Status, Distribution, and Management of Gopher Tortoises in Highly Urbanized Southeastern Florida

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Abstract - *Gopherus polyphemus* (Gopher Tortoise) populations are declining throughout their range. Western Gopher Tortoise populations have received strict legal protections and substantial research, yet similarly declining populations in southeastern Florida have received far less conservation and research attention. Herein we conduct the first review of Gopher Tortoise populations in extreme southeastern Florida (Palm Beach, Broward, and Miami-Dade counties), an area heavily impacted by anthropogenic stressors such as urbanization, habitat fragmentation, and climate change. Our objectives were to document the existing distribution of Gopher Tortoises in southeastern Florida, to assess age structure, to evaluate habitat associations, and to review habitat-management activities at focal sites in this region. Among the authors, we knew of 8 focal Gopher Tortoise sites in South Florida. We supplemented this site knowledge with occurrence records from community-science databases, and we found 30 additional ground-verified, tortoise localities across the study area. We surveyed burrows at the 8 focal sites and measured burrow width at 1283 burrows across 6 of these focal sites to estimate age structure. Tortoise populations were generally in small, protected areas (average of 43 ha, median of 18 ha). Of our 6 sites with burrow-size data, all showed presence of adult and juvenile burrows consistent with reproduction, but 4 showed bimodal size structures suggesting low or intermittent survival of subadult tortoises. This data synthesis should be foundational for the development of evidence-based conservation planning for populations of the species confronted by impacts from urbanization and climate change. We highlight conservation and research needs for tortoise populations in extreme southeastern Florida.

Introduction

Gopherus polyphemus (Daudin) (Gopher Tortoise) is a resident of upland *Pinus* (pine) communities of the southeastern coastal plain of the United States, where it is threatened range-wide through habitat loss and habitat degradation, impacts of other anthropogenic activities, and emerging infectious disease (Ashton and Ashton

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2008, Auffenberg and Franz 1982, Folt et al. 2022, FWC 2012, Mushinsky et al. 2006, Smith et al. 2006). Gopher Tortoises are protected by state endangered species laws in all states where they naturally occur, and western populations of the species are protected as threatened under the US Endangered Species Act. Gopher Tortoises serve an important ecological role as ecosystem engineers by creating deep burrows, which perturb soil and serve as a refuge for ~360 species of animals, some of which themselves are threatened or endangered species (Dziadzio and Smith 2016, Lips 1991). Furthermore, as generalist herbivores, the tortoises consume and disperse seeds of dozens of plant species (Birkhead et al. 2005, Carlson et al. 2003, Figueroa et al. 2021, Hanish et al. 2020), and significantly influence plant community structure (Gilliam et al. 2021; Lloyd et al 2023; Richardson and Stiling 2019a, b). Because of the Gopher Tortoise's role in increasing the diversity of organisms where it occurs, it is considered a keystone species and has been classified as a species of greatest conservation concern in Florida (FWC 2012).

Gopher Tortoises have been the subject of intense research and conservation efforts through much of their range (Auffenberg and Franz 1982, Folt et al. 2022, Mushinsky et al. 2006, Schwartz and Karl 2005, Smith et al. 2006). Still, there exists distinct confusion over the presence, status, and conservation needs of Gopher Tortoises in southeastern Florida (FWC 2012, Page-Karjian et al. 2021, Whitfield et al. 2022). In southeastern Florida (herein defined as Palm Beach, Broward, and Miami-Dade counties), tortoise populations face heavy impacts from habitat loss, urbanization, and climate change (Folt et al. 2022).

The earliest western science accounts of Gopher Tortoises in the study area are from European settlers who describe Gopher Tortoises as a food source in the 19th and early 20th century (Ammidown 1982, Monroe 1943, Worth 2012). Naturalists reported Gopher Tortoises from the area in the 20th century (Carr 1940, Duellman and Schwartz 1958, Simpson 1920), although details were scant with regard to abundance or distribution. Auffenberg and Franz (1982) conducted population estimates for all of Florida in the late 1970s and estimated 100 tortoises in Palm Beach County, 100 in Broward County, and 700 in Miami-Dade County; they also predicted extirpation of the species in this part of its range by the year 2000. Several studies have outlined aspects of the biology of Gopher Tortoises in Palm Beach County (e.g., Cooney et al. 2019; Huffman et al. 2018; Lauck et al. 2013; Moore and Dornburg 2014; Moore et al. 2006, 2009; Scholl et al. 2012), and 2 studies have reported on aspects of biology in Miami-Dade County (Whitfield et al. 2018, 2022), but none have attempted to estimate population size or evaluate distribution beyond a single site. In the present century, this area has been largely excluded from range-wide studies of population status (Folt et al. 2022, Smith et al. 2006) and range-wide genetics (Ennen et al. 2012, Gaillard et al. 2017, Osentoski and Lamb 1995, Richter et al. 2011, Schwartz and Karl 2005). The Gopher Tortoise management plan by the Florida Fish and Wildlife Conservation Commission (FWC) is primarily based on information from Gopher Tortoises in their northern ranges, and both acknowledges a lack of information for and encourages research on populations in southeastern Florida (FWC 2012).

In southeastern Florida, Gopher Tortoises face unique challenges both from underlying geology and the highly urbanized anthropogenic landscape (Auffenberg and Franz 1982, Zwick and Carr 2006). Predominant habitats are permanently or seasonally flooded environments of the Greater Everglades Ecosystem and differ from upland habitats used by tortoises elsewhere in their range (Baskaran et al. 2006, Lau and Dodd 2015, Smith et al. 2006, Tuberville et al. 2007). The region is mostly flat, with low elevation and a water table relatively close to the surface, which may inhibit burrowing by tortoises. Upland habitats in the area, like those harboring Gopher Tortoises elsewhere in their range, are rare and restricted to the Atlantic Coastal Ridge (Halley and Evans 1983, Hoffmeister 1974), a narrow strip of upland habitat that runs through the region. The Atlantic Coastal Ridge is relatively dry; thus, it is the part of the study area where urbanization is intense and human population density is very high and rapidly growing (Zhu et al. 2015, Zwick and Carr 2006).

The objective of this study is to synthesize information that will clarify the status of Gopher Tortoises in southeastern Florida and improve the scientific foundation for their conservation and management. Specifically, we used burrow surveys from focal sites to synthesize data on age structure to describe the tortoise populations and their habitats. We use community-science reports and ground-truthing of sites to evaluate distribution and abundance beyond our focal sites. We also review management actions in areas where tortoises occur to evaluate ongoing management programs and management needs distinct to southeastern Florida.

Methods

Study area

The study area we address is extreme southeastern Florida, an area that is climatically, geologically, and socio-ecologically distinct from other regions of Florida (Fig. 1). Southeastern Florida has far milder winters than much of the northern range of Gopher Tortoises, and rarely drops below freezing temperatures, resulting in year-round tortoise activity and reproduction (Moore et al. 2009), though high-temperature extremes in this region are lower than those in the central part of the tortoises' range. The western, inland portion of our study area includes seasonally and permanently flooded areas of the Greater Everglades Ecosystem (Myers and Ewel 1990). The eastern, upland portion of our study area lies along the Atlantic Coastal Ridge, a relatively narrow limestone ridge (Hoffmeister 1974, Myers and Ewel 1990). The upland habitats found along the ridge include rare Florida scrub and pine flatwoods ranging from Palm Beach County through northern Miami-Dade County, ultimately transitioning into the critically endangered pine rocklands in the southern two-thirds of Miami-Dade County (Possley et al. 2008).

Human impacts and urbanization in the area are pervasive. The human population in the study area has grown from <15,000 people in 1900 to ~ 5,007,000 in 2000 to ~6,118,000 in 2020, and urbanization has been rapid and extensive (Pickens et al. 2017, Romañach et al. 2020). Urban expansion in the region is most intense within upland habitats, with more than 60% declines in sand scrub statewide (Richardson

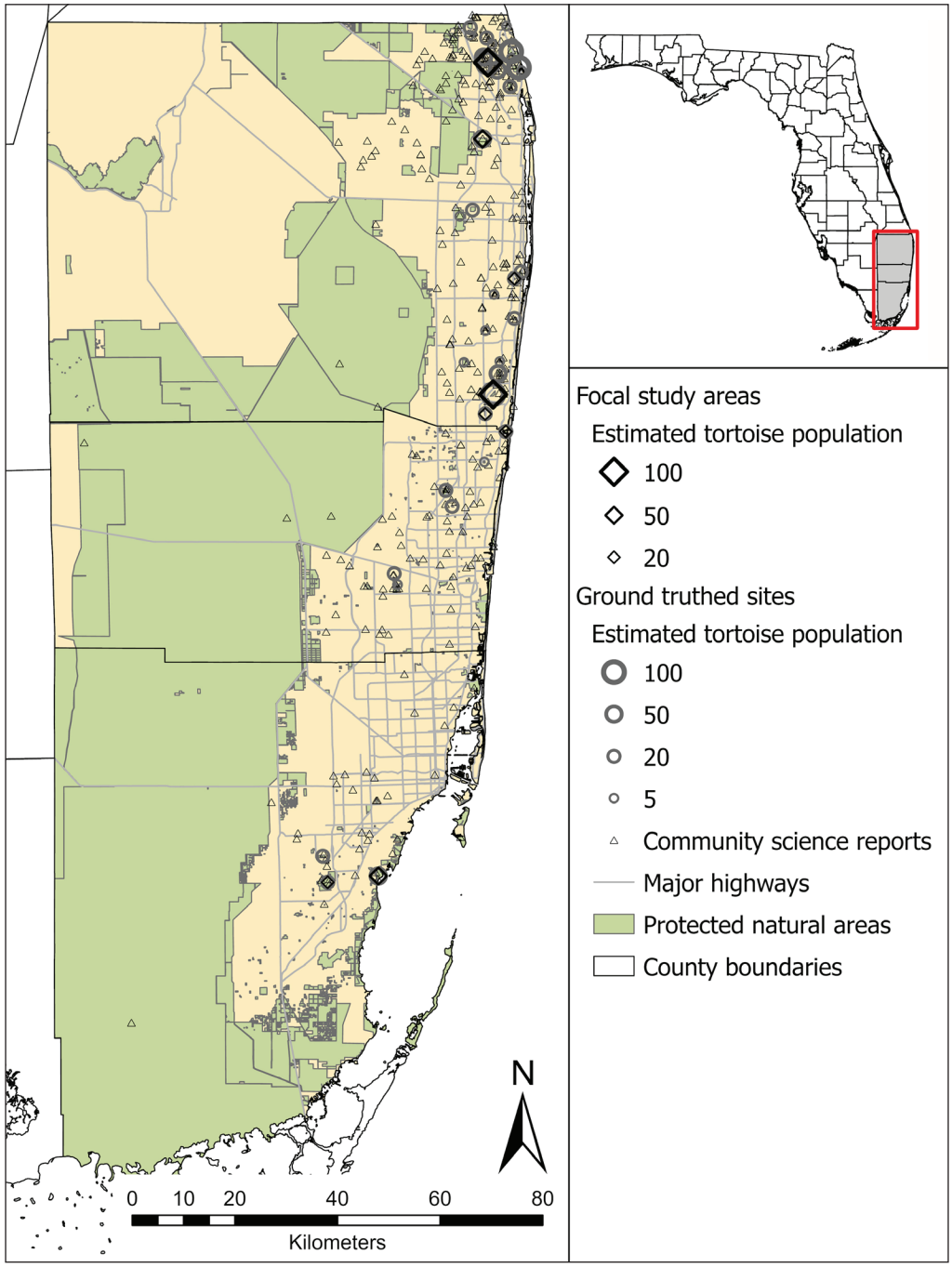

Figure 1. Map of the study area in Florida, including locations of Gopher Tortoise populations, protected areas, and major roads. Focal populations are known study sites documented by the authors in previous research. Ground-truthed sites are populations of tortoises identified by community-science reports and verified by the authors.Despite large contiguous protected areas in the region, tortoises occur almost entirely within urban areas, predominantly because urbanization has been focused on upland habitats.

1989) and more than 98% loss of pine rocklands (Jones and Koptur 2017, Possley et al. 2008).

Gopher Tortoise surveying methods

We used several methods to document presence, abundance, distribution, and age structure of Gopher Tortoises in southeastern Florida. These included burrow surveys and population monitoring from our past and ongoing research (e.g. Moore et al. 2009, Scholl et al. 2012, Whitfield et al. 2022) and community-science reports of tortoise locations (Telenius 2011). To evaluate ongoing management efforts and future management needs, we reviewed management plans from sites harboring tortoise populations in the region.

Burrow surveys at focal research sites. We surveyed Gopher Tortoise burrows from 8 focal tortoise populations known from our research (Figueroa et al. 2021, 2023; Hanish et al. 2020; Karlin 2008; Lauck et al. 2013; Moore and Dornburg 2014; Moore et al. 2006, 2009; Page-Karjian et al. 2021; Scholl et al. 2012; Wetterer and Moore 2005; Whitfield et al. 2022). These 8 focal sites offer the most detailed information available through our study region. As we compiled information from our own past work at these sites, methods varied among sites, but we present brief details here.

We conducted complete burrow surveys at 4 sites in Palm Beach County (Rosemary Scrub, Florida Atlantic University [FAU] Ecological Site, Abacoa Greenway, and Blazing Star Preserve). We sampled each site from May to October 2011 using belt transects ≤5 m wide, depending on the thickness of vegetation, placed side by side to cover the entire site. We measured the burrow width of each active and inactive burrow following McCoy et al (2006). Further details on these survey methods have been reported previously (Scholl et al. 2012).

Also in Palm Beach County, we sampled for burrows at Winding Waters Natural Area using radiotelemetry monthly from 2017 to 2021. We equipped waif tortoises translocated to this site with VHF transmitters and monitored tortoises using radiotelemetry. To the best of our knowledge, this is the only site among our focal sites that contains waif tortoises. Waif tortoises are defined as those that have been removed from the wild without an FWC relocation permit, usually as a result of medical issues (FWC 2012). We recorded burrow coordinates using a GPS device when they were located opportunistically or in the course of telemetry. We did not measure burrow width at this site.

In Broward County, we surveyed Deerfield Island Park in 2015–2016, using line transects placed 5 m apart and covering 100% of the island habitat. We updated locations and classifications of burrows yearly from 2017 to 2019, allowing for recording of new burrow locations through opportunistic encounters. We recorded burrow coordinatess using a handheld GPS unit, but we did not measure burrow widths at this site.

In Miami-Dade County, we surveyed 2 known tortoise populations. At Zoo Miami's ecological preserve (part of the larger Richmond Tract pine rocklands), we located burrows through opportunistic encounters between 2015 and 2019 and through radio-telemetry of tortoises between 2016 and 2019. At Deering Estate,

we located burrows through line transects of the 2 pine rockland parcels between February and March 2017. We measured the width of each burrow. Further details on these survey methods have been reported previously (Whitfield et al. 2022).

We calculated burrow density for each site by dividing the number of burrows detected by the area of each site. For sites where we measured burrow widths, we estimated the size structure of the resident tortoise population, based on carapace length (CL), using a published conversion formula (Alford 1980). We classified these estimated tortoise sizes into 3 life stages: juveniles (<13 cm CL), subadults (13–22 cm CL) and adults (>22 cm CL) (Diemer 1992, Mushinsky et al. 1994).

Community-science data

To supplement distribution records from our 8 focal sites, we searched for records of Gopher Tortoise sightings from 2 sources of community-science data: FWC's Gopher Tortoise reporting website (FWC 2021) and the Global Biodiversity Information Facility (GBIF 2021). GBIF reports were aggregated from iNaturalist (iNaturalist Contributors 2022), though accessing iNaturalist observations through GBIF ensures research-grade data quality (GBIF 2021). We cropped observations from both FWC and GBIF to the study area using the 'raster' package (Hijmans 2023) in the R program (version 4.2.3; R Core Team 2023). We removed any records that were from before 2011, were not live human observations (e.g., museum specimens), were duplicates, were of tortoise mortality, or were labeled by staff during data validation as "other", "no tortoise", or "different species", Occurrences before 2011 and museum records were removed due to the rapid development in South Florida and because the earliest of our burrow surveys were conducted in 2011.

Of the remaining occurrences, ~400 points, many were located outside of natural areas (i.e., low- to medium-density residential areas or commercial-zoned regions). We defined potential natural areas as any area of at least 2500 m^2 not made up of an impervious, anthropogenic surface such as concrete. We reviewed these points using Google Earth. When there were clusters of 2 or more tortoise sightings inside a potential natural area, or 4 or more tortoise sightings near (i.e., within ~1600 m of) a potential natural area, we marked this natural area as a site with a high probability of tortoise presence. Potential natural areas included named parks and preserves as well as anonymous natural areas. Potential natural areas that did not have 2 or more sightings within their boundaries or 4 near them but had at least 1 sighting associated with them, were marked as low probability of tortoise presence. Hereafter, all sites acquired from the community-science data as previously described are referred to as community-science–derived (CSD) sites.

Ground-truthing of populations and assessment of habitat quality. To assess the accuracy of the potential CSD sites, we randomly selected 26 high-probability CSD sites and 4 low-probability CSD sites for ground-truthing. We focused our efforts on high-probability sites because our goal was primarily to locate additional tortoise sites and only secondarily to evaluate the accuracy of our CSD categories. To ground-truth, we visited CSD sites on clear days with temperatures between 20 °C and 27 °C in November and December of 2021. Tortoises in south Florida are active

year-round (Moore et al. 2009), and burrows can be detected at any time of year. We surveyed each CSD site using Gaia GPS tracking software (Boulder, CO) to conduct broad belt transects varying from 20 to 100 m in width. Larger transects were used at larger CSD sites so that we surveyed ~25% of each site or until we found 10 active burrows. At each CSD site, we categorized site quality as either poor (mostly overgrown, very little open canopy, many invasive plants), good (somewhat overgrown, about half open canopy, some invasive plants), or excellent (not overgrown, mostly open canopy, few to no invasive plants) based on our transects. For each CSD site, we extrapolated the number of total burrows based on the number of burrows found and the proportion of area surveyed. We then converted this burrow number to a tortoise estimate based on the 50% occupancy rate prescribed by FWC (2012). Because our estimates were crude and to prevent overinterpretation of the results, we rounded the resulting tortoise number to the nearest category of 5, 20, 50, 100, or >100 tortoises. We assumed that tortoises do not inhabit swamp habitat or water features (lakes, ponds). Thus, we did not include these in our CSD site area calculations, surveys, or when estimating tortoise numbers for each site. Our survey estimates and site-quality categories should be interpreted cautiously as we did not conduct exhaustive surveys at any CSD site.

Site-management efforts. We accessed and reviewed management plans for 7 of our 8 focal sites (Abacoa Greenway, Rosemary Scrub, FAU Boca Campus, Winding Waters, Deerfield Island Park, Deering Estate, and Zoo Miami), but no management plan was available for Blazing Star Preserve. We recorded whether Gopher Tortoises were mentioned in management plans, whether plans indicated a need for surveys, whether plans indicated a need for habitat management, whether (and what type of) management actions had been conducted, and whether (and what type of) threats to tortoises were addressed.

Results

Burrow surveys and age structures

We compiled a total of 1283 burrows across our 8 focal sites. The number of burrows per site varied from 50 to 308 (Table 1). The density of burrows among

Table 1. Focal Gopher Tortoise populations examined in this study. Data in this table are synthesized from our past research in the region. Counties: PBC = Palm Beach County, BC = Broward County, and MDC = Miami-Dade County. Est. *N* = estimated number of tortoises in the population.

Site	Latitude (°N)	Longitude (°W)	Area (ha)	Habitat quality	# of burrows	Est. *N*	County
Abacoa Greenway	26.896	80.114	33.99	Excellent	308	>100	PBC
Winding Waters Natural Area	26.777	80.124	221.77	Good	298	50	PBC
Rosemary Scrub Natural Preserve	26.559	80.068	5.67	Good	50	20	PBC
FAU Boca Campus Natural Area	26.377	80.106	37.07	Good	289	100	PBC
Blazing Star Natural Area	26.347	80.119	9.71	Poor	49	20	PBC
Deerfield Island Park	26.319	80.083	21.57	Poor	80	20	BC
Deering Estate	25.620	80.306	179.68	Good	72	50	MDC
Zoo Miami	25.610	80.395	172.40	Good	137	50	MDC

sites varied over an order of magnitude. The highest-density sites were Abacoa Greenway (9.06 burrows/ha) and Rosemary Scrub Natural Area (8.82 burrows/ha), and the lowest density sites included Deering Estate (0.79 burrows/ha) and Zoo Miami (0.40 burrows/ha). All 6 sites where we had measurements of burrow size included adult, sub-adult, and juvenile-sized burrows. Burrow-size distributions were nearly always left-skewed, and in the case of Abacoa Greenway and FAU Boca Ecological Preserve were clearly bimodal (Fig. 2).

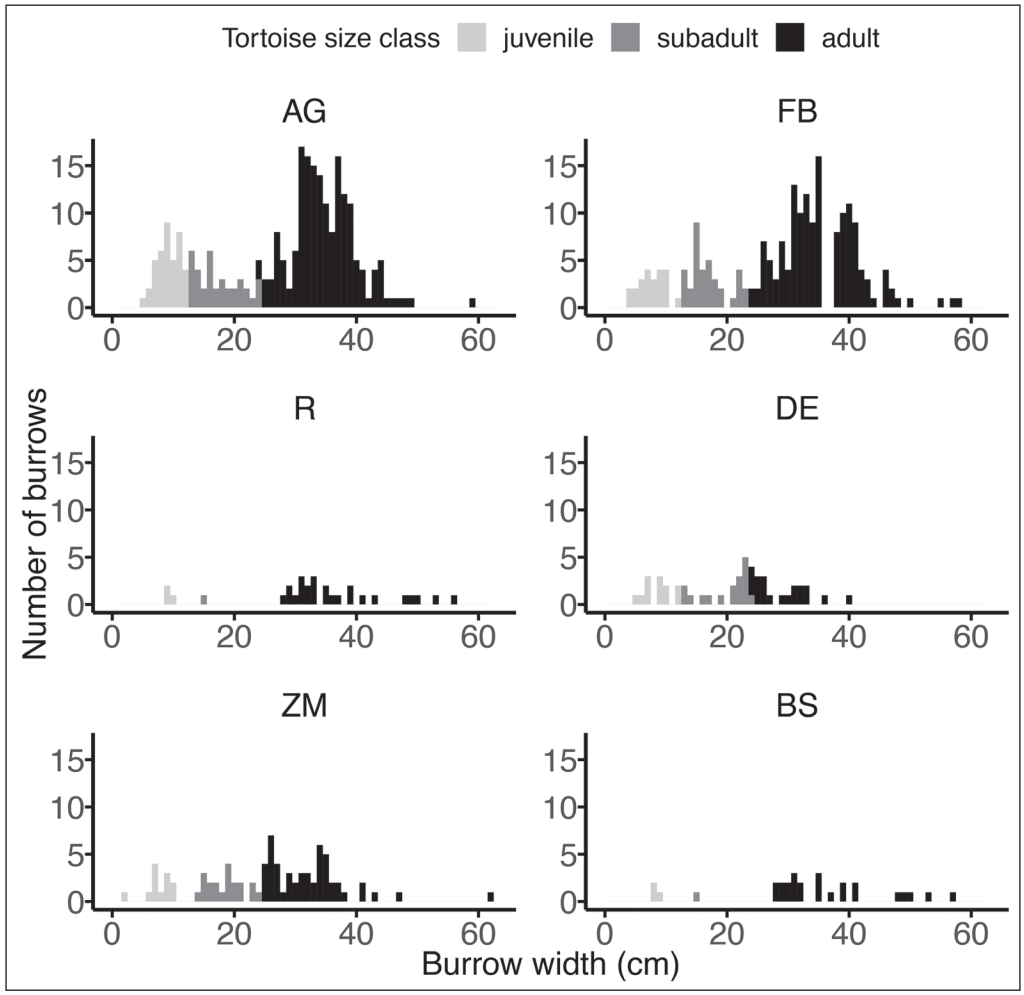

Figure 2. Gopher Tortoise burrow widths and estimated life stages across several studied populations in our study area. Tortoise life stages were based on carapace length (CL), which was estimated from burrow-width measurements using Alford's (1980) conversion formula. We classified estimated CL measurements into 3 life stages: juveniles (<13 cm CL), subadults (13–22 cm CL) and adults (>22 cm CL). All populations contained burrows representing each of the 3 life stages. Some populations (AG, FB) showed a bimodal population structure, which may be consistent with low recruitment. Site abbreviations: AG = Abacoa Greenway South, BS = Blazing Star, DE = Deering Estate, FB = Florida Atlantic University Boca Campus Conservation Area, R = Rosemary Scrub, ZM = Zoo Miami.

Community-science data

Community-science records yielded 399 tortoise observations within our study area (Fig. 1). Of these, 255 derived from the FWC tortoise-reporting system, and 144 from GBIF (exclusively submitted through iNaturalist). Of these, 292 were in Palm Beach County, 72 in Broward County, and 35 in Miami-Dade County. Using these data, we found 30 sites deemed to have a high probability of tortoise presence and 43 deemed to have a low probability of tortoise presence (Figs. 1, 3). Four of these were part of our 8 focal sites so this effort added 69 sites to our 8 focal sites (Table 1). Of these 77 sites, 46 were in Palm Beach County, 19 were in Broward County, and 12 were in Miami-Dade County. Of the 26 high-probability CSD sites and 4 low-probability sites we selected for ground-truthing, we detected tortoises at

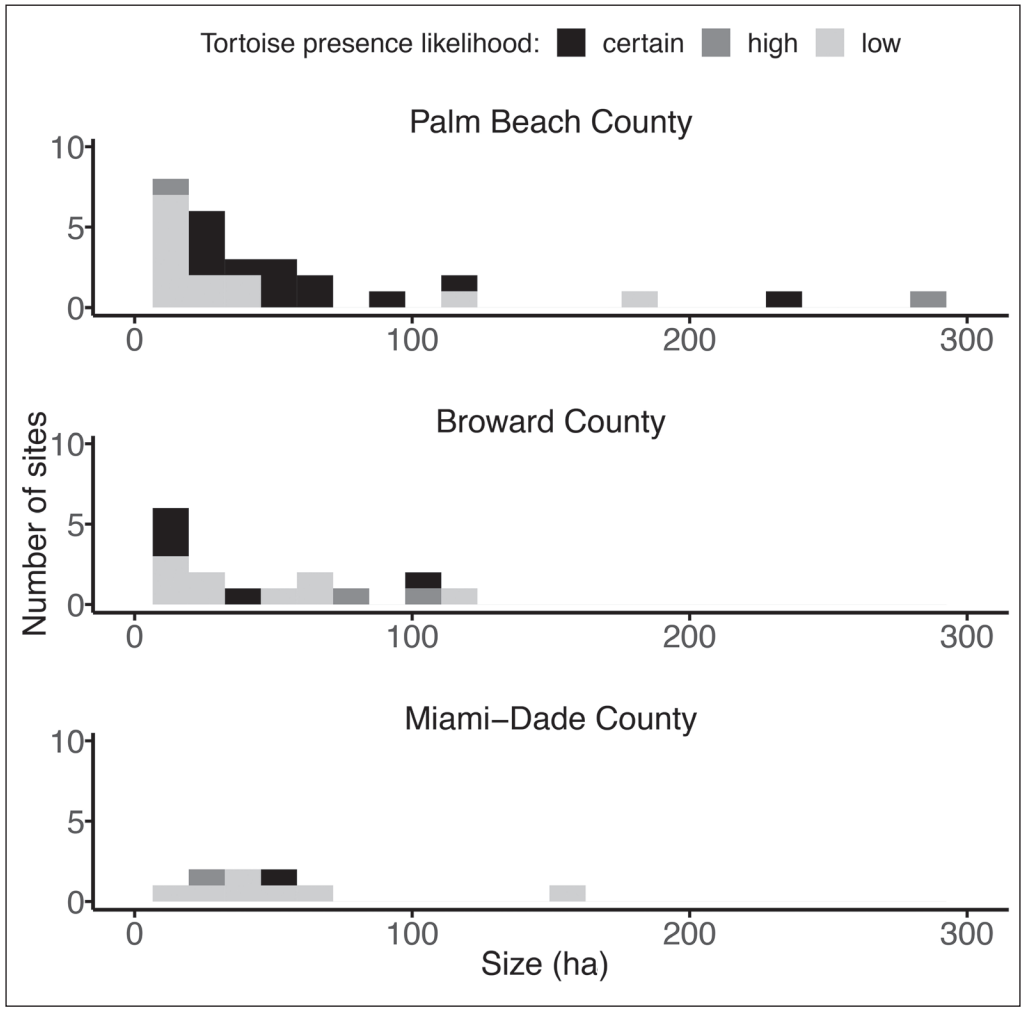

Figure 3. Likelihood of Gopher Tortoise presence at the 77 sites that were added to our list of 8 focal sites based on the community-science data from GBIF and FWC. Community-science reports indicate tortoises are more widely distributed across all 3 counties than existing burrow surveys suggest.

all but 2 high-probability CSD sites. We estimated that most CSD sites we checked had 5–20 tortoises, although several had 50–100 tortoises, and 2 had >100. Site quality was poor for 9 sites, good for 11 sites, and excellent for 10 sites. Excellent CSD sites tended to be in Palm Beach County. Palm Beach County CSD sites were the only sites with estimates of ≥50 tortoises.

Site-management plans

Of the 7 focal sites with available management plans, 6 explicitly mentioned the presence of Gopher Tortoises (Table 2). Four of the 7 sites state a need for tortoise surveys, and 4 of the 7 also state a need for habitat management for tortoises (Table 2). Five of the 7 sites name specific threats to tortoises, including fire suppression, herbicide use, genetic effects (inbreeding or outcrossing depression), harassment by people, road mortality, predation by exotic predators, and exotic plants. Six of the 7 sites mentioned specific management activities that benefit these tortoises—whether intentional or not—including prescribed fires, vegetation thinning, exotic plant removal, and fencing that enclose tortoises within preserves.

Discussion

Here, we synthesize information from a variety of sources to characterize tortoise populations and habitats in southeastern Florida. We provide evidence for persistent reproductive populations based on burrow-size measurements of tortoises in upland habitats throughout the area. We find that populations are typically small and usually occur within small natural areas, yet population density varied widely among sites. Finally, we show that tortoise populations are tracked by community-science platforms and management needs are recognized by local preserve managers. Tortoise populations in this area are small, entirely fragmented by urban areas, and face ongoing anthropogenic threats; yet, despite these threats, they persist in reproductive populations.

The data we synthesize here is at odds with tortoise population syntheses at a regional scale, which have presumed that tortoise populations have been extirpated from this area or are not viable. Auffenburg and Franz (1980) surveyed this

Table 2. Information from management plans for 7 of our 8 focal Gopher Tortoise population sites examined in this study. Management plans typically acknowledged the presence of tortoises, encouraged surveys, called for additional management, and acknowledged specific threats.

Site	County	Tortoises mentioned	Need for tortoise surveys	Need for tortoise management	Threats considered
Rosemary Scrub	Palm Beach	Y	Y	Y	Y
Abacoa Greenway	Palm Beach	Y	Y	Y	Y
FAU Boca Campus	Palm Beach	Y	Y	Y	N
Winding Waters	Palm Beach	Y	N	N	Y
Deerfield Island Park	Broward	Y	Y	Y	Y
Deering Estate	Miami-Dade	N	N	N	N
Zoo Miami	Miami-Dade	Y	N	N	Y

region and predicted the 3 counties would see extirpation of Gopher Tortoise populations by 2000. Smith et al. (2006) conducted range-wide population reviews and presented no tortoise populations from this part of the range. Several studies of putatively range-wide genetics did not include tortoises from this region within their work (Ennen et al. 2012, Gaillard et al. 2017, Osentoski and Lamb 1995, Richter et al. 2011, Schwartz and Karl 2005). Concerningly, data limitations prevented a recent federal decision considering listing eastern populations of Gopher Tortoises under the Endangered Species Act from accurately reflecting the number and distribution of these tortoises in that part of their range (Folt et al. 2022, USFWS 2022). Tortoise populations in this area appear to be so small as to fall under a detection threshold both by most Gopher Tortoise biologists and by wildlife management agencies.

The data we present highlight a stark contrast between the policy provisions for Gopher Tortoise populations in the westernmost and southernmost extent of the range. Gopher Tortoises in the western portion of the range (west of the Mobile and Tombigbee rivers) have been treated as a distinct population segment (the Western DPS) on the basis of extent of genetic distinctiveness, extent of habitat loss, and projected trajectory of populations in coming decades. The Western DPS lost more than 75% of their habitat, and its populations are small, and most have low resiliency and are highly fragmented (USFWS 2022). The populations we describe have likely lost far more than 75% of suitable habitat (as upland habitats have been largely converted to urban lands) and are also susceptible to extirpation from small population size and habitat fragmentation.

Regardless of federal-level policy considerations for Gopher Tortoises in southeastern Florida, populations are not likely to persist without management considerations that reflect the specific biological and socio-ecological threats in this area. Population density, habitat loss, and urbanization are all more intense in this region than elsewhere in the Gopher Tortoises' range (Auffenberg and Franz 1982, Zwick and Carr 2006). Tortoise populations are fragmented and isolated by urban areas, in particular roads. This hostile urban matrix will likely prohibit or prevent any natural dispersal between populations even over short distances. Most tortoise populations in this area are in natural areas that lack secure fencing to prevent tortoises dispersing into the urban matrix, where rates of survival are likely low because of road density and direct human interference (Howell and Seigel 2019). Even within natural areas, prescribed fire is difficult because preserves are entirely nested within urban areas, thereby adding to the cost of fire treatments per hectare and increasing resistance to fire treatments by surrounding communities. Without specific management recommendations for tortoise populations nested within urban areas, it is not clear that adequate regulatory mechanisms persist to prevent the extirpation of Gopher Tortoise populations in this part of the species' range. A federal recovery plan for a congeneric tortoise population in the Mojave Desert lists fencing for a management priority for the urban–wildland interface (USFWS 2011), and such actions would be warranted for these Gopher Tortoise populations as well.

It is unclear whether southern populations would represent a unique DPS. The populations we report here have not been included in several putatively range-wide genetic assessments. The Western DPS and Eastern DPS are divided by the Mobile and Tombigbee Rivers, which has been shown in multiple studies to limit gene flow. Still, Gaillard et al (2017) found that there exist 4 population subgroups within peninsular Florida and state that Gopher Tortoises in the Atlantic coastal ridge may represent 1 of these distinct subgroups. While several studies have examined genetics of Gopher Tortoises (Clostio et al. 2012, Ennen et al. 2012, Gaillard et al. 2017, Schwartz and Karl 2005), only 1 has included a single individual from within our study area (Osentoski and Lamb 1995), thus prohibiting evaluation of genetic distinctiveness or loss of genetic diversity. While no major rivers serve as barriers between our study area and other parts of the species' range, wetland habitats of the Greater Everglades Ecosystem likely do serve as a major geographical barrier.

The community-science reports and ground-truthing we report here are no substitute for rigorous, formal surveys. Instead, they clarify for the first time the necessity for formal surveys within this region, an area from which most biologists assumed tortoises were extirpated for decades. Indeed, both FWC's management plan and management plans from natural areas encourage formal surveys of tortoise populations. We urge more detailed surveys using statistically robust methodology throughout the region.

Our study illustrates a compelling need for long-term planning for protected areas in upland habitat adjacent to and surrounding currently urbanized areas, not only in south Florida, but range-wide. Zwick and Carr (2006) project that Florida's population will double from 17 million to 35 million by 2060, and developed lands may double as well. This timeline is well within the expected natural lifespan of many tortoises alive in Florida today, and as with current development, will be focused on upland habitats where tortoises occur. Protection of upland habitats surrounding urban areas today is critical to maintain the viability of tortoise populations and ensure the continuation of the ecosystem services they provide.

Conservation implications

Herein, we identify a fundamental disparity in policies regarding Gopher Tortoises at the extremes of their geographic distribution. The western-most populations have been federally listed as a threatened species since 1987, as the species had lost more than 75% of its habitat west of the Mobile and Tombigbee rivers to urbanization, agriculture, and other uses. However, a far greater percentage of habitat in southeastern Florida has been lost. For example, more than 98% of upland pine rockland habitat has been destroyed outside of Everglades National Park (Possley et al. 2008). The extent of population loss in southeastern Florida is so great that populations in the region were apparently presumed to be locally extirpated for decades (Schwartz and Karl 2005, Smith et al. 2006). Populations of tortoises in this area warrant an increase in management and conservation attention and will likely require novel strategies for mitigating urban impacts and high rates of displacement by humans. Nonetheless, there is great value in managing these tortoise populations for the ecosystem services they provide commensal species

through habitat modifications and the surrounding plant communities via herbivory and seed dispersal.

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