
OVERWINTERING ECOLOGY OF JUVENILE GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*)

BESS B. HARRIS^{1,2,5,6}, TERRY M. NORTON^{3,4}, NATHAN P. NIBBELINK²,
AND TRACEY D. TUBERVILLE¹

¹University of Georgia's Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802, USA

²Daniel B. Warnell School of Forestry and Natural Resources, 180 E Green Street,
University of Georgia, Athens, Georgia 30602, USA

³Jekyll Island Authority's Georgia Sea Turtle Center, 214 Stable Road, Jekyll Island, Georgia 31527, USA

⁴St. Catherines Island Foundation, 182 Camellia Road, Midway, Georgia 31320, USA

⁵Current affiliation: Florida Fish and Wildlife Conservation Commission, Lovett E. Williams, Jr.
Wildlife Research Laboratory, 1105 SW Williston Road, Gainesville, Florida 32641, USA

⁶Corresponding author, e-mail: bess.harris@myfwc.com

Abstract.—The Gopher Tortoise (*Gopherus polyphemus*) is a large terrestrial turtle that excavates and occupies extensive burrows, which protect individuals from predators and temperature extremes. Individuals can thermoregulate behaviorally by adjusting their position inside the burrow and through surface activity, even in winter when they are thought to be relatively inactive. Much of what is known about the overwintering behavior of Gopher Tortoises is based on adults; however, the ecology of juveniles may differ due to their smaller body size and higher surface area to volume ratio. We investigated the overwintering ecology of 11 juvenile Gopher Tortoises on St. Catherines Island, Georgia using externally attached temperature loggers. Temperatures experienced by tortoises were compared to burrow and surface air temperatures collected at the same site, allowing us to infer surface activity of individuals. We examined the onset, termination, and duration of overwintering and occurrences of juvenile surface activity during the overwinter period. Tortoises initiated overwintering over a 48-d period (median date of 14 November) and terminated overwintering over a 32-d period (median date of 8 April). Mean overwintering duration was 130 ± 7 d (1 SE). Individuals emerged on 2–22 d during the 2012–2013 winter. Mean temperature experienced by overwintering tortoises was $17.9 \pm 0.02^\circ$ C (range 11.5–38.5 °C) and the minimum surface air temperature when a juvenile tortoise emerged from its burrow to bask was 15.8 °C. Timing of overwintering in juvenile Gopher Tortoises is similar to that reported for adult tortoises from similar latitudes. However, juveniles are active more frequently on the surface during the winter and emerge from burrows at lower air temperatures than has been reported for adults.

Key Words.—activity; dormancy; Georgia; reptile; temperature

INTRODUCTION

Winter can be a challenging and even risky period for most reptiles, requiring physiological and behavioral changes to combat low temperatures and avoid mortality (Gregory 1982; Ultsch 2006). Reptiles seek refugia to avoid temperature extremes, and for terrestrial turtles and tortoises, this often means finding an underground retreat (Hutchison 1979; Gregory 1982; Ultsch 2006). Although multiple exogenous factors may influence overwintering ecology in reptiles, air temperature is the one most commonly investigated and has been identified as exerting strong influence on overwintering timing in some reptiles (Hutchison 1979; Gregory 1982). For instance, when unable to maintain a preferred body temperature, the Prairie Rattlesnake (*Crotalus viridis*; Jacob and Painter 1980) and the Chuckwalla (*Sauromalus obesus*; Case 1976) initiate overwintering, suggesting that a change in temperature or temperature instability may be an important stimulus for initiating

overwintering in other reptile species. Overwintering has been studied extensively in freshwater turtles, particularly with regard to delayed emergence from the nest by hatchlings (Gibbons and Nelson 1978; Gibbons 2013), refugia selection (e.g., Greaves and Litzgus 2008; Edge et al. 2009), and associated physiological changes (e.g., Ultsch 1989; Jackson and Ultsch 2010). However, research has been limited with regards to terrestrial turtles, particularly tortoises (Ultsch 2006; Nussear et al. 2007). If temperature is one of the primary factors driving overwintering ecology of turtles, we might expect that terrestrial turtles face different thermal challenges than aquatic turtles, which are buffered by water from large daily fluctuations in temperatures.

Of the North American tortoise species, Gopher Tortoises (*Gopherus polyphemus*) are most closely tied to their extensive burrows, which they use year round for thermoregulation, nesting, and protection from predators (Ernst and Barbour 1972). Burrows provide buffering from daily and seasonal air temperature fluctuations

(DeGregorio et al. 2012; Pike and Mitchell 2013). In central Florida, Douglass and Layne (1978) reported that temperatures in adult burrows oscillated $< 1\text{ }^{\circ}\text{C}$ in a day in summer even though air temperatures could fluctuate $13\text{ }^{\circ}\text{C}$ throughout the day. Likewise, burrows of adult Gopher Tortoises and adult Desert Tortoises (*Gopherus agassizii*) also provide temperature buffering capacity during winter, with daily temperature fluctuations inside the burrow typically $< 1.5\text{ }^{\circ}\text{C}$ (Nussear et al. 2007; DeGregorio et al. 2012). The infrequency of emergence by adult tortoises from their burrows during winter underscores the importance of burrows during the overwintering period (Nussear et al. 2007; DeGregorio et al. 2012). However, studies of overwintering in North American tortoises have primarily focused on adults (Bailey et al. 1995; Nussear et al. 2007; DeGregorio et al. 2012). If burrows are of central importance to successful overwintering by tortoises, we might expect that the overwintering ecology of juveniles might be different from that of adults. Juveniles presumably dig shallower burrows, which might provide less buffering capacity, and are of smaller body size, which gives them a higher surface area to volume ratio.

Indeed, the few studies that have monitored juvenile tortoises during winter found that winter surface activity was relatively common in juveniles (Wilson et al. 1994, 1999; DeGregorio et al. 2012). DeGregorio et al. (2012) concluded that juveniles in their South Carolina study population were much more likely than adults to emerge from their burrows in winter to bask for short periods, but their sample size was small. Wilson et al. (1999) monitored 71 juvenile Desert Tortoises in California, documenting that the juveniles would often emerge on the warm winter days to bask. These studies suggest juvenile tortoises may spend more time active during the winter than do adults (Diemer 1992; Wilson et al. 1999; DeGregorio et al. 2012). In this study, we examined the overwintering ecology of juvenile Gopher Tortoises on a barrier island in Georgia. Our objectives were to (1) determine the timing of the onset, termination, and duration of overwintering; (2) quantify the amount of surface activity during winter; (3) identify the temperatures tortoises experience during overwintering; and (4) identify environmental temperatures triggering winter surface activity in juvenile tortoises.

MATERIALS AND METHODS

Study site and study population.—St. Catherines Island is a privately owned 5,670 ha Georgia barrier island with a 102 ha former cattle pasture managed for Gopher Tortoises. The pasture is comprised of a few mature mixed pines (primarily Longleaf Pine, *Pinus palustris*, but also Loblolly Pine, *P. taeda*), no midstory canopy, and an open understory primarily composed of both native and nonnative grasses and forbs. The open

pasture is maintained through periodic mowing. The Gopher Tortoise population, which is not native to the island, was established through multiple translocations and subsequent natural recruitment (Tuberville et al. 2008, 2011).

Data collection.—We initially trapped juvenile Gopher Tortoises at their burrows starting 11 May 2012 and equipped them with radio-transmitters as part of a spatial ecology study (data to be presented elsewhere). However, we monitored these same individuals through the subsequent 2012–2013 overwintering period, which is the focal period for this study. We targeted juvenile tortoises $> 200\text{ g}$, defining juveniles as individuals with $\leq 230\text{ mm}$ carapace length (Landers et al. 1982) and no signs of sexual dimorphism, indicating they had not reached sexual maturity. We placed live animal traps (Havahart®, Lititz, Pennsylvania, USA) at active juvenile burrows, covered traps with burlap for shading, and checked them at least twice daily. We recorded mass (g), straight-line carapace length (SCL; nearest mm), and estimated age based on growth annuli (Landers et al. 1982) for each tortoise. If an individual was not previously marked, we assigned it a unique ID and notched the corresponding marginal scutes (Cagle 1939).

To the carapace of each juvenile tortoise, we attached a transmitter (3.8 g; Holohil Systems Ltd., PD-2, Ontario, Canada) with two part putty epoxy, and also a temperature logger (3.3 g; Thermochron iButton® DS1921G, Embedded Data Systems, Lawrenceburg, Kentucky, USA) with two part 5-minute liquid epoxy. We attached transmitters to the first left costal scute with the antenna secured along the length of the carapace within aquarium tubing secured to the shell using putty epoxy (modified from Boarman et al. 1998). We completely encased temperature loggers in putty epoxy and attached them to the first right costal scute. Each temperature logger had a resolution of $0.5\text{ }^{\circ}\text{C}$, accuracy of $\pm 1.0\text{ }^{\circ}\text{C}$, and could store up to 2,048 recordings. We disabled the roll-over feature and programmed them to record temperatures every two hours (12 times a day) for 171 days until loggers filled the following spring. A temperature-logger attached to the carapace did not measure the actual body temperature of the tortoise but rather it measured the environmental temperatures to which an individual was exposed. However, the temperature of the carapace is strongly correlated to body temperature in turtles (Congdon et al. 1989; Grayson and Dorcas 2004; Nussear et al. 2007; Pittman and Dorcas 2009).

We also deployed temperature-loggers at four locations within our study area to measure environmental temperatures. At each location, we measured shaded air temperatures 10 cm above the ground surface (adapted from Hubbart 2011) and burrow

temperatures 1 m inside an unoccupied juvenile burrow at each location. We encased environmental temperature loggers in putty epoxy (similarly to those attached to tortoises) and programmed them to record temperatures every two h starting at midnight. Due to a prescribed fire in North Pasture, we removed and disabled environmental temperature loggers during 20–22 February 2013. We attempted to capture tortoises approximately every 6 mo to replace transmitters and download temperature data. We downloaded environmental temperature loggers approximately every 4 mo. We report here only the temperature data collected during the 2012–2013 winter period.

Data analysis.—We inferred surface activity (i.e., an emergence event) for individual tortoises by examining the temperatures recorded by the temperature logger of an individual. Here we define activity only in relation to whether an individual likely emerged from its burrow; we cannot determine the type of activity or whether a tortoise exhibited movement activity away from its burrow based on temperature data alone. Because the maximum fluctuation in daily temperatures of burrows recorded during our study was < 3.0 °C, we considered an individual to have emerged on days during which its temperatures fluctuated ≥ 3.0 °C. From these data, we determined the overwintering onset and termination dates for each individual monitored. We modeled our analyses after DeGregorio et al. (2012) and Nussear et al. (2007), defining onset as the date after which a tortoise did not emerge from its burrow for the following seven consecutive days. We defined termination as the date after which the tortoise emerged on at least seven days within a 14-d period (modified from DeGregorio et al. 2012). We calculated duration of overwintering for individuals for which we were able to determine both an onset and a termination date. Two tortoises were not captured within 30 d after their temperature data loggers stopped recording data (i.e., their data memory was full) and we could not identify their exact termination date. However, for these tortoises we calculated overwintering duration based on assigning the date their temperature loggers stopped recording as their earliest possible emergence date. We then estimated the median overwintering termination date using the date when the sixth of 11 tortoises terminated overwintering.

We examined winter activity (emergences throughout the overwintering period) of each tortoise to determine at what air temperature each tortoise emerged from the burrow. We estimated when an active tortoise first emerged from its burrow to be when its temperature began to increase relative to burrow temperatures. We were able to determine the air temperatures when tortoises emerged from their burrows and the minimum air temperature when tortoises became active above ground. All data are reported as means \pm 1 SE.

We encountered missing data points at some environmental stations due to malfunctioning or damaged temperature loggers. To obtain a complete record of temperatures for both air and burrow temperatures throughout the winter, for each temperature sampling event (every 2 h) we averaged the available data collected from the four station locations. The compiled environmental data provided a continuous record of both air and burrow temperatures during the 2012–2013 winter study period.

RESULTS

We were able to recapture 11 juvenile Gopher Tortoises in spring 2013 to download their temperature loggers for the 2012–2013 overwintering period. Temperature loggers for six tortoises filled up prior to overwintering termination; however, four of these tortoises were captured within seven days after the temperature data stopped recording and could still be used for all other analyses, using their capture date as the termination date. Because we used a minimum termination date for calculating overwintering duration for the remaining two tortoises, overwintering duration is likely to be underestimated.

Tortoises initiated overwintering over a 48-d period (4 November to 21 December), with a median start date of 14 November 2012 (Table 1). Tortoises terminated overwintering over a 32-d period (9 March to 9 April) with a median date of 8 April. Tortoises overwintered for a mean duration of $130 \text{ d} \pm 7 \text{ d}$ (Table 1, Fig. 1). Of the nine tortoises for which we were able to calculate overwinter duration, most tortoises emerged on relatively few days (range 2–9 d) but three of the 11 tortoises emerged frequently (19–22 different days) during the winter period (Table 1). One tortoise exhibited surface activity on 22 (12%) d during the total overwintering period. The three individuals with ≥ 19 overwinter emergences each had two discrete dormancy periods, based on our threshold of seven consecutive days of emergence during a 14-d period (Fig. 1). Tortoise 720 had dormancy periods from 24 November to 1 December (8 d) and 18 December to 9 March (82 d); tortoise 761 had dormancy periods from 22 November to 1 December (10 d) and 17 December to 10 March (84 d); and tortoise 762 had dormancy periods from 21 December to 11 January (22 d) and 19 February to 10 March (20 d).

Overwintering tortoises experienced a mean temperature of 17.9 ± 0.02 °C, with a minimum carapace temperature of 11.5 °C and a maximum of 38.5 °C (Table 1). Tortoises experienced the highest recorded temperatures during winter emergences (probably basking events). Between 1 November 2012 and 2 April 2013, the minimum air temperature when a juvenile tortoise emerged from its burrow was 15.8 °C (Table 2);

TABLE 1. Individual ID, straight line carapace length (SCL), first overwintering onset date, last overwintering termination date, and overwintering duration (days); mean, minimum, and maximum overwintering tortoise temperatures experienced during the overwintering period; and number of overwintering emergence days for each juvenile Gopher Tortoise (*Gopherus polyphemus*) monitored at St. Catherines Island, Georgia, during the 2012–2013 overwinter period. For termination dates with asterisks (*), the temperature logger became full prior to the tortoise terminating overwintering but capture date could be used to determine termination date, and no date for those without a calculated termination date because their data logger stopped recording before they emerged in spring. The date the data logger stopped recording was used to calculate a minimum overwintering duration.

Tortoise ID	SCL (mm)	Onset	Termination	Duration (days)	Mean Temperature °C (± 1 SE)	Minimum Temperature °C	Maximum Temperature °C	Emergences
1	164	14 Nov 2012	8 April 2013*	146	18.4 ± 0.06	15.5	35.0	8
7	217	13 Nov 2012	—	> 143	17.4 ± 0.05	13.0	31.0	≥ 5
18	174	14 Nov 2012	11 Mar 2013	140	18.0 ± 0.09	11.5	38.5	8
422	215	10 Nov 2012	—	> 146	17.4 ± 0.05	14.0	35.0	≥ 2
720	179	24 Nov 2012	9 Mar 2013	106	18.0 ± 0.08	12.5	34.0	20
761	142	22 Nov 2012	10 Mar 2013	109	18.7 ± 0.08	14.0	37.5	19
762	199	21 Dec 2012	10 Mar 2013	80	21.0 ± 0.09	16.0	37.5	22
792	147	21 Nov 2012	9 April 2013*	140	16.7 ± 0.06	13.0	35.5	5
793	230	14 Nov 2012	8 April 2013*	146	17.9 ± 0.06	14.0	33.0	9
823	140	14 Nov 12	8 April 2013*	146	16.6 ± 0.06	13.0	33.5	9
831	130	4 Nov 12	15 Mar 2013	132	16.6 ± 0.06	11.5	35.0	5

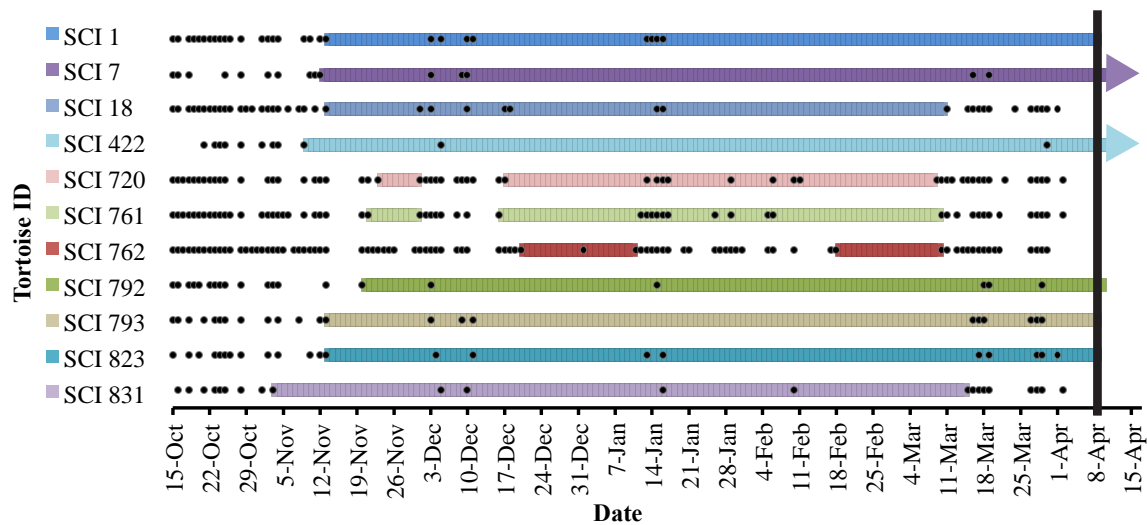


FIGURE 1. Overwintering duration for 11 juvenile Gopher Tortoises (*Gopherus polyphemus*) at St. Catherines Island, Georgia, during the 2012–2013 winter. Duration from onset to termination is depicted by a solid line for each tortoise. The vertical black bar at 8 April 2013 indicates the date when tortoise temperature loggers filled and stopped recording temperatures. Four tortoises were captured within seven days after the temperature loggers stopped recording and their capture date was used as the termination date. Lines ending in arrows indicate tortoises that were not captured soon enough (i.e., > 30 d) after temperature loggers filled to estimate termination date. Broken lines correspond to tortoises that had discontinuous overwintering periods comprised of two discrete dormancy events. Each day a tortoise was recorded as active is indicated by a black circle for each individual tortoise.

however, the mean air temperatures associated with initiation of emergence was 20.9 °C ± 1.0 °C. Individuals emerged frequently throughout the 2012–2013 winter (Fig. 1) and multiple individuals emerged from their burrows on the same days (Fig. 2). During the period coinciding with tortoise overwintering, shaded

air temperatures 10 cm above the ground (Fig. 3) ranged from -6.8 to 36.6 °C, with daily temperature fluctuations averaging 17.4 °C (3.5–30.8 °C) in a given day. In contrast, temperatures 1 m inside burrows ranged from TABLE 2. St. Catherines Island air temperatures (°C) on days when at least one Gopher Tortoise (*Gopherus polyphemus*) emerged from

its burrow during the 2012–2013 overwintering period (1 November 2012 to 2 April 2013). Temperatures reported are those occurring at the time an individual first emerged from its burrow, summarized across emergence events to calculate mean, minimum, and maximum air temperatures at initial emergence. Summaries are reported based on number of individual tortoises known to have emerged on a specific day.

Count of Tortoises Emerging	Mean Temperature °C (± 1 SE)	Minimum Temperature (°C)	Maximum Temperature (°C)
1	24.5 ± 0.5	15.8	31.5
2	25.3 ± 0.4	18.5	31.5
3	26.3 ± 0.5	18.5	31.3
4	27.4 ± 0.5	24.3	35.0
5	29.2 ± 0.8	25.3	35.5
6	27.2 ± 0.2	25.5	28.4

9.3 to 24.2 °C, but daily fluctuation averaged only 1.01 °C (range = 0.0–2.8 °C).

DISCUSSION

Burrows function as important refugia by acting as thermal buffers against extreme temperatures (Douglass and Layne 1978; Nussear et al. 2007; Pike and Mitchell 2013). Previous studies have shown that adult Gopher Tortoises experience relatively stable temperatures inside their extensive burrows (Douglass and Layne 1978; DeGregorio et al 2012; Pike and Mitchell 2013), which can be up to 7.9 m long and 3.7 m deep (Kinlaw et al. 2007). Our study demonstrated that juvenile burrows also provide remarkable thermal buffering despite their shorter length and shallower depth (pers. obs.). Temperature at 1 m inside juvenile burrows typically fluctuated by only 1 °C throughout the day during winter, while air temperatures outside the burrow fluctuated as much as 30 °C.

A substantial proportion of the juvenile life stage is spent in dormancy. Juvenile Gopher Tortoises in our study spent approximately a third of the year overwintering, beginning around mid-November and ending approximately mid-March. Although overwintering duration may vary throughout the range of the Gopher Tortoise based on local climate conditions, the duration of time juveniles spent overwintering at our coastal site (130 ± 7 d) was similar to that reported for adults by DeGregorio et al. (2012; 127 ± 9 d) at the northern extent of the range of the species. Although juveniles in our study did exhibit surface activity during winter, our radio-telemetry monitoring did not detect any movements by juveniles away from their winter burrow that would indicate they might be foraging (data presented elsewhere). Thus, the overwintering period represents an extensive amount of time when tortoises

are not gathering resources, which is especially important for juveniles that are presumably directing most of their available energy into growth.

Winter activity by juveniles in our study was strikingly different than that reported for adults in the literature in terms of both minimum temperatures at which they are active and how often they exhibit surface activity during the overwintering period. Two previous studies reported that the minimum air temperature at which adult Gopher Tortoises exhibit activity is 21 °C (Douglass and Layne 1978; McRae et al. 1981), although Diemer (1992) reported observing adult activity at temperatures as low as 18 °C near Gainesville, Florida. In contrast, juveniles in our study initiated basking at air temperatures as low as 15.8 °C, although the mean air temperature at which they began emerging was around 21 °C. The smaller body size and higher surface area to volume ratio of juveniles relative to adults allows them to heat and cool more rapidly, which may explain why juveniles will exit burrows at lower air temperatures (Gregory 1982; Berry and Turner 1986; Keller et al. 1997). Juveniles in our study had an average mean carapace temperature of 18° C, while DeGregorio et al. (2012) found adult tortoises had a mean carapace temperature of 12.5 °C. Thus, juveniles at our study site were able to maintain warmer temperatures on average throughout the winter than adults observed by DeGregorio et al. (2012).

Although juveniles have been reported to be more active in winter than adults in several tortoise species, including Gopher Tortoises, the frequency of winter surface activity by juveniles in our study was surprising. All juveniles in our study emerged numerous days (2–22 overwinter emergences) during the 2012–2013 overwintering period. In fact, for three individuals (27.3%), the winter was punctuated by so many emergence events that we identified two discrete dormancy periods based on our criteria. However, in reality, their emergence patterns likely reflect two similar periods of reduced activity punctuated by an intervening period in which individuals opportunistically took advantage of warm environmental temperatures. In addition, tortoise temperature records revealed that as many as 73% of juveniles emerged on the warmest days, suggesting that juvenile Gopher Tortoises may be cueing in on the same stimuli. Diemer (1992) also noted that juveniles were more likely to emerge from their burrows in winter than were adults. Similarly, DeGregorio et al. (2012) reported that juvenile Gopher Tortoises monitored with automated temperature loggers in South Carolina emerged more frequently (four to five times) in winter than adults (one to two times), although sample sizes were small. Hatchling Spur-thighed Tortoises (*Testudo graeca*) have also been reported to be more

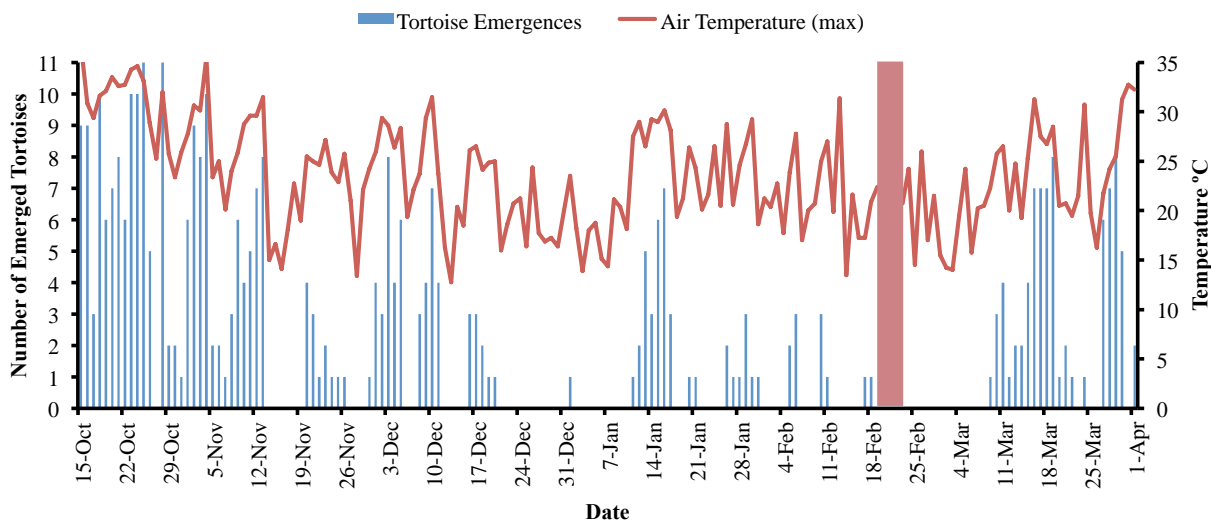


FIGURE 2. The number of juvenile Gopher Tortoises (*Gopherus polyphemus*) that emerged each day (blue bars) and the maximum daily air temperature (red line) from 15 October 2012 to 2 April 2013. Air temperatures were not collected 20–22 February 2013 (marked by the pink bar) due to a prescribed fire in North Pasture where the environmental stations were located.

active than adults and to exhibit discontinuous hibernation (Keller et al. 1997).

Although adult Gopher Tortoises do occasionally bask during winter, activity appears to be limited to warm days and it is unusual for healthy tortoises to exhibit frequent or extended surface activity. The single adult Gopher Tortoise in the DeGregorio et al. (2012) study that exhibited numerous winter emergences was an individual (female #95) that tested as suspect for upper respiratory tract disease (URTD) and had also experienced complications due to anesthesia in the activity season preceding the overwintering period in which temperatures were measured (Hernandez et al. 2011). Likewise, McGuire et al. (2014) found that adults severely afflicted by URTD experienced greater temperature fluctuations than asymptomatic or mildly-symptomatic adults and exhibited abnormal thermoregulatory behavior (i.e., exhibited behavioral fever). All juveniles in our study appeared to be healthy, showing no clinical symptoms of URTD or other disease. Thus, we suspect that the surprisingly frequent winter surface activity by juveniles in our study reflects normal juvenile activity. Our findings add to the growing body of literature regarding activity of juvenile tortoises during the overwintering period and how it differs from adult conspecifics.

There may be advantages to juvenile tortoises being active during winter or being active at lower environmental temperatures than adults. Because growth in turtles occurs primarily during the juvenile stage (Congdon et al. 2013), maximizing resource acquisition and growth is critical for juveniles. Most winter surface activity by Gopher Tortoises has been

attributed to basking, with foraging only very rarely observed (McRae et al. 1981, Wilson et al. 1994), thus activity in winter is unlikely to provide foraging opportunities for juveniles, particularly if sudden decreases in daily temperatures could interfere with subsequent digestion. However, their ability to heat quickly and be active at lower environmental temperatures may extend their activity season relative to adults, thereby increasing opportunity for resource acquisition and accumulation. For example, hatchling Spur-thighed Tortoises exhibit improved body condition and an early season growth spurt during the period immediately following spring emergence (Keller 1997). In addition, activity on warm winter days, particularly near the end of overwintering period, may physiologically prime juveniles such that they may be able to more quickly obtain and sustain body temperatures optimal for foraging, digestion, and assimilation. Collectively, these potential benefits may explain why juveniles exhibit such frequent surface activity during winter, despite the risk of predation.

In addition to its potential consequences for individual growth, juvenile activity during winter has important implications for habitat management. When actively managed, Gopher Tortoise habitats are periodically treated with fire or, alternatively, mechanical disturbance such as mowing. These habitat treatments are often applied in winter, a time when both adult and juvenile tortoises have been presumed to be relatively inactive. However, our study reveals that juveniles exhibit frequent activity during winter, with surface activity by at least one tortoise documented on 48% of days. Due to

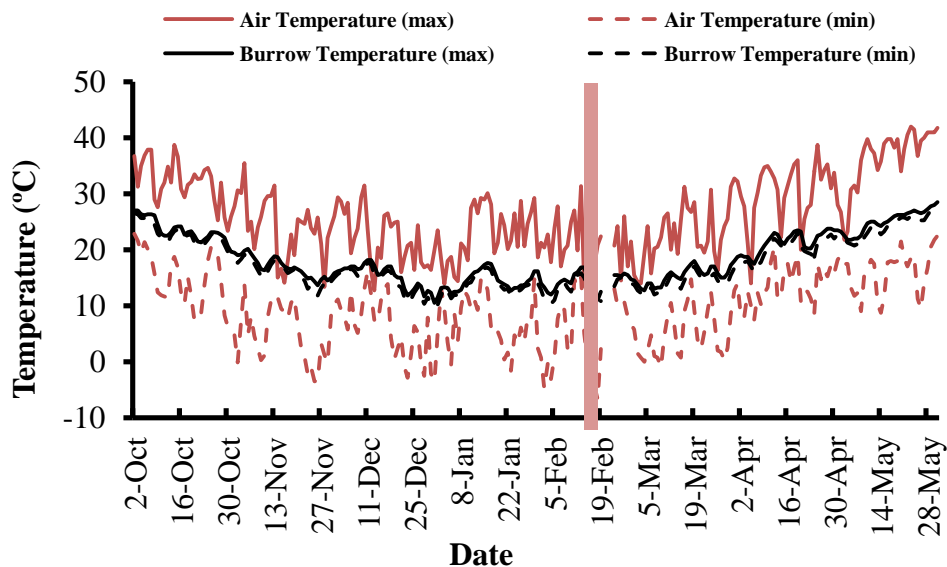


FIGURE 3. Environmental temperatures at the study site of juvenile Gopher Tortoises (*Gopherus polyphemus*) during winter 2012–2013 at the St. Catherines Island, Georgia, including daily maximum (solid red line) and minimum (dashed red line) air temperatures, as well as daily maximum (solid black line) and minimum burrow temperatures (dashed black line). During 20–22 February 2013 a prescribed fire was conducted at the study site, which required environmental stations to be pulled from the field, resulting in three days for which data were not collected (represented by a pink bar).

their small size, juveniles are inherently less detectable, as are their burrows, and might not be observed during management activities. Although juveniles are probably unlikely to stray from their burrows and could presumably retreat quickly back into the burrow, managers should consider the likelihood of juvenile surface activity when planning management activities during winter and take special precautions, such as planning habitat management activities on days when maximum air temperatures are $< 16^{\circ}\text{C}$.

Acknowledgments.—We extend our gratitude to Veronica Greco and the St. Catherines Island interns that assisted in deploying and collecting temperature loggers and in processing turtles. We thank Jack Tuberville for constructing environmental stations. We are grateful for the assistance Elizabeth Hunter provided in capturing tortoises prior to winter. We are especially appreciative of the logistical support provided by Royce Hayes and the St. Catherines Island Foundation staff throughout the study. Jessica McGuire, Brett DeGregorio, Brian Crawford, and Elizabeth Schlimm provided valuable feedback during the preparation of this manuscript. Funding was provided by grants from the St. Catherines Island Foundation, TERN: Friends of Georgia's Nongame Wildlife, and Riverbanks Zoo and Garden Conservation Support Fund. Data analysis and manuscript preparation was supported by the Department of Energy under Award Number DE-FC09-07SR22506 from Department of Energy to the

University of Georgia Research Foundation. All research was conducted in accordance with Georgia scientific collecting permits 29-WBH-12-166 and 29-WJH-13-83 and using procedures approved by University of Georgia's Institutional Animal Care and Use Committee under Animal Use Proposal #A2011 05-20-Y1.

LITERATURE CITED

- Bailey, S.J., C.R. Schwalbe, and C.H. Lowe. 1995. Hibernaculum use by a population of Desert Tortoises (*Gopherus agassizii*) in the Sonoran Desert. *Journal of Herpetology* 29:361–369.
- Berry, K.H., and F.B. Turner. 1986. Spring activities and habits of juvenile Desert Tortoises, *Gopherus agassizii*, in California. *Copeia* 1986:1010–1012.
- Boarman, W.I., T. Goodlet, G. Goodlet, and P. Hamilton. 1998. Review of radio transmitter attachment techniques for turtle research and recommendations for improvement. *Herpetological Review* 29:26–33.
- Cagle, F.R. 1939. A system of marking turtles for future identification. *Copeia* 1939:170–173.
- Case, T.J. 1976. Seasonal aspects of thermoregulatory behavior in the Chuckwalla, *Sauramalus obesus*, (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology* 10:85–95.
- Congdon J.D., R.E. Gatten, Jr., and S.J. Morreale. 1989. Activity of box turtles (*Terrapene carolina*) in South Carolina. *Journal of Herpetology* 23:179–181.

- Congdon, J.D., J.W. Gibbons, R.J. Brooks, N. Rollinson, and R.N. Tsaliagos. 2013. Indeterminate growth in long-lived freshwater turtles as a component of individual fitness. *Evolution and Ecology* 27:445–459.
- DeGregorio, B.A., K.A. Buhlmann, and T.D. Tuberville. 2012. Overwintering of Gopher Tortoises (*Gopherus polyphemus*) translocated to the northern limit of their geographic range: temperatures, timing, and survival. *Chelonian Conservation and Biology* 11:84–90.
- Diemer, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. *Journal of Herpetology* 26:158–165.
- Douglass, J.F., and J. N. Layne. 1978. Activity and thermoregulation of the Gopher Tortoise (*Gopherus polyphemus*) in Southern Florida. *Herpetologica* 34:359–374.
- Edge, C.B., B.D. Steinberg, R.J. Brooks, and J.D. Litzgus. 2009. Temperature and site selection by Blanding's Turtles (*Emydoidea blandingii*) during hibernation near the species' northern range limit. *Canadian Journal of Zoology* 87:825–834.
- Ernst, C.H., and R.W. Barbour. 1972. *Turtles of the United States*. University Press, Lexington, Kentucky, USA.
- Gibbons, J.W. 2013. A long-term perspective of delayed emergence (aka overwintering) in hatchling turtles: some they do and some they don't, and some you just can't tell. *Journal of Herpetology* 47:203–214.
- Gibbons, J.W., and D.H. Nelson. 1978. The evolutionary significance of delayed emergence from the nest by hatchling turtles. *Evolution* 32:297–303.
- Grayson, K.L., and M.E. Dorcas. 2004. Seasonal temperature variation in the Eastern Painted Turtle (*Chrysemys picta*). *Herpetologica* 60:325–336.
- Greaves, W.F., and J.D. Litzgus. 2008. Chemical, thermal, and physical properties of sites selected for overwintering by northern Wood Turtles (*Glyptemys insculpta*). *Canadian Journal of Zoology* 86:659–667.
- Gregory, P.T. 1982. Reptilian hibernation. Pp. 53–154 *In* *Biology of the Reptilia*. Gans, C. (Ed.). Academic Press, New York, New York, USA.
- Hernandez, S.M., T.D. Tuberville, P. Frank, S.J. Stahl, M.M. McBride, K.A. Buhlmann, and D.J. Divers. 2011. Health and reproductive assessment of a free-ranging Gopher Tortoise (*Gopherus polyphemus*) population following translocation. *Journal of Herpetological Medicine and Surgery* 20:84–93.
- Hubbart, J.A. 2011. An inexpensive alternative solar radiation shield for ambient air temperature micro-sensors. *Natural Environmental Sciences* 2:9–14.
- Hutchison, V.H. 1979. Thermoregulation. Pp. 207–228 *In* *Turtles: Perspectives and Research*. Harless M., and H. Morlock (Eds.). John Wiley & Sons, Inc., New York, New York, USA.
- Jackson, D.C., and G.R. Ultsch. 2010. Physiology of hibernation under the ice by turtles and frogs. *Journal of Experimental Zoology Part A—Ecological Genetics and Physiology* 313A:311–327.
- Jacob, J.S., and C.W. Painter. 1980. Overwinter thermal ecology of *Crotalus viridis* in the north-central plains of New Mexico. *Copeia* 1980:799–805.
- Keller, C., C. Díaz-Paniagua, and A.C. Andreu. 1997. Post-emergent field activity and growth rates of hatchling Spur-thighed Tortoises, *Testudo graeca*. *Canadian Journal of Zoology* 75:1089–1098.
- Kinlaw, A.E., L.B. Conyers, and W. Zajac. 2007. Use of ground penetrating radar to image burrows of the Gopher Tortoise (*Gopherus polyphemus*). *Herpetological Review* 38:50–55.
- Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and maturity of the Gopher Tortoise in Southwestern Georgia. *Bulletin of the Florida State Museum, Biological Science* 27:81–110.
- McGuire, J.L., L.L. Smith, C. Guyer, and M.J. Yabsley. 2014. Effects of mycoplasma upper-respiratory-tract disease on movement and thermoregulatory behavior of Gopher Tortoises (*Gopherus polyphemus*) in Georgia, USA. *Journal of Wildlife Diseases* 50:745–756.
- McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement patterns and home range of the Gopher Tortoise. *American Midland Naturalist* 106:165–179.
- Nussear, K.E., T.C. Esque, D.F. Haines, and C.R. Tracy. 2007. Desert Tortoise hibernation: temperatures, timing, and environment. *Copeia* 2007:378–386.
- Pike, D.A., and J.C. Mitchell. 2013. Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Animal Conservation* 16:694–703.
- Pittman, S.E., and M.E. Dorcas. 2009. Movements, habitat use, and thermal ecology of an isolated population of Bog Turtles (*Glyptemys mühlenbergii*). *Copeia* 2009:781–790.
- Tuberville, T.D., T. M. Norton, B.D. Todd, and J.S. Spratt. 2008. Long-term apparent survival of translocated Gopher Tortoises: a comparison of newly released and previously established animals. *Biological Conservation* 141:2690–2697.
- Tuberville, T.D., T.M. Norton, B.J. Waffa, C. Hagen, and T.C. Glenn. 2011. Mating system in a Gopher Tortoise population established through multiple translocations: apparent advantage of prior residence. *Biological Conservation* 144:175–183.
- Ultsch, G.R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. *Biological Reviews* 64:435–516.
- Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Review* 1:1–29.
- Wilson, D.S., H.R. Mushinsky, and E.D. McCoy. 1994. Home range, activity and use of burrows of juvenile

Herpetological Conservation and Biology

Gopher Tortoises in Central Florida. Pp. 147–160 *In* Biology of North American Tortoises. R.B. Bury, and D.J. Germano (Eds.). Fish and Wildlife Research Report 13, US Department of the Interior, National Biological Survey, Washington DC, USA.

Wilson, D.S., D.J. Morafka, C.R. Tracy, and K.A. Nagy. 1999. Winter activity of juvenile Desert Tortoises (*Gopherus agassizii*) in the Mojave Desert. *Journal of Herpetology* 33:496–501.



BESS B. HARRIS is a Biological Scientist with the Florida Fish and Wildlife Conservation Commission. She has worked with numerous reptile and amphibian species including examination of contaminant exposure on long-lived species such as aquatic turtles and the American Alligator (*Alligator mississippiensis*). She has a B.A. (2010) in Biology from Agnes Scott College and M.S. (2014) in Wildlife Biology from the University of Georgia (UGA) Warnell School of Forestry and Natural Resources, and has worked as a technician at UGA's Savannah River Ecology Laboratory. Her graduate work focused on juvenile Gopher Tortoise ecology on St. Catherines Island, Georgia. She loves working with all wildlife, but is passionate about working with herpetofauna and their conservation needs. (Photographed by Walton Harris).



NATHAN P. NIBBELINK is an Associate Professor of Spatial Ecology and GIS in the Warnell School of Forestry & Natural Resources at the University of Georgia (UGA). He has an M.S. in Oceanography and Limnology from the University of Wisconsin where he developed an individual-based model investigating the effects of Bluegill (*Lepomis macrochirus*) habitat selection on population size structure in Wisconsin lakes. His Ph.D. is in Zoology and Physiology from the University of Wyoming where he investigated the influence of landscape structure on trout populations. He and his students at UGA use spatial models to better understand species response to climate and landscape change. He also currently serves as Director of the Center for Integrative Conservation Research, whose mission is to facilitate innovative research that blends social and natural science perspectives to address global conservation and sustainability challenges. (Photographed by Shannon Albeke).



TERRY M. NORTON earned his Doctor of Veterinary Medicine at Tufts University in 1986 and completed a residency in Zoo and Wildlife Medicine at the University of Florida in 1989. He became a Diplomate in the American College of Zoological Medicine in 1992. Terry provides veterinary care for the Georgia Sea Turtle Center and St. Catherines Island Foundation programs. Additionally, he is the Director of the Georgia Sea Turtle Center. He enjoys working with all wildlife but has a true passion for working with all types of turtles. (Photographed by Tracey D. Tuberville).



TRACEY D. TUBERVILLE is an Associate Research Scientist at the University of Georgia's (UGA) Savannah River Ecology Laboratory, near Aiken, South Carolina. She received her B.S. in Biology from Furman University (1993), M.S. in Conservation Ecology and Sustainable Development (1998) and Ph.D. (2008) in Ecology from University of Georgia. Her research interests are in applied conservation and management of reptiles and amphibians, including translocation and reintroduction as conservation tools. (Photographed by Kurt A. Buhlmann).