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Understanding Occupancy Patterns in a Low-density Gopher Tortoise (*Gopherus polyphemus*) Population

Houston C. Chandler[1,2,7]***, Steven J. Goodman***[1,3]***, Jennifer A. Smith***[1,4,5]***,***
Thomas A. Gorman[1,6]***, and Carola A. Haas***[1]

[1]*Department of Fish and Wildlife Conservation, Virginia Tech, 310 West Campus Drive, Blacksburg, Virginia 24061, USA*
[2]*The Orianne Society, 11 Old Fruitstand Lane, Tiger, Georgia 30576, USA*
[3]*Current address: National Parks Conservation Association, 1 Rankin Avenue, 2nd Floor, Asheville, North Carolina 28801 USA*
[4]*Department of Biological Sciences, Virginia Tech, 926 West Campus Drive, Blacksburg, Virginia 24061, USA*
[5]*Current address: Department of Environmental Science & Ecology, University of Texas at San Antonio, One UTSA Circle, San Antonio, Texas 78249, USA*
[6]*Current address: Aquatic Resources Division, Washington State Department of Natural Resources, 1405 Rush Road, Chehalis, Washington 98532, USA*
7Corresponding author, e-mail: houstonc@vt.edu

Abstract.—**Assessing population trends for imperiled species that occur at low densities across large geographic areas can be challenging. Standard sampling techniques are often designed for small areas where target species can be easily observed across most of the study site. We evaluated the use of an occupancy framework for sampling a low-density Gopher Tortoise (*Gopherus polyphemus*) population found on Eglin Air Force Base, Florida, USA. We examined the effects of habitat type and proximity to historic Gopher Tortoise observations on site occupancy across the base. We surveyed 469 1-ha sites using two observers to walk 10 m transects across the survey site. We determined occupancy using the presence of active or inactive tortoise burrows as a surrogate for actual tortoise observations. We surveyed approximately 58% of sites twice to estimate the probability of burrow detection. We encountered Gopher Tortoise burrows at 53 survey sites (11%), and the detection probability for burrows was high ($p = 0.951$). Occupancy probability decreased from 0.42 to 0.01 as the distance from historic tortoise burrow observations increased, regardless of the habitat type. Power analyses indicated that a 3–5% annual decline in Gopher Tortoise occupancy would likely be detected by repeat surveys within 5–10 y. While our approach does not estimate tortoise abundance or density changes over time, it offers natural resource managers a technique to monitor the area occupied by tortoises over a large geographic area and broadly assess the effects of ongoing management actions.**

Key Words.—burrow; coastal plain; Florida; power analysis; reptile; sandhills; Testudines

Introduction

Monitoring programs for species of conservation concern often have limited resources and must balance efficiency and rigor to detect meaningful changes in population status or environmental characteristics over time (Field et al. 2005). Long-term monitoring programs can enhance understanding of population trends through time and provide an in-depth assessment of ongoing management actions designed to enhance wildlife populations (Lindenmayer et al. 2012). Such projects have been used successfully to document population declines, implement management actions, and assess the success or failure of these actions (Mullin et al. 2020). For populations that are patchily distributed and occur at low densities, careful consideration must be given to selecting a sampling approach for long-term monitoring when faced with limited resources, including a realistic assessment of the ability to detect population changes over time (Lurz et al. 2008).

Gopher Tortoises (*Gopherus polyphemus*) are a critical component of Longleaf Pine (*Pinus palustris*) uplands across a large portion of the southeastern U.S. (Auffenberg and Franz 1982; Ernst and Lovich 2009). Often described as a keystone species or ecosystem engineer, Gopher Tortoises excavate 4–8 m long burrows into the sandy soils that dominate this region (Diemer 1986). These burrows provide a source of shelter for tortoises but are also used by over 300 other species (Jackson and Milstrey 1989; Pike and Mitchell 2013), including imperiled (e.g., the Gopher Frog, *Rana capito*) and federally listed as threatened species (e.g., the Eastern Indigo Snake, *Drymarchon couperi*). Furthermore, burrow creation and maintenance impact the environment surrounding the burrow, promoting plant diversity and environmental heterogeneity (Kaczor and Hartnett 1990). Gopher Tortoise populations have declined significantly across their range, primarily because of extensive habitat loss and degradation resulting from fire suppression (Auffenberg and Franz 1982; Diemer 1986; Frost 1993; McCoy et al. 2006). As a result, Gopher Tortoise populations in the western portion of its range were listed federally as threatened under the U.S. Endangered Species Act in 1987 (U.S. Fish and Wildlife Service [USFWS] 1987), and the remaining populations are currently considered a candidate for federal listing (USFWS 2011). Current management plans commonly focus on conserving remaining habitat and improving habitat conditions to promote stability in extant populations, but well-designed monitoring programs do not always accompany these management actions.

Line-transect distance sampling (LTDS) is a commonly used method for monitoring Gopher Tortoise populations (e.g., Nomani et al. 2008; Smith et al. 2009; Stober and Smith 2010; Castellón et al. 2015). This approach is a reliable survey method at sites with moderate to high population densities and easily defined site boundaries (Smith et al. 2009). LTDS can be unfeasible, however, when low tortoise densities, particularly across large areas of suitable habitat, lead to low encounter rates (Smith et al. 2009; see Stober et al. 2017 for low density modifications to traditional LTDS techniques). LTDS also requires observers to determine occupancy status of at least some Gopher Tortoise burrows using scoping cameras, which can increase the effort and cost required to complete surveys at a landscape scale. Furthermore, success of burrow scoping can range from approximately 30–95% across different habitat types and experience levels (Smith et al. 2005; Stober and Smith 2010; Castellón et al. 2015; Stober et al. 2017). Without sufficient resources, it may be difficult for managers to implement LTDS across large landscapes with low tortoise densities. Thus, in certain situations, alternative sampling approaches to LTDS may be needed.

Measuring occupancy probability at the site level, while accounting for imperfect detection, has become a common component of many wildlife monitoring programs in recent years (Weir et al. 2009; Bauder et al. 2017). Compared to distance sampling, measuring site occupancy has been shown to be more efficient and robust (capable of detecting a 5% annual decline after 10 y of sampling) when used to monitor populations of Sonoran Desert Tortoise (*Gopherus morafkai*); Zylstra et al. 2010). Similarly, Erb et al. (2015) showed that a 10% decline in occupancy between 5-y sampling rounds could be detected for low-density populations of Eastern Box Turtles (*Terrapene carolina carolina*), highlighting the use of this approach. Despite its recent popularity and successful application with other chelonian species, occupancy sampling has not been previously applied to Gopher Tortoise populations at a landscape scale.

Indirect signs of animal presence (e.g., footprints, burrows, or hair) can be used as surrogates for actual observations of the target species, potentially allowing observers to efficiently assess large geographic areas or low-density populations when target species are secretive (Stanley and Royle 2005; Rhodes et al. 2011). Gopher Tortoises are well suited to this approach because their burrows are a conspicuous feature, and individuals will often construct and maintain multiple burrows (McRae et al. 1981; Diemer 1992; Smith et al. 1997; Eubanks et al. 2003). Tortoise burrows are more easily observed than tortoises themselves because tortoises spend a large percentage of time underground (Smith 1995). When inferring occupancy from indirect signs, it is important to understand the underlying relationships between the animal and the sign that it is producing (Stanley and Royle 2005; Rhodes et al. 2011). For tortoise burrows, identifying site-specific rates of burrow collapse and disappearance should give managers confidence that observed burrows were created or actively maintained within a certain time span, which would ideally be shorter than the return interval for future surveys in a long-term monitoring program (minimizing false positives).

Eglin Air Force Base (hereafter, Eglin) is a large military installation spanning 188,459 ha in the Gulf Coastal Plain of the Florida, USA, panhandle. This base contains approximately 155,600 ha of potential Gopher Tortoise habitat (USFWS 2011), making it a regionally important landscape for tortoise conservation. The potential tortoise habitat primarily consists of Longleaf Pine-dominated sandhills that are interspersed with pine plantations and treeless, open test ranges (areas used for bombing and artillery). These habitats are sometimes suitable for tortoise use, and the active habitat management program at Eglin has improved habitat quality through the application of prescribed fire, Sand Pine (*Pinus clausa*) and oak (*Quercus* spp.) removal, and Longleaf Pine planting. Despite abundant suitable habitat, Gopher Tortoises on Eglin occur at low densities, with small, isolated populations scattered across the base. Using unpublished data from Jackson Guard (Eglin Natural Resource Division), we estimated that tortoise density outside of these known populations was approximately 0.008 tortoises/ha and that the effort required to conduct LTDS across the area of interest would be beyond the scope of our project (Smith et al. 2009). Thus, Eglin represents an important but challenging landscape for managers to quantify trends in the Gopher Tortoise population.

The goal of this study was to test whether measuring site occupancy using Gopher Tortoise burrows as a surrogate for tortoise observations could be a viable method for monitoring low-density tortoise populations. We investigated the potential value of this approach in tracking changes in site occupancy over time (e.g., Eraud et al. 2007; Weir et al. 2009). We expected that the detection probability for tortoise burrows would be high, limiting the need to conduct repeat surveys across all sites (see below). Furthermore, we expected that the effort required to sample sites in an occupancy framework would compare favorably to other common survey techniques for Gopher Tortoise populations. A secondary objective of this study was to assess the current distribution and habitat use of Gopher Tortoises on Eglin by incorporating historic tortoise records and habitat types into our survey design. We used the results of our surveys to provide guidelines for future monitoring of the Gopher Tortoise population on Eglin.

Methods and Materials

Study design.—We used the Florida Cooperative Land Cover Map to map potential Gopher Tortoise habitat (Florida Fish and Wildlife Conservation Commission [FWC] and Florida Natural Areas Inventory [FNAI] 2014). We identified all potential habitat using four land cover categories represented in the Florida Land Cover Map: sandhills, non-forested, pine production, and upland pine. Sandhills composed approximately 63% of the study area and were defined as areas of Longleaf Pine-dominated uplands, typically on well-drained soils. Through on-the-ground validation surveys, we found that there was substantial variation in habitat characteristics (i.e., heterogeneity in canopy cover and herbaceous ground cover) within the sandhills designation. Thus, we used the Ecological Condition Model (ECM) developed by the Air Force Wildland Fire Center at Eglin to refine this habitat category (Wiens et al. 2009; Hiers et al. 2012). This model integrated remotely sensed image classifications with geographical, inventory, and management datasets to classify sandhill habitat into a low- and a high-quality category, which were based on the amount of canopy cover and herbaceous vegetation present (Wiens et al. 2009).

Non-forested sites were primarily military test ranges (10% of the study area), where vegetation was cleared to improve line-of-site or create buffer zones for Air Force missions. Test range habitat ranged from minimal shrub cover with planted non-native grasses to high native shrub and herbaceous vegetation cover. Pine production sites consisted of tree plantations and post-harvest natural regeneration, varying widely in age, species, and management history (20% of study area). Upland pine composed just 4% of the study area and was characterized by mesic pine woodlands. The remaining 3% of the study site was comprised of mesic

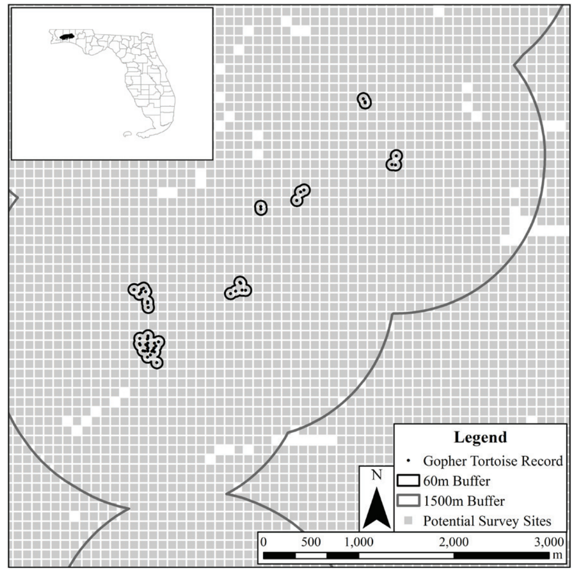

Figure 1. Occupancy surveys conducted for Gopher Tortoises (*Gopherus polyphemus*) on Eglin Air Force Base, Florida, USA, by sampling randomly selected 1-ha survey sites from a grid covering all suitable tortoise habitat (example shown above). Survey sites were sampled proportionately to overall availability based on habitat type and distance to historic burrow observations of Gopher Tortoises. Unsuitable habitat is represented by blanks in the survey grid.

flatwoods, which we did not include in our study design because this habitat is unsuitable for Gopher Tortoises. This process resulted in five habitat categories (high-quality sandhills, low-quality sandhills, non-forested areas, pine production, and upland pine). We partitioned all potential Gopher Tortoise habitat across Eglin into a grid of 1-ha survey sites (Fig. 1). We based the size of survey sites in part on mean estimated male home range (1.1 ha; Eubanks et al. 2003) and inter-burrow movement distances (median movement distances near 100 m; Guyer et al. 2012). We stratified all survey sites based on the dominant habitat type within that site (i.e., > 50% coverage). The habitat classifications assigned to each site were verified during surveys. All habitat classification work was conducted in ArcGIS 10.2 (Esri, Redlands, California, USA).

We then classified each survey site into one of three distance categories based on their proximity to historic Gopher Tortoise burrow observations available through Jackson Guard or data from recent area-constrained surveys on Eglin (Carola Haas, unpubl. data). For this classification, we excluded burrow records > 20 y old, burrows that were abandoned at the time of observation, and isolated single burrows that were > 60 m from at least one other tortoise burrow. We used distance categories of < 60 m, 60–1,500 m, or > 1,500 m from the nearest tortoise observation (measured from the center of the survey site; Fig. 1). Most daily tortoise movements are < 60 m, and this distance represents the approximate radius of a male home range (Eubanks et al. 2003). We used the second cutoff of 1,500 m because it approximates the distance of tortoise dispersal. Tortoises making movements ranging from 700–1,500 m have been considered dispersing in other studies (Diemer 1992; Eubanks et al. 2003).

***Gopher Tortoise surveys*.**—We conducted surveys for Gopher Tortoise burrows from 29 July through 5 December 2014, attempting to survey the maximum number of sites over this approximately 4.5 mo period. We randomly sampled 1-ha sites using a stratified sampling design where sites were sampled in proportion to their availability based on the five habitat types and three distance categories. We excluded sites in areas that were inaccessible because of ongoing military operations or that required special security clearance. There were > 100,000 potential 1-ha survey sites, and the removal of inaccessible sites did not impact our ability to representatively sample sites based on the categories described above.

We determined the presence or absence of Gopher Tortoise burrows at each site using methods modified from FWC (2012). Two observers walked together along 10 m-wide straight-line transects (11 transects/ha) that together covered the entire survey site. Observer 1 used a compass and Garmin GPSMap78 (Garmin International Inc., Olathe, Kansas, USA) to navigate, record data, and survey 1 m on either side of the transect. Observer 2, positioned 5 m from the transect, surveyed 4 m on either side of their position. A second survey, conducted with different observers, occurred at 274 (58%) of the survey sites within one week. Following the recommendation of MacKenzie and Royal (2005), we determined that a single repeat survey at approximately half of the survey sites was sufficient to estimate burrow detection probability because of a high burrow detection rate (p = 0.87) using the same survey methods at other sites on Eglin (Carola Haas, unpubl. data).

During each survey, we classified Gopher Tortoise burrows as active, inactive, or abandoned based on the following criteria. Active burrows were those with signs of recent tortoise activity, including footprints, scat, plastron scraping, and/or recent tortoise digging near the burrow entrance (Auffenberg and Franz 1982; McCoy and Mushinsky 1995; Smith et al. 2005). We classified burrows as inactive if there were no obvious signs of recent activity, and no vegetation blocking the entrance to the burrow, although debris could be present in the entrance (Smith et al. 2005). These parameters suggest relatively recent maintenance by a tortoise (Auffenberg and Franz 1982), and burrows were functionally available for tortoise use (McCoy and Mushinsky 1995). Finally, abandoned burrows were characterized by entrances that were substantially degraded due to soil accumulation from erosion, ceiling collapse, or vegetation growing at the entrance (Auffenberg and Franz 1982; Smith et al. 2005). Major burrow modification would be needed for abandoned burrows to become available for tortoise use (McCoy and Mushinsky 1995). We ended the survey when an active or inactive burrow was located and considered the site occupied.

***Statistical analyses*.**—We developed a Single-season Occupancy Model to estimate site occupancy of Gopher Tortoises across Eglin (MacKenzie et al. 2002; MacKenzie et al. 2006). We fit a set of candidate models where occupancy probability (Ψ) varied by distance category, habitat category, or their additive and interactive effects. We held detection probability (p) constant in all models for two reasons: first, previous work indicated that burrow detection probability was high and consistent at multiple sites on Eglin; and second, the number of occupied sites with both detections and non-detections was low and did not span all the categories of the predictor variables. We also excluded the 52 surveys conducted at 38 upland pine sites from our analyses because this habitat occurred on the landscape infrequently, was not represented in all three distance categories, and had no tortoise detections. Thus, all results are based only on four landcover types (high- and low-quality sandhills, non-forested, and pine production), which accounted for 93% of the total study area.

We evaluated the candidate models using an information theoretic approach and assessed the fit of the global model using a χ^2 goodness-of-fit test (MacKenzie and Bailey 2004). We used quasi-Akaike's Information Criterion (AIC) corrected for overdispersion (i.e., ĉ-hat for global model > 1) and for small sample size ($QAIC_c$) to select the model with the most support. We then calculated $\Delta QAIC_c$ and model weights (w_i) to examine the relative support of each model (Burnham and Anderson 2002). We considered the top-ranking model as the model with the lowest $QAIC_c$ value and models with $\Delta QAIC_c \leq 2$ were considered to have equivalent support.

Using the parameter estimates from the top model, we simulated the power of different survey designs to detect changes in site occupancy for the Gopher Tortoise population on Eglin. We used the methodology outlined by Guillera-Arroita and Lahoz-Monfort (2012) and ran 5,000 simulations for each of the following scenarios. First, we examined the effects of varying overall survey effort (300, 500, or 1,000 follow-up surveys) to detect changes in occupancy assuming that sites were randomly sampled across the base (i.e., a mean occupancy probability of 0.137 as derived from the top model). Second, we assessed the power of the same sampling design focused only on sites that had

Table 1. One-ha survey sites (n = 469) stratified by habitat type and distance to historic Gopher Tortoise (*Gopherus polyphemus*) burrow observations, sampled across Eglin Air Force Base, Florida, USA. The number in parentheses represents the number of sites that were confirmed occupied by tortoises.

	Distance category		
Habitat category	< 60 m	60–1,500 m	> 1,500 m
High-quality Sandhills	39 (17)	55 (5)	85 (0)
Low-quality Sandhills	6 (2)	34 (0)	66 (0)
Non-forested	41 (20)	36 (4)	5 (1)
Pine Production	7 (0)	36 (2)	59 (2)

Table 2. Occupancy models describing the effects of habitat and distance to known Gopher Tortoise (*Gopherus polyphemus*) observations on tortoise occupancy and detection probabilities at Eglin Air Force Base, Florida, USA. Acronyms are k = number of parameters, QAICc = second order Akaike's Information Criteria (AIC) for overdispersed data, ΔQAICc = change in QAICc, and w_i = relative amount of support for each model.

Model	k	QAICc	ΔQAICc	w_i
psi(distance), p(.)	5	115.1	0.00	0.83
psi(habitat + distance), p(.)	8	118.3	3.23	0.16
psi(habitat + distance + habitat*distance), p(.)	14	125.1	10.04	0.01
psi(habitat), p(.)	6	136.0	20.97	0.00
psi(.), p(.)	3	146.2	31.14	0.00

the highest probability of being occupied by Gopher Tortoises (occupancy probability = 0.418). Finally, we evaluated the length of time in years that it would take to detect an annual decline in site occupancy of 1%, 3%, or 5%. For this scenario, we assumed that 500 follow-up surveys would be completed on sites with the highest occupancy probability (0.418). We ran all simulations using a constant detection probability of 0.951 (derived from the top model) with two repeat visits to 1-ha survey sites as described above. We considered a power of 0.8 or greater to be an acceptable estimate of future ability of surveys to detect changes (Jennions and Møller 2003; Guillera-Arroita and Lahoz-Monfort 2012). We conducted all statistical analyses in R (R Core Team 2020).

Results

From July through December 2014, we surveyed 469 sites for Gopher Tortoises on Eglin, completing 743 surveys (274 sites surveyed twice). The habitat at most sites was categorized as either high (179) or low (106) quality sandhills, while pine production (102) and non-forested sites (82) made up a smaller proportion of surveys (Table 1). Over 80% of the survey sites were located > 60 m from the nearest known Gopher Tortoise burrow observation, falling within the two highest distance classes. Just 93 survey sites were within 60 m of a known Gopher Tortoise burrow observation. We detected Gopher Tortoise burrows on 91 surveys and at 53 sites (Table 1). For the 469 initial surveys, mean survey time for unoccupied sites was 33.4 ± (standard error) 0.6 min (range, 10–105 min), and mean survey time for occupied sites was 22.7 ± 3.2 min (range, 1–115 min).

Of the five models included in our candidate model set, one model received the most support from the data (model weight = 0.83; Table 2). The top ranked model included a constant detection rate (p = 0.951) and an occupancy probability that varied by the distance to the nearest known tortoise burrow observation. Occupancy estimates from this model indicated that the probability of site occupancy for Gopher Tortoises was highest at sites that were closer to known Gopher Tortoise burrow observations than those farther away (< 60 m: $\Psi = 0.42 \pm 0.05$, 95% confidence interval [CI] = 0.32–0.52; 60–1,500 m: $\Psi = 0.07 \pm 0.02$, 95% CI = 0.04–0.12; > 1,500 m: $\Psi = 0.01 \pm 0.01$, 95% CI = 0.004–0.043). All other models had a $\Delta QAIC_c > 2$ (Table 2).

Power estimates indicated that future surveys would be able to detect a 30–50% change in tortoise occupancy, depending on the number of sites that were included in the sampling design (Fig. 2). If surveys were restricted to just sites within 60 m of known Gopher Tortoise occurrence (i.e., with a higher occupancy probability), then it would be possible to detect a 15–25% change in occupancy with 80% power (Fig. 2). Similarly, it would be possible to detect an annual 3% or 5% decline in Gopher Tortoise occupancy between 4–9 y after it began. Surveys would be less likely to detect a 1% annual decline in occupancy probability, however, within 20 y of that decline initiating (Fig. 3).

Discussion

Our study is the first to use an occupancy modeling framework to monitor Gopher Tortoise populations and highlights the potential usefulness of this approach for low-density populations that cover large geographic areas. We were able to conduct approximately 800 surveys (including upland pine sites excluded from analyses) in just over 4 mo using a small group of observers. By using highly visible tortoise burrows as a surrogate for tortoise observations, our survey methodology had a detection probability near 1.0, allowing us to conduct repeat surveys at only 58% of sites. Furthermore, because we were only interested in site occupancy, the effort required to sample each site was low (i.e., no burrow scoping, stopping the survey after first burrow detection at a site). Our estimates of survey effort are similar to LTDS conducted without scoping burrows (Nomani et al. 2008) and approximately 2–5 times faster than LTDS when scoping burrows and total count methodologies (Nomani

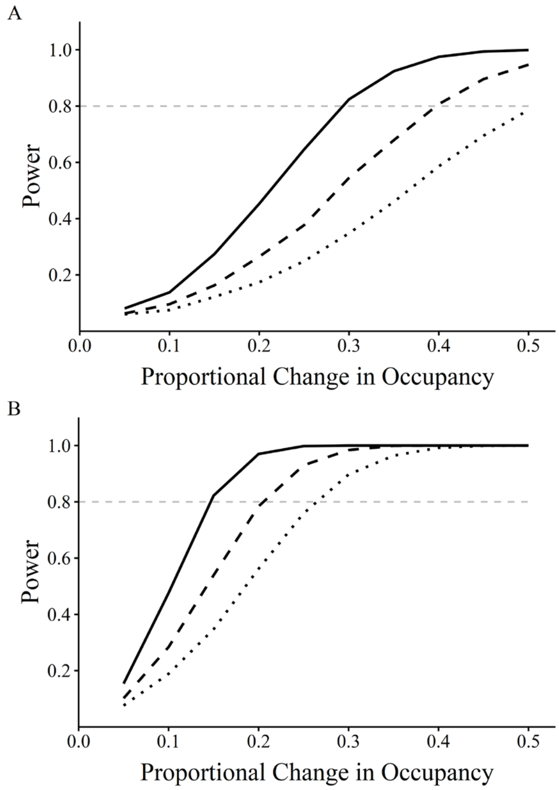

Figure 2. Probability of detecting proportional changes in Gopher Tortoise (*Gopherus polyphemus*) occupancy on Eglin Air Force Base, Florida, USA, based on baseline surveys of 469 sites across the base. Power estimates were based on simulations using a constant detection probability of 0.951, assuming either 300 (dotted line), 500 (dashed line), or 1,000 (solid line) sites were sampled twice. The initial occupancy probability is (A) an average across the entire base (0.137) or (B) the occupancy probability for sites within 60 m of a historic tortoise observation (0.4183). The dashed horizontal line represents an estimated power of 80%.

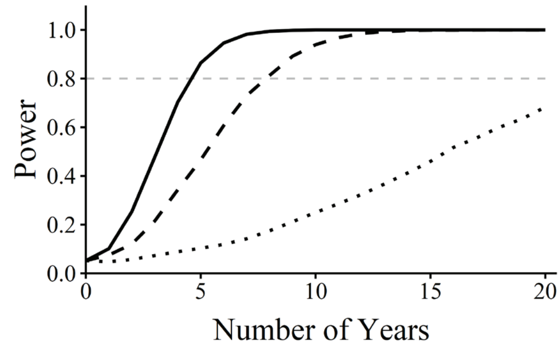

Figure 3. Probability of detecting a 1% (dotted line), 3% (dashed line), or 5% (solid line) annual decline in Gopher Tortoise (*Gopherus polyphemus)* site occupancy on Eglin Air Force Base, Florida, USA. Power estimates were based on surveying 500 sites two times using an initial occupancy probability of 0.4183. The detection probability was constant at 0.951. The dashed horizontal line represents an estimated power of 80%.

et al. 2008; Smith et al. 2009). Another advantage of this approach is that it does not require a burrow camera or GPS equipment with sub-meter accuracy, both of which can be prohibitively expensive for monitoring programs. Thus, we believe monitoring Gopher Tortoise populations using an occupancy modeling approach that considers indirect signs of occupancy to be a useful extension of existing monitoring techniques, particularly at large spatial scales.

A significant limitation of this monitoring approach is that it does not provide site-specific estimates of any demographic parameters that could be used to understand population trends (Loehr 2017). Rather, it is designed to provide a landscape-scale estimate of trends in site-occupancy. Because Gopher Tortoises can live > 60 y (Germano 1994), an individual or small group of individuals could persist for decades with no successful recruitment. This could lead to sites being occupied even if the tortoise population in that area is not viable. A useful extension of the presented methodology would be to completely survey all sites (not stopping after an initial burrow detection) and measure burrow widths of all detected tortoise burrows. Burrow width is correlated with the size and age of the tortoise using the burrow (Alford 1980; Landers et al. 1982), and width measurements would provide additional demographic data about the population (e.g., presence of juvenile tortoises). Managers could also record information from opportunistic encounters that may provide additional insight into population dynamics (e.g., the presence of any dead tortoises). These expanded efforts would increase the use of an occupancy monitoring approach for Gopher Tortoise populations, while adding little to the overall survey effort.

Our approach provided an Eglin-wide assessment of Gopher Tortoise occupancy in areas of potentially suitable tortoise habitat (an estimated area of 155,600 ha). These results will serve as a baseline from which future long-term occupancy trends can be monitored, allowing natural resource managers on Eglin to assess threats and potential benefits of ongoing management actions. Our power analyses indicated that both a 3% and 5% annual decline in tortoise occupancy could be detected within 5–10 y. Goodman et al. (2018) reported that approximately 63% of active and/or inactive burrows on Eglin were collapsed, filled in, or substantially degraded after 2 y, 82% after 3 y, and 100% after 5 y. Thus, surveying tortoises on time scales longer than every 3–5 y would minimize false positives using this approach. It is important to recognize, however, that these burrow degradation rates may be specific to the sandy soils on Eglin and may not apply to other locations. Gopher Tortoise site occupancy rates are likely to change slowly over time, and conducting repeat surveys over a 10–15-y period would maximize the chances of detecting changes in occupancy and allow enough time for occupancy rates to change via demographic processes (e.g., deaths, immigration, or emigration). Shorter time intervals between repeat surveys may be useful if testing the specific effects of a management or habitat change on tortoise occupancy. In addition, shorter time intervals between surveys may be needed to generate a sufficient sample size for statistical assessment of trends. Finally, because of low tortoise densities on Eglin, sampling sites with a higher overall occupancy rate (i.e., closer to known sites) would increase the chances that changes in occupancy would be detected by future monitoring efforts.

Although we conducted this research as a pilot study to test a potential survey methodology, the results can be directly applied to our understanding of the tortoise population on Eglin. Previous studies suggest that habitat characteristics (e.g., the availability of well-drained soil in which to burrow, herbaceous biomass for food, and sunlit nesting sites) can affect the presence of Gopher Tortoises (Diemer 1986; Breininger et al. 1994; Aresco and Guyer 1999; Castellón et al. 2012). We found relatively limited support for models that included an effect of habitat type on occupancy probability. There are trends in the habitat data that are worth noting, however. At distances > 60 m from known sites, both non-forested sites (12.2%) and pine production sites (4.2%) were occupied at higher or similar proportions than high-quality sandhills (3.6%). Given the potential conflicts with ongoing military activities in pine production and non-forested habitats, it is important for future research to understand why Gopher Tortoises are frequently using these habitat types. In addition, no low-quality sandhill sites were occupied in the larger distance categories, and only 1.9% of low-quality sandhill sites (n = 106) were occupied at all (compared to 12.3% of high quality sandhills sites), indicating that the habitat quality of these sandhills may be poor relative to other habitat types.

Our results did suggest that occupancy probability was negatively associated with increasing distance from a previous tortoise burrow observation. This trend highlights the clumped distribution of Gopher Tortoises on Eglin despite abundant suitable habitat across a large portion of the base (USFWS 2011). Isolated clusters of Gopher Tortoises may reflect historical constraints on occurrence that are not reflected in the current distribution of suitable habitat. Similar to most Longleaf Pine uplands, Eglin experienced widespread fire suppression for many decades, leading to large areas of degraded habitat that have been restored over the last several decades (Provencher et al. 2001; Varner et al. 2005). Even with increased management in recent years, fire frequency, intensity, and effectiveness can all vary spatially, creating a gradient of habitat quality that can reduce movement in tortoise populations (McCoy et al. 2013). Our results suggest there are still sites on Eglin where habitat quality for Gopher Tortoises can be improved. Furthermore, human predation on tortoises was historically widespread in Florida (Taylor 1982), and easily accessible populations may have been unable to withstand consistent mortality from human exploitation. Once tortoise populations are reduced to low densities, movements of individuals to interact with other tortoises are shorter (typically < 80 m) than those in higher density populations (Guyer et al. 2012), which could further reinforce the clumped distributions of tortoises across Eglin. Gopher Tortoise populations on Eglin appear to be slow to expand from areas where populations have persisted into areas where habitat has been recently improved by appropriate fire management.

Most known Gopher Tortoise sites at Eglin are likely to contain fewer than 25 tortoises (based on burrow counts mostly below 50). The presence and number of smaller burrows at intensively surveyed sites indicates that recruitment is occurring in some, but not all, locations (Steve Goodman and Carola Haas, unpubl. data). Further, anecdotally, management activities designed to create more open canopy in an area with a low-density tortoise population resulted in a > 100% increase in active burrows and a more than three-fold increase in subadult-sized burrows. In light of this, the current management goals at Eglin are to maintain open canopy in and increase connectivity among extant populations and to conduct internal translocations to create larger clusters of tortoises (Jeremy Preston, pers. comm.).

Given that Gopher Tortoise populations on Eglin appear to be isolated and clustered at certain locations, we propose two approaches to increase and expand the current low-density populations. First, conservation and management actions should be focused on core areas (< 1,500 m from known occurrences) to allow dispersal and colonization from existing tortoise colonies. The effects of these management actions could be assessed using the occupancy design outlined in this study. Second, translocation of tortoises could augment existing low-density populations or establish populations in unoccupied suitable habitat. Translocating Gopher Tortoises has become a widespread management strategy in recent years (Tuberville et al. 2008; Bauder et al. 2014), and efforts are already underway to significantly increase the tortoise population on Eglin through external translocations from central and southern Florida (Kobilinsky 2017). Managers can strategically target sites for future releases of translocated animals by identifying areas with high quality habitat and within close proximity to existing tortoise populations. Finally, the results of our surveys provide sampling site-specific information that managers can use to assess the impacts of future projects relating to the military mission on Eglin. Spatially explicit data on tortoise occupancy could allow future projects to minimize habitat fragmentation around tortoise populations, which can promote dispersal (BenDor et al. 2009).

To be successful, monitoring programs must have clearly defined goals and be designed in such a way that the data collected can directly address those goals. Occupancy modeling through the collection of presence-absence data can be used to understand large-scale landscape trends in site occupancy. These data could be complemented with additional monitoring approaches to address questions at various spatial and temporal scales, which has been successfully implemented for the tortoise population on Eglin (Goodman et al. 2018). Finally, management programs should clearly identify points when interventions or additional management actions are needed (Lindenmayer et al. 2013; Robinson et al. 2018). Understanding the limitations of any monitoring technique is critical to implementing it successfully and addressing identified problems. We believe the above methodology can be employed effectively to complement existing survey techniques for Gopher Tortoises.

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Houston Chandler received his B.S. in Biology from Georgia College, Milledgeville, USA, in 2012 and an M.S. in Fish and Wildlife Conservation from Virginia Tech, Blacksburg, USA, in 2014. Currently, he is a Ph.D. student at Virginia Tech studying the effects of climate change on an endangered salamander. He is also Science Director for the nonprofit organization The Orianne Society, which focuses on reptile and amphibian conservation. He is broadly interested in applied research that has direct monitoring or management applications for imperiled herpetofauna. (Photographed by Cailin Lutz).

Steven Goodman is a Conservation Biologist currently leading a wildlife connectivity research project in the Pigeon River Gorge in North Carolina and Tennessee, USA. With 20 y of experience researching, monitoring, and managing sensitive wildlife with university, state wildlife agency, and nonprofit settings, his driving objective is to find the balance between the need for novel research and using existing, best available information to make timely decisions to conserve wildlife and landscapes. (Photographed by Rebecca Goodman).

Jennifer Smith is a Wildlife Ecologist whose research aims are to evaluate the effects of global change on the spatial ecology, demography, and behavior of wildlife. Her research often takes a mechanistic approach by incorporating field observations, experiments, and statistical and geospatial analyses. Much of her work addresses the effects of land-use and management decisions in rural landscapes but has recently expanded to consider urbanization. Overall, her objective is to conduct research that informs policy and promotes sustainable land uses that consider the conservation of wildlife and human well-being. (Photographed by Larkin Powell).

Thomas Gorman is an Assistant Division Manager in the Aquatic Resources Division of the Washington State Department of Natural Resources, Chehalis, USA, and is an Affiliated Research Scientist in the Department of Fish and Wildlife Conservation, College of Natural Resources and Environment, Virginia Tech, Blacksburg, USA. He received a B.S. in Wildlife Ecology from the University of Maine, Orono, USA, a M.S. in Biology from Minnesota State University, Mankato, USA, and Ph.D. in Fisheries and Wildlife Sciences from Virginia Tech. His interests include management and conservation of rare species, habitat and restoration ecology, and the intersection of science and policy. (Photographed by Jessica Homyack).

Carola Haas is a Professor in the Department of Fish and Wildlife Conservation at Virginia Tech, Blacksburg, USA. She received a B.A. from Wellesley College, Wellesley, Massachusetts, USA, a Ph.D. from Cornell University, Ithaca, New York, USA, and did postdoctoral training at Yamanashi University, Kofu, Japan, and the Wild Bird Society of Japan Research Center. She is interested in breeding and movement behavior of amphibians and reptiles (including birds). She studies wild populations on managed landscapes, with a goal of improving land use practices to conserve native biodiversity while achieving landowner goals. (Photographed by Olivia Coleman).