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Behavior and temperature modulate a thermoregulation–predation risk trade-off in juvenile gopher tortoises

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Abstract

Ectotherms frequently thermoregulate behaviorally to improve physiological processes such as digestion and growth, but basking and other thermoregulatory activities can also increase predation risk. Organismal and environmental characteristics can, in some species, influence predation risk associated with thermoregulation and thereby relax or tighten constraints on thermoregulatory behavior, physiological performance, and, ultimately, life history traits. Providing one of the first such investigations in turtles, we examine whether behavior and thermal environment modulate a thermoregulation–predation risk trade-off in juvenile gopher tortoises (*Gopherus polyphemus*). Young gopher tortoises experience very high predation pressure, and their declining species faces many challenges, including human-induced increased shading of its environment. We hypothesized that in response to simulated predator approach, basking hatchling and juvenile tortoises would: (i) hide inside burrows; (ii) hide for shorter durations in cooler burrows presumably due to greater constraints on physiological performance; and (iii) spend greater time at the surface following disturbance in cool environments because individuals would need to bask more to maintain preferred body temperatures. Basking tortoises always hid inside burrows when approached and exhibited very long flight initiation distances ($\bar{x} = 45$ m) that increased with age/size. Individuals fled into burrows even when it was not possible for them to see the approaching researcher, suggesting the use of vibrations (aerial/ground) to detect potential predators and a possible antipredator function for exceptionally large otoliths characteristic of the species. Tortoises hid for short durations ($\bar{x} = 18.3$ min), especially in cool burrows, suggesting that they optimize hiding responses to balance physiological costs and antipredator benefits. Additionally, surface activity following disturbance consisted primarily of basking and correlated negatively with burrow temperature. These findings suggest that thermal environment influences predation risk in ectotherms whose surface activity is driven primarily by thermoregulatory requirements and highlight potential benefits of warm, well-insolated habitats, such as endangered longleaf pine (*Pinus palustris*) ecosystems, for juvenile gopher tortoises.

KEYWORDS

basking, flight initiation distance, *Gopherus polyphemus*, otolith, thermal ecology, turtle

1 | INTRODUCTION

Many ectotherms regulate body temperature behaviorally, which can enhance physiological processes such as digestion and growth, but thermoregulatory activities, including basking and shuttling movements between sun and shade, can expose individuals to increased predation risk (Angilletta, 2001; Huey, 1974; Huey & Slatkin, 1976; Lillywhite, Licht, & Chelgren, 1973). These and other costs may influence the extent to which reptiles thermoregulate and can impose constraints on physiological performance and life history traits (Huey, 1974; Huey & Slatkin, 1976; Sears et al., 2016; Vickers, Manicom, & Schwarzkopf, 2011). For example, predator scent caused garden skinks (*Lampropholis guichenoti*) to spend less time in optimal foraging and thermoregulatory microhabitats and to grow more slowly (Downes, 2001). Similarly, some snakes limit basking as juveniles, possibly in response to avian predators, a thermoregulatory strategy that may result in lower growth rates (Lelièvre et al., 2013; Webb & Whiting, 2005). However, limited basking may not be an optimal, or even demographically feasible, strategy if juveniles grow very slowly and remain vulnerable to predators during other activities (e.g., sheltering in refugia or foraging).

Although basking in open habitats can increase exposure to predators, organismal traits such as cryptic coloration and specialized sensory capacities can reduce predation risk during thermoregulation (Robert & Thompson, 2007; Smith et al., 2016; Vitousek, Adelman, Gregory, & St Clair, 2007). Ectotherms can also optimize trade-offs between costs and benefits of thermoregulatory behavior that may vary with environmental conditions through careful microhabitat selection and other responses (Huey, 1974; Huey & Slatkin, 1976). Considerable data support the hypothesis that prey, including basking individuals, modify flight initiation distance (FID) to balance predation risk against flight costs (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). Costs and benefits can also influence subsequent refuge use. For example, after entering a refuge in response to a predator, some lizards hide longer when the refuge is warm or when external temperatures are low, presumably because physiological costs of refuge use are not as great (Amo, López, Martín, & Douglas, 2003; Cooper & Wilson, 2008; Martín & López, 1999, 2001, 2010). Similarly, in warm environments, ectotherms may be able to maintain preferred body temperatures without having to bask and expose themselves to predators as much as when basking (Akins et al., 2014; Webb & Whiting, 2005).

Most investigations of trade-offs to predator avoidance in reptiles focus on lizards (Cooper & Blumstein, 2015; Downes, 2001; Martín & López, 2015). Comparatively, turtles are understudied in this regard (Cooper, 2015), and even FIDs remain largely undocumented (but see Costa, 2014; Polich & Barazowski, 2016), especially for juvenile turtles. Studying how organismal traits and environmental conditions influence a trade-off between thermoregulation and predator avoidance in turtles provides an opportunity to assess the generality of relevant predator avoidance hypotheses (e.g., Lima & Dill, 1990; Martín & López, 2015; Ydenberg & Dill, 1986) in a distinct lineage and potentially reveal novel evolutionary responses to a fundamental problem confronting many ectotherms (Cooper & Blumstein, 2015). In

contrast to many studies of small lizards (Blouin-Demers & Nadeau, 2005; Sears et al., 2016), few studies of turtles report precise thermoregulation, but this may reflect the scarcity of field investigations into the thermoregulatory behavior of small juvenile chelonians. Moreover, investigating temperature relations in turtles is important because as climate change progresses, turtles may encounter not only first-order effects on activity, development, and sex ratios (Hawkes, Broderick, Godfrey, & Godley, 2007; Janzen, 1994; Van Houtan, Halley, & Marks, 2015), but potentially second-order impacts on predator-prey interactions, which remain far less examined (Cavallo et al., 2015; Lovich et al., 2014).

The gopher tortoise (*Gopherus polyphemus*), a threatened burrowing herbivore of the southeastern USA (USFWS et al., 2013), has experienced dramatic changes to its thermal environment. Fire suppression and other human activities have led to grand-scale conversion of longleaf pine (*Pinus palustris*) savannahs, highly biodiverse ecosystems that once dominated the southeast and are hypothesized to be primary ancestral habitats of the gopher tortoise, to more shaded, cooler environments (Guyer & Hermann, 1997; Van Lear, Carroll, Kapeluck, & Johnson, 2005; Watson & Gough, 2012). Small juvenile gopher tortoises spend almost all of their time in or near self-constructed burrows that provide individuals protection against temperature extremes and a variety of predators, including snakes, mammals, and birds (Perez-Heydrich, Jackson, Wendland, & Brown, 2012; Pike & Grosse, 2006; Wilson, 1991; Wilson, Mushinsky, & McCoy, 1994). Although the literature is mixed regarding the extent to which juvenile gopher tortoises bask outside the relative safety of their burrows, multiple studies indicate that juveniles regularly bask on the bare patch of soil located just in front of their burrows (referred to as the burrow "apron") and experience an important trade-off between thermoregulation and predator avoidance (Harris, Norton, Nibbelink, & Tuberville, 2015; Johnston, 1996; Pike & Grosse, 2006; Wilson, 1991; Wilson et al., 1994). Some authors also suggest that this trade-off may be amplified in cool months if young must bask more to maintain elevated body temperatures (Wilson, 1991; Wilson et al., 1994). However, information regarding how young tortoises balance thermoregulation and predator avoidance, and how this dynamic may be influenced by thermal environment, is unavailable.

Here, we examine potential behavior and temperature influences on a thermoregulation-predation risk trade-off in hatchling and juvenile gopher tortoises. At our study site in southwest Georgia (USA), juvenile tortoises bask extensively just in front of their burrows to maintain body temperatures within preferred ranges (T.A. Radzio and M.P. O'Connor, unpublished data). We considered tortoises to be at greater risk of predation while basking outside of burrows than when inside burrows (Wilson, 1991; Wilson et al., 1994). We investigate: (i) basking tortoise responses to simulated predator approach; (ii) potential associations between temperature and hiding time following approach; and (iii) potential associations between temperature and surface activity following approach. We predicted: (i) basking tortoises would hide inside burrows when approached and exhibit substantial FIDs, even if they were unable to

visually observe the approaching researcher; (ii) hiding time following disturbance would correlate positively with burrow temperature; and (iii) amount of surface activity during the hour following disturbance would correlate negatively with surface and burrow operative temperatures.

2 | MATERIALS AND METHODS

2.1 | Study site

We studied tortoise behavior on Arcadia Plantation (30°45' N, 84°0' W), located in Thomas County in southwest Georgia, USA. The site (957 ha) was dominated by mature (>80 years) longleaf pine forest and included the Wade Tract, an 80-ha old-growth ecological preserve that has never been heavily cut and contains many old trees (>200 years; Platt, Evans, & Rathbun, 1988). Ground vegetation on both the Wade Tract and surrounding areas of Arcadia Plantation was dominated by wiregrass (*Aristida stricta*), oaks (*Quercus* spp.), and a diverse assemblage of other native plants. Soils at the site were a mix of sand and clay. The study area was managed using frequent prescribed fire (≤ 2 -years return intervals).

2.2 | Simulated predator approaches

During April–August 2013, one of us (TAR) performed systematic approaches on 20 basking hatchling (<1 year) or juvenile (1–4 years; aged following Aresco & Guyer, 1998) gopher tortoises. Carapace lengths and masses of approached individuals were approximately 54–106 mm and 39–243 g, respectively. Most approached tortoises were recently captured (but not within at least 19 days preceding approaches) and fitted with miniature radio transmitters with short, flexible trailing antennas and iButton (Maxim Integrated Products, Sunnyvale, CA, USA) temperature loggers for another study. For the smallest study animals, post-winter hatchlings, combined equipment and epoxy mass totaled ~4–5 g, or ~6%–10% of body mass ($n = 3$ individuals with a transmitter and iButton and 3 with only an iButton) and did not noticeably affect behavior or movement, including time required to enter burrows following disturbance (always <2 s in this study) or righting ability following naturally occurring overturning events captured on video (T.A. Radzio and M.P. O'Connor, unpublished data). Hatchlings fitted with equipment and measured 1 month later ($n = 5$ individuals) increased in carapace length ($\bar{x} = 3.3$ mm, range = 0.6–4.9 mm), midline plastron length ($\bar{x} = 3.0$ mm, range = 0.8–4.7 mm), and in four of five instances, mass ($\bar{x} = 8.3$ g, range = –1.4–15.0 g).

Prior to the approach day, we set up two video cameras at the focal burrow: one to record tortoise activity and a second to determine from a distance when the focal tortoise was basking to properly time the researcher approach. A time-lapse video camera (Plotwatcher Pro, Day 6 Outdoors, Inc., Columbus, GA, USA) continuously (1 frame per second) recorded tortoise activity during daylight hours at the focal burrow. The camera was mounted to a 1.2-m wooden pole, pushed ~0.2 m into the ground ~1 m from the burrow. Using a similar pole setup, we positioned a surveillance camera that facilitated remote viewing of

tortoise activity from 108 m away via a coaxial cable connected to a liquid crystal display (LCD) monitor.

One of us (TAR) performed all approaches on sunny days, between 11:00 and 15:00 hr, always wearing the same clothing type and color. Before each approach, the researcher used the remote camera and LCD monitor to determine from 108 m away whether the focal tortoise was on its burrow apron. When the tortoise was observed on the apron, the researcher initiated a steady walk (~1.5 m/s; speed determined by recording walking time in most approaches) toward the burrow, following the outstretched coaxial camera cable to ensure a straight path. After reaching the focal burrow, the researcher briefly placed his hand in front of the video camera to facilitate later determination of how much time passed between when the tortoise initiated a flight response and when the researcher arrived at the burrow, information that was used in conjunction with approach speed to estimate FID (see below). The researcher then immediately turned around and left the area, allowing the tortoise to reemerge undisturbed.

On several occasions, the researcher mistook a shadow or other feature on the video feed for a basking tortoise and therefore approached burrows when individuals were either inside or away. In one instance, a tortoise left the burrow area just as the researcher initiated his approach. These individuals were approached again on a subsequent day. Additionally, we excluded one approach and repeated it on another day because the burrow temperature logger malfunctioned.

2.3 | Operative temperatures

Prior to approach days, we set out recording devices to measure burrow and apron operative temperatures. We used an iButton miniature temperature logger to record temperature 10 cm inside the burrows of approached tortoises at 10-min intervals. This distance inside the burrow represents the warmest location available to tortoises within burrows during times of day when we performed approaches (T.A. Radzio and M.P. O'Connor, unpublished data). The iButton was affixed with epoxy to the end of a thin wooden spike such that the two objects created a nail-like shape. We then pushed the wooden spike into the sidewall of the burrow until the iButton laid securely flat against it.

We used simple operative temperature models to record operative temperatures on burrow aprons of approached tortoises. Models consisted of thin-walled aluminum jars with aluminum lids, measuring 2.6 × 5.0 cm (small models used on the aprons of 0.5- to 2.0-year-old turtles) or 4.3 × 8.2 cm (large models used on the aprons of 2.5- to 4.0-year-old turtles), and painted gray using Rust-Oleum Painter's Touch 2x Ultra Cover flat gray primer (model number 249088). An iButton temperature logger, epoxied inside the center of the hollow models atop a small plastic spacer, recorded apron operative temperatures at 10-min intervals.

To assess the accuracy of operative temperature models, we compared small model temperatures to the internal temperatures of a dried neonate gopher tortoise carcass set out in an open field. We recorded carcass internal temperature by inserting a small thermistor, connected by wire to a temperature logger (HOBO 64K Pendant

Waterproof Temperature/Alarm Data Logger; Onset Computer Corporation, Bourne, MA, USA), into the body cavity through a small hole in the skin above a hind limb that was sealed with silicone. We compared temperatures of a small model and the carcass at 5-min intervals in an open field during midday hours on three partly cloudy days during March–September. Operative temperatures during testing times ranged between 20 and 55°C. The mean difference between temperatures recorded by metal models and the dry carcass was 1.8 ± 1.5 (1 SD)°C. Differences did not exceed 4.5°C, except briefly during very rapid temperature changes when they differed by as much as 8.2°C, which we largely attribute to differences in the heat capacity of the heavier metal model and the dry hatchling carcass.

Validation of operative temperature model accuracy is incomplete, particularly with regard to operative temperatures in rapidly changing environments, for older, larger-sized juvenile tortoises. However, large and small models recorded nearly identical temperatures. Predictably (Gates, 1980), large models recorded higher temperatures in full sun conditions, but only by ~1–2 °C. We conclude that in most cases models were satisfactory for our need, which was assessing if surface operative temperatures would allow basking tortoises to reach preferred body temperatures.

2.4 | Statistical analyses

We estimated FID as the product of approach speed (1.5 m/s) and number of seconds between when an approached tortoise initiated flight response and when the approaching researcher arrived at the burrow (both documented by the video camera). We tested for relationships between FID and tortoise age, carapace length, and mass using Pearson correlations. To visually represent the relationship between FID and tortoise age, we used a linear least square regression (LLSR). We visually inspected data to assess linearity and homoscedasticity and performed logarithmic transformations where appropriate.

We quantified two measures of hiding time: “appearance” time (when a tortoise’s head first appeared in the burrow entrance) and “re-emergence” time (when the tortoise’s head fully emerged out of the burrow). Young gopher tortoises routinely bask in burrow entrances with only their heads and a portion of their body above ground (T.A. Radzio and M.P. O’Connor, unpublished data). In most instances, appearance and reemergence times were very similar and preceded further movements out of the burrow seconds later. However, after hiding for 3.7 min in response to the approaching researcher, one tortoise extended its nose out of the burrow entrance for only 1 s, but was not visible again until 12.4 min later when it reemerged with its head fully out of the burrow. We tested for relationships between burrow temperature at 10 cm, the warmest temperature available to tortoises within burrows during approach times (T.A. Radzio and M.P. O’Connor, unpublished data), and appearance time and reemergence time by performing Pearson partial correlations (PPC; Package “ppcor” in R, Kim, 2015) with age as a covariate. To satisfy linearity assumptions, we performed these analyses on log-transformed hiding times. We first conducted the above analyses using data from all approaches ($n = 20$). However, disturbed tortoises may be less inclined to reemerge

when surface operative temperatures are low. Therefore, to better isolate potential burrow temperature associations with hiding time, we repeated the analyses using only approaches where apron operative temperatures were $>33^\circ\text{C}$ ($n = 17$), the approximate preferred body temperature of fed hatchling gopher tortoises (Johnston, 1996; T.A. Radzio and M.P. O’Connor, unpublished data). We visually represent simple relationships between burrow temperature and log hiding times without accounting for possible covariate effects by performing LLSRs.

We tested for relationships between surface activity during the hour following researcher approach and two variables, mean burrow temperature at 10 cm, and mean apron temperature during the hour following approach, by performing PPCs with tortoise age as a covariate. We visually represented simple relationships between burrow temperature and surface activity during the hour following researcher approach without accounting for possible covariate effects by performing LLSRs. We conducted all analyses in RStudio version 1.0.136 (RStudio Team, 2016). Statistical tests were two-tailed, with $\alpha = 0.05$.

3 | RESULTS

3.1 | Response to researcher approach

Tortoises on burrow aprons or in burrow entrances ($n = 20$) always responded to researcher approach by entering burrows. Mean FID was 45 ± 22 (1 SD) m (range = 13–101 m) and correlated positively with age (PC, $r = .84$, $df = 18$, $p < .00001$, Figure 1), carapace length (PC, $r = .81$, $df = 17$, $p = .0001$), and mass (PC, $r = .82$, $df = 17$, $p = .0001$). Individuals did not make movements prior to initiating flight that would suggest substantial differences between FIDs and alert distances.

Upon initiating flight response, tortoises quickly entered burrows without first changing body orientation. In other words, if a tortoise

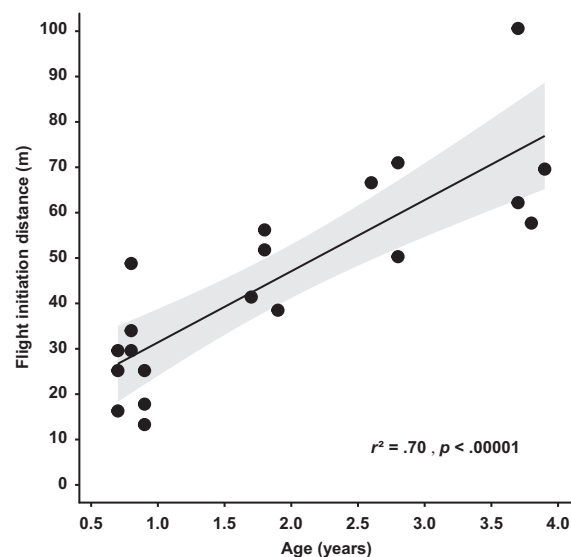


FIGURE 1 Relationship between gopher tortoise age and flight initiation distance in response to researcher approach. Solid line depicts linear least square regression, and shading represents 95% confidence interval

was facing away from the burrow entrance, it quickly backed into the burrow, rather than first turning around and then entering. On average, tortoises filmed at 1 frame/s ($n = 19$) completely entered burrows within at least 1.7 s of initiating flight (range: 1–3 s). One tortoise, inadvertently filmed at 0.2 frames/s, completely entered the burrow within at least 5 s of initiating flight (the fastest measurable speed given the reduced frame rate). On average, tortoises entered burrows in a similar rapid manner only 0.7 times (median = 1, range = 0–2, $n = 20$ tortoises) in the 60 min of burrow entrance or apron activity preceding researcher approach. Cameras did not document any potential predators when tortoises made these rapid movements into burrows. These movements were not in response to the researcher because he avoided focal tortoises prior to approaches.

3.2 | Hiding time

On average, tortoises appeared in burrow entrances 18.3 ± 11.7 min (3.4–50.0 min; $n = 20$) following disturbance by the approaching researcher. Log appearance time was not partially correlated with burrow temperature at time of approach (PPC with age as a covariate, $r = .42$, $df = 17$, $p = .074$, Figure 2a), but log reemergence time was (PPC with age as a covariate, $r = .52$, $df = 17$, $p = .022$, Figure 2b). Similarly, when only approaches with apron operative temperatures exceeding 33°C were included in the analyses ($n = 17$), log appearance time was not partially correlated with burrow temperature (PPC with age as a covariate, $r = .49$, $df = 14$, $p = .052$, Figure 2c), but log reemergence time was (PPC with age as a covariate, $r = .64$, $df = 14$, $p = .007$, Figure 2d). Understandably, burrow temperature also correlated with

approach time (PC, $r = .76$, $df = 18$, $p < .001$), Julian day (PC, $r = .83$, $df = 18$, $p < .00001$), and apron temperature (PC, $r = .82$, $df = 18$, $p < .00001$).

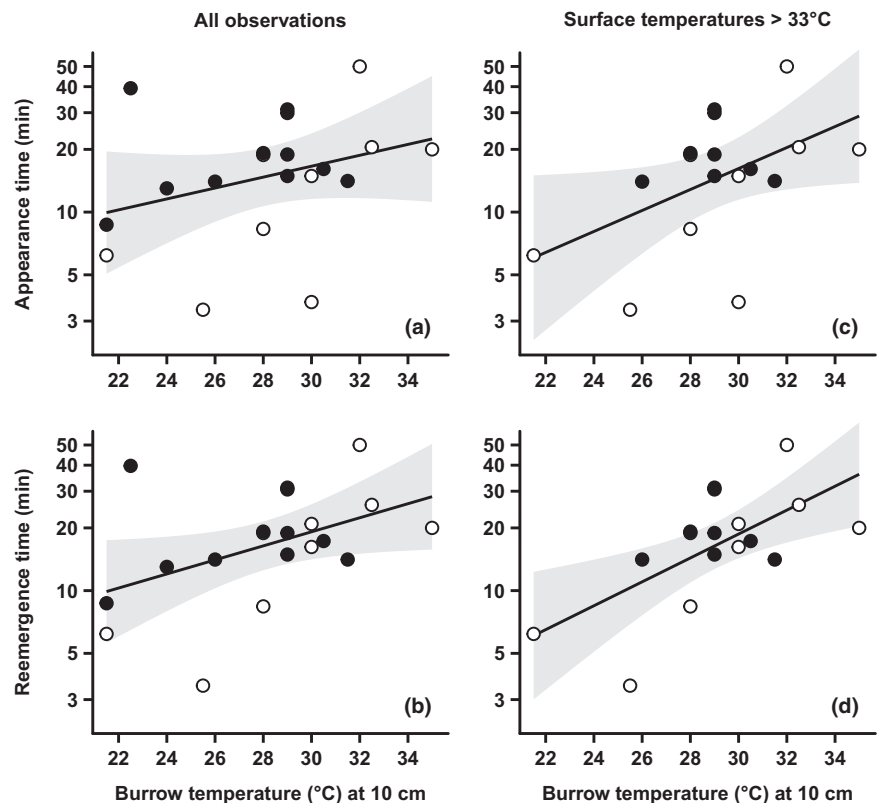
3.3 | Surface activity during the hour following approach

Surface activity during the hour following approach was almost entirely (525.8 of 547.4 min) restricted to burrow entrances and aprons and consisted primarily of basking and movements in and out of burrows. In fact, only 1 of 20 tortoises engaged in surface activity away from its burrow entrance or apron. Surface activity during the hour following researcher approach exhibited a negative partial correlation with mean burrow temperature (PPC with age as a covariate, $r = -.55$, $df = 17$, $p = .015$, Figure 3), but not mean apron operative temperature during the hour following approach (PPC with age as a covariate, $r = -.43$, $df = 17$, $p = .069$). Mean burrow temperature during the hour following approach also correlated with Julian day (PC, $r = .84$, $df = 18$, $p < .00001$), approach time (PC, $r = .74$, $df = 18$, $p < .0001$), and mean apron operative temperature (PC, $r = .74$, $df = 18$, $p < .0001$).

4 | DISCUSSION

Combining simulated predator approaches with remote video observations revealed exceptionally long FIDs ($\bar{x} = 45$ m) for young gopher tortoises, much greater than typically reported for other small reptiles (Cooper, Pyron, & Garland, 2014; Costa, 2014; but see Legler & Vogt,

FIGURE 2 Relationships between: (a) burrow temperature (at 10 cm) and gopher tortoise appearance time for all observations (linear least square regression [LLSR], $r^2 = .10$, $p = .173$); (b) burrow temperature and gopher tortoise reemergence time for all observations (LLSR, $r^2 = .21$, $p = .044$); (c) burrow temperature and appearance time for observations with burrow apron operative temperatures $>33^\circ\text{C}$ (LLSR, $r^2 = .25$, $p = .042$); (d) burrow temperature and reemergence time with burrow apron operative temperatures $>33^\circ\text{C}$ (LLSR, $r^2 = .42$, $p = .005$). Statistics are performed on log-transformed hiding times (note log scales on y-axis). Open circles represent <1 -year-old tortoises, and filled circles represent 1- to 4-year-old individuals. Solid lines are linear least square regression lines, and shading represents 95% confidence intervals. See text for alternative Pearson partial correlation analyses that control for potential age effects



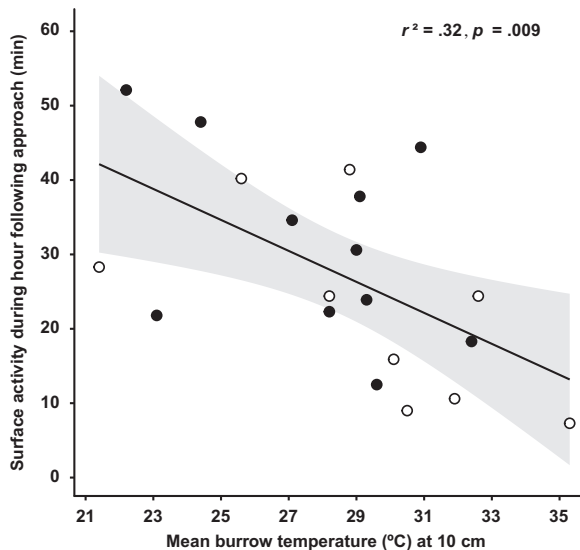


FIGURE 3 Relationship between mean burrow temperature at 10 cm and immature gopher tortoise surface activity during the hour following researcher approach. Open circles represent <1-year-old tortoises, and filled circles represent 1- to 4-year-old individuals. Solid line depicts linear least square regression, and shading represents 95% confidence interval. Surface activity was confined almost entirely (96.1%) to burrow entrances and aprons. See text for an alternative Pearson partial correlation analysis that controls for potential age effects

2013; Polich & Barazowski, 2016; Figure 1). Due to dense herbaceous vegetation and long FIDs, the approaching researcher never visually observed a tortoise before it hid inside its burrow. Similarly, we believe that in all or most cases it was not possible for tortoises to visually observe the approaching researcher, especially in two instances, where tortoises were oriented toward burrows with their heads completely belowground when approached (FIDs = 49 and 52 m). Thus, we hypothesize that young gopher tortoises use vibrational cues (aerial or ground) to detect predators early and reduce predation risk associated with basking. Long FID s may be common in turtles (Legler & Vogt, 2013; Polich & Barazowski, 2016), but very few data are available for this group. Optimal escape theory predicts that prey will modify FID to balance potential costs and benefits of fleeing (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). A unique factor potentially contributing to the long FIDs and rapid flight movements of young gopher tortoises may be that individuals are unable to always reliably assess if vibrational cues correspond to a “loud” predator that is far away or a “quiet” one that is nearby and often hide immediately upon detecting any irregular or signature vibration.

Detecting potential predators via non-visual cues seems particularly useful in longleaf pine ecosystems where a dense herbaceous layer limits line-of-sight for small ground-dwelling animals. However, tortoises may be less perceptive to vibrational cues when walking (e.g., manuring burrow aprons, foraging) or in noisy environments (e.g., high winds, near highways, or foraging conspecifics). Tortoises may also waste energy and miss thermoregulatory opportunities by responding incorrectly to vibrations that are not associated with

a potential predator. Video-recorded hatchlings routinely flee into burrows in response to non-threatening animals, such as fox squirrels (*Sciurus niger*) and adult tortoises (Video S1; T.A. Radzio and M.P. O'Connor, unpublished data). In this study, basking tortoises made on average 0.7 rapid, presumably antipredator, movements into burrows during the hour of surface activity preceding simulated predator approach, but in no instance ($n = 13$) was an actual predator observed visiting burrows. Despite potential energetic and thermoregulatory costs, young tortoises appear to err on the safe side and hide inside burrows in response to false-positive threat cues, perhaps because failing to respond to a real threat can be lethal.

Vigilance and apparent use of vibrations to detect potential predators suggest an ecological function for the greatly exaggerated inner ear morphology of gopher tortoises. Bramble (1982) describes the “enormous” otolith (ear bones) of gopher tortoises to be larger than those of any living tetrapod, and Bramble and Hutchison (2014) state that they are the species' most striking feature, more so than any specializations for digging burrows (e.g., fused carpals). Among other potential functions, Bramble (1982) hypothesized that the massive otoliths and other specialized inner ear structures of gopher tortoises function as hypersensitive seismic sensors that provide individuals inside burrows information about predator activity at the surface that can be used to decide when to safely emerge. We extend this hypothesis to include that they may reduce costs associated with extensive thermoregulatory activity by increasing the ability of basking individuals to detect predators and hide inside burrows before being attacked. Notably, the gopher tortoise's closest living relative, *G. flavomarginatus*, also exhibits very large otoliths and very long FIDs in response to humans (Bramble, 1982; Bramble & Hutchison, 2014; Legler & Vogt, 2013).

Flight initiation distance increased with tortoise age and size, despite likely declines in predation risk as individuals become larger (Perez-Heydrich et al., 2012; Tuberville, Todd, Hermann, Michener, & Guyer, 2014; Wilson, 1991). In lizards, similar positive correlations between FID and body size, occurring within and among species, may reflect a greater reliance on crypsis for predator avoidance in smaller, slower-moving individuals (Cooper, 2011, 2015; Cooper et al., 2014). Although there are other potential explanations, such as, perhaps, greater flight costs in smaller individuals, we are intrigued by the possibility that greater sensory constraints on the ability of younger tortoises to detect vibrations could underlie the ontogenetic pattern we observed. Hatchlings and small juveniles have soft shells, composed primarily of keratin, that do not fully ossify until tortoises are well beyond the sizes of our study animals (Wilson 1991). Perhaps as young gopher tortoises become larger, heavier, and more ossified, their ability to conduct and sense vibrational cues increases.

Consistent with a hypothesized thermoregulation–predator avoidance trade-off (Harris et al., 2015; Wilson, 1991; Wilson et al., 1994), tortoises generally reappeared from burrows soon after hiding in response to the approaching researcher ($\bar{x} = 18.3$ min, Figure 2). Field observations at our Georgia study site and a laboratory growth experiment indicate that hatchlings and juveniles usually must emerge from burrows and bask to achieve body temperatures at which growth

rates are highest (~33°C; T.A. Radzio and M.P. O'Connor unpublished data). By limiting time in burrows following disturbance, tortoises can maintain high body temperatures and reduce physiological costs of predator avoidance.

This investigation is the first to examine whether turtles adjust hiding times in response to temperature. As documented in various lizard species (Amo et al., 2003; Cooper & Wilson, 2008; Martín & López, 1999, 2001, 2010), thermal costs appear to constrain hiding time in hatchling and juvenile tortoises. Reemergence times were shorter when burrows were cooler, presumably because physiological costs were greater. We suspect that this phenomenon is more widespread in turtles, including aquatic species that terminate aerial basking in response to disturbance (Moore & Seigel, 2006; Polich & Barazowski, 2016; Selman, Qualls, & Owen, 2013). Adjusting hiding time in response to refuge temperature also suggests a precise thermoregulatory strategy. Indeed, at our study site hatchlings and juveniles exploit most thermal opportunities available at burrows and burrow aprons to maintain body temperatures within ranges that promote rapid growth (T.A. Radzio and M.P. O'Connor, unpublished data).

To our knowledge, this is also the first study to examine relationships between temperature and time spent outside refugia following real or simulated predator disturbance. This parameter, though requiring extended observation to measure, can be important because predation risk may remain elevated if a predator stays in the area, but prey do not always accurately assess predation risk upon reemergence. Juvenile tortoise surface activity during the hour following disturbance correlated negatively with burrow temperature, and basking accounted for most surface activity following disturbance, providing preliminary support for the hypothesis that thermal environment determines the minimum amount of time individuals must spend basking to maintain preferred body temperatures (Wilson, 1991; Wilson et al., 1994), and thus, time outside burrows following disturbance. We conclude that burrow temperature and, perhaps to some extent, apron temperature influenced hiding time and surface activity following disturbance, and feel that time of day and day of year were simply correlated with burrow thermal environment.

Despite antipredator responses and extensive basking, hatchling and small juvenile gopher tortoises exhibit low survivorship, and individuals from forested sites at similar latitudes typically require approximately 15–20+ years to reach maturity (Aresco & Guyer, 1999; Landers, McRae, & Garner, 1982; Perez-Heydrich et al., 2012; Wilson, 1991), putting a premium on juvenile growth and survivorship. The ability to detect potential predators using non-visual cues likely reduces predation risk associated with thermoregulatory basking in hatchling and juvenile gopher tortoises. We speculate that hypertrophied otoliths and specialized inner ear morphology (Bramble, 1982; Bramble & Hutchison, 2014) may represent key sensory features allowing young gopher tortoises to exploit thermal opportunities required for rapid growth while also maintaining predator-induced mortality at demographically feasible levels. Our data also indicate that in warmer environments young tortoises hide longer when disturbed and spend less time outside the relative safety of their burrows following disturbance.

In the setting of temporal and thermal constraints on the energetics of ectothermic herbivores (van Marken Lichtenbelt, 1992; Tracy, Flack, Zimmerman, Espinoza, & Tracy, 2005; Troyer, 1987; Zimmerman & Tracy, 1989), this trade-off between predator avoidance and basking highlights the importance of endangered longleaf pine ecosystems, where much solar radiation reaches and warms the ground, to this threatened species (Guyer & Hermann, 1997; Van Lear et al., 2005; Watson & Gough, 2012).

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