Gopher Tortoise (Gopherus polyphemus) Burrow Densities in Scrub and Flatwoods Habitats of Peninsular Florida

TRACI D. CASTELLÓN1, BETSEY B. ROTHERMEL1, AND SAIF Z. NOMANI2

1Archbold Biological Station, 123 Main Dr, Venus, Florida 33960 USA [castellon@archbold-station.org; brothermel@archbold-station.org]; 2Western EcoSystems Technology, Inc, 2003 Central Ave, Cheyenne, Wyoming 82001 USA [saifnomani@yahoo.com]

ABSTRACT. – Gopher tortoises (Gopherus polyphemus) occur in a variety of habitats, but are primarily associated with sandhill communities. In peninsular Florida, however, mesic flatwoods make up the largest area of habitat, and scrub often replaces sandhill on inland ridges. Tortoise ecology is poorly understood in these habitats and few data are available to guide management. We surveyed tortoise burrows and assessed vegetation in scrub, flatwoods, and pine plantations on flatwoods soils at Avon Park Air Force Range in south-central Florida. Densities of noncollapsed burrows in scrub (1.93/ha) and flatwoods/plantations (1.42/ha) were generally lower than is typical for sandhill (3.25–9.95/ha), although total abundance was high (>20,000) because of the large habitat area. In scrub, low burrow densities may be due to low abundance of food plants. Nonetheless, the burrow density in scrub was significantly higher than in flatwoods/plantations, where food was abundant but soils were poorly drained and burrows were often flooded. The percentage of collapsed burrows was significantly higher in scrub (53%) than in flatwoods/plantations (35%), although a higher percentage of the remaining (noncollapsed) burrows were active in scrub (23%) than in flatwoods/plantations (16%). These patterns (and data from a subsequent radiotelemetry study) suggest that tortoises in scrub maintain strong fidelity to individual burrows, and frequently abandon others, whereas tortoises in flatwoods share burrows and move among them regularly, but rarely abandon them. This sharing and continual reuse of available burrows suggests a possible limitation on suitable conditions for burrow construction in flatwoods, probably related to the high water table. We suggest that scrub and flatwoods may constitute suboptimal habitats for gopher tortoises, due to low abundance of food in scrub and poorly drained soils in flatwoods. Nonetheless, large numbers of tortoises may occupy scrub and flatwoods, necessitating better understanding of their ecology in these habitats.

KEY WORDS. – Reptilia; Testudines; Gopherus polyphemus; pine flatwoods; Florida scrub; burrow densities; line-transect distance sampling

The gopher tortoise (Gopherus polyphemus) is listed as threatened under the federal Endangered Species Act in its western range, and is a candidate for listing throughout the remainder of its range (US Fish and Wildlife Service 1987, 2011). Gopher tortoises occur in a variety of habitats, yet most studies of their ecology have been conducted in sandhill communities (e.g., Auffenberg and Franz 1982; Diemer 1986; MacDonald and Mushinsky 1988; Tuberville and Dorcas 2001), and few data are available to guide management in other habitats. In peninsular Florida, which is considered a stronghold for the gopher tortoise, the dominant upland habitat is pine flatwoods rather than sandhill (Abrahamson and Hartnett 1990), and scrub vegetation largely replaces sandhill along major sand ridges (Myers 1990). Although previous studies have found relatively low tortoise densities in flatwoods and scrub (e.g., Auffenberg and Franz 1982; Hipes 2008), these habitats may sustain large tortoise populations in some parts of the range, despite low densities, owing to their large spatial extent. Given ongoing population declines, and the increasingly common use of tortoise relocation as a management tool (Florida Fish and Wildlife Conservation Commission 2008; Tuberville et al. 2008), it is important to develop a stronger understanding of gopher tortoise demography and population densities in all potentially suitable habitats, especially when these are used as recipient sites for translocation.

Our study site, Avon Park Air Force Range (APAFR), is a 42,000-ha military training area in south-central Florida, with flatwoods and scrub as the dominant upland habitats. This Air Force range is one of only a few remaining areas of undeveloped land within the gopher tortoise range that is large enough to support a viable, self-sustaining population (McCoy and Mushinsky 2007; Styrsky et al. 2010; US Fish and Wildlife Service 2011). However, the current size and demographic trajectory of the tortoise population at APAFR is unknown. We conducted the first comprehensive survey of adult-sized tortoise burrows at APAFR in scrub, flatwoods, and pine plantations on flatwoods soils. Our survey results indicate presence of a large tortoise population overall, but relatively low burrow densities. Patterns of burrow use also suggest that demography and carrying capacity in these habitats may differ substantially from those in the better-studied sandhill communities.
METHODS

Habitat Description and Stratification. — The dominant upland habitats at APAFR are mesic and dry-mesic flatwoods (7421 ha), slash pine (Pinus elliottii) plantations on mesic and dry-mesic flatwoods soils (5442 ha), and Florida scrub (2572 ha). Mesic flatwoods are characterized by low flatland with poorly drained sandy soils, open canopy, and frequent fires (Abrahamson and Hartnett 1990). Groundwater is relatively close to the surface (usually ≤ 1.2 m deep) for most of the year, and standing water or sheet-flow may be present during periods of high rainfall. Dense groundcover (mostly grasses) is usually present if fire is relatively frequent. Pine plantations at APAFR principally occupy flatwoods soils. Both the natural flatwoods and plantations are burned every 2 to 3 yrs, although plantations are burned only during winter (US Air Force 2000). Plantations are managed as even-aged stands, with a typical harvest age of 40 to 50 yrs and periodic thinning to maintain basal area between 9 and 16 m²/ha (T. Meade, APAFR, pers. comm., 2010), well below the recommended maximum (30 m²/ha) for maintaining tortoise habitat quality (Aresco and Guyer 1999).

The well-drained sand ridges at APAFR support several scrub assemblages, including sand pine (Pinus clausa) scrub, oak (Quercus spp.) scrub, mixed scrub and scrubby flatwoods. Current management prescriptions at APAFR call for controlled burning every 7 to 20 yrs, but a higher-than-normal proportion was burned during the years preceding our survey due to a backlog in the burning schedule (US Air Force 2000). Like sandhill, Florida scrub occurs on droughty, infertile uplands, though scrub tends to occupy drier, lower-nutrient soils (Myers 1990). The habitat is typically dominated by stunted oak shrubs with sparse groundcover.

Habitat stratification for our survey relied on a geographic information system (GIS) vegetation classification produced by APAFR (E. Bridges and E. Orzell, unpubl. data, 2000). We combined several fine-scale vegetation classes into 3 broad categories likely to support gopher tortoises: scrub (all scrub types, including scrubby flatwoods), flatwoods (mesic and dry-mesic flatwoods, excluding wet flatwoods), and pine plantations (plantations on soils that would otherwise support mesic and dry-mesic flatwoods). We excluded all areas delineated as wetland, and those supporting cutthroat grass (Panicum abscissum), an indicator of groundwater seepage. The dominant flatwoods soil was Myakka, followed distantly by Immokalee and Basinger Sands. Dominant scrub soils were Satellite, Narcoossee, Duette, Archbold, Daytona, and Zolfo Sands.

Tortoise Burrow Surveys. — Burrow surveys were conducted between April and October 2009, using line-transect distance sampling (LTDS; Buckland et al. 2001). We chose this method because it better reflects spatial variability across large study areas than the traditional method, which involves burrow counts within isolated survey plots (Nomani et al. 2008). The method also accounts for imperfect detection of burrows by statistically modeling the decrease in detection probability with increasing distance from the transect (Buckland et al. 2001).

For random placement of transects within each habitat, we generated a set of random points across the APAFR map using a GIS, then used randomly selected points within each habitat stratum as starting locations for 1-km-long transects. Transects were oriented east to west, approximately perpendicular to the major elevation gradients. Where a habitat patch was too narrow to accommodate a 1-km-long transect, the transect was interrupted at the edge of the patch and picked up again at a location 100 m to the north or south, or within the nearest patch of the specified habitat.

We used a survey method adapted from Smith et al. (2009), wherein one observer searched for burrows while walking slowly along the transect, navigating using a global positioning system (GPS) unit with real-time, submeter accuracy (Trimble GeoXT, Sunnyvale, CA), to stay as close as possible to the line. Other members of the survey team searched adjacent to each transect (one on each side), meandering back and forth to a maximum distance of approximately 20 m from the transect, but burrows observed in this way were treated separately from those detected by the observer walking directly on the transect (see data analysis). Burrow locations were recorded with the GPS, and perpendicular distances from the transects to the burrows were measured in the lab using GIS.

All burrows were visually examined and classified based on external characteristics. Given the subjectivity of the traditionally used burrow classification system (i.e., active, inactive, and abandoned; see Smith et al. 2005), we developed a set of strict (more objective) criteria to classify burrows as active, usable, or collapsed. We classified burrows as active only if there were clearly distinguishable footprints or plastron drag marks at the mouth. Burrows were classified as collapsed only if they were occluded or collapsed ≤ 1 m from the entrance, to the point that excavation would be required for a tortoise to enter. All other burrows were classified as usable. Most of these usable burrows were in good condition, having the characteristic half-moon shape, with the mouth relatively clear of debris, although some appeared less maintained. We use the phrase “all noncollapsed burrows” when discussing the active and usable burrow classes combined.

We used a video camera burrow scope (built by E. Wester, Auburn, AL) to view inside each burrow (excluding collapsed burrows that could not be scoped), in an effort to determine occupancy. However, at our site, occupancy could not be determined for 33% of burrows in scrub and 71% in flatwoods and plantations (combined). Difficulties with scoping were due to partial or complete flooding of the burrows with groundwater (mainly in
flatwoods and plantations), or presence of roots or complex burrow architecture that interfered with maneuverability of the scope (mainly in scrub). Occupancy was also undetermined in some cases because of the camera’s limited field of view.

Because of difficulties determining burrow occupancy, our analyses here deal exclusively with burrow densities and activity status, without direct consideration of occupancy by tortoises. Population size is estimated based on an index, assuming an abundance of 1 tortoise per active burrow. This index was expected to produce a conservative estimate of population size because some usable burrows without clear tortoise sign at the mouth may have been occupied, especially given frequent summer rainfall in south-central Florida, which could obscure tortoise sign. Use of this index was considered the least biased means of comparison between scrub and flatwoods/plantations, given that proportions of burrows with unknown occupancy differed by habitat (see McCoy and Mushinsky 1992).

**Vegetation Surveys.** — We sampled vegetation at intercept points located every 250 m along each transect, using methods adapted from the State of Florida’s gopher tortoise permitting guidelines (Florida Fish and Wildlife Conservation Commission 2008). Percentage of cover was estimated (using the following ranges: 0%, 1%–25%, 26%–50%, 51%–75%, 76%–100%) within a 1-m² quadrat at each intercept point for the following ground-cover categories: broadleaf grasses and grass-like vegetation (e.g., sedges), wiregrass (*Aristida* spp.), forbs, palmetto (either saw palmetto [*Serenoa repens*] or scrub palmetto [*Sabal etonia*]), woody vegetation, and bare ground. Indices of shrub and canopy cover were also calculated as follows. At each intercept point, an observer took 20 steps perpendicular to each side of the transect and recorded presence or absence of shrubs and canopy at each alternate step (10 observations on each side). To classify shrub presence, the observer created a ‘‘T’’ with two 1-m-long rods, with the vertical rod touching the ground and the horizontal rod placed atop and perpendicular to it. If the horizontal rod touched a shrub (woody plant 1–3 m tall), shrubs were recorded as present. Presence of overhead canopy was determined using a densitometer, with canopy recorded as present if any portion of a tree crown intersected the center point of the vertical lens. The cover indices for shrub and canopy were then calculated for each intercept point by summing the numbers of observations with shrubs or canopy present, then dividing by 20.

**Data Analysis.** — We used program Distance 5.0 (Thomas et al. 2006) to generate burrow detection functions by fitting several models to the LTDS data. Because the activity status of burrows could potentially influence detectability, we compared models with and without burrow status as a covariate, and selected the most parsimonious models based on Akaike’s Information Criterion (AIC; Burnham and Anderson 2002). The models we evaluated included the following key functions and series expansions: half-normal/hermite polynomial, hazard-rate/cosine, and hazard-rate/simple polynomial. For models without burrow status as a covariate, uniform/cosine and uniform/simple polynomial were also evaluated. Only adult-sized burrows (≥23 cm) were used for these analyses because burrow detection is influenced by size, and combining different size classes into a single LTDS detection function would be questionable. To minimize outliers, data were truncated by discarding the 5% of observations at the greatest distances from transects.

Models were developed independently for scrub habitat data because the vegetation structure differed substantially from flatwoods and plantations, and was expected to influence the detection function. However, groundcover was similar in flatwoods and plantations, so detection functions were modeled jointly for these strata. Burrow density estimates for flatwoods and plantations were initially generated for both pooled and stratified data, but coefficients of variation (CV) for stratified estimates were unacceptably high, so we combined the flatwoods and plantation data in all further analyses. We also examined the effect of using all burrow observations for LTDS modeling, including burrows detected by observers searching the areas adjacent to the transects. Including these observations nearly tripled the sample size, but it did not substantially reduce CVs, so we chose to use only burrows observed from the transect lines because it is more consistent with the model assumption that distance from the line is the primary factor influencing detection.

Mean proportions of adult-sized burrows that were active, usable, active and usable combined (i.e., all noncollapsed), and collapsed, were estimated for each habitat by calculating the proportions of burrows in each category along each transect, and then calculating the mean across all transects. We used the mean across transects because, although transects were independent, the proportions of active, usable, and collapsed burrows along individual transects were not. For each habitat, the mean proportion of burrows in each category was then multiplied by the total burrow density (derived from the best LTDS model) to generate density estimates by activity class. All comparisons of burrow densities between habitats were based on confidence intervals. Mean proportions of burrows by activity status were compared using *t*-tests. Vegetation cover data were compared using Kruskal-Wallis analysis of variance and Duncan’s multiple range tests.

**RESULTS**

**Tortoise Burrow Surveys.** — Total survey effort included 51 km of transects in scrub and 44 km in flatwoods/plantations. We detected 1089 tortoise burrows while searching on and adjacent to the transects. Of these,
were detected by an observer walking directly on the transect, of which 260 were adult-sized (182 in scrub, 78 in flatwoods/plantations). These 260 burrows comprised the data used for LTDS analysis.

Detection function models fit the data well for both scrub and flatwoods/plantations (Table 1). In each case, we accepted the model with the lowest AIC. The total burrow density was highest in scrub (4.12/ha), and all scrub patches were occupied. This density yielded an abundance estimate of 10,605 adult-sized burrows in scrub across the entire APAFR site. In comparison, density in flatwoods/plantations was lower (2.18/ha), although the total abundance was high (27,979 burrows). Notably, in the flatwoods/plantations, burrows were found on only 65% of transects, compared to 94% in scrub.

Inclusion of burrow activity status (active, usable, collapsed) as a covariate in the LTDS models did not improve AIC values either for scrub (AIC without covariate: 636.84; with covariate: 639.59) or flatwoods/plantations (without covariate: 256.94; with covariate: 259.49), indicating lack of evidence for an effect of burrow status on detectability. Therefore, we chose to use data for all 947 adult burrows (260 observed from the transect line plus 687 detected by observers searching adjacent to the transects) to calculate the proportions of burrows in each activity class. These proportions were then used to calculate the densities and abundances of burrows in each activity class for each habitat (Table 2). These calculations produced an estimated total abundance of 1435 active burrows across all scrub habitat at APAFR, and 2694 across all mesic and dry-mesic flatwoods/plantations.

Densities of active burrows, as well as active and usable burrows combined (i.e., all noncollapsed burrows), were significantly higher in scrub (active 0.56/ha; noncollapsed 1.93/ha) than in flatwoods/plantations (active 0.21/ha; noncollapsed 1.42/ha), based on confidence intervals (Table 2). However, mean percentages of usable burrows, and mean percentages of all noncollapsed burrows, were significantly higher in flatwoods/plantations than in scrub (usable: scrub 33%, flatwoods/plantations 56%; \( t_{50} = 3.51, p = 0.001 \); noncollapsed: scrub 47%, flatwoods/plantations 65%; \( t_{50} = 3.16, p = 0.002 \)), whereas mean percentages of active burrows were similar in scrub (14%) and flatwoods/plantations (10%; \( t_{50} = -1.01, p = 0.316 \)). In addition, there were significant differences between scrub and flatwoods/plantations in both density (scrub 2.19/ha, flatwoods/plantations 0.76/ha; Table 2) and mean percentages of collapsed burrows (scrub 53%, flatwoods/plantations 35%; \( t_{50} = -3.16, p = 0.002 \)). Thus, although a higher percentage of burrows in scrub was collapsed, more of the remaining noncollapsed burrows were active in scrub (23%) than in flatwoods/plantations (16%).

### Table 1. Model-fitting results for estimation of gopher tortoise burrow densities (per hectare) and abundance for all adult-sized burrows (active, usable, and collapsed) using line-transect distance sampling at Avon Park Air Force Range, Florida. Abundance estimates were extrapolated across the entire installation for the specified habitats. Data from flatwoods and plantations were combined because stratification did not improve Akaike's Information Criterion (AIC) values. Key functions of the best models were uniform (U) and hazard-rate (HR). Adjustment terms are cosine (Cos) and simple polynomial (SP). None indicates that use of an adjustment term was not justified based on Delta AIC. Only models with \( \Delta \text{AIC} \leq 2.00 \) are presented.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Key function/adjustment</th>
<th>N*</th>
<th>Burrow density</th>
<th>Burrow abundance</th>
<th>95% CI</th>
<th>CV</th>
<th>df</th>
<th>Parameter</th>
<th>( \Delta \text{AIC} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scrub</td>
<td>U/Cos</td>
<td>173</td>
<td>4.12</td>
<td>10,605</td>
<td>3.13–5.44</td>
<td>13.91</td>
<td>57.06</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>U/SP</td>
<td>173</td>
<td>4.11</td>
<td>10,571</td>
<td>3.08–5.48</td>
<td>14.48</td>
<td>66.59</td>
<td>2</td>
<td>1.49</td>
</tr>
<tr>
<td>Flatwoods &amp; Plantations</td>
<td>U/Cos</td>
<td>74</td>
<td>2.18</td>
<td>27,979</td>
<td>1.42–3.33</td>
<td>21.52</td>
<td>55.22</td>
<td>2</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>HR/None</td>
<td>74</td>
<td>2.39</td>
<td>30,755</td>
<td>1.41–4.06</td>
<td>27.15</td>
<td>52.98</td>
<td>2</td>
<td>1.49</td>
</tr>
</tbody>
</table>

N* is the number of observations included in the model after data were truncated by discarding the 5% of observations at the farthest distance from the transects to eliminate outliers.
Vegetation Surveys. — Groundcover vegetation comparisons among habitats revealed significant differences in percentage of cover for all vegetation categories (broadleaf: grass $\chi^2 = 162.32$, $p < 0.001$; wiregrass: $\chi^2 = 42.04$, $p < 0.001$; forbs: $\chi^2 = 50.41$, $p < 0.001$; woody vegetation: $\chi^2 = 54.22$, $p < 0.001$; bare ground: $\chi^2 = 27.42$, $p < 0.001$; Fig. 1) except palmetto, which was common in all habitats (mean cover 25.9–29.2%; $\chi^2 = 2.94$, $p = 0.23$). Duncan’s multiple range tests ($\alpha = 0.05$) revealed significantly lower cover by broadleaf grasses, wiregrass, and forbs in scrub than in other habitats, but significantly higher cover by woody vegetation and bare ground (Fig. 1). Of all scrub plots, 89% had ≤ 5% broadleaf grass cover, and 63% had 1%. Wiregrass was somewhat more common, although 66% of scrub plots had ≤ 5% cover. Forbs were extremely scarce in scrub, with 61% of plots having < 1% cover.

Groundcover in flatwoods and plantations differed significantly only in percentage of cover by wiregrass and woody vegetation. Broadleaf grasses were present in 87% and 90% of flatwoods and plantation plots, respectively, although > 70% of plots in each had ≤ 25% cover. Wiregrass was also present in most flatwoods (74%) and plantation (63%) plots, although cover was significantly lower in plantations (57% of plots had ≤ 5% cover by wiregrass), whereas 90% in flatwoods had > 5%. Forbs were present in 67% and 74% of flatwoods and plantation plots, respectively, but forb cover was ≤ 5% in most plots for both habitats. Woody vegetation was present in most flatwoods and plantation plots, but cover was > 25% in 45% of flatwoods plots, whereas it was ≤ 25% in 81% of plantation plots.

The mean index values for canopy and shrub cover also differed significantly among habitats (canopy cover: $\chi^2 = 16.41$, $p < 0.001$; shrubs: $\chi^2 = 215.55$, $p < 0.001$). Not surprisingly, Duncan’s multiple range tests indicated that canopy cover was significantly higher in plantations (2.77 ± 0.64 SD) than in scrub (1.35 ± 0.64 SD) or flatwoods (1.96 ± 3.25 SD); although canopy in the plantations was still relatively open. Canopy in the scrub was very sparse, with most points (65%) lacking canopy. Shrub index values were significantly higher in scrub (6.23 ± 2.17 SD) than in flatwoods (1.10 ± 2.40 SD) or plantations (1.05 ± 2.17 SD), with 74% of plots in flatwoods and 67% of plots in plantations lacking shrubs entirely.

DISCUSSION

Characteristics of Flatwoods, Plantations and Scrub Habitats at APAFR. — At APAFR, like much of peninsular Florida, mesic flatwoods and pine plantations make up the largest area of habitat and Florida scrub,
rather than sandhill, dominates the sand ridges. With respect to groundcover, flatwoods are dominated by woody vegetation and wiregrass, and plantations are dominated by broadleaf grasses and palmetto (Fig. 1). Scrub is dominated by woody vegetation and bare ground, with significantly lower cover of plants used as forage by tortoises (i.e., broadleaf grasses, wiregrass, forbs).

In flatwoods and plantations at APAFR, the active fire program and periodic thinning of trees in plantations support open conditions and lush groundcover (Fig. 1). The weighted mean time-since-fire in the flatwoods/plantation sites we surveyed was 2.47 ± 0.05 yrs SD, and the only significant difference in groundcover vegetation between flatwoods and plantations was a lower percentage of cover by woody vegetation and wiregrass in plantations. Lower wiregrass cover may be due to the winter-season burn prescription used in plantations. This contrasts with the growing-season burns conducted in the natural flatwoods, which promote wiregrass flowering and seed production (Outcalt 1994). For the scrub sites we surveyed, the weighted mean time-since-fire was 3.18 ± 0.04 yrs SD due to recent application of prescribed fire over a large area that had not been burned for many years (US Air Force 2000).

**Densities of Gopher Tortoise Burrows in Scrub, Flatwoods and Plantations.** — We estimated densities of active, adult-sized gopher tortoise burrows (having clearly visible tortoise footprints or plastron drag marks at the mouth) in scrub and flatwoods/plantations at APAFR as an alternative to estimating population densities based on burrow occupancy rates. Our efforts at occupancy estimation (via burrow scoping) were hindered by the presence of water in flatwoods/plantation burrows, and the presence of roots or complex architecture that interfered with maneuverability of the scope in scrub burrows, forcing us to rely on burrow activity status as an indicator of tortoise occupancy. Despite the many factors that confound interpretation of burrow densities when occupancy rates are unknown, a general index can be obtained by assuming 1 adult tortoise per active adult burrow. This index yielded a total abundance estimate of 1435 adult tortoises in scrub habitats at APAFR, and 2694 in flatwoods/plantations (Table 2).

We found a significantly higher density of active burrows in scrub compared to flatwoods/plantations, despite significantly lower availability of food plants in scrub (Table 2; Fig. 1), which runs counter to previous research showing positive correlations of tortoise densities with herbaceous cover (e.g., Auffenberg and Iverson 1979; Auffenberg and Franz 1982). However, most existing data on gopher tortoise ecology are derived from studies in sandhill, which provides both dense herbaceous groundcover and well-drained soils. Habitats at APAFR may not fit this model because, although fire-maintained flatwoods/plantations support abundant forage, their poorly drained soils may be less suitable for tortoises. Conversely, the scrub habitats that dominate suitable soils tend to have sparse herbaceous food.

Our data, showing higher densities of active burrows in scrub compared to flatwoods/plantations, suggest that tortoises at APAFR may prefer scrub habitat over the more mesic flatwoods/plantations, although scrub may be somewhat less suitable than the better studied sandhills, due to low abundance of herbaceous plants. Although our LTDS data were unsuited for statistically assessing the burrow distribution pattern, we also noted that the distribution of burrows in flatwoods/plantations appeared patchy. Large expanses of flatwoods/plantations lacked burrows entirely, and burrows were only found along 65% of flatwoods/plantation transects, compared to 94% in scrub. Yet, where burrows occurred in flatwoods, local-scale densities were sometimes comparable to scrub (Castellón and Rothermel 2012). Thus, further research may be required to identify factors that influence gopher tortoise distribution in flatwoods habitats.

The patterns of burrow activity status we observed also raised some interesting questions. For example, the density (Table 2) and percentage of collapsed burrows (scrub 53%; flatwoods/plantations 35%) were significantly higher in scrub than in flatwoods/plantations. In contrast, a higher percentage of the remaining (non-collapsed) burrows were active in scrub (23%) than in flatwoods/plantations (16%). This suggests a somewhat higher occupancy rate of noncollapsed burrows in scrub (i.e., a higher tortoise-to-burrow ratio), but a stronger propensity to abandon burrows than in flatwoods/plantations. This could occur if tortoises in scrub are forced to relocate when food is depleted. However, radiotelemetry data from the same study area do not support this hypothesis, as tortoises (especially females) in the scrub appear to retain strong fidelity to a single burrow for long periods, allowing other burrows to go unmaintained, often until they collapse (Castellón and Rothermel 2012).

Alternatively, the high percentage of burrows in flatwoods/plantations that are usable, but not active, may suggest that tortoises maintain and move frequently among multiple burrows, but rarely abandon them. This idea is supported by our radiotelemetry data (Castellón and Rothermel 2012), but the frequent movements we observed are difficult to explain given availability of high-quality food within the immediate vicinity of most burrows. One possible explanation is that burrows with suitable hydrologic conditions (i.e., nonflooded burrows) may be a limited resource in flatwoods/plantations, and construction of new burrows may be hindered by the frequently high water table. In fact, the radiotelemetry data indicated that individual burrows in flatwoods/plantations were regularly used by several tortoises (though rarely at the same time), a situation that occurred infrequently in scrub. Thus, tortoises in flatwoods/plantations appear to move frequently among existing burrows, potentially in response to hydrologic conditions...
Potential Constraints on Gopher Tortoise Demography in Scrub and Flatwoods. — Potentially suboptimal habitat conditions in scrub and flatwoods may have demographic consequences for many of Florida’s extant tortoise populations. Gopher tortoises have 3 recognized habitat constraints: a need for herbaceous cover, sunlight at ground level, and soils appropriate for burrowing (Auffenberg and Franz 1982; Diemer 1986). At APAFR, given the active fire management program and low tree-stocking densities in forest stands, canopy closure and lack of sunlight probably are not major limiting factors. However, herbaceous cover is naturally sparse in Florida scrub habitat, which could translate into low quality and quantity of food for tortoises. This scarcity of high-quality forage could lead to lower fecundity, via small clutch sizes and/or poor egg quality (Ashton et al. 2007), lower survival of juveniles due to lack of palatable/nutrient-rich foods required by this age group (MacDonald and Mushinsky 1988; Mushinsky et al. 2003), or slower growth rates and later age at first reproduction (Aresco and Guyer 1999) than are typical of higher-quality habitats. Each of these factors could potentially limit population growth in scrub at APAFR.

Although availability of herbaceous forage is high in flatwoods and plantations at APAFR, mesic soil conditions in these habitats may be less than optimal. It is suggested that soil type might be less important for tortoises than either food or sunlight, as long as the soil is at least minimally suitable (Diemer 1992). In fact, tortoises sometimes occur in areas with poorly drained or dense soils, and they are even known to tolerate partial flooding of their burrows for extended periods (McRae et al. 1981; Means 1982; Breininger et al. 1988; Guyer and Hermann 1997). Nonetheless, they are not usually associated with wetlands, and Diemer (1992) speculated that prolonged inundation might induce movement to higher ground. Dispersal of a radio-tagged female from a flatwoods site at APAFR (after spending 2 nights under a pile of woody debris) during a period when most burrows were completely flooded supports this hypothesis (Castellón and Rothermel 2012). However, many tortoises remained at the site, inhabiting burrows that were partially flooded for long periods. Nonetheless, given the low density and apparently patchy distribution of burrows in mesic flatwoods/plantations at APAFR, we suggest that soil conditions may approach the limits of gopher tortoise tolerance for moisture or flooding.

Flooding of mesic flatwoods by shallow surface water or sheet-flow during periods of high rainfall is common in this part of Florida, and most flatwoods burrows we scoped were at least partially flooded throughout most of the year. Although adult tortoises may tolerate these periods of inundation, flooding of eggs would likely cause nest failure. The hypothesis that flatwoods hydrology may limit nest success is supported by near complete lack of juvenile-burrow observations along transects in flatwoods/plantations (1.75% of observations), compared to 16.3% in scrub (Castellón and Rothermel 2012). One possibility that requires further investigation is that females in flatwoods may travel to drier habitats for nesting, although our radiotelemetry data provided no evidence that this occurs.

Alternatively, despite the seemingly suboptimal conditions in scrub and flatwoods, it is possible that climatic factors in peninsular Florida provide opportunities for some forms of demographic compensation in these habitats. For example, despite our observation that the quality and quantity of forage was low in scrub, warm winters provide opportunities for year-round foraging (Douglass and Layne 1978; Diemer and Moore 1994), which could ameliorate some negative demographic consequences of lower habitat quality. This is plausible given that climate is the presumed explanation for rapid growth rates in Florida compared to more northern sites (Iverson 1980; Mushinsky et al. 1994). Although many local factors, such as herbaceous cover, will obviously influence growth rates, faster growth (leading to earlier
age at first reproduction) in more southern regions is a potential mechanism that could enable population persistence in otherwise suboptimal habitats. Likewise, although nest success may be low in flatwoods during most years (due to periodic flooding), recruitment may be high during droughts, potentially allowing flatwoods to function as source habitat during some years. These potential compensatory mechanisms raise intriguing questions that warrant further research.

In conclusion, little is known about gopher tortoise population dynamics in the habitat types that dominate peninsular Florida, yet careful management may be especially critical if populations in these habitats are unstable due to suboptimal conditions. Population dynamics and habitat use patterns may also be more complex in landscapes dominated by less than optimal habitats, especially if source–sink dynamics and/or landscape supplementation (Dunning et al. 1992) play important roles. Our survey provides important information on gopher tortoise densities in scrub and flatwoods habitats of peninsular Florida, and suggests avenues for additional research to understand mechanisms driving the patterns we observed.

Research is even more urgent if these habitats continue to be proposed as recipient sites for translocated tortoises. Our survey results suggest that even actively managed scrub and flatwoods do not typically support tortoise densities as high as those permitted for translocation recipient sites in Florida (Florida Fish and Wildlife Conservation Commission 2008). Although the State’s translocation guidelines do not establish habitat-specific stocking densities, “suitable” habitats may be stocked at densities of approximately 5–10 tortoises/ha, depending on a number of habitat quality criteria. Given our estimated densities of 0.56 active burrows/ha in scrub, and 0.21/ha in flatwoods/plantations, we suggest that additional research is needed to establish whether the densities we observed represent the typical carrying capacity for these habitats and, if so, whether stocking criteria should be adjusted accordingly. Finally, given the candidate status of gopher tortoises under the Endangered Species Act, density estimates in well-managed examples of all occupied habitat types will ultimately be needed to develop realistic recovery goals.

Acknowledgments

This work was supported by many people and organizations, including C. MacLaughlin, P. Ebersbach, M. Fredlake, B. Bonner, S. Orzell, C. Brown, and many others at APAFR, and H. Swain, G. Schrott, L. Gilson, M. Dent, B. Rolek, J. Rodriguez, R. Bowman, A. Thompson, E. Stein, M. George, and others at Archbold Biological Station. Valuable advice on implementation of field surveys was provided by L. Smith, T. Tuberville, H. McCoy, E. Mushinsky, and J. McGuire. We are grateful to research assistants E. McCluskey, K. Pollack, J. Lopez, Z. Forsburg, L. Rankin, D. Rankin, J. Ross, T. Demers, K. Powers, R. Percino-Daniel, K. Foley, A. Harrar, J. Miller, G. Kamener, L. Peters, M. McMillian, M. LaFave, T. Simpson, J. Daskin, J. O’Connor, A. Verpoorten, S. Rogers, A. Johnson, and S. Caster, and to K. Ashton for reviewing a draft of the manuscript. Funding was provided by the US Air Force under Cooperative Agreement W81XWH-06-2-0026 and research was conducted under Florida scientific collecting permit LSSC-10-00043.

LITERATURE CITED


US FISH AND WILDLIFE SERVICE. 2011. 12-Month finding on a petition to list the gopher tortoise (Gopherus polyphemus) as threatened in the eastern portion of its range. Federal Register 76:45130–45162.


Received: 7 November 2011
Revised and Accepted: 28 June 2012
Handling Editor: Jeffrey E. Lovich