Gopher Tortoise (*Gopherus polyphemus*) Densities and Habitat Suitability Across a Xeric-Mesic Gradient in Peninsular Florida, USA

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Abstract.—The Gopher Tortoise (*Gopherus polyphemus*) is a burrowing, keystone species of the southeastern USA. Factors influencing habitat suitability for this declining species in the southern portion of its range are unclear, due to its broad habitat associations and lack of detailed demographic data. We used Line-transect Distance Sampling of burrows to determine densities and estimate age-class structure of Gopher Tortoises across a gradient of xeric to mesic habitats on Avon Park Air Force Range (APAFR) in south-central Florida. We also examined the influence of soil characteristics on burrow encounter rates. Tortoise densities were highest in Florida scrub (0.95 adult and subadult tortoises/ha), intermediate in pine flatwoods (0.73) and pine plantations (0.44), and lowest in prairies (0.18). Despite persistent burrow flooding that hindered precise density estimation for mesic habitats, we estimated that APAFR harbors a regionally significant population of 7,899–11,109 adult and subadult tortoises. We encountered more burrows per km in soils with intermediate available water capacity ($r^2 = 0.45$, df = 2,11, $P = 0.036$,), suggesting a tradeoff in habitat suitability between wetter soils that may support the most forage and drier soils that may be most appropriate for burrowing and nesting. Burrow size-class distributions were skewed towards adult sizes, particularly in pine and prairie communities. Variation in tortoise densities and age-class structure across this xeric-mesic gradient implies differences in recruitment and survival arising from corresponding variation in habitat quality. Our study provides useful reference densities for species management and new insights regarding Gopher Tortoise use of poorly drained soils and non-forest habitats.

Key Words.—abundance; distance sampling; Florida scrub; pine flatwoods; pine plantations; prairies; soils

Introduction

Spatial variation in population density arises from complex demographic and behavioral responses to differences in environmental conditions and resource availability. The specific processes regulating population size and density can be difficult to ascertain for reptiles that are long-lived or hard to observe. These traits are characteristic of chelonians, most of which are also experiencing severe population losses due to anthropogenic modification and other stressors (Lovich et al. 2018; Stanford et al. 2020). An example is the Gopher Tortoise (*Gopherus polyphemus*), a fossorial species endemic to southeastern U.S. Coastal Plain ecosystems. Gopher Tortoise populations are declining, principally due to habitat loss and degradation, and receive some level of legal protection in all six states within the historic range of the species (U.S. Fish and Wildlife Service [USFWS] 2021). Sea-level rise, urbanization, and decreased habitat management pose significant threats to long-term persistence of the species (Folt

et al. 2022). Although Gopher Tortoises are known to use varied upland habitats (Auffenberg and Franz 1982; Diemer 1986), a lack of habitat-specific data on vital rates hinders our understanding of population dynamics. This in turn makes it difficult to prioritize habitat protection and management efforts, estimate impacts of further habitat loss, determine appropriate densities for translocation programs, and set realistic recovery goals. These conservation activities are all the more important considering the ecological importance of Gopher Tortoises and their burrows to the ecosystems in which they occur (Catano and Stout 2015; Johnson et al. 2017).

The U.S. Department of Defense initiated Gopher Tortoise monitoring at several military installations pursuant to the 2008 Candidate Conservation Agreement (USFWS 2012; Partners in Amphibian and Reptile Conservation [PARC] 2022), which advocated use of Line-transect Distance Sampling (LTDS). The difficulty in directly estimating vital rates for populations of a long-lived species such as the Gopher Tortoise has led to using interpretations

of density to inform management, for example, when assessing population viability (Gopher Tortoise Council 2013) or setting stocking thresholds for translocations (Florida Fish and Wildlife Conservation Commission 2023). Line-transect Distance Sampling is an efficient and statistically robust method for estimating density, particularly with recent advances that enable implementation across sites and habitats having widely varying population densities (Buckland et al. 2001, Stober et al. 2017). These flexible LTDS approaches have proven useful at our study site, Avon Park Air Force Range (APAFR), a large military training area in south-central Florida (Fig. 1). In this and other large, undeveloped landscapes, heterogeneity in population densities is reflective of historical conditions and the natural ecological factors dictating carrying capacity for Gopher Tortoises. The varied ecological communities of APAFR provide an opportunity to examine Gopher Tortoise density in relation to the distinctive soil, vegetation, and hydroclimatic conditions of peninsular Florida.

As currently understood, the habitat requirements of Gopher Tortoises include herbaceous ground cover for foraging, ground-level sunlight for thermoregulating, and soils appropriate for burrowing and nesting (Auffenberg and Iverson 1979; Auffenberg and Franz 1982; Diemer 1986; Mushinsky et al. 2006; Pudner et al. 2021). The Gopher Tortoise is typically associated with sandy, well-drained soils characteristic of Longleaf Pine (*Pinus palustris*) savanna and sandhill ecosystems. In peninsular Florida, Longleaf Pine savanna and sandhill are scarce, largely replaced by Florida scrub assemblages (Myers 1990) or habitats that can be broadly classified as grasslands, such as dry prairie, dune and coastal grasslands, pine flatwoods, and pine rocklands (Noss 2013). Prairie-type habitats once covered more than 809,000 ha of peninsular Florida, but have been reduced by about 90%, mostly due to conversion to pasture (Noss 2013). Although Gopher Tortoises readily use these habitats (Castellón et al. 2012; Pawelek and Kimball 2014; Whitfield et al. 2022), the ecological significance of prairies and other grasslands in Florida, and the loss of these habitats, are largely underappreciated.

Pine flatwoods and Florida scrub assemblages comprise the majority of suitable habitat for Gopher Tortoises in peninsular Florida. Although fire-maintained pine flatwoods and scrub habitats both provide suitable open-canopy conditions, tortoises occur at relatively low densities in these habitats (Auffenberg and Franz 1982; Hipes 2008; Castellón et al. 2012), which suggests habitat quality may be limited with respect to soils and forage availability. Soils in Florida scrub are amenable for burrow construction and nesting, but herbaceous forage is extremely sparse (Myers 1990; Castellón et al. 2012). In contrast, pine flatwoods have abundant forage, but the poorly drained soils are less suitable for burrowing and frequently flood during the summer wet season (Abrahamson and Hartnett 1990; Castellón et al. 2012). Nevertheless, Gopher Tortoises in southern Florida frequently use these relatively poorly drained soils and will continue to occupy inundated burrows (Means 1982; Diemer 1992; Castellón et al. 2018), suggesting the fundamental niche of this species may be broader than traditionally recognized. The importance of soil hydrological characteristics is not well understood, however, especially in light of the high annual variation in precipitation typical of Florida. Furthermore, prairie communities occur on similar soil associations as pine flatwoods, but Gopher Tortoise use of prairies is poorly studied (but see Enge et al. 2014).

Our primary study objective was to estimate and compare densities of Gopher Tortoises and burrows across a gradient of xeric to mesic habitats in south-central Florida. By expanding our surveys into previously unsampled prairie communities, we aimed to clarify the tolerance of poorly drained soils by the species. In addition to determining habitat-specific densities, we produced the first estimate of total abundance of Gopher Tortoises at APAFR to aid in range-wide conservation planning.

Materials and Methods

Habitat description and stratification.—Avon Park Air Force Range (42,910 ha) is located within Highlands and Polk counties, Florida, USA. The range is bisected by the Bombing Range Ridge, a sandy ridge 5−6.5 km wide rising to elevations of 12−20 m above the surrounding Osceola and Okeechobee Plains (White 1970; U.S. Air Force [USAF] 2022). Habitat stratification for our survey relied on a geographic information system (GIS) vegetation classification produced by APAFR (Edwin Bridges, unpubl. report) and soil mapping produced for Highlands and Polk counties (Carter et al. 1989; Ford et al. 1990). To delineate suitable habitats, we combined several fine-scale vegetation classes into four broad categories likely to support Gopher Tortoises based on suitable soils: scrub (2,577 ha),
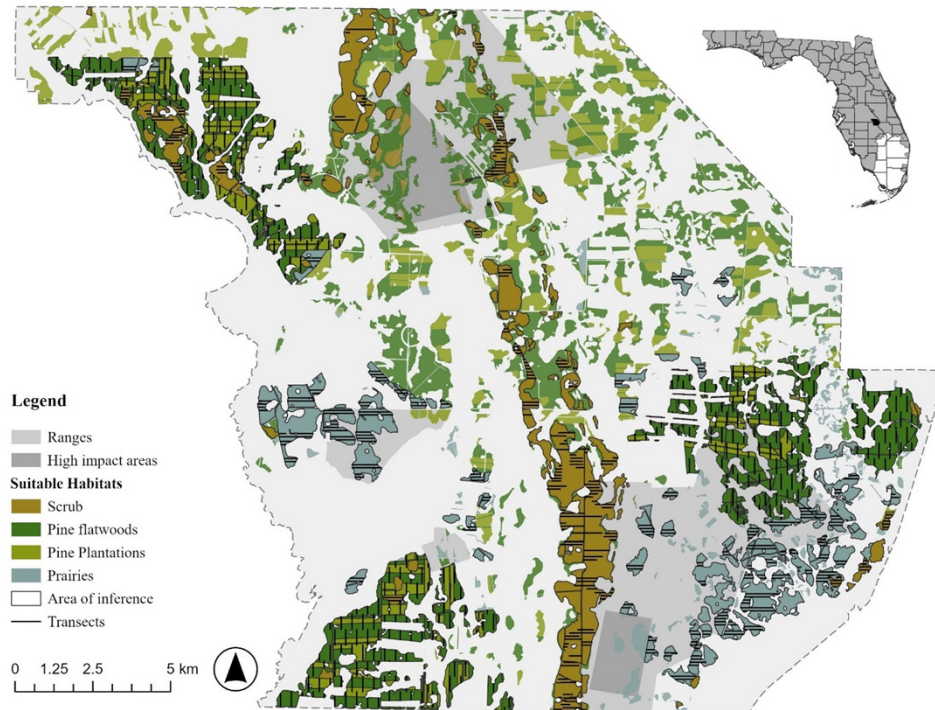
FIGURE 1. Gopher Tortoise (*Gopherus polyphemus*) population survey using Line-transect Distance Sampling methodology during 2022 and 2023 in suitable scrub, pine, and prairie communities at Avon Park Air Force Range (APAFR), Florida, USA. Suitable habitat was delineated based on soils suitable for Gopher Tortoises. The area of inference in each habitat is outlined; suitable habitat not included in the area of inference is slightly lighter in color. Shaded region in the map of Florida (upper right) is the species distribution in the State, with APAFR as a black polygon.

pine flatwoods (7,018 ha), pine plantations (3,302 ha), and prairies (2,156 ha; Fig. 1, Fig. 2). We determined soil suitability within the target communities by reviewing the literature (i.e., USFWS and Natural Resources Conservation Service 2012) and following recommendations made by APAFR botanist Steve Orzell (pers. comm.). For purposes of transect placement, we excluded small, isolated patches of habitat (generally patches <10 ha) and habitat within impact ranges where access is restricted, resulting in a slightly smaller area of inference for generating model estimates (Fig. 1). Soils in Florida with similar seasonal high water tables (SHWT) were grouped into drainage classes defined by the U.S. Department of Agriculture (Schuster 2015). Scrub communities occur on a mix of well-drained soils (SHWT >150 cm; Archbold Sand), moderately well-drained soils (SHWT: 60–120 cm; Pomello, Daytona, and Duette Sands), and somewhat poorly drained soils (SHWT: 30–75 cm; Satellite, Adamsville, Narcoossee, and Zolfo Sands), whereas pine and prairie communities occur predominantly on poorly drained soils (SHWT 0–45 cm; Myakka, Immokalee, Eau Gallie, and Oldsmar Sands). Small amounts of poorly drained Wabasso Sand, Basinger Sand, and St. John's Basinger Placid Soils were also included in our study area.

The Bombing Range Ridge is characterized by well-drained to somewhat poorly drained soils and a patchy mosaic of scrub vegetation communities, including oak scrub, sand pine scrub, scrubby flatwoods, and small areas of sandhill. Scrub assemblages typically occur with or without pine canopy (Sand Pine, *Pinus clausa*, South Florida Slash Pine, *P. densa*, and/or *P. palustris*) over a subcanopy of scrub oaks (Chapman Oak, *Quercus chapmanii*, Sand Live Oak, *Q. geminata*, and Myrtle Oak, *Q. myrtifolia*) and ericaceous shrubs (Fetterbush, *Lyonia lucida*, Coastalplain Staggerbush, *L. fruticosa*, and Tarflower, *Bejaria racemosa*) interspersed with openings of bare sand and sparse herb cover. Scrub communities of the ridge grade into pine flatwoods/savannas and prairie communities in the surrounding plains. Pine flatwoods are the most extensive vegetation community on APAFR and are characterized by a sparse to moderately dense canopy of *P. densa* or *P. palustris* and a continuous, fire-maintained ground cover of grasses (bluestem, *Andropogon* spp. and Wiregrass, *Aristida beyrichiana*), sedges (*Carex* spp.), forbs, and low shrubs (Saw Palmetto,
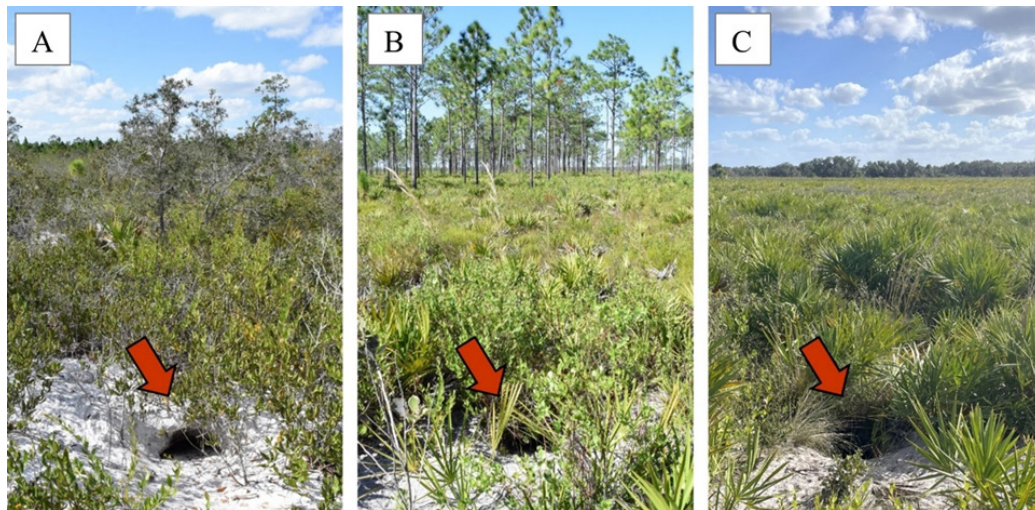
FIGURE 2. Adult-sized Gopher Tortoise (*Gopherus polyphemus*) burrows in (A) scrub, (B) flatwoods, and (C) prairie at Avon Park Air Force Range, Florida, USA. Red arrows indicate burrow entrances**.**

Serenoa repens, Dwarf Live Oak, *Quercus minima*, and staggerbush and fetterbush, *Lyonia* spp.). The boundary between pine flatwoods and prairies is often gradual and not clearly distinguished, as overstory density of pine flatwoods may be very low in some areas due to cyclic changes in tree maturation and fire frequency. Pine flatwoods and prairies occur as dry-mesic and mesic vegetation associations (Orzell and Bridges 2006). Current management prescriptions at APAFR call for controlled burning every 7–20 y in scrub and every 2–3 y in pine flatwoods and prairies.

Pine plantations included in our survey were even-aged stands of Slash Pine (*Pinus elliottii*) planted on soils that would otherwise support mesic or dry-mesic pine flatwoods. Pine plantations were established in the 1960s and 1970s with sawlogs and mulchwood being primary production end states (USAF 2022). A reforestation program initiated in 1999 sought to replace *P. elliottii* with *P. densa* and *P. palustris*, and since then, forest management has followed an adaptive ecological and restorative approach. Following this shift in management, clearcut pine plantations are treated with prescribed fire and planted back with local seed-sourced pine. Pre-commercial thinning is used in planted and natural pine stands to reduce competition and maintain desirable understories. We surveyed pine plantations representing all stages of production, including areas that had historically been planted and managed for pine production but were left fallow to regenerate naturally. Pilot surveys revealed absence of Gopher Tortoises in un-thinned pine plantations that had been planted between 2000 and 2012 (10–20 y since planting), leading us to exclude these pine plantations from the final sampling frame of suitable habitat. Pine plantations are burned every 2–3 y between December and April.

Survey design.—We implemented a random survey design in scrub and prairie communities (Fig. 1). To enable long-term population monitoring in scrub, we resampled approximately the same set of randomly placed transects surveyed by Castellón et al. (2012). We added 2.2 km of additional randomly placed transects to replace transects in areas of restricted access, and we adjusted the length of some transects to allocate effort roughly in proportion to the relative extent of each scrub community type. When Gopher Tortoises are patchily distributed, as expected in sub-optimal habitats such as prairie, between-transect variation in burrow encounters has a large influence on overall variance and constrains the precision of population abundances, especially when using a random survey design such as the one we implemented in scrub (Buckland et al. 2001; Stober et al. 2017). Despite this, we moved forward with a random design in prairie communities due to time and logistical limitations and because our primary goal was to gather preliminary data in a poorly studied habitat. To replicate the efficiency of pseudo-circuits used by Stober et al. (2017), we created pairs of transects spaced 100 m apart at

randomly selected locations and stratified effort to be roughly proportional to the relative extent of dry-mesic and mesic community types in our study area.

To inform a full survey design in pine communities, we conducted a pilot survey in January and February 2023 comprising 29.6 km of pseudo-circuits randomly placed across the entire extent of suitable pine communities. We detected 14 adult-sized tortoises in 127 non-collapsed adult-sized burrows, yielding an encounter rate of 0.47 tortoises/km (4.29 burrows/km). Given this encounter rate, the projected full survey effort to achieve a coefficient of variation (CV) of 20% was 158 km (Buckland et al. 2001). Due to the large spatial extent of pine communities at APAFR, we predicted tortoise density and occupancy would vary not only with local factors such as soils, but also in relation to connectivity to other suitable habitat. Time constraints imposed by the short duration of the dry season and military training activities led us to implement a full survey of systematically placed transects focused in three regions of pine communities (Fig. 1). The systematic approach ensured representative coverage of pine flatwoods and pine plantation communities, while focusing effort in only three regions captured spatial heterogeneity of burrows at a finer scale than a systematic design of the same survey length spread across all regions. Furthermore, we expected that surveying a smaller spatial extent more thoroughly would result in greater precision in model estimates (Buckland et al. 2001).

We placed systematic north-south-oriented transects in pine flatwoods and pine plantation communities using the Create Fishnet and Generate Transect Along Line tools in ArcGIS Pro (version 3.0.2). Transects were 500 m long separated by 300 m east to west and 500 m north to south. At our study site, portions of native pine flatwoods were converted into pine plantations, creating interspersed strips of native pine flatwoods and pine plantations oriented east-west longwise. Thus, we oriented our transects perpendicularly to cover both habitat types more effectively and avoid oversampling edge habitat. We elected to adapt our full survey design to consist of unpaired transects rather than pseudo-circuits, which allowed us to survey a greater spatial extent in the time available.

Tortoise burrow surveys.—As recommended by Castellón et al. (2012), we conducted LTDS surveys during the later part of the dry season to minimize the proportion of burrows that were inundated, thereby improving the likelihood that tortoises would be detected by scoping burrows with a camera. We conducted burrow surveys January-April 2022 in scrub, May 2022 in prairie, and March-May 2023 in pine flatwoods and pine plantations. One observer navigated while searching for burrows on and near the transect line while two additional observers searched for burrows outward from the transect, walking 3–5 m from the observer on the centerline (Smith et al. 2009). We used a handheld Trimble TDC600 unit paired with a Trimble R1 Global Navigation Satellite System (GNSS; Trimble, Westminster, Colorado, USA) with sub-meter accuracy and real-time data correction to record transect start and end points and navigate the transect line. Real-time data correction ensured the center observer closely navigated the transect. We made every effort to find all burrows on the centerline to satisfy key assumptions of distance modeling that every burrow on the transect itself is detected, that detection probability decreases with increasing distance from the transect, and that perpendicular distances are measured accurately (Buckland et al. 2001). Sub-meter accuracy allowed us to obtain accurate perpendicular distances from burrows to the centerline without measuring distances in the field. In addition to the assumptions of distance modeling, we also assumed burrow occupancy rates were equal across the study period to account for the nonoverlapping timing of surveys.

We recorded the location and scoping outcome of every burrow detected along each transect in the Trimble using TerraFlex software (Version 5.6.1.1). To determine occupancy, we scoped every burrow greater than 0.5 m long and 14 cm diameter using a burrow camera system consisting of a camera attached to a 7.5-m-long flexible hydraulic hose wired to a video monitor (Environmental Management Systems, Canton, Georgia, USA). Burrows ≤ 14 cm wide were too small to accommodate the camera. After scoping, we classified burrows as occupied, unoccupied, or undetermined occupancy (due to presence of water or complex burrow architecture that prevented scoping). We also classified the activity status of each burrow based on its length, presence of tortoise sign (tracks or shell drag marks), and presence of debris in the entrance, resulting in four classifications: (1) collapsed, burrows that were fully occluded by soil < 1 m from the entrance; (2) active, tortoise sign present at the entrance of the burrow; (3) possibly active - maintained, tortoise sign absent and burrow entrance was free of debris; and (4) possibly active - not maintained, tortoise sign

absent and burrow entrance contained debris. We refer to active and possibly active burrows combined as non-collapsed burrows. We measured burrow width 50 cm inside the burrow using calipers (Smith et al. 2009). Because burrow width is correlated with tortoise size (Martin and Layne 1987), burrow widths indicate the size and thus approximate age class of the resident tortoise. We classified burrows as adult-sized (≥ 23.5 cm), subadult-sized (≥ 14.5 and ≤ 23 cm), or juvenile-sized (≤ 14 cm; Smith 1995). If a juvenile-sized burrow was too narrow for our calipers, we measured approximate burrow width at the entrance using a tape measure.

In pine communities, we measured the degree of concealment by vegetation at each burrow using a Robel Pole (Robel et al. 1970). The pole consisted of a 1.5-m-long PVC pipe with a diameter of 3.5 cm. The pole was marked with 30, 5-cm increments numbered one through 30 starting from the bottom of the pole. Concealment was measured as the lowest increment that was at least 50% unobscured. We aligned the pole with the mouth of the burrow and an observer estimated concealment from an eye-level of 1 m above the ground. We estimated concealment 3 m from the burrow entrance in three cardinal directions and used the average of the three measurements.

Data analysis.—To prepare the data for analysis, we determined transect length by converting start and end points to lines in ArcGIS. The length of transects varied, but never exceeded 1.2 km. We then calculated perpendicular distance from the transect line to each burrow using the Near tool. Total study area, transect lengths, perpendicular distances, and possible covariates such as burrow width, burrow activity status, and vegetation concealment were formatted and uploaded into Program Distance 7.3 Release 2 (Thomas et al. 2010).

For each vegetation community, we ran a series of models following Smith and Howze (2016) with the conventional distance sampling engine using combinations of key functions (half normal, uniform, and hazard rate) and series expansion functions (cosine and simple polynomial). We truncated the farthest 5% of detections in all models to remove outliers and aid in model fitting (Buckland et al. 2001; Thomas et al. 2010). For scrub and pine communities, we used a standard analysis that included only the occupied burrows when modeling the detection function. We generated stratified tortoise abundance and density estimates for pine flatwoods and pine plantations using a single global detection function. Due to small sample size, we used a cluster analysis in prairie communities that first estimated usable burrow abundance and then corrected for burrow occupancy to estimate tortoise abundance (Stober et al. 2017). Tortoise density and abundance were estimated as the weighted average stratified by dry-mesic and mesic prairie types.

We included detection covariates using the multiple covariate distance sampling engine in Distance when factors might influence the rate of the detection function curve but not the shape. Specifically, the scrub and pine community models included burrow width as a covariate because these datasets included subadult- and adult-sized tortoises/burrows and we expected detection probability to be lower for smaller burrows. We modeled detection in prairie communities using only adult-sized burrows as we did not detect subadult tortoises in prairies. We also included burrow activity status as a covariate in all vegetation communities to account for potential differences in detection rate based on apron appearance. In pine communities, we included vegetation concealment as a covariate because vegetation density and height tend to be greater compared to scrub communities but also varies among different areas of pine. We expected burrows to be more detectable in areas with shorter vegetation such as soon after fire (Howze and Smith 2019; Gaya et al. 2023). For the cluster analysis of prairie data, we also ran models that included occupancy status (occupied or unoccupied) to confirm the assumption that detectability of unoccupied usable burrows was the same as occupied burrows (Stober et al. 2017). These models did not support that detection varied with occupancy, so we omitted this covariate from subsequent models.

We assessed the fit of each model using Kolmogorov-Smirnov tests and by examining the shape of the detection curve and the linearity of the quantile-quantile plot (Thomas et al. 2010; Buckland et al. 2015). We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to compare models with and without covariates. When models were equally well supported ($\Delta AIC \leq 2$), we deemed the model with the lowest CV and/or the one with the most probable detection curve to be the best model for estimating tortoise density and population size.

We determined overall tortoise density by using habitat-specific density estimates and associated variances to calculate a weighted average across all suitable habitats (Eric Rexstad, pers. comm.). We then used this global density to calculate a log-based

Table 1. Summary of sampling effort and detections of burrows and Gopher Tortoises (*Gopherus polyphemus*) during 2022 Line-transect Distance Sampling surveys of scrub and prairie communities and 2023 LTDS surveys of pine communities at Avon Park Air Force Range, Florida, USA. Numbers of burrows are the numbers observed before truncating data for further analyses.

	Scrub 2022	Pine Flatwoods 2023	Pine Plantations 2023	Prairie 2022	All communities
Total transect length (km)	56.8	80.5	30.6	59.2	227.1
Total no. of adult and subadult non-collapsed burrows detected	470 (8.3/km)	684 (8.5/km)	131 (4.3/km)	119 (2.0/km)	1,404 (6.2/km)
No. of adult and subadult tortoises detected	120 (2.1/km)	104 (1.3/km)	25 (0.8/km)	19 (0.3/km)	268 (1.2/km)
No. of burrows with undetermined occupancy (no. due to water)	28 (3)	124 (113)	25 (22)	3 (3)	180 (141)
Burrow occupancy (%)	25.5	15.2	19.1	16.0	19.1

confidence interval (Supplemental Information: Combining density and variance estimates across geographic strata). Applying the density estimate and confidence interval across the entire area of suitable habitat, we estimated total population size. We also extrapolated the pine community density estimates from the area of inference (the three sampled regions) to all suitable pine communities, with the assumption that variance in tortoise encounter rate across all pine communities is equal to the observed variance in the area of inference.

To complement habitat-specific population estimates, we examined patterns in burrow encounter rate and size-class distributions with respect to vegetation communities and soil characteristics. For these analyses, we used the entire dataset of non-collapsed burrows (before 5% truncation). As reference, soil drainage refers to the frequency and duration of wet periods, and available water capacity is a measure of the quantity of water that a soil can store for use by plants. For each vegetation community, we used Chi-squared Goodness-of-fit tests to compare proportional distribution of subadult- and adult-sized burrows in different soil drainage classes to the expected distribution based on sampling effort. Given the relatively small proportion of well-drained and moderately well-drained soils present in pine flatwoods, pine plantations, and prairies compared to scrub, we used an alpha level of 0.10 and accepted the greater probability of a Type I error for this test. We then used adjusted standardized residuals to identify the soil drainage classes that significantly contributed to observed differences, where residuals > 1.96 or < -1.96 indicated a significant contribution (Sharpe

2015). We also fitted a regression to the relationship between burrow encounter rates and available water capacity in each soil pooled across all suitable habitats. We obtained soil data for our inference area from the Web Soil Survey database (https://websoilsurvey. sc.egov.usda.gov/App/WebSoilSurvey.aspx).

Results

We surveyed 56.8 km of transects in scrub, 80.5 km in pine flatwoods, 30.6 km in pine plantations, and 59.2 km in prairies (Fig. 1). We detected 1,404 non-collapsed subadult- and adult-sized burrows and 268 tortoises (Table 1). Including burrows for which occupancy could not be determined, burrow occupancy ranged from 15.2% in pine flatwoods to 25.5% in scrub (Table 1). We could not determine occupancy for 6% of burrows in scrub, 18% in pine flatwoods, 19% in pine plantations, and 3% in prairie. An unnavigable obstruction (sharp turn, soft sand, roots) was the most common cause of undetermined occupancy in scrub, whereas presence of water in the burrow was the most common cause in pine and prairie communities (Table 1).

The burrow size-class distributions derived from our LTDS surveys were strongly skewed toward adult sizes (Fig. 3). This trend was more pronounced in pine (flatwoods, plantations) and prairie communities, where 93–95% of non-collapsed burrows were adult-sized compared to 74% of burrows in scrub. Subadult- and juvenile-sized burrows represented 15% and 11% of non-collapsed burrows in scrub, respectively, whereas only 3–5% and 1–2% of non-collapsed burrows in pine flatwoods, pine plantations,
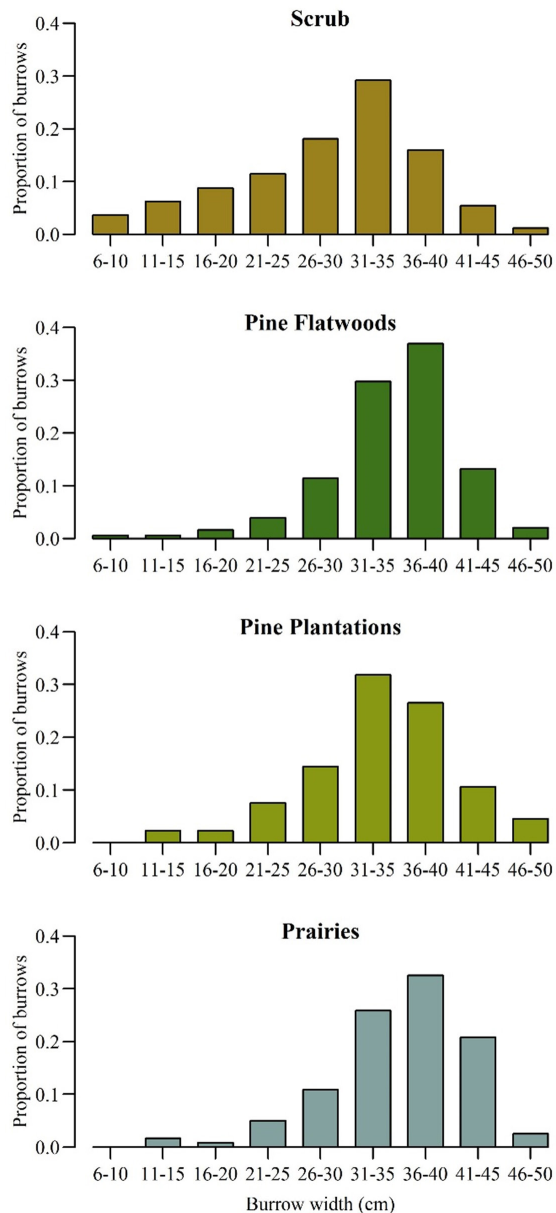
FIGURE 3. Size-class distributions of non-collapsed Gopher Tortoise (*Gopherus polyphemus*) burrows detected during Line-transect Distance Sampling surveys in (A) scrub, (B) pine flatwoods, (C) pine plantations, and (D) prairies at Avon Park Air Force Range, Florida, USA, in 2022–2023. We classified burrows as adult-sized (≥ 23.5 cm), subadult-sized (≥ 14.5 and ≤ 23 cm), or juvenile-sized (≤ 14 cm; Smith 1995). Histograms are colored as in Figure 1.

and prairies were subadult- and juvenile-sized.

The proportion of adult- and subadult-sized burrows found in each soil drainage type differed significantly from the proportion surveyed for scrub (X^2 = 10.3, df = 3, P = 0.016), pine flatwoods (X^2 = 5.1, df = 2, P = 0.079), and pine plantations

(X^2 = 4.4, df = 1, P = 0.047; Fig. 4). In scrub, we found a smaller proportion of burrows in well-drained soils and a greater proportion in somewhat poorly drained soils than expected based on survey effort. In pine communities, we detected a smaller proportion of burrows in poorly drained soils than expected. Although we detected juvenile-sized burrows in all four soil drainage classes, sample sizes were not sufficient to assess trends. The encounter rate of subadult- and adult-sized burrows related to available water capacity in a quadratic manner (Fig. 5; burrows = -2,575.98 × water capacity^2 + 391.75 × water capacity - 5.293; $F_{2,11}$ = 4.541; P = 0.036; r^2 = 0.45). Burrow encounter rates were very low in soils with available water capacity greater than 0.10, whereas encounter rates in Zolfo and Pomello sands were disproportionately high compared to the values predicted by the regression.

For estimating abundance and density of subadult- and adult-sized Gopher Tortoises, we found strong support for multiple detection models in each vegetation community (ΔAIC ≤ 2; Table 2). Inclusion of burrow width as a covariate in the LTDS models did not improve AIC values in any vegetation community, thus we did not include these models in Table 2. For scrub, we selected the uniform simple polynomial model with no covariates as the best model (based on shape and CV; see Supplemental Information Fig. S1). For pine communities, we determined the hazard rate model with vegetation concealment as a covariate was the best model for inference. Though it did not have the lowest AIC, goodness-of-fit was much higher than the half normal key function (0.986 compared to 0.668). In pine communities, detection decreased at a faster rate with increased vegetation concealment. For prairies, models including burrow activity status were better supported than models with no covariates, and the half normal model with activity status was the best-fit model based on AIC. In prairies, detection of active burrows did not vary with distance, whereas detection of possibly active burrows decreased with distance from the centerline.

The encounter rate of subadult- and adult-sized tortoises decreased monotonically from scrub (2.1/ km) to prairies (0.3/km; Table 1). Estimated tortoise density decreased in the same manner, from 0.95 tortoises/ha in scrub (CV 12.0%) to 0.18 tortoise/ ha in prairies (CV 30.3%; Table 3). Sample sizes were too small to obtain estimates with CV < 20% in pine plantations and prairies. Despite obtaining density estimates with CV ≤ 15% in scrub and pine

TABLE 2. Best-fit detection models for Line-transect Distance Sampling surveys of Gopher Tortoises (*Gopherus polyphemus*) conducted in 2022 and 2023 at Avon Park Air Force Range, Florida, USA. Sample size (n) shown after 5% data truncation. Estimates for scrub and pine communities were derived from standard analyses (n = number of tortoise detections). Estimates for prairies were derived from cluster analysis (n = number of usable burrow detections). The abbreviation ESW = effective strip width (m). An asterisk (*) indicates selected models. Goodness-of-fit (GOF) was assessed with Kolmogorov-Smirnov tests. See Supplemental Information for associated detection curves and quantile-quantile plots.

Key function + adjustment term	n	Detection probability (CV)	ESW	ΔAIC	GOF p-value
Scrub					
Uniform + simple polynomial*	114	0.70 (0.04)	10.51	0.00	0.899
Hazard Rate	114	0.78 (0.06)	11.76	1.58	0.972
Half Normal	114	0.72 (0.10)	10.85	1.77	0.978
Uniform + cosine	114	0.68 (0.17)	10.26	1.99	0.990
Pine Flatwoods and Pine Plantations					
Half Normal + veg concealment	123	0.50 (0.07)	9.44	0.00	0.668
Hazard Rate + veg concealment *	123	0.45 (0.07)	8.49	1.57	0.986
Prairies					
Half Normal + activity status*	98	0.52 (0.07)	7.88	0.00	0.915
Hazard Rate + activity status	98	0.51 (0.07)	7.83	1.41	0.696

flatwoods, the 95% confidence intervals spanned approximately 0.50 tortoises/ha and the considerable overlap indicated no difference in density between these vegetation communities. In fact, scrub and prairies represented the only habitat-specific pairwise comparison that differed significantly in tortoise density. Estimated global tortoise density across suitable scrub, pine flatwoods, pine plantations, and prairie communities on APAFR was 0.62 tortoises/ha

(95% confidence interval [CI] = 0.52–0.74), which yielded a total abundance of 9,367 subadult and adult tortoises (95% CI = 7,899–11,109; Table 3).

We estimated tortoise abundance in prairies as a weighted average stratified by prairie type with mean cluster sizes of 0.23 ± 0.052 (standard error) in dry-mesic prairie and 0.069 ± 0.048 in mesic prairie. After data truncation, our dataset consisted of 66 adult-sized burrows detected in 26.0 km of transects
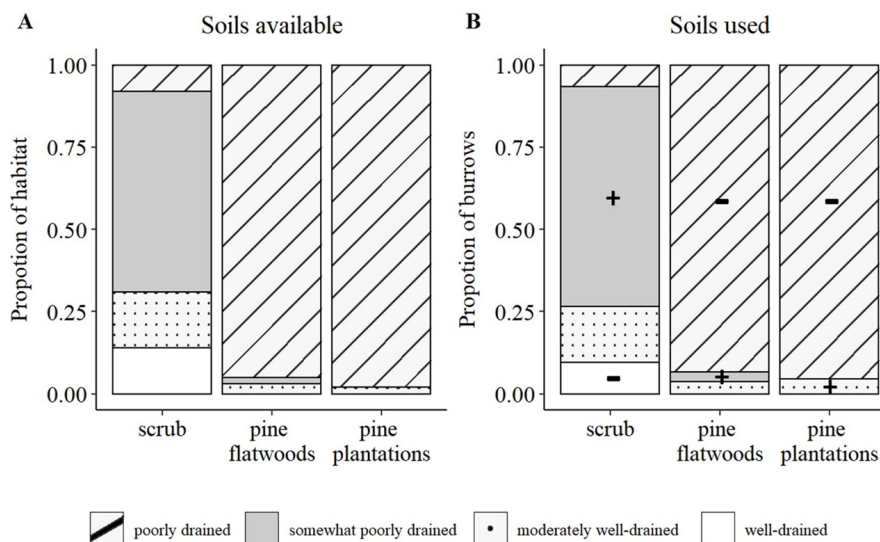

FIGURE 4. Distribution of surveyed habitat (left) and non-collapsed subadult- and adult-sized Gopher Tortoise (*Gopherus polyphemus*) burrows (right) with respect to four soil drainage classes. Soil classes contributing to significant differences are denoted with plus (+) if the proportion of burrows was greater than expected and (-) if the proportion of burrows was less than expected. All soils in prairie communities were poorly drained and are not shown here.

TABLE 3. Estimated Gopher Tortoise (*Gopherus polyphemus*) density (D) and abundance (n) in different vegetation communities at Avon Park Air Force Range, Florida, USA, based on selected Line-transect Distance Sampling models in Table 2. Units of measurement are ha (area), number of adult and subadult tortoises per ha (density), and number of adult and subadult tortoises combined (abundance). An asterisk (*) indicates we estimated tortoise abundance as the habitat-specific density estimate and associated 95% Confidence Interval (CI) multiplied by the habitat-specific area of suitable habitat. The abbreviation CV = coefficient of variation.

Habitat	Suitable habitat	Area of inference	Tortoise density			Tortoise abundance	
			D	95% CI	CV	n	95% CI
Scrub	2,577	2,493	0.95	0.75–1.21	12.0	2,379	1,879–3,011
Pine Flatwoods*	7,018	3,211	0.73	0.55–0.98	15.1	5,140	3,830–6,899
Pine Plantations*	3,302	1,244	0.44	0.26–0.76	27.7	1,464	856–2,503
Prairies	2,156	2,156	0.18	0.10–0.32	30.3	384	214–688
All communities*	15,053	9,104	0.62	0.52–0.74	8.7	9,367	7,899–11,109

in dry-mesic prairie and 32 adult-sized burrows detected in 33.2 km of transects in mesic prairie. Our selected model predicted a higher density of adult tortoises in dry-mesic prairie (0.37 tortoises/ha; 95% CI = 0.19–0.69) than in mesic prairie (0.04 tortoises/ha; 95% CI = 0.01–0.16). This corresponded to 331 tortoises (95% CI = 176–622; CV = 32.8%) in dry-mesic prairie and 53 tortoises (95% CI = 14–205; CV = 75.3%) in mesic prairie. We did not detect any subadult tortoises in prairies.
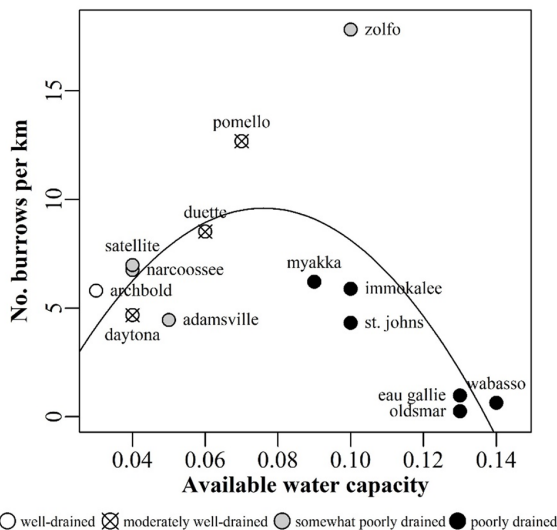

FIGURE 5. Encounter rates of non-collapsed subadult- and adult-sized Gopher Tortoise (*Gopherus polyphemus*) burrows versus available water capacity for 14 soil types surveyed at Avon Park Air Force Range, Florida, USA, in 2022–2023.

DISCUSSION

The patterns of burrow distribution and tortoise density we observed within this naturally heterogeneous, fire-managed landscape revealed how soils and other factors influence habitat suitability for Gopher Tortoises. In habitats of peninsular Florida there appears to be a trade-off between soils suitable for burrowing and soils that support adequate forage (Castellón et al. 2012). Available water capacity explained 45% of the variance in soil-specific burrow encounter rates at APAFR. Tortoises in xeric scrub communities preferentially used somewhat poorly drained soils that may be marginally suitable for burrowing but tend to have greater water capacity to support forage. In contrast, tortoises in mesic habitats tended to burrow in moderately well-drained soils, somewhat poorly drained soils, or poorly drained soils with relatively lower water capacity, such as Myakka and Immokalee sands. Differences in management history and vegetation structure are other factors that likely affect relative habitat suitability (Pudner et al. 2021) and may explain the disproportionately high burrow encounter rates in Pomello and Zolfo sands. Overall, the variation in subadult and adult densities across the xeric-mesic habitat gradient on APAFR implies differences in demographic rates (recruitment and survival) arising from corresponding variation in habitat quality (Folt et al. 2021).

Prairies seem to represent the boundary of the tolerance for mesic habitats by Gopher Tortoises, and our data fill a knowledge gap concerning this habitat type. According to our stratified distance model for prairies, more than 80% of the estimated tortoise abundance was in dry-mesic prairie habitat. This may be because saturated soil conditions of mesic prairie (Orzell and Bridges 2006) make it difficult for tortoises to excavate and maintain usable burrows. Castellón et al. (2020) hypothesized that tortoises in pine flatwoods cope with saturated soils and fluctuating water tables by seeking burrow sites with higher microtopographic elevations. Under these conditions, Gopher Tortoises may use more burrows and move more frequently among them (Castellón et al. 2018). Whether tortoises residing

in prairies exhibit similar behavioral responses to these dynamic hydrological conditions is unknown. The lower encounter rate of non-collapsed burrows in prairie compared to pine flatwoods could be a result of fewer tortoises present to maintain usable burrows, given that the entrance of burrows can completely collapse in as little as a few months if not maintained by a tortoise (Goodman et al. 2018). Guyer et al. (2012) found that movement and social patterns of Gopher Tortoises occurring at densities < 0.4 tortoises per ha were probably not conducive to viable populations. This threshold exceeds our density estimate (and 95% CI) for prairies overall but is bounded by the confidence interval for density in dry-mesic prairies (0.19−0.69 tortoises per ha; CV = 32.8%). In combination, these lines of reasoning lead us to propose that the low density of tortoises in prairies may limit the behavioral mechanisms (with respect to burrow use and mate-seeking behaviors) needed for long-term population persistence. In short, prairies may be sink habitats.

In the absence of habitat-specific vital rates and measures of individual fitness, it is difficult to draw conclusions regarding mechanisms that regulate populations of Gopher Tortoises inhabiting marginal habitats; that is, do Gopher Tortoise populations exhibit source-sink or resource-regulated population dynamics? Spatially extensive, transect-based surveys can only address this question superficially, especially given the lower detection rate of juvenile-sized burrows (Smith et al. 2009, Howze and Smith 2019). Nevertheless, burrow size-class distributions are frequently used to understand whether juvenile recruitment is occurring (e.g., Smith 1995; Tuberville et al. 2014; Folt et al. 2021), which in turn may reflect habitat quality (McCoy and Mushinsky 2007) and nest success (Castellón et al. 2022). In our 2023 survey, as well as past LTDS surveys at APAFR (Castellón et al. 2022), the dominance by adult-sized burrows was more extreme in pine communities. Additionally, when Castellón et al. (2022) conducted more intensive burrow mapping of selected pine flatwoods and scrub communities, they found that juvenile-sized burrows comprised 11–41% of burrows in scrub and < 3% of burrows in pine flatwoods. The consistency of these trends leads us to speculate that scrub may act as a source habitat, despite the lack of a significant difference in our tortoise density estimates for scrub and pine flatwoods. Goessling et al. (2021) found that periodic emigration and immigration among local aggregations of tortoises were important

aspects of population viability in the low-density populations of Alabama. Telemetry data from APAFR, on the other hand, revealed frequent forays by males to adjacent habitats, presumably to court females, but high site fidelity and little movement between habitats for female tortoises (Castellón et al. 2018). Tortoises were only followed for an average of 13 months, however, which could have been too short to capture immigration events. If immigration into low-density habitats is truly low, and individuals exhibit similar levels of fitness across habitats, then we could conclude that populations are regulated by available resources, as in two herbivorous marsupials occupying marginal habitat (Johnson et al. 2005). This question is unresolved for Gopher Tortoises and could have significant implications for future conservation and population management strategies, as populations regulated by source-sink dynamics are sensitive to disturbance to source habitats (Gilroy and Edwards 2017).

Our methods improved population estimates compared to Castellón et al. (2012), whose surveys were hindered by very high prevalence of burrow inundation in APAFR pine communities. Even so, apparently high baseline levels of burrow flooding, particularly in 2023, reduced the precision of our estimates. We explored cluster-based analysis (Stober et al. 2017) to increase precision of detection modeling for pine flatwoods, but ultimately deemed it less reliable because of the high proportion of burrows with unknown occupancy. Essentially, the uncertainty surrounding accurately estimating occupancy outweighed the benefits of having a larger sample size to estimate the detection function. The use of a cluster analysis for these habitats is further complicated by yearly variation in rainfall during the wet season preceding LTDS surveys. Even though the 2023 field season was characterized by La Niña conditions, which are typified by extremely low rainfall, we observed burrow flooding throughout the duration of the study. We attribute this to heavy rainfall associated with hurricanes Ian and Nicole in Fall 2022, leading to prolonged elevation of the water table. Twelve percent of burrows in pine communities were flooded during May 2023, further demonstrating that restricting surveys to even the driest months does not guarantee lower water tables. On the other hand, cluster analysis was appropriate for prairies given that we surveyed that habitat in a relatively dry year (2022) during the driest month (May), resulting in only < 3% of burrows being

flooded. The precision of our prairie estimates was instead limited by low sample size and high variance in encounter rates of burrows between transects resulting from patchy distribution. The use of systematic transect placement, pseudo-circuits, and measurement of visual obstruction could be used in the future to overcome these challenges in prairies and other low-density habitats, as we demonstrated in pine communities. Overall, obtaining usable LTDS estimates for these habitats required beneficial timing and careful consideration of alternative survey designs and analytical approaches. Combining LTDS methods with spatial modeling, such as density surface models (Miller et al. 2013), might provide additional insights into relationships between habitat-specific densities and soil hydrology (e.g., available water capacity, depth to water table), vegetation structure, and other environmental covariates.

By employing advanced LTDS methods across a variety of vegetation communities, we determined that APAFR supports a regionally significant population of 7,899–11,109 adult and subadult Gopher Tortoises. As noted by Castellón et al. (2012), densities of non-collapsed burrows in scrub and pine flatwoods communities at APAFR are within the typical range for these habitats in Florida but tend to be lower than in sandhill and longleaf pine ecosystems, both within Florida and elsewhere. Although Florida scrub and pine flatwoods may not be optimal habitats for Gopher Tortoises, the estimated landscape-level density of 0.52–0.74 subadult and adult tortoises per ha at APAFR greatly exceeds landscape-level densities on some publicly owned sites in other parts of the range, such as Conecuh National Forest, Alabama (0.14–0.32 tortoises per ha; Goessling et al. 2021) and Fort Gordon Army Installation, Georgia (0.02–0.03 subadults/adults per ha; Stober et al. 2017). Densities on APAFR are also similar to or greater than densities estimated for 11 of 26 state-owned sites surveyed in Florida using LTDS in 2016 (Lora Smith and Jennifer Howze, unpubl. data). Given current thinking regarding the minimum viable population criteria for Gopher Tortoises of 250 adults with a density of no less than 0.4 tortoises/ha (Gopher Tortoise Council 2013), APAFR clearly harbors at least one, but likely many, viable populations. The degree of connectivity among local aggregations within this landscape is unknown. Movement or genetic data are needed to delineate local populations and prioritize relatively isolated, occupied habitats that might benefit from more management attention

because of limited immigration from other occupied areas.

Gopher Tortoise use of mesic pine flatwoods, prairies, and other non-forest habitats expands our understanding of their ecological niche. While their use of dry-mesic prairie and (to a much lesser extent) mesic prairie is not a novel finding, our study provides the first density estimate for Florida prairie habitat and provides new insights into the relative suitability of specific soil types for Gopher Tortoises in the southern portion of their range. Until there is better understanding of the roles of immigration and recruitment in maintaining Gopher Tortoise populations in pine and prairie communities dominated by poorly drained soils, it is unclear how to prioritize and manage these populations. For now, the lack of intensive demographic monitoring at most sites means that management decisions will continue to be based on careful interpretation of density data and supplemental information like age-class structure. Unbiased estimates of tortoise densities from well-managed landscapes, such as those reported here, may serve as reference densities for assessing impacts of future habitat loss and setting appropriate stocking densities for translocation and population augmentation efforts.

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