GOPHER TORTOISES (GOPHERUS POLYPHEMUS) AS MICROCLIMATE ENGINEERS: FINE-SCALE ENVIRONMENTAL HETEROGENEITY PROMOTES NEAR-SURFACE THERMAL OPTIONS AT BURROW SITES

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Abstract.—Understanding how organisms respond to thermal heterogeneity (i.e., spatio-temporal variation of thermal conditions) requires quantification of thermal environments collected at spatial and temporal scales that are relevant to the scale at which individuals perceive their surroundings. Although the thermal implications of burrow use by Gopher Tortoises (Gopherus polyphemus) have been well-studied, near-surface microclimates (i.e., entrances and aprons) that are routinely used have received much less research attention. During summer, we deployed models equipped with temperature sensors to quantify thermal variation at burrow sites, and cameras to assess subsequent microsite use and behavioral responses by Gopher Tortoises. We found that burrow sites offer a wide range of thermal options for Gopher Tortoises at fine spatial scales (< 2 m), including ranging from 19.8°-66.9° C across all diurnal periods sampled during summer. Entrances provided substantially cooler microclimates by an average of up to 11.3° C, exhibited less hour-to-hour variability, and were less prone to extreme temperatures (i.e., $> 40^{\circ}$ C) than aprons. Although most Gopher Tortoise observations occurred at aprons (64%), entrances were used approximately twice as much for basking and sitting, demonstrating how fine-scale thermal heterogeneity can promote fine-scale behavioral differences. In addition to their role as ecosystem engineers, these findings reinforce that more attention should be paid to the role that Gopher Tortoises play as microclimate engineers. Doing so will not only provide more information on the thermal niche of Gopher Tortoise but will also help researchers identify the mechanisms that drive burrow use by commensal species.

Key Words.-activity; microsite use; temperature; thermal environment

INTRODUCTION

Understanding how organisms respond to thermal heterogeneity (i.e., spatio-temporal variation of thermal conditions) is a fundamental question in ecology, yet it is not well understood for many species (Angilletta 2009; Faye et al. 2016). Much of this poor understanding stems from a lack of information on how landscape patterns influence thermal conditions, and consequently, the space use and behavior of organisms (Potter et al. 2013; Carroll et al. 2016; Elmore et al. 2017). Although broad-scale climate data can be informative for studying a wide range of ecological questions, such as predicting species distributions (Buermann et al. 2008; Fancourt et al. 2015), most organisms experience temperature at finer scales (Potter et al. 2013; Schefers et al. 2014; Carroll et al. 2015, 2016). As a result, weather station data (i.e., macroclimate) alone often does not fully represent the thermal heterogeneity experienced by organisms (Schefers et al. 2014; Pincebourde et al. 2016). Addressing this discrepancy fundamentally requires collecting microclimate data at spatial and temporal scales that are relevant to the scale at which individuals perceive their surroundings (Potter et al. 2013; Pincebourde et al. 2016). In doing so, researchers can achieve a better understanding of the thermal niche of species (Goller et al. 2014; Martin et al. 2015) and can gain baseline information on the thermal context of different life stages (Angilletta 2009; Carroll et al. 2015, 2018).

Considered to be ecosystem engineers (Kinlaw and Grasmueck 2012; Catano and Stout 2015), the burrows constructed and inhabited by Gopher Tortoises (*Gopherus polyphemus*) provide critical habitat for hundreds of other native species (Landers and Speake 1980). Gopher Tortoise populations have undergone a precipitous decline (~80%) mostly due to large scale habitat loss as a result of land development as well as modern agricultural and forestry practices (Landers and Speake 1980; Auffenberg and Franz 1982). Despite their ecological importance and population decline, several fundamental aspects of Gopher Tortoise ecology (e.g., thermal biology, activity, space use) remain understudied, creating potential barriers

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to future management and conservation efforts. While it is widely acknowledged that subterranean burrows shelter Gopher Tortoises from suboptimal or extreme thermal environments (Douglas and Layne 1978; Pike and Mitchell 2013), quantifications of fine-scale thermal heterogeneity at near-surface microsites (e.g., entrances and aprons), which may promote or constrain activity, are scarce. For example, near-surface microclimate has been shown to be a primary driver of Desert Tortoise (Gopherus agasizzii) behavior (i.e., foraging, basking, etc.,), microhabitat use, and body temperature (Zimmerman et al. 1994), yet it remains an understudied aspect of Gopher Tortoise ecology. Therefore, modeling the thermal environments available to Gopher Tortoises at burrow sites provides a way to gain previously unknown, and potentially important, baseline information on the thermal niche of the species (Radzio and O'Connor 2017), and helps to achieve a better understanding of finescale microsite use and behavior.

Because undisturbed behavior of Gopher Tortoises is difficult to observe, gaining observations of activity and behavior are limited to traditional observational techniques. Using automated wildlife cameras, however, provides a way to efficiently and continuously observe behavior while eliminating disturbance caused by onsite observers (Vine et al. 2009; Millar and Hickman 2021). Researchers are also able to simultaneously record and pair fine-scale temperature measurements with camera data for the purpose of assessing the influence of microclimate on activity and microhabitat use in real-time (Carroll et al. 2018). Accordingly, camera data have also been useful for elucidating previously unobserved temperature-dependent behavior in Desert Tortoises (Agha et al. 2015) and Gopher Tortoises (Radzio and O'Connor 2017).

The main prerequisites of Gopher Tortoise habitat are sandy soils to promote burrow construction, as well as frequent fire and sparse tree canopies, which promote the growth of preferred forage plants (Diemer 1986; Jones and Dorr 2004). As ectotherms, Gopher Tortoise thermoregulation is contingent upon the thermal conditions in the immediate environment (i.e., microclimate; Auffenberg and Franz 1982), yet landscape structure often dictates the thermal conditions that organisms are exposed to (Milling et al. 2018). While thermal environments within burrows have been well-studied (Douglas and Layne 1978; Pike and Mitchell 2013), near-surface microclimates that are routinely used by Gopher Tortoises (i.e., entrances and aprons) for essential activities such as basking, mating, and nesting, have received much less attention. Therefore, our primary objectives were to: (1) quantify spatial and temporal variation of thermal conditions (i.e., thermal heterogeneity) available to Gopher Tortoises at burrow sites during the summer; (2) assess subsequent Gopher Tortoise activity in relation to nearsurface thermal environments; and (3) investigate the effects of site-specific characteristics on microclimate at burrow sites.

MATERIALS AND METHODS

Study site.—We collected data at the John W. and Margaret Jones Langdale Forest, located in southcentral Georgia, USA. Specifically, we sampled Gopher Tortoise burrows across a Southeastern Coastal Plain sandhill community in two stands. The first stand (16.8 ha) predominantly consisted of Slash Pine (*Pinus elliottii*; basal area about 14 m2/ha; Grant Rentz pers. comm.) that was burned in 2019. The second adjacent stand (9.6 ha) consisted primarily of Loblolly Pine (*Pinus taeda*; basal area of about 25 m2/ha; Grant Rentz, pers. comm.). Dominant shrubs and vines include gallberry (*Ilex spp.*), blueberry (*Vaccinium spp.*), Running Oak (*Quercus pumila*), Winged Sumac (*Rhus copallinum*), and Muscadine (*Vitis rotundifolia*).

Microclimate measurements.—To provide an index of thermal environments, we measured the cumulative effects of ambient temperature, solar radiation, and wind, using thermal models (T_{model}) that we painted flat black (i.e., black bulb temperature; Bakken et al. 1985; Hovick et al. 2014; Carroll et al. 2015, 2018; Rakowski et al. 2019). We constructed models by securing a Thermochron iButton (Maximum Integrated, San Jose, California, USA) inside of a small round aluminum jar (Radzio and O'Connor 2017), which was 4 cm diameter \times 1.7 cm deep and about 15 mm in volume. We used a small amount of tape to attach and secure an Ibutton to a small foam spacer glued to the center of each thermal model. In addition, we secured each thermal model in the burrow sidewall using a wooden dowel (Radzio and O'Connor 2017) attached to the base and pinned in place into the substrate. Although they provided a means to measure fine-scale thermal environments at burrow sites, the size of the thermal models did not match that of our study species and thus did not necessarily match the body temperature of Gopher Tortoises. Nevertheless, the use of these types of thermal models provides an effective and standardized way to gain a relative index of the spatiotemporal variability of thermal conditions across different microsites (Forrester et al. 1998; Carroll et al. 2015, 2016; Rakowski et al. 2019). Using an onsite weather station, we collected hourly solar radiation (S_{rad}) and ambient temperature (T_{air}) measurements to compare T_{air} to T_{model} observed during the study. The weather station was positioned approximately 1.5 m aboveground and was located approximately 1.5 km from the site where sampling was conducted. All temperature data (i.e., Tair and Tmodel) were collected at 15-min intervals.

We sampled microclimate at adult burrow sites (i.e., entrances and aprons) across each of the four survey rounds in both summer 2020 and 2021 (June-August). We sampled eight Gopher Tortoise burrows during each round (7-d rounds in 2020, and 10-d rounds in 2021) resulting in 64 monitoring periods. We randomly drew sampled burrows from the pool of known Gopher Tortoise burrows in the stand resulting in 44 different burrows sampled (13 in 2020 and 31 in 2021).

At each burrow site, we deployed a thermal model on the outermost periphery of the apron (i.e., excavated soil mound), and flush with the burrow sidewall approximately 10 cm inside the entrance (Radzio and O'Connor 2017). We placed the thermal model on the apron so that it would not be in the direct line of regular travel or use by Gopher Tortoises as evidenced by trails or a preponderance of tracks. The small size and placement of the thermal models ensured that they did not interfere with Gopher Tortoise movement or influence behavior and activity at either microsite.

Camera observations.--We monitored Gopher Tortoise activity at each of the burrow sites where thermal sampling occurred using passive infrared motion sensor cameras (Moultrie D300; Moultrie Feeder, Birmingham, Alabama, USA and Bushnell Trophy Camera; Bushnell Corporation, Overland Park, Kansas, USA). Previous studies have documented the limitations of using cameras to detect and monitor ectotherms (Ariefiandy et al. 2013), especially for small-bodied species (Pagnucco et al. 2011) and/or when the body temperature of an organism approximates the ambient temperature in the surrounding environment (Meek et al. 2012). Despite these limitations, cameras have been shown to be effective for monitoring the activity of Desert Tortoises and Gopher Tortoises (Agha et al. 2015; Radzio and O'Connor 2017; Knapp et al. 2018; Rautsaw et al. 2018; McHugh et al. 2019). Moreover, cameras have been used extensively to detect the use of Gopher Tortoise burrows by commensal species (e.g., reptiles,

mammals, and birds; Alexy et al. 2003; Dziadzio and Smith 2016). At each burrow sampled, we mounted a camera on a wooden stake, aimed at the burrow (Agha et al. 2015; McHugh et al. 2019) and slightly angled downward to increase visibility into the entrance. We positioned cameras at a height of approximately 40 cm (McHugh et al. 2019) and 75–100 cm from the entrance. We generally followed the camera positioning protocol used by McHugh et al. (2019; i.e., camera positioned 36-76 cm from the entrance); however, we periodically positioned our cameras slightly farther from the entrance to simultaneously maintain both the ability to observe activity in the entrance as well as on the apron in front of the burrow. For each detection event, we programmed cameras to collect three high-definition photographs with a motion detection delay of 30 sec. Cameras recorded a time stamp (i.e., date and time) for each image, and we compared images to temperature data collected in real time to assess the influence of changes in thermal environments on Gopher Tortoise microsite and observable behavior.

Microsite use data can be an informative proxy for how organisms, including ectotherms, respond to thermal heterogeneity (Attum et al. 2013; Goller et al. 2014; Carroll et al. 2015; Milling et al. 2018). We categorized observations of microsites occupied by Gopher Tortoises as either entrance or apron. We defined Gopher Tortoise microsite use as entrance if we observed a portion of the body of the tortoise in the entrance of the burrow chamber (i.e., burrow mouth), and as apron if we observed individuals on the mound of excavated soil outside and in front of the burrow chamber. Observations of Gopher Tortoises behind or adjacent to burrow sites were rare (< 1%) and we did not use them for our comparative analysis of microsite use. We classified behavior as: (1) basking; (2) sitting; (3) locomotion; (4) maintenance; (5) foraging; (6) mating; (7) alert; and (8) sleeping (Table 1; Fig. 1) based on postures, movement, and/or behavior detailed in previous studies (Ruby and Niblick 1994; Buteler et al. 2022).

TABLE 1. Behavioral states observed for Gopher Tortoises (Gopherus polyphemus) in southern Georgia, USA, Summer 2020 and 2021.
Definitions are based on postures, movement, and/or behavior described by Ruby and Niblick (1994) and Buteler et al. (2022).

Behavior	Defintion
Basking	Plastron contacting the ground with legs sprawled and skin exposure to sunlight maximized (Fig. 1).
Sitting	Motionless with plastron contacting the ground. Not exhibiting other obvious basking behavior (e.g., sprawled posture).
Locomotion	Alternating limb movement.
Maintenance	Digging and soil excavation.
Foraging	Active feeding or chewing.
Mating	Copulating/mounting.
Alert	Motionless posture with neck extended and eyes pointed forward.
Sleeping	Resting with eyes closed.



FIGURE 1. Trail camera photograph of a Gopher Tortoise (*Gopherus polyphemus*) basking on the apron of a burrow in southern Georgia, USA, summer 2020.

Microsite measurements.—To estimate tree canopy cover, we used a spherical crown densiometer (Forestry Suppliers, Jackson, Mississippi, USA) centered above each burrow (Hayes et al. 1981). Additionally, we measured burrow orientation (i.e., the aspect that burrows faced) using a Suunto MC-2G Navigator compass (Suunto, Vantaa, Finland). We also measured other burrow characteristics including entrance width, entrance height, apron length (i.e., left to right when facing the burrow), and apron width (i.e., at the widest point from the burrow entrance to the edge of the apron in front of the burrow entrance).

Statistical analyses.--Mean values are reported with standard errors and we performed all analysis of temperature data in R (R Development Core Team, 2020). We used univariate statistics to test for differences in thermal environments at microsites used by Gopher Tortoises. Prior to analyzing temperature data, we used a Shapiro Wilks normality test (Zar 1999) and found that the data exhibited a non-normal distribution for aprons (W = 0.97, P < 0.001) and entrances (W = 0.79, P < 0.001). Therefore, we used a Wilcoxon Rank Sum Test (Zar 1999) to test for differences among model temperature (T_{model}) at entrances and aprons for diurnal periods (0700-1900) and during the hottest period of the day (1100-1500). To evaluate hour-to-hour microclimate variability, we calculated the standard deviation of T_{model} for each hour of the diurnal period. We assessed variation in thermal patterns using Linear Regression to examine T_{model} in relation to T_{air} at entrance and apron microsites, respectively. Accordingly, we calculated hourly average T_{model} from measurements recorded at 15-min intervals to allow for comparisons of T_{air} that were collected at hourly intervals (Carroll et al. 2015, 2016). We compared slopes of regression lines

for entrances and aprons using Analysis of Covariance (ANCOVA), and we used an alpha value of 0.05 for all statistical procedures.

Because photographs recorded within each threeimage observation event (i.e., collected at 30 sec intervals) may not be independent, we randomly sampled one image from each observation event (Agha et al. 2015). We compared distributions of behavior type observations across diurnal time periods (0700-1000, 1100-1500, and 1600-1900) and the most commonly observed behaviors (e.g., basking, locomotion, and sitting; 87.3%) among microsites using Chi-square To assess potential drivers of microclimate Tests. at burrow sites, we used Generalized Linear Mixedeffects Models using the nlme package in R (Pinheiro and Bates 2022; R Development Core Team 2020). Specifically, we modeled the influence of T_{air}, burrow orientation, canopy density, and burrow width as fixed effects, and burrow site as a random effect on T_{model} (i.e., dependent variable). We modeled T_{model} measured from 1100–1500 because this period experienced the greatest thermal variability and corresponded with the majority of Gopher Tortoise observations at entrances and aprons (65.8%).

We ranked models by Akaike Information Criterion (AIC) values, and we considered models within AIC < 2 to have equal plausibility (Burnham and Anderson 2002). Prior to analysis, we assessed potential correlation of variables by calculating Pearson's Correlation Coefficients. Entrance width and height (r = 0.64, t = 40.08, df = 2,312, P < 0.001) and apron length and width (r = 0.71, t = 50.21, df = 2485, P <0.001) were significantly correlated, and thus we removed entrance height and apron width from all respective candidate models. Moreover, T_{air} and S_{rad} were also significantly correlated for entrances (r =0.60, t = 36.56, df = 2312, P < 0.001) and aprons (r =0.61, t = 38.69, df = 2485, P < 0.001), and therefore we removed S_{rad} from all respective candidate models. We coded burrow orientation as dummy variables with four categories, each corresponding to north (315°-44°), east (45°-134°), south (135°-224°), and west (225°-314°), respectively (Evans 2018; Carroll et al. 2020).

To analyze the effects of orientation and canopy density categories (i.e., 0-25%, > 25%-50%, > 50%-75%, and > 75%) on T_{model}, we used a Kruskal-Wallis Test (Zar 1999). We evaluated pairwise comparisons using a Dunn's Test (Dunn 1964; Zar 1999) given that this test is appropriate when the number of observations between groups are not equal (Elliot and Hynan 2011). We adjusted *P*-values using the Benjamini-Hochberg method (Benjamini and Hochberg 1995). To investigate non-uniformity in burrow orientation, we used a Rayleigh's Test (Zar 1999).



FIGURE 2. (A) Distribution of model temperature (Tmodel) observed at ambient temperatures (Tair) recorded at an on-site weather station during diurnal periods (0700–1900) at Gopher Tortoise (*Gopherus polyphemus*) burrow aprons. (B) Distribution of model temperature (Tmodel) observed at ambient temperatures (Tair) recorded at an on-site weather station during diurnal periods (0700–1900) at Gopher Tortoise burrow entrances. (C) Linear relationship of model temperature (Tmodel) observed at ambient temperatures (Tair) recorded at an on-site weather station during diurnal periods (0700–1900) at Gopher Tortoise burrow entrances. (C) Linear relationship of model temperature (Tmodel) observed at ambient temperatures (Tair) recorded at an on-site weather station during peak diurnal heating (1100–1500) at Gopher Tortoise burrow aprons (red) and burrow entrances (blue) in southern Georgia, USA, Summer 2020 and 2021.

RESULTS

Microclimate and microsite measurements.-To assess microclimate relevant to Gopher Tortoises, we recorded 97,796 black bulb temperature measurements (T_{model}). Burrow sites (including entrances and aprons combined) exhibited substantial thermal heterogeneity (e.g., average hourly T_{model} ranging from 19.8°-66.9° C during summer) at fine spatial scales (< 2 m) (Fig. 2). Entrance T_{model} differed from apron T_{model} during diurnal periods (0700–1900; W = 29, df = 278,338, P < 0.001), as well as during the hottest period of the day (1100-1500; W = 53, df = 46,177, P < 0.001), and differences in T_{model} between entrances and aprons increased as T_{air} increased (Fig. 2). Specifically, T_{model} at entrances were an average of 9.6° C cooler than at aprons from 1100-1500 and were up to 11.3° C cooler at 1300 (Fig 3). Moreover, from 1100-1500 we observed that 40.0% and 14.2% of apron T_{model} measurements exceeded 40° C and 50° C, respectively. In contrast, we observed that 3.6% and 0.9% of entrance $\mathrm{T}_{\mathrm{model}}$ measurements, exceeded 40° C and 50° C, respectively.

Linear relationships observed between T_{model} and T_{air} were significantly stronger at aprons ($F_{1,6679} = 8,824, P$

 $< 0.001, r^2 = 0.57$) than at entrances (F_{1,6358} = 3,651, P < 0.001, $r^2 = 0.36$; Fig. 2) during diurnal periods (0700– 1900). In addition, the slopes of the relationship between T_{air} and T_{model} differed significantly between entrance and apron microsites ($F_{3,13037} = 6,434$, P < 0.001, $r^2 = 0.60$). Furthermore, average T_{model} at entrances remained cooler than T_{air} from 0700-1900, although the difference was not significant (Fig. 3). In addition to being generally cooler and less prone to thermal extremes, entrances experienced substantially less hour-to-hour variability in T_{model} (Fig. 3). Specifically, hour-to-hour variability in T_{model} (assessed as standard deviation) at entrances and aprons were 3.0° C and 5.4° C, respectively, during diurnal periods, and 4.4° C and 8.9° C respectively, from 1100-1500. Thus, hour-to-hour variability was approximately 75% greater and 100% greater at aprons than at entrances during diurnal periods and from 1100-1500, respectively. Peak hour-to-hour variability occurred at 1400 for both entrances (5.3° C) and aprons (10.0° C; Fig. 3) and mean hour-to-hour variability of T_{air} was 2.8° C during diurnal periods and 3.0° C from 1100-1500.

Average entrance width and height were 31.5 ± 1.3 cm and 16.8 ± 0.6 cm, respectively, and average apron

FIGURE 3. (A) Average hourly temperature and, (B) standard deviation for Tmodel at Gopher Tortoise (*Gopherus polyphemus*) burrow aprons (black), Tmodel at burrow entrances (gray), and Tair (dashed) recorded from 0700–1900 in southern Georgia, USA, Summer 2020 and 2021. Errors bars for temperatures shown in A are standard errors.

length and width were 131.8 ± 5.7 cm and 116.5 ± 7.5 cm, respectively. We found a weak, but significant, correlation between entrance T_{model} and entrance width (r = -0.19, t = -15.13, df = 6,025, P < 0.001), entrance height (r = -0.18, t = 13.88, df = 6,025, P < 0.001), as well as, apron T_{model} and apron length (r = -0.04, t =-3.38, df = 6,463, P < 0.001) and apron width (r = -0.06, t = -4.50, df = 6,463, P < 0.001). Entrance T_{model} differed significantly by orientation (H=228.3, df=3, P<0.001) during diurnal periods, and all pairwise comparisons demonstrated statistical significance (P < 0.05). Apron T_{model} also differed by orientation (H = 56.11, df = 3, P < 0.001) during diurnal periods, and all pairwise comparisons differed significantly (P > 0.05) except for east-west orientations. However, Gopher Tortoise burrow orientation monitored in our study exhibited a uniform distribution (i.e., random; r = 0.126, P = 0.509), indicating no pattern for specific orientations. We found significant differences (H = 234.4, df = 3, P < 0.001) in entrance T_{model} among all canopy density categories, except for 0–25% and > 50–75% comparisons (Dunn's Test, P > 0.05). Among canopy density categories, we observed no significant differences in apron T_{model} (H = 3.39, df = 3, P = 0.336).

The most plausible model for assessing the drivers of entrance microclimates based on AIC ranking included T_{air} , canopy density, and orientation (AIC = 11,387.3), but the global model received similar support (AIC = 11,388.4; Δ AIC < 2). For the highest ranked model, lower T_{model} was associated with lower T_{air} , greater canopy

FIGURE 4. Observed Gopher Tortoise (*Gopherus polyphemus*) microsite use (i.e., burrow entrance or apron) at burrow sites in southern Georgia, USA, Summer 2020 and 2021.

density, and north orientation. We found no significance (P > 0.05) for south, east, and west orientation. For apron microclimates, the model that received the greatest support based on AIC ranking included T_{air} and orientation (AIC = 15,252.8). At aprons, higher T_{model} was associated with greater T_{air} and south orientation, which were the only significant parameters (P < 0.05).

Camera observations.—Camera monitoring vielded 3,077 observation events of Gopher Tortoises at burrow sites. Most Gopher Tortoise observations (64.0%) were made at aprons compared to entrances (36.0%; Fig. 4). We observed that most Gopher Tortoise observations occurred from 1100-1500 (65.8%) compared to 0700-1000 (7.2%) and 1600-1900 (27.0%; Fig. 5), and we found strong evidence to support a relationship between microsite use and diurnal time period (i.e., 0700-1000, 1100–1500, 1600–1900; $X^2 = 17.77$, df = 2, P < 0.001). Specifically, the frequency of observations was greatest during midday for entrances (70.9%) and aprons (63.3%). Thus, entrances and aprons were more likely to be used during the midday than morning or evening periods (Fig. 4). With the exception of 0700 and 0800, the number of observations at aprons were 1.3-2.7-fold greater than for entrances during each diurnal hourly period (Fig. 4).

We found that 87.3% of observed Gopher Tortoise behavior at burrow entrances and aprons consisted of basking (41.1%), locomotion (31.7%), and sitting (14.5%; Fig. 5). Less commonly observed behaviors included burrow maintenance (5.3%), mating (4.8%), as well as other behaviors (i.e., foraging, alert, sleeping combined at 2.6%; Fig. 5). The three most commonly observed behaviors, basking, locomotion, and sitting, accounted for 59.6%, 11.9%, and 21.2% of total entrance observations events, respectively, compared to 30.3%, 43.4%, and 10.6% of apron observations events, respectively (Fig. 5). Moreover, we found a significant relationship between microsite use and behavior (i.e., basking, locomotion, and sitting; $X^2 = 401.9$, df = 2, P < 0.001). Specifically, basking was observed at

FIGURE 5. Camera observations of Gopher Tortoise (*Gopherus polyphemus*) behavior at burrow microsites (i.e., burrow entrance or apron) in southern Georgia, USA, summer 2020 and 2021.

considerably greater frequencies at entrances than aprons, whereas locomotion was observed much more frequently at aprons than entrances (Fig. 5). In addition, we observed two or three individuals simultaneously using burrow sites in 23.8% and 0.63% of observation events, respectively.

DISCUSSION

Our results demonstrate that burrow sites (i.e., aprons and entrances) offer a wide-range of thermal options for Gopher Tortoises at fine spatial scales (< 2 m), including ranging from 19.8°-66.9° C during summer. Entrances provided substantially cooler microclimates by an average of up to 11.3° C, exhibited less hourto-hour variability, and were less prone to extreme temperatures than aprons. While it is well established that the subterranean depths of Gopher Tortoise burrows are decoupled from aboveground thermal environments (Hansen 1963; Douglas and Layne 1978), these results suggest that entrance and apron microclimates are also decoupled from each other, but at much finer spatial scales (< 2 m). Notably, the substantial differences in T_{model} that we observed at burrow sites demonstrates fine-scale thermal heterogeneity that is similar to, or greater than, that which is observed across larger spatial scales on other landscapes (Hovick et al. 2014; Carroll et al. 2016; Rakowski et al. 2019), including southeastern pine forests (Roe et al. 2017). Therefore, in addition to their role as ecosystem engineers (Kinlaw and Grasmueck 2012; Dziadzio and Smith 2016), the thermal heterogeneity that we report at burrow sites reinforces that more attention should be paid to the role that Gopher Tortoises play as microclimate engineers (Pike and Mitchell 2013).

The frequency of extreme heat in the southeastern U.S. is predicted to increase in the future due to global climate change (Christensen et al. 2007; Carter et al. 2018). Because they provide comparatively cool and stable microclimates in summer, the subterranean

reaches of burrows have been identified as critical thermal refuge sites for Gopher Tortoises and commensal species in the face of future climate change (Pike and Mitchell 2013). The influence of climate change on other aspects of Gopher Tortoise habitat and thermal ecology, however, are poorly understood. We found that differences in T_{model} between entrances and aprons increased concomitantly to increased Tair, suggesting that temperatures at entrances will rise at a slower rate than aprons under increasing T_{air} associated with future climate change. These findings of greater thermal buffering at entrances are further supported given that they also tended to be substantially cooler and subject to fewer heat extremes (i.e., 14.2% vs. 0.9% of T_{model} in excess of 50° C) than nearby apron microsites. In addition, the overall juxtaposition of microclimates associated with burrows is evident given that the average entrance temperatures we found (29.3° C) were warmer than those reported for subterranean burrow retreats (about 27° C during summer; Douglas and Layne 1978; Pike and Mitchell 2013), but we found that they remained much cooler than average apron temperatures (38.9° C) from 1100-1500.

By providing moderated microclimates, our findings suggest that entrances serve as important intermediate microsites (i.e., positioned between thermally disparate aprons and subterranean burrow chambers) despite not necessarily providing the coolest or warmest available conditions. This was demonstrated by our observations that Gopher Tortoise entrances were used primarily for basking, but that individuals also shuttled to and from aprons periodically. Moreover, Gopher Tortoises that occupy entrances may incur reduced energetic costs given that they are able to remain close to basking, mating or foraging opportunities at the surface, while also having access to the cooler microclimates and shelter from predators afforded by subterranean portions of the burrow (Radzio and O'Connor 2017). Thus, while thermal refuge is often considered as being sites that provide the most moderated microclimates (i.e., that buffer against potentially lethal extremes; Carroll et al. 2015; Martin et al. 2015; Rakowski et al. 2019), these results reinforce that other less buffered sites may still have thermal value depending on their spatial juxtaposition relative to other resources (White et al. 2019; Olsoy et al. 2022). In the future, a better understanding of tortoise thermal ecology would benefit from the role that moderated microclimates play in mitigating thermal extremes while also potentially reducing energetic costs incurred by Gopher Tortoises engaging in critical behaviors (e.g., basking, mating, nesting, etc.,). Accomplishing this will fundamentally require future research aimed at quantifying the entire thermal landscape to better understand Gopher Tortoise behavior and space use.

The effectiveness of thermoregulation is contingent upon the behavioral adjustments that ectotherms make relative to the thermal suitability of available microhabitats (Pincebourde and Suppo 2016; Laspiur et al. 2021). Similar to previous studies, we observed that Gopher Tortoise summer activity at burrow sites primarily occurs during the heat of midday (i.e., unimodal) (Douglas and Layne 1978; Alexy et al. 2003). Interestingly, however, we found that most activity at entrances and aprons not only corresponded to peak diurnal ambient temperatures (Douglas and Layne 1978) but was also associated with increases in spatial and temporal T_{model} variability, which likely maximized fine-scale thermal choices for Gopher Tortoises. In response to these thermal choices, Gopher Tortoises regularly used both microsites, albeit oftentimes for different behaviors. Specifically, observations of basking and sitting were approximately two-fold greater at entrances than aprons. Conversely, aprons accounted for more (> three-fold) observations of locomotion than entrances. Locomotion was typically observed when Gopher Tortoises were moving across the burrow apron, potentially visiting the burrow and/or checking the burrow for conspecifics (e.g., mates; Ruby and Niblick 1994). These observations demonstrate how fine-scale thermal heterogeneity appears to promote fine-scale differences in Gopher Tortoise behavior and helps to explain why a high proportion of activity is concentrated around burrow sites (Mushinsky et al. 2006; Radzio and O'Connor 2017; McHugh et al. 2019), often within 1 m (Douglas and Layne 1978).

Gopher Tortoises may use more than one burrow during a diurnal period (Diemer 1992; Mushinsky and Esman 1994) and can alternate the burrows that they occupy (Mushinsky and Esman 1994). Therefore, our findings only apply to the microsite use that we observed as a result of our camera monitoring and simultaneously recorded temperatures at each respective burrow site. Due to the difficulty of visually differentiating individuals in photographs, we were unable to collect demographic information (i.e., ID, sex, or age) using camera data. Given that some behavioral responses to thermal conditions were likely sex-dependent (Douglas and Layne 1978), the inability to visually distinguish sexes in our study reduces the behavioral detail that we were able to glean. Despite this, our sampling methodology allowed for an assessment of Gopher Tortoise activity and a depiction of the natural variance of behavior relative to previously unquantified thermal heterogeneity occurring in real-time.

Despite being in close proximity (< 2 m), data from T_{model} at entrances were best explained by a different combination of variables than at aprons. These findings provide further evidence that microclimate variation occurs due to the synergistic effects of biotic

and abiotic factors at fine spatial and temporal scales (Potter et al. 2013; Carroll et al. 2016; Pincebourde et al. 2016), including at Gopher Tortoise burrow sites. For example, lower T_{model} values were associated with lower Tair, greater canopy cover, and north orientation at entrances, whereas at aprons, greater T_{model} values were associated with greater T_{air} and south orientation. While it is not surprising that T_{air} and orientation (i.e., potential exposure to solar radiation) influenced T_{model} at both microsites, it is unclear why canopy density influenced $\mathrm{T}_{\mathrm{model}}$ at entrances but not at aprons. Nevertheless, these differences demonstrate the complexity associated with understanding fine-scale thermal heterogeneity and provide further evidence that entrance and apron microclimates are thermally decoupled. We observed differences in T_{model} at entrances and aprons for certain orientation and canopy cover comparisons, yet our results agree with previous studies that burrow orientation exhibits no directional pattern (i.e., they are randomly situated; McCoy et al. 1993). Thus, the structural variation resulting from the excavation of burrow sites (i.e., burrows and aprons), and the resulting thermal heterogeneity that we observed, may have provided a wide enough range of temperatures to override any potential thermal benefits associated with selection for a particular burrow orientation.

Conclusions.—Our study demonstrates how thermal environments supported by entrances and aprons provide a wide range of thermal choices that are available for exploitation and are routinely used by Gopher Tortoises. To help inform conservation efforts, future research would benefit from investigating how thermal variation manifests across landscapes inhabited by Gopher Tortoises under different forest management regimes (e.g., thinning, prescribed burning, road construction, etc.). Without such information, the ability of managers to fully understand how their practices influence Gopher Tortoise habitat is hindered. Ultimately, our findings also suggest that more research to fully understand the mechanisms driving the role of Gopher Tortoises as not only ecosystem engineers (Jones et al. 1994; Kinlaw and Grasmueck 2012), but also as microclimate engineers (Pike and Mitchell 2013), is needed. Doing so would be instructive for understanding how burrow sites and their construction may influence present and future habitat quality for Gopher Tortoises and commensal species.

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