Effects of habitat type on the use of Gopher Tortoise (*Gopherus polyphemus*) burrows by burrow associates on a large military installation in Florida

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ABSTRACT

The Gopher Tortoise (*Gopherus polyphemus*) has been declining throughout most of its geographic range. With the most potential Gopher Tortoise habitat (155,600 ha) of all Department of Defense lands, Eglin Air Force Base (Eglin) is a regionally significant landscape for current and future tortoise conservation. Yet, the ecology of tortoises and their burrow associates across dominant habitats in this landscape is poorly understood. Here, we compared tortoise burrow densities and the prevalence of their burrow associates between 8 treeless military test ranges and 4 forested sites. Burrow density was higher on test range as compared to forested sites, and test ranges had a considerably higher range of densities, including for smaller burrows. On average, tortoise burrows on test ranges supported a lower diversity of burrow associates than those on forested sites. However, the federally-petitioned Gopher Frog (*Lithobates capito*) was significantly more abundant on test ranges, but we cannot rule out that this may be an artifact of pond location. The occurrences and richness of burrow associates that are potential predators of Gopher Tortoise eggs and juveniles were lower on test ranges, suggesting a potential advantage to nesting tortoises at those sites. Given the higher incidence of potential predators of Gopher Tortoise eggs and young on the forested sandhills sites, it is possible that Gopher Tortoise populations there are constrained by predator activity. A better understanding of nesting success and whether there are artificially elevated predator populations because of human subsidies in forested areas of the base may be needed.

INTRODUCTION

Gopher Tortoises (*Gopherus polyphemus*) primarily inhabit Longleaf Pine (*Pinus palustris*)-dominated sandhill communities in the southeastern Coastal Plain of the United States (Auffenberg and Franz 1982) where they are considered a keystone species because their burrows provide shelter, habitat, and food for approximately 60 vertebrate and 300 invertebrate species (Young and Goff 1939, Jackson 1989, Kent et al. 1997, Alexy et al. 2003, Dziadzio and Smith 2016). Despite previously being widespread and abundant, Gopher Tortoises are considered federally threatened under the Endangered Species Act (ESA) in the western portion of their range, and as a candidate for listing in the eastern portion of its range (USFWS 2011) as a result of habitat loss and fragmentation. The listing of Gopher Tortoises has stimulated applied studies aimed at informing habitat management practices (e.g. Hermann et al. 2002, Yager et al. 2006). Yet, few studies have considered how taxa associated with Gopher Tortoise burrows (hereafter 'burrow associates') respond to differing habitat conditions. Of the existing studies that have focused on burrow associates, most have provided lists of species observed in burrows (e.g., Young and Goff 1939, Roznik and Johnson 2009), or have focused on the effects of burrow status (e.g., active or inactive; Witz et al. 1991, Dziadzio and Smith 2016) or density on burrow associate diversity (Catano and Stout 2015). In contrast, few studies have considered the associations between burrow associates and habitat (but see Lips 1991, Kent et al. 1997, White and Tuberville 2017) and those that have done so have focused on a limited number of habitat types. To effectively manage Gopher Tortoises as a keystone species, it is critical that we develop a better understanding of the ecology of burrow associates on military landscapes.

Some of the largest remaining tracts of available Gopher Tortoise habitat occur on Eglin Air Force Base (Eglin) in the Florida panhandle. Eglin is an active military installation containing approximately 155,600 ha of potential habitat, making it a regionally critical landscape for Gopher Tortoise conservation (USFWS 2011). The habitat primarily consists of Longleaf Pine-dominated sandhills interspersed with several non-forested test ranges that are used primarily for munitions testing, and to a lesser extent drop zones, artillery ranges, and ground troop maneuvers. Tortoises became established on many of these test ranges decades ago, most likely as they emigrated from surrounding forests that were fire-suppressed. Once established, tortoises have appeared reluctant to move away from test ranges, even after adjacent forested areas have been restored through mechanical and fire management. During a base wide occupancy survey, Gorman et al. (2015; Legacy Project 14-762) found that test ranges are more likely to be occupied by tortoises compared to other habitat types within Eglin, including mature sandhills. However, the concomitant effects of habitat type on burrow associates in this landscape are unknown.

Potential burrow associates on Eglin include several imperiled species such as the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*), Pine Snake (*Pituophis melanoleucus mugitus*), Indigo Snake (*Drymarchon couperi*), Gopher Frog (*Lithobates capito*), and the Florida Mouse (*Podomys floridanus*). Several of these are dependent on tortoise burrows for persistence; the Gopher Frog relies on burrows to avoid predation and desiccation (Roznik and Johnson 2009), and the Florida Mouse (*Podomys floridanus*) relies on burrows for nesting (Layne and Jackson 1994). Of the vertebrate species documented as burrow associates, several have been reported as predators of Gopher Tortoises or their eggs (Table 3; Roosevelt 1917, Vetter 1970, Mount 1975, Douglas and Winegarner 1977, Causey and Crude 1978, Fitzpatrick and Woolfenden 1978, Landers et al. 1980, Auffenberg and Franz 1982, Maehr and Brady 1984, Wilson 1991, Butler and Sowell 1996, Mushinsky et al. 2006, Ernst and Lovich 2009, Aresco et al. 2010, Stevenson et al. 2010, Perez-Heydrich et al. 2012, Smith et al. 2013), or as potential predators based on reports of predation on other turtle species, including those in the genus *Gopherus* (Table 3; Nelson 1933, Hamilton 1951, Fordham et al. 2006, Fordham et al. 2008, Mayer and Brisbin 2009, Jolley et al. 2010, Holcomb and Carr 2013, Whytlaw et al. 2013, Lovich et al. 2014). While many of these species occur on Eglin, their associations with Gopher Tortoise burrows within test ranges and nearby forested sites remains unknown.

Here, we evaluated associations between Gopher Tortoise burrows and potential burrow associates within test ranges and forested sites on Eglin using camera trapping. Specifically, we compared species richness, diversity, and community composition of burrow associates between these two habitat types. We also evaluated the effect of habitat type on the richness and diversity of vertebrate burrow associates that are considered predators of Gopher Tortoise juveniles or Gopher Tortoise eggs. Because test ranges have a simpler habitat structure (no tree canopy) and less diverse native plant communities than forested sites, we predicted that test ranges would have lower diversity of burrow associates compared to forested sites.

METHODS

STUDY AREA AND PLOT SELECTION. — To begin to address these questions, after conducting tortoise burrow surveys at 8 test range and 4 forested study sites on Eglin, we conducted camera trapping for each site across 4 seasons in 2016–2017 to assess vertebrate burrow associate (hereafter burrow associate) use of burrows. Eglin is a large military installation (188,459 ha) located in the Florida Panhandle (Figure 1a). The area primarily consists of Longleaf Pine (*Pinus palustris*)-dominated sandhills characterized by scattered Longleaf Pine, a sparse to dense midstory consisting of Turkey Oak (*Quercus laevis*) and Sand Live Oak (*Quercus geminata*), and sparse to dense rich ground cover consisting of native forbs and grasses. Sandhills habitat is interspersed with large areas (<1–4000 ha) of treeless open test ranges (areas used for bombing and artillery, as well as their associated safety buffer areas), characterized by low and sparse native shrubs and a ground cover that includes native forbs and grasses along with varying amounts of native ruderal species and non-native grasses. In addition, moderate acreages of pine plantations and smaller acreages of mesic upland pine and flatwoods habitats occur across the landscape. Eglin is primarily underlain by the Lakeland Soil Series (Soil Survey Staff, USDA 2013) which is characterized by nearly 100% sand soil horizons. Over the last two decades, Eglin has maintained an active habitat management program through prescribed burning (upwards of 40,000 ha/year, Air Force Wildland Fire Center, Eglin, pers. comm.), Sand Pine (*Pinus clausa*) and oak (*Quercus* spp.) removal, and Longleaf Pine planting, but had a history of fire suppression in most areas prior to that. Habitat management on test ranges includes, or has included as recently as the mid to late 1990s, bush hogging (hereafter mowing), prescribed fire, herbicide treatments (i.e., Velpar), and roller drum chopping. The purpose of habitat management depends on the individual range and specific missions and includes maintaining and creating conditions suitable for munitions scoring, line-of-sight, drop zone safety, and fire control. Intensity of management can vary from annual routine maintenance (primarily once-a-year mowing) to 2-3 mowing events per year along with fire or herbicide management to meet mission-specific needs (pers. comm., Don McRaney and USAF Wildland Fire Center).

Using Jackson Guard's (Eglin Natural Resources Branch) Gopher Tortoise burrow observation database, we selected 12 study plots (8 test range and 4 forested) where we expected to observe at least 10 burrows within a 10-ha survey plot.

BURROW SURVEYS. — Our survey goal for each study site was to observe at least 10 active and/or inactive tortoise burrows. If we did not observe this number in the original 10 ha surveyed, we expanded the survey boundary until we did. We conducted all surveys during Spring-Summer 2016 using a two-observer 10 m transect method with repeat surveys conducted by different observers (Gorman et al. 2015). Upon detection of each burrow, we recorded the location (UTM) using a Garmin GPSMap78 (Garmin International, Inc., Olathe, KS) and measured burrow tunnel width at 50 cm depth (McCoy et al. 2006). A strong correlation exists between Gopher Tortoise burrow width and individual carapace length (Alford 1980, Martin and Layne 1987, Wilson et al. 1991) and between size class and age class (Landers et al. 1982). Juvenile Gopher Tortoises are generally considered as those with carapaces below 110–120

(Landers et al. 1982), while adults are considered as those with carapace lengths above 220-230 mm (Wilson 1991, Landers et al. 1982, Diemer 1992, Berish 2014, Rostal et al. 2014, Tuberville et al. 2014). Given that we predict, based on pilot work, that commensal use of burrows may vary with burrow size we categorized burrows using the following categories: juvenile (<130 mm), subadult (≥ 130 mm < 230 mm), and adult (≥ 230 mm). Burrow density was calculated for each site, broken down by burrow size category.

CAMERA TRAPPING. — We conducted camera trapping at all sites across all seasons (defined as calendar dates of astronomical seasons). Actual trapping dates within each season were as follows: Summer, 1 July to 05 September 2016; Fall, 14 October to 15 December 2016; Winter, 23 December 2016 to 24 February 2017; and Spring, 20 March to 18 June 2017. Cameras were placed 1.5 m from burrow entrances atop 0.6 m stakes and angled to include within the viewing frame, the burrow entrance, most of the apron, and approximately 6–12 cm behind the burrow entrance. To maximize the capabilities of the camera model chosen (Moultrie M-990i Gen 2), and to maximize tortoise and burrow associate detections based on estimated seasonal activity periods, we programmed the cameras to record activity via time lapse during specified time periods (Table 1). When time lapse was inactive, the cameras were programmed so that the motion detection function was active. Once deployed, cameras were checked after a maximum of five trap days (i.e., one trapping period) at which time the cameras were retrieved. Test range (n=8) and forested sites (n=4) were paired for each camera trapping period to minimize intra-seasonal differences. We sampled each of the four, forested sites twice during each season and each of the eight test range sites once or twice during a given season. During each trapping period, camera traps were set at 10 burrows at each site, except for the winter, when only five adult burrows were camera trapped per site. For each trapping period, we recorded the number of unique individuals (when discernable) for each species of burrow associate observed entering the burrow, utilizing any part of the apron, or within 6‒12 cm behind the top of the burrow. When we tallied these occurrences of each species, we made a conservative estimate within each trapping period. We considered an occurrence to be a unique individual determined either because we could see multiple individuals in a single camera frame (for example, 3 Gopher Frogs in a single camera frame would be counted as three occurrences) or observation of individuals of the same species that were clearly distinct (for example, a juvenile Eastern Coachwhip (*Masticophis flagellum*)and a large adult Eastern Coachwhip exiting and entering the burrow multiple times during a trapping period would count as two occurrences). Across burrows and across trapping periods, we summed occurrences, so it is possible that the same individuals were counted multiple times if they were using multiple burrows and/or were present in multiple seasons. For quality control and future reference, at least one representative photo was typically archived for each individual of each species encountered for each burrow during each trapping period.

We compared mean number of occurrences and richness of all burrow associates combined, herpetofauna, and potential Gopher Tortoise predators for test ranges and forested sites across seasons. Our measures of occurrence and richness consider all burrow associates detected. Because we were not always able to identify individual burrow associates, we acknowledge that our approach is not an accurate or unbiased estimate of abundance.

STATISTICAL ANALYSIS. — To determine burrows commensal associate community composition, we used the site-specific number of observations for each species to estimate alpha (i.e., average species richness), gamma, and beta diversity indices (Whittaker 1972). Additionally, for each site-specific survey (i.e., all burrows surveyed within a site during a given season) we determined richness and Shannon index (Hill 1973) to use as response variables for subsequent analyses. To determine how richness or diversity varied between habitat types, season, burrow size, and total number of burrows surveyed, we used a generalized linear mixed effects model with Poisson error distribution while we used a linear mixed effects model for Shannon diversity index. For both models, we included site identity as a random intercept as some sites were surveyed multiple times within a given season. For both models, we included fixed effects for habitat type (categorical), season (categorical), number of burrows surveyed (continuous), and the proportion of burrows surveyed that were juvenile (continuous – see *Burrow Surveys* for more information). We graphically assessed quantile-quantile plots of residuals to check the assumption that residuals were normally distributed (linear mixed effects model) while we checked that our dispersion parameter (generalized linear mixed effects model) did not show evidence of over-dispersion (i.e., > 1). We determined significance of fixed effects using likelihood ratio tests and used a Tukey *post hoc* test to identify significant differences across seasons when applicable (i.e., when the effect of season was significant – see *Results*). Lastly, we determined if forested and range communities were significantly different in community composition by first computing a distance matrix using the Jaccard method (Minchin 1987), and performing an analysis of variance using these distance matrices. We subsequently visualized these data by using nonmetric multidimensional scaling (NMDS), and represented these data along two axes along with each habitat type.

We used Program R for all statistical analyses (R Core Team, 2017). We used the *lme4* package (Bates et al. 2015) for mixed effects models, *lmtest* package (Zeileis and Hothorn 2002) for likelihood ratio tests, *multcomp* package (Hothorn et al. 2008) to perform posthoc comparisons, and the *vegan* package (Oksanen et al. 2017) for all community analyses.

RESULTS

BURROW SURVEYS. — Plot size ranged from 10.0 to 16.5 ha for test range sites (n=8) and 9.9 to 13.0 ha for forested sites (n=4). Total burrow density was generally higher (but more variable) on test range sites compared to forested sites (Table 2), ranging from 0.84/ha to 1.72 and 0.30 ha to 4.33, respectively. Variation in subadult and juvenile burrow densities were also generally higher for test ranges (Table 2).

BURROW ASSOCIATES. — Burrowing Owls (*Athene cunicularia)* are not native to Eglin AFB and were established on only one test range study site, so they were not included in any of the analyses.

For all seasons combined, we had 1,197 camera trap days for test ranges and 1,054 trap days for forested sites. The number of photos taken and analyzed for test ranges were 4,824,735 and for forested sites, 4,282,892. We observed 451 occurrences of 31 species of burrow associates on test ranges (n = 8 sites) and 475 occurrences of 48 species on forested sites (n = 4 sites; Table 3). We also observed 66 occurrences of 7 species of known or likely Gopher Tortoise predators on test ranges (n = 8) and 111 occurrences of 12 species on forested sites (n = 4; Table 3). We found that forested sites had higher values for all three diversity indices (except predator beta diversity) compared to test range sites, which indicates that forest sites had a greater total diversity, site-level diversity, and a greater variation in diversity among sites compared to test range sites (Table 4).

At the site level, we found that sites in forested habitats had higher commensal richness (χ^2 = 9.928; df = 1; P = 0.002; χ^2 is chi squared test statistic, df is degrees of freedom, and P is the associated probability value, indicating statistical significance, for that test statisitic and degrees of freedom) and Shannon indices (χ^2 = 4.918; df = 1; P = 0.027) compared to those in range habitats (Table 5). While we also found that season had a significant effect on site commensal richness (χ^2 = 8.121; df = 3; P = 0.044), post-hoc comparisons revealed no significant differences among seasons (Table 5).

Furthermore, commensal communities were significantly different between forested and test range sites ($F_{1, 64}$ = 3.371; P = 0.001; $F_{1, 64}$ refers to the F statistic with a numerator, or treatment effect, degrees of freedom of 1 and a denominator, or error, degrees of freedom of 64). Species found on test range sites were typically also found in forested sites whereas forested sites contained many unique species that were not found to be associated with burrows on test ranges (Figure 2). While occurrences and richness were, on average, generally lower on test ranges, the federally-petitioned Gopher Frog was more abundant on test ranges (Table 6). We expect this is because test range sites were closer to known Gopher Frog breeding ponds than forested sites.

DISCUSSION

Although military test range sites on Eglin contain Gopher Tortoise burrows at comparable or higher densities than sites in natural Longleaf Pine sandhills, the community of burrow associates in test range sites appears to be depauperate. In order to reduce potential conflicts with military activities and provide access to burrows in locations that are more beneficial to a wide array of burrow associates, it would be helpful to develop and implement management strategies that would retain or increase Gopher Tortoise populations in forested sandhills. However, given the higher incidence of potential predators of Gopher Tortoise eggs and young on the forested sandhills sites, it is possible that Gopher Tortoise populations there are constrained by predator activity. A better understanding of nesting success and whether there are artificially elevated predator populations because of human subsidies in forested areas of the base may be needed (Boarman et al. 2006, Esque et al. 2010, Smith et al. 2013).

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TABLES

Table 1. Time periods for which trail cameras were programmed to record the activity of Gopher Tortoises and their burrow associates at burrows on Eglin Air Force Base, FL between 2016 and 2017. Times are provided in Central Time, 24-hour clock (military time).

Camera Settings	Summer 2016	Fall 2016	Winter 2016	Spring 2017
Time lapse 1	0600-1300	0600-0900	0600-1600	1000-2100
Time lapse 2	1800-2200	1200-2000	–	–

Table 2. Burrow density for different size classes with mean and SE (parentheses) for each habitat type.

Habitat Type	Density			
	Adult	Subadult	Juvenile	Total
Test Range (n=8)	0.47 (0.08)	0.41 (0.20)	0.53 (0.26)	1.40 (0.45)
Forested (n=4)	0.41 (0.05)	0.32 (0.14)	0.46 (0.15)	1.19 (0.19)

Table 3. Occurrences of Gopher Tortoise burrow associates during camera trapping on test ranges (n=8) and forested (n=4) sites for all seasons from 2016-2017. The number of sites within each habitat that each species was found is shown in parentheses. Known or likely Gopher Tortoise predators are highlighted in gray.

Group	Species	Common Name	Range	Forested
Herpetofauna	*Anaxyrus terrestris*	Southern Toad	18 (7)	38 (4)
	Anolis carolinensis	Green Anole	2 (1)	22 (4)
	Aspidoscelis sexlineata	Eastern Six-lined Racerunner	97 (8)	95 (4)
	Cemophora coccinea	Scarlet Snake	1 (1)	1 (1)
	Coluber constrictor priapus	Southern Black Racer	11 (6)	6 (3)
	Crotalus adamanteus	Eastern Diamondback Rattlesnake	0	1 (1)*
	Eurycea cirrigera	Southern Two-lined Salamander	0	1 (1)
	Heterodon platirhinos	Eastern Hognose Snake	1 (1)	1 (1)
	Hyla sp.		0	1 (1)
	Lithobates capito	Gopher Frog	58 (6)	16 (2)
	Masticophis flagellum flagellum	Eastern Coachwhip	33 (8)	68 (4)
	Micrurus fulvius	Eastern Coral Snake	0	1 (1)
	Pantherophis guttatus	Eastern Corn Snake	2 (2)	0
	Pituophis melanoleucus mugitus	Florida Pine Snake	2 (2)	1 (1)
	Plestiodon egregius	Northern Mole Skink	0	1 (1)
	Plestiodon laticeps	Broad-headed Skink	0	3 (3)
	Sceloporus undulatus	Eastern Fence Lizard	0	8 (2)
	Scincella lateralis	Ground Skink	1 (1)	5 (2)
	Sistrurus miliarius barbouri	Dusky Pygmy Rattlesnake	5 (4)	1 (1)
	Tantilla coronata	Southeastern Crowned Snake	0	5 (3)
	Terrapene carolina carolina	Eastern Box Turtle	0	1 (1)
Mammals	*Canis latrans*	Coyote	12 (5)	5 (1)
	Dasypus novemcinctus	Nine-banded Armadillo	1 (1)	7 (1)

	Didelphis virginiana	Virginia Opossum	1 (1)	5 (3)
	Geomys pinetis	Southeastern Pocket Gopher	0	1 (1)
	Glaucomys volans	Southern Flying Squirrel	0	1 (1)
	Lynx rufus	Bobcat	0	2 (2)
	Mephitis mephitis	Striped Skunk	3 (1)	12 (2)
	Neotoma floridana	Florida Woodrat	1 (1)	0
	Odocoileus virginianus	White-tailed Deer	4 (4)	12 (4)
	Peromyscus polionotus	Oldfield Mouse	125 (8)	47 (4)
	Procyon lotor	Common Raccoon	0	5 (3)
	Sciurus carolinensis	Eastern Grey Squirrel	0	3 (1)
	Sciurus niger	Fox Squirrel	0	3 (2)
	Sigmodon hispidus	Hispid Cotton Rat	0	1 (1)
	Sus scrofa	Feral Pig	1 (1)	3 (2)
	Sylvilagus floridanus	Eastern Cottontail	32 (4)	40 (4)
	Urocyon cinereoargenteus	Grey Fox	0	3 (2)
	Ursus americanus	Florida Black Bear	0	1 (1)**
Birds	*Ammodramus savannarum*	Grasshopper Sparrow	1 (1)	0
	Antrostomus carolinensis	Chuck-will's-widow	0	1 (1)
	Athene cunicularia	Burrowing Owl	78 (5)	0
	Catharus guttatus	Hermit Thrush	0	3 (1)
	Colinus virginianus	Northern Bobwhite	0	5 (2)
	Corvus brachyrhynchos	American Crow	15 (7)	1 (1)
	Falco sparverius	American Kestrel	0	1 (1)
	Megascops asio	Eastern Screech Owl	2 (1)	7 (4)
	Mimus polyglottos	Northern Mockingbird	1 (1)	0
	Myiarchus crinitus	Great Crested Flycatcher	0	1 (1)
	Passerculus sandwichensis	Savanah Sparrow	14 (7)	0
	Peucaea aestivalis	Bachman's Sparrow	0	2 (1)
	Polioptila caerulea	Blue-gray Gnatcatcher	0	1 (1)
	Sayornis phoebe	Eastern Phoebe	3 (1)	19 (4)
	Setophaga palmarum	Palm Warbler	1 (1)	5 (3)

Spizella passerina	Chipping Sparrow	0	1 (1)
Troglodytes aedon	House Wren	1 (1)	0
Turdus migratorius	American Robin	0	3 (2)
Tyrannus tyrannus	Eastern Kingbird	1 (1)	0
Zonotrichia albicollis	White-throated Sparrow	1 (1)	0

*A single individual was observed entering a study burrow during camera setup.
**Bear knocked down camera on first day

Table 4. Diversity indices for vertebrate species associated with Gopher Tortoise burrows on Eglin Air Force Base. We separated indices for herpetofauna and potential Gopher Tortoise predators (see species list in Table 3).

	Total		Herpetofauna		Predators	
Index	Range	Forest	Range	Forest	Range	Forest
Alpha	1.34	1.65	0.68	0.91	0.21	0.35
Beta	22.10	28.18	16.55	19.92	32.91	27.48
Gamma	31	48	12	19	7	10

Table 5. Results of generalized linear mixed effects (richness) and linear mixed effects models (Shannon index) to assess the effects of habitat type (forest vs. range), season, burrow size, and total number of burrows surveyed on richness and diversity. Post-hoc comparisons and associated P values are shown among seasons for richness, while for Shannon index effects of season are compared to fall. χ^2 is chi squared test statistic, df is degrees of freedom, and P is the associated probability value (indicating statistical significance) for that test statistic and degrees of freedom.

Response	Fixed Effect	χ^2 (df)	P value	Post-hoc comparisons	Estimate (SE)	Post-hoc P value
Richness	Habitat (Forest-Range)	9.928 (1)	0.002	–	-0.385 (0.107)	–
	Season	8.121 (3)	0.044	Spring-Fall	-0.193 (0.142)	0.484
				Summer-Fall	0.003 (0.134)	1.000
				Winter-Fall	-1.316 (0.590)	0.097
				Summer-Spring	0.196 (0.139)	0.453
				Winter-Spring	-1.123 (0.584)	0.191
				Winter-Summer	-1.319 (0.562)	0.074
	Total burrows	1.200 (1)	0.273	–	-0.123 (0.115)	–
	Proportion juvenile burrows	0.309 (1)	0.579	–	-0.402 (0.723)	–
Shannon index	Habitat (Forest-Range)	4.918 (1)	0.027	–	-0.356 (0.111)	–
	Season	5.981 (3)	0.113	Spring	-0.289 (0.143)	–
				Summer	-0.098 (0.142)	–
				Winter	-1.460 (0.550)	–
	Total burrows	0.641 (1)	0.423	–	-0.153 (0.106)	–
	Proportion juvenile burrows	1.871 (1)	0.171	–	-0.576 (0.775)	–

Table 6. Number of Gopher Frog observations from Gopher Tortoise camera trapping on test ranges and forested sites on Eglin Air Force Base across seasons.

Season	Forest	Test Range
Summer	11	24
Fall	4	14
Winter	0	9
Spring	1	11
Total	16	58

FIGURES

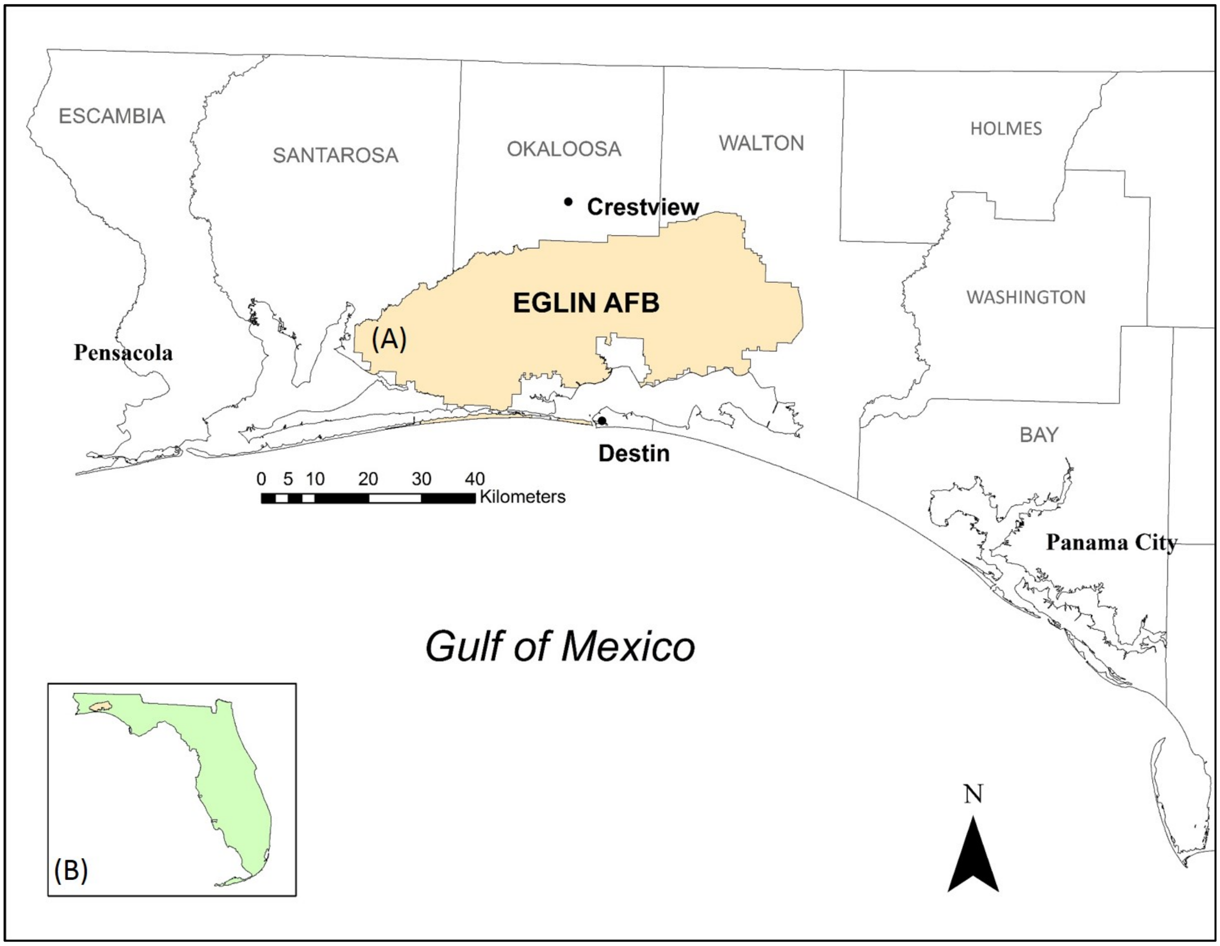

Figure 1. The location of Eglin Air Force Base (Eglin) (A) in the Florida panhandle (B). Eglin is >184,000 ha and spans the counties of Santa Rosa, Okaloosa, and Walton.

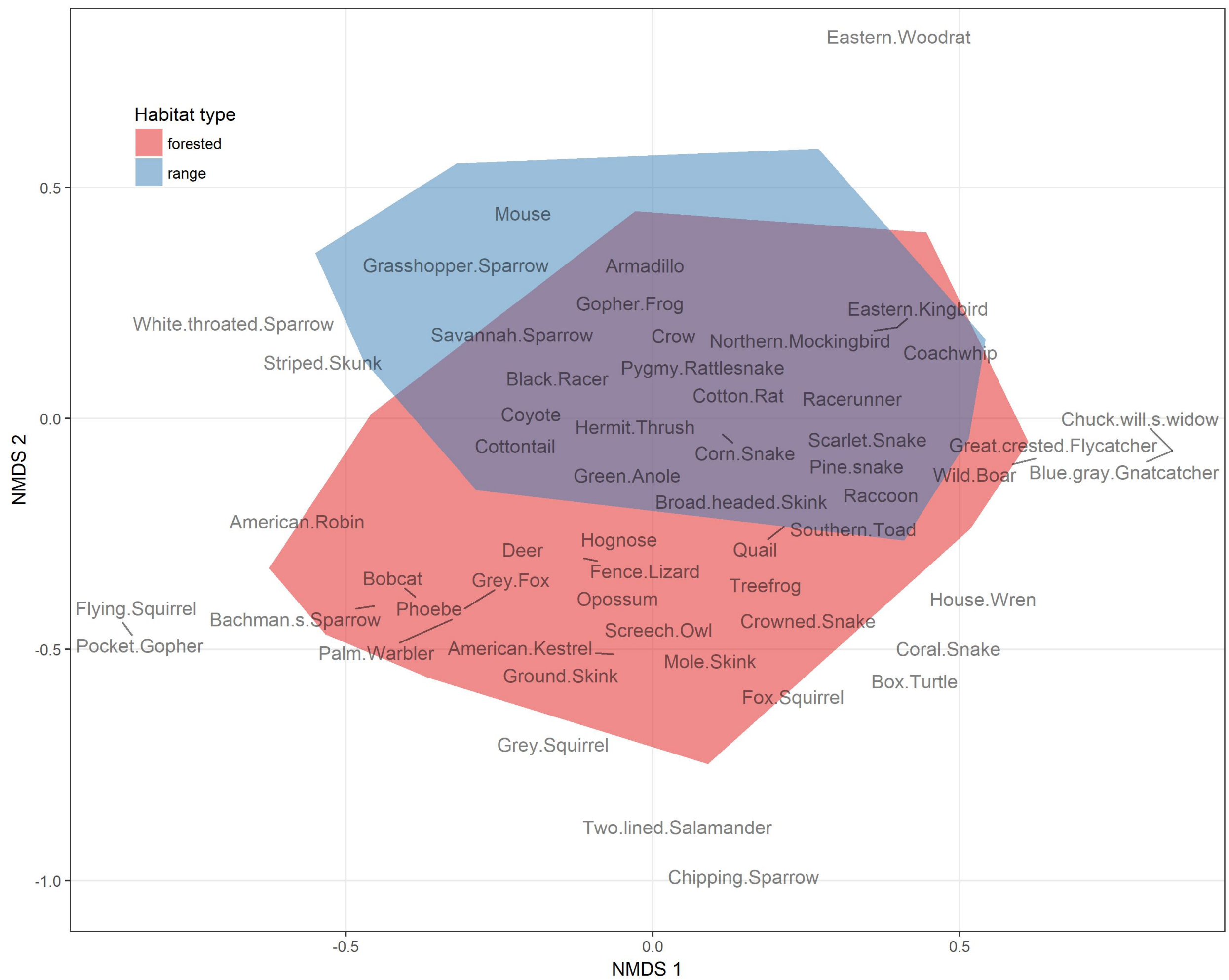

Figure 2. Forested and range habitats along the first two NMDS axes along with each species of Gopher Tortoise burrow associate on Eglin Air Force Base. See Table 3 for a complete list of species and numbers found in each habitat.