperson & Heise 2003, Pike & Seigel 2006), forage quality may be directly linked to a site's recruitment potential as achieving larger body size is inversely related to predation risk (Wilson 1991, Butler et al. 1995, Innes 2009).

Both test ranges and forested sites with diverse herbaceous groundcover therefore probably provide adequate foraging opportunities (i.e. availability) for adult tortoises and many plant taxa reported to be important to gopher tortoises in the literature (e.g. *Andropogon*, *Aristida*, *Galactia*, *Pityopsis, Tephrosia* etc, Garner & Landers 1981, Macdonald & Mushinsky 1988) are commonly found on Eglin within both vegetation types. However, most test range herbaceous assemblages, despite their considerable diversity, were generally distinct from those in forested sandhills, and may be more representative of ruderal/early successional communities than typical longleaf pine understory. Forage value for many disturbance-prone species is unknown, though Garner & Landers (1981) suggested that ruderal forage plants contained higher nutrients than typical vegetation in more natural sites. At least one ruderal species common on Eglin's test ranges, poor Joe (*Diodia teres*), was reported as a high-quality forb that is readily eaten by Gopher Tortoises (Garner & Landers 1981, Macdonald and Mushinsky 1988). Alternatively, woody goldenrod (*Chrysoma pauciflosculosa*), a shrub that becomes dominant in mechanically disturbed areas, produces compounds that inhibit germination of nearby plants

including common sandhill grasses (Manelaou et al. 1992), and may limit herbaceous forage availability where it has become well-established. The abundance of woody goldenrod on B70E and C52 in particular may contribute to the relatively patchy vegetation (especially graminoids) observed at these sites, and possibly to the comparatively low burrow densities (particularly within juvenile size-classes) due to limited foraging opportunities.

Mechanical Disturbance of Burrows and Nests: I did not find an obvious relationship between management histories (mowing and fire) over the last 10 years and burrow densities or vegetation characteristics for most sites. However, direct effects of heavy machinery on Gopher Tortoises, potentially more so than their impacts on vegetation, may limit tortoise densities on some test ranges. In July 2017, two test ranges, C62N and C62S, were mowed and tortoise burrows were not avoided, collapsing or occluding all revisited burrows and leaving deep ruts in their aprons. Adult gopher tortoises are generally able to excavate themselves from burrows collapsed by heavy machinery (Landers & Buckner 1981, Diemer & Moler 1982, Mendonca et al. 2007), and most active burrows showed signs that the resident tortoise had extracted itself within a week.

While burrow collapse usually does not result in direct mortality of adults, these mowing events occurred during the nesting season (~ May – June in south Georgia and north Florida, hatching occurring in August - September) when female Gopher Tortoises typically deposit eggs in shallow nests located in the burrow apron (Landers et al. 1980). Due to the timing of these mowing events, there is a high probability that most, if not all nests were destroyed during the 2017 season at those sites. Landers and Buckner (1981) documented destroyed nests that had been run over by heavy equipment as well as one adult and multiple juvenile tortoises killed by disking and road grading. The smallest size classes often hide in shallow pallets, beneath litter, or

excavate shallow burrows and may be crushed by heavy machinery (Innes 2009). Even if mowing does not directly cause mortality in juvenile tortoises, they may be exposed to predators and extreme temperatures if they are frequently required to excavate new burrows or find alternative sources of shelter. If consistent nest failure and/or high juvenile mortality limits recruitment but conditions on test ranges continue to attract adult tortoises, these habitats may be acting as ecological traps.

Management techniques currently used on test ranges are not as intensive as in the past when roller chopping was apparently used more frequently. Roller chopping generally has more dramatic effects on soil and vegetation than mowing and may have influenced Gopher Tortoise behavior on test ranges when it was used more regularly in past decades. For example, roller chopping in a dry prairie in Florida appeared to cause some gopher tortoises to emigrate from an area entirely (Tanner & Terry 1981) and frequent burrow collapse may have had a similar effect on tortoises occupying certain test ranges in the past.

Historical Conditions Including Direct Harvest: It is also important to note that this study merely provided a snapshot of vegetation conditions that currently exist within tortoise-occupied sites on Eglin and that these conditions do not necessarily reflect past habitat suitability. Gopher tortoises are long-lived, have relatively low reproductive outputs compared to many other turtles, and population-level responses to changes in the environment, either positive or negative, are often delayed and may not be apparent for years (Iverson 1980, Landers et al. 1982, Yager et al. 2007, Berish et al. 2012, Tuberville et al. 2014). It is therefore possible that Eglin's extant gopher tortoise populations are relics of management practices, habitat conditions, and/or harvest by locals for food that occurred years or decades prior, rather than the conditions now present where populations still persist.

Regardless of current habitat suitability, it is important to note that few, if any, of Eglin's remaining tortoise populations (excluding translocated animals) appear to meet Tuberville et al.'s (2009) adult population criterion for long-term viability (see Tuberville et al. 2009), and may represent various stages of decline. The current model-based consensus among experts is that a minimum viable gopher tortoise population requires at least 250 adults and 100 ha or more of potential habitat to persist for 200 years or longer (Tuberville et al. 2009, Gopher Tortoise Council 2013). Where recent burrow surveys have been conducted on Eglin, only two sites (test ranges C61A and B71) had more than 20 burrows > 130 mm in width within ~10 to 20 ha survey areas. Further, based on occupancy surveys, it seems unlikely that large undocumented populations are persisting outside of those survey areas or elsewhere on base (Gorman et al. 2015).

Tuberville et al. (2009) did note, however, that activities that increase survival rates in juvenile size classes would have the greatest effect on long-term population viability. Test ranges may host a different assemblage of predators compared to forested sites (Goodman et al. 2018) and it is not clear whether nest success and juvenile survival rates differ between vegetation types. The expansive exposed conditions found on test ranges are not favorable to mesocarnivores such as raccoons and skunks that are significant predators of nests and juvenile gopher tortoises. Alternatively, test ranges appear to provide desired conditions for coyotes, documented predators on juvenile tortoises and potentially larger size classes as well (see Walkup et al. 2019 for account of coyote depredation of an adult tortoise at a translocation pen on Eglin). In 2018 on test range C62, a coyote dig was found where a juvenile tortoise burrow had previously been located with juvenile tortoise scutes in the scat next to entrance. Further, a

lack of cover on test ranges may also make juvenile tortoises more susceptible to avian predation.

Management Considerations and Future Directions

Test ranges at Eglin Air Force Base occupied by gopher tortoises exhibited a wide array of vegetation conditions with herbaceous communities that shared a number of native species with forested sandhills, but were also generally distinct in composition. However, the mechanisms that have shaped vegetation communities on test ranges, as well as those responsible for declines in gopher tortoise populations across base within otherwise suitable habitat remain ambiguous. Sandhills with dense midstories and canopies where gopher tortoises currently occur may require more frequent/intense prescribed burns to support populations long-term, and in some cases more intensive restoration efforts may be needed. Some sites may be too degraded or their populations may be too small to recover naturally. In these cases, translocation to consolidate tortoises from degraded sites and/or into suitable areas and augment small populations may be the best management decision. Translocation efforts are currently underway and Eglin serves as a recipient site for tortoises relocated from elsewhere in the state while resident tortoises are taken from unsuitable areas on base and relocated together to preserve local genetics.

While some test ranges appear to provide necessary conditions for gopher tortoises, it remains to be seen whether they can serve as long-term viable habitats, and may need to be evaluated on a case-by-case basis. Test ranges where reproduction seems to be high but with low adult tortoise densities may be used in a supporting role for other sub-populations on base through the collection of eggs and juveniles to be used in head starting efforts. Should some populations remain on test ranges, further work should address forage quality as well as nest

success, growth, and survival of juveniles. Detailed management records will be necessary to both better understand management effects on vegetation as well as their direct impacts on gopher tortoises. Communication with natural resource personnel and test range managers is critical in determining whether management practices are, and will remain, suitable for tortoise populations to persist on test ranges, or if relocation is a more viable option. Ideally, mowing would occur outside the nesting season and preferably during a time that would not expose tortoises to extreme temperatures should they need to excavate new burrows; though, it seems unlikely that routine maintenance is this flexible. A more viable option may be to flag burrows and aprons (and other areas of exposed soils that may be used as nesting sites, see Dziadzio et al. 2016) prior to mowing events to minimize the possibility of collapse or nest destruction.

Further, determining the management strategies used at sites such as C61A where tortoise populations appear to be growing and thriving would provide an ideal starting point in determining best management practices, assuming that maintaining test range populations is compatible with mission objectives. Human-disturbed/ruderal habitats such as Eglin's test ranges are often overlooked despite sometimes harboring large gopher tortoise populations. It is imperative that anthropogenic habitats receive more attention as they may play an increasingly important role in future Gopher Tortoise conservation efforts, particularly should rates of habitat loss and degradation maintain their current course.

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Appendix A

Table A1. All plant species encountered during vegetation surveys (both scales) at Eglin Air Force Base Florida.

Code refers to the unique identifier for each species (typically the first three letters of the genus followed by the first three letters of the specific epithet). Cover class refers to major vegetative cover class (cactus, fern, forb, graminoid, legume, shrub, vine, yucca, and disturbance) to which a species was assigned. Disturbance associated species (used to estimate total disturbance-prone species cover) were assigned to one of the other cover classes in addition to classification as a disturbance species (i.e. they contributed to estimates of both disturbance cover and whichever vegetative growth classification they were also assigned to). Vegetation type refers to whether the species was encountered (regardless of sampling scale) only in forested sites, only on test ranges, or in both vegetation types. For certain species that were difficult to identify consistently (e.g. some grasses in genera *Andropogon* and *Aristida* without flowering structures) and that were typically lumped under another species code (e.g. ANDspp or ARIspp), vegetation type is listed as N/A.

Family	Species	Common Name	Code	Cover Class	Vegetation Type
Acanthaceae	*Ruellia caroliniensis*	Carolina wild petunia	RUECAR	forb	both
Agavaceae	*Yucca filamentosa*	Adam's needle	YUCFIL	yucca	both
Anacardiaceae	*Rhus copallinum*	winged sumac	RHUCOP	shrub	both
Apocynaceae	*Asclepias humistrata*	pinewoods milkweed	ASCHUM	forb	test range
	Asclepias verticillata	whorled milkweed	ASCVER	forb	both
Aquifoliaceae	*Ilex ambigua*	Carolina holly	ILEAMB	shrub	forested
	Ilex vomitoria	yaupon	ILEVOM	shrub	both
Arecaceae	*Serenoa repens*	saw palmetto	SERREP	shrub	both
Asteraceae	*Balduina uniflora*	oneflower honeycomehead	BALUNI	forb	both
	Berlandiera pumila	soft greeneyes	BERPUM	forb	test range
	Chaptalia tomentosa	pineland daisy	CHAPTOM	forb	both
	Chrysoma pauciflosculosa	woody golden rod	CHRPAU	shrub/ disturbance	both
	Chrysopsis gossypina	cottony goldenaster	CHRGOS	forb	both
	Chrysopsis mariana	Maryland goldenaster	CHRMAR	forb	N/A
	Erigeron strigosus	prairie fleabane	ERIGSTR	forb	both
	Eupatorium compositifolium	yankeeweed	EUPACOM	forb	both
	Euthamia caroliniana	slender flattop goldenrod	EUTCAR	forb	both
	Helianthus spp.	sunflower	HELspp	forb	both
	Hieracium gronovii	queen-devil	HIEGRO	forb	both
	Liatris gracilis	slender gayfeather	LIAGRA	forb	both
	Liatris secunda	fewflower blazing star	LIASEC	forb	both
	Liatris tenuifolia	shortleaf gayfeather	LIATEN	forb	both
	Pityopsis aspera	pineland silk grass	PITASP	forb	both
	Pityopsis graminifolia	narrowleaf silk grass	PITGRA	forb	forested
	Silphium compositum	kidneyleaf rosinweed	SILCOM	forb	both
	Solidago odora	sweet goldenrod	SOLODO	forb	both
	Symphyotrichum adnatum	scaleleaf aster	SYMADN	forb	both
	Symphyotrichum dumosum	rice button aster	SYMDUM	forb	both
Cactaceae	*Opuntia humifusa*	pricklypear	OPUHUM	cactus	both

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Caryophyllaceae	*Paronychia patula*	pineland nailwort	PARPAT	forb/ disturbance	both
	Stipulicida setacea	pineland scalypink	STISET	forb	both
Chrysobalanaceae	*Licania michauxii*	gopher apple	LICMIC	forb	both
Cistaceae	*Crocanthemum spp.*	frostweed	CROCspp	forb	test range
	Lechea sessiliflora	pineland pinweed	LECSES	forb	both
Clusiaceae	*Hypericum gentianoides*	pineweeds, orangegrass	HYPGEN	forb	both
	Hypericum suffruticosum	pineland St. John's-wort	HYPSUF	forb	both
Commelinaceae	*Commelina erecta*	whitemouth dayflower	COMERE	forb	both
	Tradescantia hirsutiflora	hairyflower spiderwort	TRADHIR	forb	both
Convolvulaceae	*Stylisma patens*	coastal plain dawn flower	STYPAT	forb	both
Cyperaceae	*Bulbostylis ciliatifolia*	capillary hairgrass	BULCIL	graminoid	both
	Bulbostylis warei	Ware's hairsedge	BULWAR	graminoid	both
	Cyperus filiculmis	wiry flatsedge	CYPFIL	graminoid	both
	Cyperus retrofractus	rough flatsedge	CYPRET	graminoid	both
	Rhynchospora filifolia	threadleaf beaksedge	RHYNFIL	graminoid	both
	Rhynchospora grayi	Gray's beaksedge	RHYNGRA	graminoid	both
	Scleria ciliata	fringed nutrush	SCLCIL	graminoid	both
Dennstaedtiaceae	*Pteridium aquilinum*	bracken fern	PTEAQU	fern	both
Ebenaceae	*Diospyros virginiana*	common persimmon	DIOVIR	shrub	both
Ericaceae	*Ceratiola ericoides*	Florida rosemary	CERERI	shrub	forested
	Gaylussacia dumosa	dwarf huckleberry	GAYDUM	shrub	both
	Vaccinium arboreum	sparkleberry	VACARB	shrub	both
	Vaccinium darrowii	Darrow's blueberry	VACDAR	shrub	both
	Vaccinium myrsinites	shiny blueberry	VACMYR	shrub	both
Euphorbiaceae	*Cnidoscolus stimulosus*	tread-softly	CNISTI	forb	both
	Croton argyranthemus	silver croton	CROARG	shrub	both
	Euphorbia discoidalis	summer spurge	EUPDIS	forb	both
	Euphorbia floridana	greater Florida spurge	EUPFLO	forb	both
	Tragia smallii	Small's noseburn	TRASMA	forb	both
	Tragia urens	wavyleaf noseburn	TRAURE	forb	both
Fabacaea	*Baptisia calycosa var. villosa*	hairy Florida wild indigo	BAPCAL	legume	both
	Baptisia lanceolata	gopherweed	BAPLAN	legume	test range
	Centrosema virginianum	spurred butterfly pea	CENVIR	legume	both
	Chamaecrista fasciculata	partridge pea	CHAFAS	legume	both
	Crotalaria purshii	Pursh's rattlebox	CROTPUR	legume	forested
	Crotalaria rotundifolia	rabbitbells	CROTROT	legume	both
	Dalea pinnata	summer's farewell	DALPIN	legume	both
	Desmodium strictum	pinebarren ticktrefoil	DESSTR	legume	test range
	Galactia erecta	erect milkpea	GALERE	legume	both
	Galactia regularis	eastern milkpea	GALREG	legume	both
	Lespedeza cuneata	Chinese lespedeza	LESCUN	legume	test range
	Lespedeza hirta	hairy lespedeza	LESHIR	legume	both
	Lupinus diffusus	skyblue lupine	LUPDIF	legume	both

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Mimosa quadrivalvis	sensitive briar	MIMQUA	legume	both
Pediomelum canescens	buckroot	PEDCAN	legume	forested
Rhynchosia cytisoides	royal snoutbean	RHYCYT	legume	both
Rhynchosia reniformis	dollarleaf	RHYREN	legume	both
Stylosanthes biflora	sidebeak pencilflower	STYLBIF	legume	both
Tephrosia chrysophylla	scurf hoarypea	TEPCHR	legume	both
Tephrosia florida	Florida hoarypea	TEPFLO	legume	forested
Tephrosia spicata	spiked hoarypea	TEPSPI	legume	both
Tephrosia virginiana	goat's rue	TEPVIR	legume	both
Fagaceae	*Quercus incana*	bluejack oak	QUEINC	shrub	both
	Quercus laevis	tuerkey oak	QUELAE	shrub	both
	Quercus laurifolia	laurel oak	QUELAU	shrub	forested
	Quercus margarettae	sand post oak	QUEMAR	shrub	both
	Quercus spp.	sand live oak	QUEspp	shrub	both
Hypoxidaceae	*Hypoxis juncea*	fringed yellow stargrass	HYPOJUN	forb	both
Lamiaceae	*Callicarpa americana*	American beauty berry	CALAME	shrub	forested
	Salvia azurea	azure blue sage	SALAZU	forb	both
Pinaceae	*Pinus clausa*	sand pine	PINCLA	shrub	both
	Pinus elliott	slash pine	PINELL	shrub	forested
	Pinus palustris	longleaf pine	PINPAL	shrub	both
Poaceae	*Andropogon spp.*	bluestem	ANDspp	graminoid	both
	Andropogon virginicus	broomsedge bluestem	ANDVIR	graminoid	N/A
	Aristida condensata	piedmont threeawn	ARICON	graminoid	N/A
	Aristida mohrii	Mohr's threeawn	ARIMOH	graminoid	both
	Aristida purpurascens	arrowfeather threeawn	ARIPUR	graminoid	both
	Aristida spp.	three-awn grass	ARIspp	graminoid	both
	Aristida stricta	wiregrass	ARISTR	graminoid	test range
	Axonopus fissifolius	common carpet grass	AXOFIS	graminoid/ disturbance	test range
	Danthonia sericea	downy Danthonia	DANSER	graminoid	test range
	Dicanthelium spp.	rosette grass	DICspp	graminoid	both
	Eragrostis spectabilis	purple lovegrass	ERASPE	graminoid	both
	Gymnopogon ambiguus	bearded skeleton grass	GYMAMB	graminoid	both
	Panicum virgatum	switchgrass	PANVIR	graminoid	both
	Paspalum notatum	bahiagrass	PASNOT	graminoid/ disturbance	test range
	Paspalum praecox	early paspalum	PASPRA	graminoid	both
	Paspalum setaceum	thin paspalum	PASSET	graminoid	both
	Paspalum spp.	crowngrass	PASspp	graminoid	both
	Schizachyrium sanguineum	crimson bluestem	SCHSAN	graminoid	both
	Schizachyrium scoparium	little bluestem	SCHSCO	graminoid	both
	Schizachyrium tenerum	slender bluestem	SCHTEN	graminoid/ disturbance	both
	Sorghastrum secundum	lopsided indian grass	SORSEC	graminoid	both
	Sporobolus junceus	pineywoods dropseed	SPOJUN	graminoid	both

Polygalaceae	*Asemeia violacea*	showy milkwort	ASEVIO	forb	test range
	Polygala polygama	racemed milkwort	POLPOL	forb	both
Polygonaceae	*Eriogonum tomentosum*	dogtongue wild buckwheat	ERITOM	forb	both
	Polygonella gracilis	jointweed	POLGRA	forb	both
Rhamnaceae	*Ceanothus microphyllus*	littleleaf buckbrush	CEAMIC	shrub	forested
Rosaceae	*Crataegus uniflora*	dwarf hawthorn	CRAUNI	shrub	both
	Rubus cuneifolius	sand blackberry	RUBCUN	shrub	both
Rubiaceae	*Diodia teres*	poor Joe	DIODTER	forb/ disturbance	both
	Galium hispidulum	coastal bedstraw	GALIHIS	forb	both
	Houstonia procumbens	roundleaf bluet	HOUPRO	forb	both
Smilacaceae	*Smilax auriculata*	earleaf greenbrier	SMIAUR	vine	both
	Smilax bona-nox	saw greenbrier	SMIBON	vine	both
Tetrachondraceae	*Polypremum procumbens*	rustweed	PLYPPRO	forb/ disturbance	both
Violaceae	*Viola palmata*	early blue violet	VIOPAL	forb	forested
Vitaceae	*Vitis spp.*	grape vine	VITspp	vine	forested

Table A2. Site-wide scale percent cover estimates of major vegetative cover classes and total disturbance species cover within all sites surveyed on Eglin Air Force Base, Fl.

Results are provided as means ± SE. Cover classes are defined as follows: Bare = bare ground cover; Forb = non-leguminous forb cover; Graminoid= graminoid cover, i.e. grasses (Family Poaceae) & sedges (Family Cyperaceae); Legume = leguminous-forb cover (Family Fabaceae); Litter = non-living plant material cover, i.e. leaves & woody debris; Shrub = woody plant cover; & Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates). Estimates were generated from 30 1-m^2 plots per site.

Year	Vegetation Type	Site	Bare	Forb	Graminoid	Legume	Litter	Shrub	disturbance
2017	Forested	201E	24.4±2.9	36.4±4.0	24.8±3.5	5.3±1.2	31.8±3.3	31.3±3.8	N/A
		Pine log	18.8±3.0	7.5±1.1	14.4±1.9	4.3±0.9	45.7±4.7	20.0±3.3	4.1±1.2
		Rogue Creek	27.4±5.1	13.8±1.3	11.5±3.0	6.6±1.6	41.8±5.5	39.6±4.1	N/A
2018		Bull Creek	22.3±2.9	42.8±3.5	34.2±3.2	16.8±1.9	35.8±3.3	13.0±2.3	2.9±0.9
		Garnier Creek	7.1±1.5	1.5±0.4	7.4±1.4	5.1±1.4	83.3±2.5	22.8±3.8	10.9±2.5
		Middle Creek	20.2±2.5	23.5±3.5	51.1±3.4	8.8±1.4	50.8±2.8	14.9±3.5	0.2±0.1
		Turtle Creek	6.3±1.1	21.1±3.1	22.0±3.1	13.3±2.0	63.8±3.3	39.1±5.1	0.8±0.5
2017	Test Range	B70C2	61.2±2.9	39.0±3.8	41.2±2.8	2.8±0.9	9.2±1.7	6.3±1.7	21.5±3.4
		B70E	26.7±3.2	8.3±1.4	29.8±4.9	2.3±0.8	24.6±3.1	16.7±2.3	24.4±4.1
		C61A	10.3±1.5	21.5±1.6	41.5±2.8	1.3±0.3	12.9±0.9	8.4±2.4	14.5±2.2
		C62S	48.3±3.0	36.7±4.1	24.0±2.2	4.8±1.0	10.0±1.1	11.3±2.8	7.3±1.9
		C64	11.2±1.4	31.0±3.0	39.3±4.3	4.5±0.9	23.0±3.5	21.1±4.5	11.5±4.0
		C72	19.7±2.8	21.4±2.4	48.8±3.6	2.4±0.7	30.3±3.4	14.9±3.9	15.2±3.2
2018		B71	50.5±3.2	31.7±3.5	41.5±3.5	2.6±0.8	21.3±2.5	20.7±3.9	22.3±3.3
		B75	49.7±3.8	37.1±2.7	59.2±2.9	6.8±1.3	19.0±2.0	14.8±3.0	10.7±2.3
		C52N	34.6±3.3	27.8±2.7	32.0±3.4	4.7±1.0	23.4±3.0	23.3±3.2	27.8±2.9
		C74	30.7±4.1	35.7±5.0	47.9±4.8	7.7±2.0	36.5±3.4	13.1±12.8	25.3±4.6

Table A3. Burrow scale percent cover estimates of major vegetative cover classes and total disturbance species cover for foraging/use (U) and paired availability (A) within all sites surveyed on Eglin Air Force Base, FL.

Results are presented as means ± SE. Cover classes are defined as follows: Bare = bare ground cover; Forb = non-leguminous forb cover; Graminoid= graminoid cover, i.e. grasses (Family Poaceae) & sedges (Family Cyperaceae); Legume = leguminous-forb cover (Family Fabaceae); Litter = non-living plant material cover, i.e. leaves & woody debris; Shrub = woody plant cover; & Disturbance = disturbance associated species cover (see methods for disturbance-prone species list used for these estimates). Estimates were generated from 10 burrows per site within both buffers around each burrow.

Year	Vegetation Type	Site	U/A	Bare	Forb	Graminoid	Legume	Litter	Shrub	Disturbance
2017	Forested	201E	U	19.2±1.7	27.5±3.8	26.2±2.5	5.2±1.1	32.0±3.4	19.9±3.5	1.7±0.8
			A	23.6±2.2	24.4±14.6	16.3±2.4	4.6±0.6	44.9±3.4	15.6±1.5	0.7±0.3
		Pine	U	19.2±2.3	16.0±3.0	22.7±1.9	6.4±0.9	45.3±2.7	17.7±4.2	6.2±1.8
		Log	A	17.3±2.0	12.6±1.1	15.0±1.6	4.0±0.6	56.4±5.0	20.8±2.9	7.3±1.9
		Rogue	U	23.7±3.2	9.1±0.8	7.1±1.1	6.5±1.0	46.8±4.0	48.8±4.9	0.1±0.1
		Creek	A	23.0±3.0	9.8±0.6	6.8±0.9	6.2±0.7	49.7±3.8	42.2±3.7	0.4±0.3
2018		Bull	U	24.8±3.1	47.3±3.9	48.5±5.0	15.4±2.2	39.1±3.2	17.2±2.3	1.1±0.5
		Creek	A	29.2±2.2	38.7±3.9	38.2±2.3	15.1±1.4	46.1±2.6	16.3±2.3	1.7±0.6
		Garnier	U	13.8±3.1	4.6±1.0	11.1±2.1	2.8±0.8	73.6±4.4	21.2±3.7	12.2±3.0
		Creek	A	8.1±2.1	4.4±0.9	7.6±1.2	3.4±0.8	80.7±3.2	19.2±3.1	11.4±2.5
		Middle	U	16.3±1.2	24.7±2.8	49.2±1.9	15.3±2.1	43.7±2.3	17.5±2.9	0.6±0.2
		Creek	A	11.6±1.0	27.9±3.7	41.3±2.0	11.4±3.3	50.4±2.1	22.1±4.4	0.6±0.3
		Turtle	U	15.6±2.7	27.6±3.4	24.3±2.8	14.0±1.3	56.3±1.6	32.7±5.7	1.2±0.6
		Creek	A	8.8±1.4	23.6±4.0	20.3±1.6	13.0±1.5	65.3±2.2	34.5±3.4	0.2±0.1
2017	Test Range	B70C1	U	34.7±3.8	29.4±3.3	36.5±2.1	5.9±1.4	17.6±2.5	13.1±3.0	16.7±2.2
			A	47.9±3.2	25.9±1.9	37.4±2.9	2.5±0.5	16.1±2.5	4.9±1.5	24.4±3.1
		B70C2	U	52.9±1.5	33.9±2.0	34.9±2.4	1.8±0.3	9.0±1.4	4.2±1.3	16.3±2.5
			A	54.8±2.2	32.6±3.0	34.9±1.9	2.0±0.4	9.7±1.4	4.7±0.7	13.9±2.1
		B70E	U	24.3±2.7	27.0±1.7	28.5±2.9	3.8±0.7	20.2±2.5	16.7±3.1	25.8±2.1
			A	27.4±2.3	24.3±2.3	25.8±2.2	3.9±1.4	20.7±1.8	17.5±1.6	24.6±1.8
		C61A	U	16.8±2.0	26.2±1.7	45.6±3.7	2.0±0.4	17.9±1.2	6.5±1.4	13.2±2.7
			A	20.3±2.0	24.4±2.0	46.9±2.9	1.8±0.3	17.5±1.3	6.2±1.4	15.0±1.7
		C62N	U	31.9±4.2	28.3±3.0	33.2±2.1	5.7±0.9	36.7±4.2	11.2±3.2	4.5±1.2
			A	34.5±2.3	30.4±2.0	30.3±1.7	4.3±0.4	33.8±4.0	8.6±3.0	4.3±1.0
		C62S	U	46.2±3.7	43.0±3.6	31.3±3.0	6.6±1.3	20.4±3.6	8.2±2.4	8.8±2.9
			A	54.3±2.6	36.4±2.9	32.4±3.0	4.8±0.7	15.3±2.7	7.7±2.9	10.0±1.8
		C64	U	24.6±5.9	32.9±2.1	31.6±2.7	4.3±0.7	19.3±2.7	17.8±3.2	10.3±2.0
			A	27.3±4.9	35.1±2.4	30.0±4.0	4.1±0.6	21.2±2.7	13.9±3.3	11.8±2.9
		C72	U	20.7±1.7	27.1±2.3	42.2±3.5	4.9±0.7	24.5±3.0	16.0±2.9	12.3±4.6
			A	19.0±1.1	27.8±2.1	45.4±3.5	4.5±0.8	22.9±2.7	10.0±2.1	20.6±3.7
		B71	U	42.5±3.7	30.3±3.4	52.3±4.9	4.4±0.8	20.2±2.9	18.6±4.7	26.5±5.5
			A	49.8±2.0	37.0±4.5	42.4±3.4	3.2±0.8	21.1±0.7	18.7±1.9	19.0±1.5
		B75	U	47.1±2.2	34.3±2.4	46.3±2.6	7.0±1.1	19.2±2.1	22.5±4.5	15.4±3.9
			A	52.0±2.2	34.6±2.1	54.2±2.8	6.0±1.5	17.9±2.1	13.3±2.6	13.1±2.7
		C52N	U	39.2±3.9	28.7±2.1	46.4±4.6	4.5±0.9	26.9±2.3	26.6±3.4	34.3±3.9
			A	39.2±1.7	30.4±7.5	41.9±3.2	2.7±0.6	28.3±2.6	25.0±3.2	32.7±2.8
		C74	U	32.9±3.2	33.7±2.2	43.7±4.0	7.4±1.6	38.3±2.0	20.1±2.3	2.7±0.5
			A	32.7±2.0	36.6±2.6	49.4±3.6	8.0±1.1	33.1±2.6	17.3±3.5	12.1±3.4

Table A4. Test range management questionnaire distributed to natural resource personnel at military installations where tortoises occur. Actual questionnaire was distributed electronically.

Introduction

All participating natural resource managers are strongly encouraged to return the survey regardless of how many questions may be applicable (**All questions are completely voluntary**, but any feedback will be helpful, even if you're only able to answer one or two questions).

On Eglin Air Force Base, many gopher tortoise populations currently reside on expansive military testing and training ranges that are maintained in an open state (i.e. vegetation kept short through some combination of mowing, roller-drum chopping, fire, chemical treatments etc.). The lack of trees and tall shrubs on test ranges creates appealing habitat to gopher tortoises and many of these sites appear to support diverse native herbaceous ground cover that tortoises eat. However, tortoise burrow densities, particularly in smaller size classes that suggest recruitment potential, vary significantly among test ranges. Different management practices, both past and present, may at least partially explain differences in burrow densities and vegetation characteristics we currently observe on Eglin.

Therefore, we feel that a broader comprehension of how these unique landscapes are managed on other tortoise-occupied installations could help mitigate future conflicts between military training objectives and gopher tortoise conservation goals. This questionnaire, in combination with field work currently being conducted on Eglin as part of DoD Legacy Project 16-818, will be useful in determining common management practices employed to maintain test ranges and other human altered habitats on DoD lands. Ideally, the results of this questionnaire will be used to inform DoD natural resource managers whether test ranges can harbor gopher tortoises long-term without impacting training objectives and, if so, what the optimal management strategies are to promote healthy tortoise populations while still maintaining desired conditions for military mission activity. Thank you for your participation.

Name of Respondent:

Properties/Installations Managed:

Contact Info if Follow-up Desired:

Phone: (   )   Email:

Request for Results Summary upon Completion (please check):

_Yes   _No

Gopher Tortoise Habitat Use/Distribution on Installation

1. On the military installation you manage, what habitat types do gopher tortoises occupy?
(check all that apply)
- ☐ **forested sites** (sandhill, pine savanna, flatwoods, xeric hammock, planted pine, scrub etc.,)
- ☐ **ruderal/disturbed areas** (check all that apply)
  - ☐ **clearcuts**
  - ☐ **power line cuts**
  - ☐ **test ranges/airfields maintained for military training operations**
  - ☐ **road edge/fire break**
  - ☐ **pasture/old field**
- ☐ **other** (please list)

- ☐ **unknown**

Habitat Management Practices Specific to Military Training/Testing Areas

2. What management practices are used to control or remove tall woody vegetation from the military testing and training areas where the tortoises are present?
- ☐ **mechanical** (check all that apply)
  - ☐ mowing
  - ☐ roller-drum chopping
  - ☐ chainsawing
  - ☐ logging
- ☐ **herbicide**
- ☐ **fire** (check all that apply)
  - ☐ prescribed burning
  - ☐ incidental (live fire, incendiary devices, lightning)
- ☐ **none**
- ☐ **other** (please list)

- ☐ **N/A**

3. If prescribed fire is used to manage testing or training areas and/or incidental fires are allowed to burn, what seasons do these sites typically burn? How frequently?

4. Are any management practices used specifically to improve/maintain gopher tortoise habitat (or habitat for threatened species, e.g. red cockaded woodpeckers) in testing or training areas?

☐ **yes** (if so, please list)

☐ **no**
☐ **N/A**

5.. What general military training/testing activities occur in the habitats occupied by gopher tortoises? (check all that apply)

☐ **tactical land vehicle use**
☐ **bivouacs**
☐ **live fire/incendiary exercises**
☐ **other** (please list)

☐ **none**
☐ **N/A**

6. If possible, please briefly comment on the frequency and variability in the application of any management practices used to maintain test ranges managed primarily for military training operations (e.g. are management practices used to suppress tall, woody vegetation fairly uniform among test ranges or do they vary widely in frequency within or among ranges and depending on mission purpose?).

Habitat Management Practices Specific to Other Ruderal/Disturbed Areas

7. What management practices are used to control or remove tall woody vegetation within disturbed/ruderal areas such as clearcuts, old fields, pastures or powerline cuts?
- ☐ **mechanical** (check all that apply)
    - ☐ mowing
    - ☐ roller-drum chopping
    - ☐ chainsawing
    - ☐ logging
- ☐ **herbicide**
- ☐ **fire** (check all that apply)
    - ☐ prescribed burning
    - ☐ incidental (live fire, incendiary devices, lightning)
- ☐ **other** (please list)

- ☐ **none**
- ☐ **N/A**

8. If prescribed fire is used to manage disturbed/ruderal areas, please comment on month/season/frequency of burns.

9. Are any management practices used specifically to improve/maintain gopher tortoise habitat within disturbed/ruderal areas such as clearcuts, old field, pastures or powerline right of ways?
- ☐ **yes (if so, please list)**

- ☐ **no**
- ☐ **N/A**

10. If possible, please briefly comment on the frequency and variability in the application of any management practices used to maintain disturbed/ruderal areas such as clearcuts, old field, pastures or powerline right of ways (e.g. are the management practices used to suppress tall, woody vegetation fairly uniform for most ruderal/disturbed areas or do they vary widely over time and from one site to the next?)

Comments and Suggestions
11. Please use the space below for additional comments, suggestions and to clarify or elaborate on any responses.