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Thermal Ecology of Spotted Turtles (*Clemmys guttata*) in Two Southern Populations

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The ecology of many ectotherms depends heavily on their ability to navigate the surrounding thermal environment in a manner that maintains body temperature (T_b) within or near some optimal temperature range at least some of the time. From April–December 2016, we measured shell temperatures (T_s) and water temperatures (T_w) in two Spotted Turtle (*Clemmys guttata*) populations in southeastern Georgia using iButton temperature loggers. We attached radio transmitters and iButtons to the carapace of adult Spotted Turtles ($n = 18$ and 11 in each population, respectively) in early spring. Temperature loggers recorded a T_s measurement every 90 minutes (accuracy = 0.5°C), and we restricted our analyses to temperatures recorded between sunrise and sunset. Monthly mean T_s ranged from 12.3±3.4 to 27.1±2.7°C (SD), and seasonal variation accounted for a majority of the observed variation in temperatures. We found a strong positive correlation between weekly mean T_s and weekly mean T_w at one site that remained flooded throughout the study ($P < 0.0001$, $R^2 = 0.99$). T_w could not be measured at the other site because it dried completely early in the study. Spotted Turtles did occasionally (<5% of total temperature observations) bask to raise T_s above that of the surrounding T_w. Gravid females achieved significantly higher daily maximum temperatures (26.2°C) than males (24.5°C) during the four weeks surrounding egg development ($P = 0.043$). In general, Spotted Turtles at the southern end of their range appear to spend a majority of their time conforming to environmental temperatures that often fall within the preferred range for the species.

TEMPERATURE plays a critical role in the biology and ecology of ectotherms. A variety of ecological and physiological processes are impacted by body temperature (T_b), including foraging efficiency, digestion efficiency, reproductive success, and disease response (Lourdais et al., 2002; Ayers and Shine, 2003; McConnachie and Alexander, 2004; McGuire et al., 2014). T_b ultimately affects fitness (Kingsolver and Huey, 2008), and ectotherms can either conform to environmental temperatures or thermoregulate to maintain T_b within some optimal range (Huey and Stevenson, 1979). Thermoregulating in a heterogeneous thermal environment can be achieved using behavior, physiology, or both (Lillywhite et al., 1973; Crawford et al., 1983; Angilletta et al., 2002; Shine, 2005). However, there are costs associated with thermoregulation (Huey and Slatkin, 1976; Herczeg et al., 2008), and a single T_b may not be optimal for all physiological processes or behaviors. The interaction between the costs and benefits of thermoregulation, the available thermal environment, and a suite of other environmental factors creates a complex thermal landscape for individuals to navigate (Brett, 1971; Sears and Angilletta, 2015).

For freshwater turtles, this complex thermal environment consists of relatively stable water temperatures (T_w) and air temperatures (T_a) that can fluctuate significantly over short time periods (Dubois et al., 2009; Shen et al., 2013). Thermally stable aquatic environments facilitate broad distributions in many species (Ernst and Lovich, 2009) and allow aquatic turtles to be active when T_a are unfavorable for other reptile species (Litzgus and Brooks, 2000). For turtle species inhabiting large geographic distributions, behavioral differences between populations at different latitudes are common, particularly when low temperatures significantly restrict activity in some portions of the range (e.g., winter dormancy). Despite inhabiting complex thermal environments, the thermal ecology of many freshwater turtle species is not well studied, either in laboratory tests or in wild populations. The need for such studies is exacerbated by the likely impact of climate change on the thermal environments of many species.

The Spotted Turtle (*Clemmys guttata*) is an example of a freshwater turtle species that ranges across a wide latitudinal gradient, spanning most of the eastern United States and stretching into southern Canada (Ernst and Lovich, 2009). In Canada and the northeastern U.S., Spotted Turtles condense the majority of their life history into a 7–8-month period broken up by a long period of hibernation each winter (Ernst, 1976; Litzgus et al., 1999). This is in stark contrast to southern populations that can be active for 12 months of the year, depending on the specific environmental conditions (Litzgus and Mousseau, 2004; Stevenson et al., 2015; Chandler et al., 2019). The thermal biology and basking behaviors in northern Spotted Turtle populations have been previously studied (Ernst, 1982; Litzgus et al., 1999; Rasmussen and Litzgus, 2010; Yagi and Litzgus, 2013), but, to date, no thermal ecology studies have been conducted in southern populations.

Quantifying the thermal environments used by southern Spotted Turtle populations over an active season is important to the conservation of this species for several reasons. First, southern populations could differ behaviorally from northern populations to cope with dramatically different environmental temperatures. Understanding when environmental conditions are ideal for activity and how they impact behavior has direct applications to monitoring populations. Second, Spotted Turtles appear to be relatively rare at the southern end of their range (Barnwell et al., 1997; Stevenson et al., 2015). Thermal stress from high temperatures could

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play a limiting role in abundance or distribution of Spotted Turtle populations in this southern portion of their range. Finally, a changing climate will likely disproportionately impact shallow ephemeral wetlands that respond primarily to precipitation and evapotranspiration rates (Brooks, 2009). Baseline temperature data are needed to frame future work examining how changes to the thermal environment in shallow wetlands are impacting Spotted Turtle populations.

The goal of this study was to quantify temperatures experienced over a nine-month period by Spotted Turtles in two populations from the Coastal Plain of southeastern Georgia. Given the overall warm climate in this region, we expected temperatures to be generally favorable for Spotted Turtle activity and predicted that individuals would spend a majority of their time conforming to environmental temperatures. We hypothesized that if temperatures were suitable for Spotted Turtle activity, then the number of basking events would be low but that they would be concentrated during the cooler times of the year. Finally, we examined the effects of both sex and the availability of water on temperatures experienced by individuals. We expected female turtles to maintain higher temperatures than male turtles during egg development. We also hypothesized that a lack of water at one site would lead to higher and more variable T_b when compared to individuals with consistent access to water, which provides a stable thermal environment (Litzgus et al., 1999; Jacobs et al., 2008).

MATERIALS AND METHODS

Study sites.—We studied two Spotted Turtle populations in the Coastal Plain of southeastern Georgia (specific locations are withheld because of collecting concerns). Both sites contain small, forested wetland complexes bordering the floodplains of small creeks (total wetland area approximately 15–30 ha). Each site is composed of a small number of discontinuous flooded areas that are separated by small sections of upland habitat. Site 1 contains both natural and artificial wetlands, including a beaver wetland and old agricultural ditches. Site 2 is a natural wetland. The hydrology of the two sites differed over the study period. Site 1 had standing water in a large portion of the wetland for the entire period, while Site 2 dried completely by the end of May, remaining mostly dry for the duration of the sampling season (precipitation events occasionally filled small pools of water after initial drying in May). Bald Cypress (*Taxodium distichum*), Swamp Black Gum (*Nyssa biflora*), and Red Maple (*Acer rubrum*) are dominant in the canopy, and Buttonbush (*Cephalanthus occidentalis*) is common in the understory at both sites. Wetlands at both sites are surrounded by a matrix of deciduous floodplain forests, pine plantations, and riparian habitats. The two study sites are located in different river drainages, approximately 145 km apart. The wetland complex at Site 1 is larger than at Site 2 (see discussion of space use in Chandler et al., 2019). Both study sites experience similar climate patterns, including mean high temperatures above 30°C during the summer months and winter temperatures that rarely dip below 0°C. Precipitation patterns are characterized by winter rains (i.e., December–February) that typically fill temporary wetlands before spring, followed by a drier April and May before an increase in precipitation rates during the summer.

Data collection.—As part of ongoing population monitoring, we captured Spotted Turtles at the two study sites from 18 March to 16 May 2016 using a combination of aquatic Jones Traps baited with sardines (Chandler et al., 2017) and visual encounter surveys. During this time period, we opportunistically attached waterproof radio transmitters (Model: SOPR-2190, Wildlife Materials International, Inc., Murphysboro, IL) and waterproofed (Roznik and Alford, 2012) iButton temperature loggers (Model: DS1922L, Maxim Integrated, San Jose, CA) to the carapace of adult Spotted Turtles. We programed iButtons to record temperatures every 90 minutes (0.5°C accuracy). We attached both radio transmitters (left rear) and iButtons (right rear) to each turtle's carapace using a waterproof epoxy. The total weight of transmitters, iButtons, and all epoxy was always less than 10% of the individual's body mass. After attaching equipment, we verified that transmitters were working and released all turtles at their point of capture within 24 hours.

All turtles included in the study were adults with midline carapace lengths ranging from 90.1–110.9 mm. We initially attached radio transmitters and iButtons to 18 adult turtles at Site 1 (10 males and 8 females) and 11 turtles at Site 2 (6 males and 5 females). However, iButtons attached to five turtles at Site 1 were not operational when removed at the end of the study period, and one iButton was lost during a failed predation event. No temperature data were recovered from these six turtles. Thus, our analysis of temperature data was restricted at Site 1 to 12 individuals (8 males and 4 females), but we present habitat and behavioral observations for all 18 individuals at this site. Although these sample sizes are relatively small, both populations included in this study are small and area-constrained (Chandler et al., 2019); thus, we believe that the number of turtles included in our study is representative of the overall variation among individuals in each population.

We located turtles 1–2 times per week over the majority of the study period (April–October). Logistical constraints forced us to decrease tracking effort to once every two weeks during November and December (see Chandler et al., 2019). On 16 May, we captured all female turtles at both sites and x-rayed them to confirm the presence of shelled eggs (Gibbons and Greene, 1979). All turtles were returned to their capture point within 24 hours. We located all turtles for the final time on December 22 at Site 1 and December 29 at Site 2. We removed radio transmitters and iButtons and used sandpaper to gently remove any additional epoxy stuck to each turtle's shell. Radio transmitter batteries on two individuals at Site 1 died unexpectedly before transmitters and iButtons were removed. However, both turtles were captured during population monitoring in March 2017, at which time we removed their transmitters and iButtons (iButtons were still recording temperature data for both turtles).

Each time a turtle was located, we recorded a general description of its surrounding habitat and behavior. We measured the canopy cover at each individual's position using a convex spherical densiometer (Lemon, 1956). To describe behavior, we first noted whether a turtle was in cover (i.e., not visible and under some type of structure) or in the open and visible to the observer. If a turtle was visible to the observer, we recorded a description of that individual's behavior (e.g., feeding, basking, courtship, etc.). On many occasions, turtle behavior was not easily classified (i.e., they were sitting or moving in the open), and we simply noted that individuals were not in cover.

In addition to monitoring turtles, we also placed two iButtons in the water at each site during the first week of April. We programmed these iButtons to record temperatures every 90 minutes. We placed iButtons in locations that were frequently used by turtles based on previous site knowledge (Chandler and Stevenson, unpubl. data) and suspended them in the water column approximately 15–30 cm from the water's surface. iButtons at both sites were located in areas of high canopy cover but were potentially exposed to small patches of sunlight during certain times of the day. We periodically adjusted iButtons to account for changing water levels. At Site 2, environmental iButtons were left in the same locations to record T_a after the wetland dried completely. At Site 1, extensive flooding as a result of Hurricane Matthew dislodged one of the environmental iButtons during mid-October. We were eventually able to recover this iButton, but it was no longer in a position to record T_w. Thus, T_w at Site 1 after 17 October were derived from a single iButton. We removed all other iButtons on December 22 and 29 at Sites 1 and 2, respectively.

Temperature data.—We estimated turtle T_b from temperature measurements recorded from iButtons attached to the carapace of each individual. Measuring shell temperatures (T_s) as a proxy for turtle T_b has been employed in other turtle species, including Spotted Turtles (Grayson and Dorcas, 2004; Millar et al., 2012; Yagi and Litzgus, 2013; Feaga and Haas, 2015). In general, T_b and T_s are correlated, especially in small freshwater turtles (Sajwaj and Lang, 2000; Grayson and Dorcas, 2004), although T_s tends to be higher than T_b (Edwards and Blouin-Demers, 2007). We refer to measured temperatures as T_s throughout this paper and consider them to be a reasonable approximation of T_b.

All temperature loggers were programmed to record a temperature measurement at the same time stamp, and prior to analyses, we aligned all temperature data so that the timestamps for each measurement were the same. For our analyses, we focused on daytime temperature measurements because Spotted Turtles are almost entirely diurnal (Ernst, 1976), and these were the time periods when turtles could potentially thermoregulate. We defined daytime temperatures as any temperature measurements that occurred between sunrise and sunset. We identified sunrise and sunset times using the coordinate for the approximate center of each study site with the R package suncalc (Thieurmel, 2019). We then extracted all temperature measurements that fell between these times. We summarized T_s measurements by calculating monthly and weekly mean temperatures across all individuals at each site. We also calculated mean monthly and weekly minimum and maximum temperatures. To do this, we first calculated a daily maximum and minimum T_s for each individual, and then calculated a mean value across months or weeks.

At Site 1, we identified potential basking events by comparing T_s to the available T_w. The mean deviance between the two iButtons placed in the water was 1.4±1.5°C (SD). Thus, we classified all shell temperatures greater than 3°C above the maximum T_w at each timestamp as times when turtle T_s was significantly higher than the available T_w (i.e., the turtle was basking). We quantified the number of potential basking events for each individual and summed the total number of events by month and sex.

Statistical analyses.—We used a mixed effects model to test the effects of sex and month on T_s, including the individual as a random effect in the model and population as a block. At Site 1, we compared both the weekly mean and maximum T_w to mean and maximum T_s using simple linear regression models. We also fit a mixed effects model to examine the effect of sex (male, female, or gravid female) on daily maximum T_s reached during a four-week period surrounding egg development (i.e., two weeks before and two weeks after shelled eggs were detected on 16 May). We included the population as a block in this model, and we used a Tukey's HSD to test for differences between sexes. All analyses were performed in R (R Core Team, 2018).

RESULTS

The number of daytime temperatures recorded per day varied over the survey season ($n = 6–10$), and most individuals had approximately 2,200 daytime T_s measurements recorded. The two individuals at Site 1 with iButtons attached until the following spring had an additional 526 daytime temperature measurements recorded. The observed variability in T_s for Georgia Spotted Turtle populations was largely attributable to seasonal variation in environmental temperatures (Table 1; Fig. 1). Mean monthly daytime T_s increased from approximately 20°C during the late spring to a high of 27.0°C (August) and 27.1°C (July) at Sites 1 and 2, respectively. Mean T_s declined during the fall and early winter to a low of 13.8°C and 12.3°C during December. Mean daily maximum T_s approached 30°C during the summer months, while mean daily minimum T_s generally ranged from 10–14°C during the late fall and early winter (Table 1). We did not detect a T_s below 0°C (including nighttime temperatures) over the course of the study.

When water was available, Spotted Turtles at both sites generally conformed to available T_w. Turtles at Site 2 only had access to intermittent standing water after early June and generally experienced more temperature fluctuations (mean variance in T_s across individuals = 24.7 at Site 1 and 36.3 at Site 2) and lower minimum temperatures than individuals at Site 1 (Fig. 1; Table 1). At Site 1, weekly mean T_s and weekly mean maximum T_s were both correlated to weekly mean and maximum T_w, respectively (weekly mean: $R^2 = 0.99$; mean weekly maximum: $R^2 = 0.59$; Fig. 2). Despite general conformity, individuals at Site 1 did occasionally raise T_s above that of the surrounding T_w (Fig. 3A). We identified 1,050 occasions when Spotted Turtles were likely basking (<5% of total daytime temperature measurements at Site 1). Basking events peaked in late spring and fall but tapered off during the summer months when T_w were highest. Female turtles tended to bask more often in May, while male turtles tended to bask more often in October and November (Fig. 3B).

There was a significant interaction effect between month and sex ($F_{8,48833} = 13.7$, $P < 0.0001$) on daytime T_s. Although a significant interaction effect between sex and month was observed, the actual temperature differences between male and female turtles were small across the entire year (Fig. 4). However, we also detected a significant effect of sex on the mean daily maximum T_s reached during the time period

Table 1. Daytime (sunrise to sunset) shell temperatures measured every 90 minutes on adult Spotted Turtles (*Clemmys guttata*) at two sites in Georgia with standard deviations in parentheses. Maximum and minimum temperatures represent the values calculated daily for each individual and then averaged across the entire month. *January and February temperatures were recorded for just two individuals that were not recaptured until the following year.

	Site 1			Site 2		
	Mean	Min	Max	Mean	Min	Max
April	19.6 (4.2)	16.1 (2.6)	24.6 (5.5)	20.1 (3.8)	16.8 (2.5)	24.4 (4.2)
May	22.3 (3.1)	19.3 (2.3)	25.5 (3.7)	21.2 (3.4)	17.5 (2.6)	24.2 (3.5)
June	25.4 (2.4)	23.0 (1.2)	28.1 (2.9)	25.3 (2.7)	22.2 (1.4)	28.4 (2.6)
July	26.9 (2.2)	24.5 (0.7)	29.6 (2.6)	27.1 (2.7)	23.2 (0.8)	30.1 (1.7)
August	27.0 (2.1)	24.1 (0.9)	29.3 (1.8)	26.7 (2.3)	23.6 (1.0)	29.2 (1.7)
September	24.7 (2.0)	22.8 (1.2)	27.0 (2.6)	24.7 (2.5)	21.3 (1.5)	26.9 (2.0)
October	21.0 (3.2)	18.4 (2.6)	24.6 (4.0)	19.8 (3.5)	15.8 (3.1)	22.6 (2.3)
November	16.1 (4.1)	13.6 (3.5)	18.7 (4.8)	14.7 (4.6)	10.2 (4.1)	18.0 (3.0)
December	13.8 (3.1)	12.3 (2.8)	15.6 (3.5)	12.3 (3.4)	10.6 (3.0)	14.2 (3.6)
January*	14.5 (5.2)	11.6 (3.5)	19.4 (6.9)	—	—	—
February*	16.9 (5.5)	12.5 (2.7)	24.1 (6.7)	—	—	—

surrounding egg production at both sites ($F_{2,19} = 4.1$, $P = 0.03$). Gravid females reached a higher T_s, on average, than did males ($P = 0.043$), but not non-gravid females ($P = 0.059$; GF = 26.2±0.6°C, F = 24.1±0.6°C, M = 24.5±0.3°C [means ±SE]).

We recorded a total of 1,246 observations of turtle behavior over the nine-month period, including the six turtles with no temperature data (Table 2). Spotted Turtles were in cover, both on land and in the water, approximately 77% of the times that they were located. We classified just six observations as basking behavior, although an additional 16 observations (1.28%) were made of turtles in the open while on land. Mean canopy cover was high at both sites (Site 1: 91.7%; Site 2: 98.4%), and there were few areas with an open canopy that received long periods of direct sunlight ideal for basking turtles.

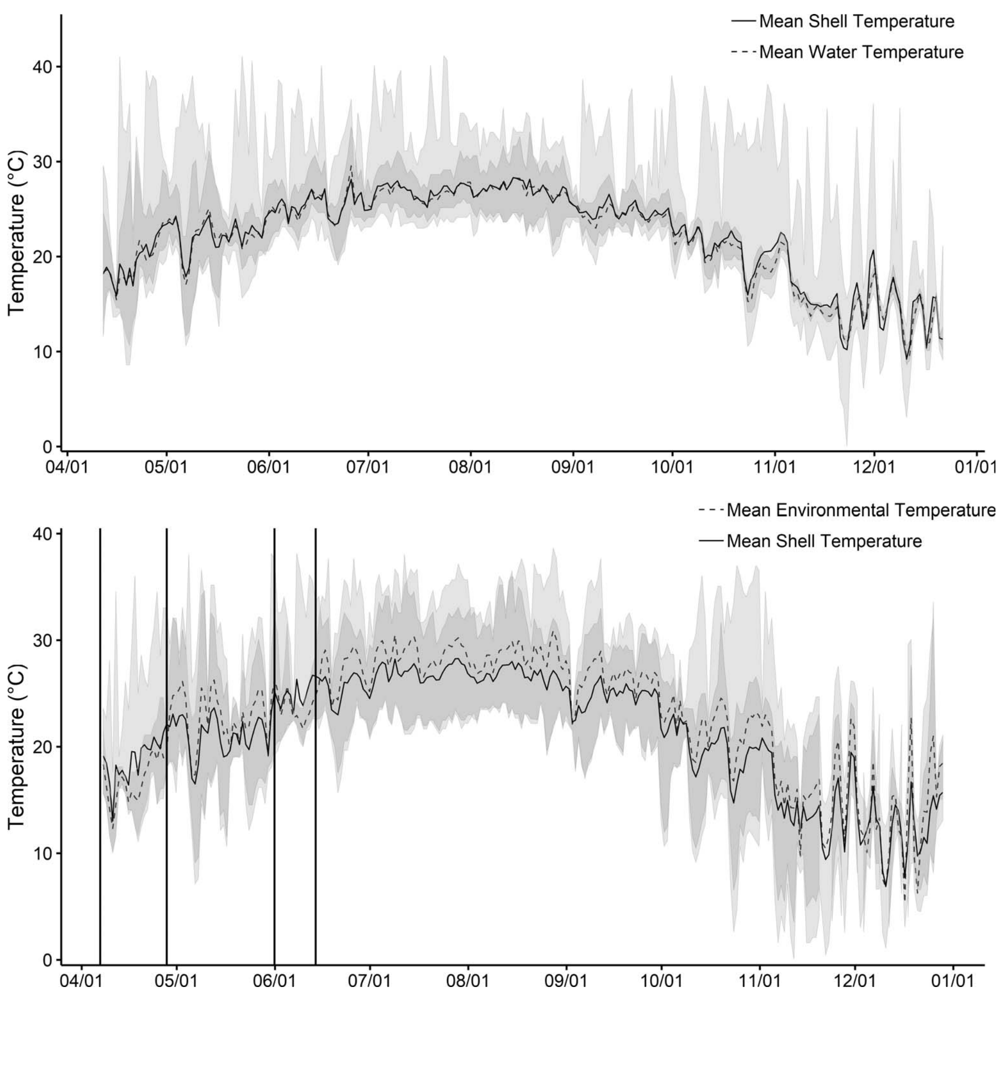

Fig. 1. Water and shell temperatures for Spotted Turtles (*Clemmys guttata*) at two sites in southeastern Georgia (Site 1 on top and Site 2 on bottom). Temperature measurements were recorded every 90 minutes during the time between sunrise and sunset, and mean, minimum, and maximum temperatures were calculated daily. Light gray shading represents minimum and maximum water temperatures, and dark gray shading represents minimum and maximum shell temperatures. At Site 2, water was only available until 27 April and then from 1–14 June (represented by vertical lines). Measurements outside of these dates represent air temperatures.

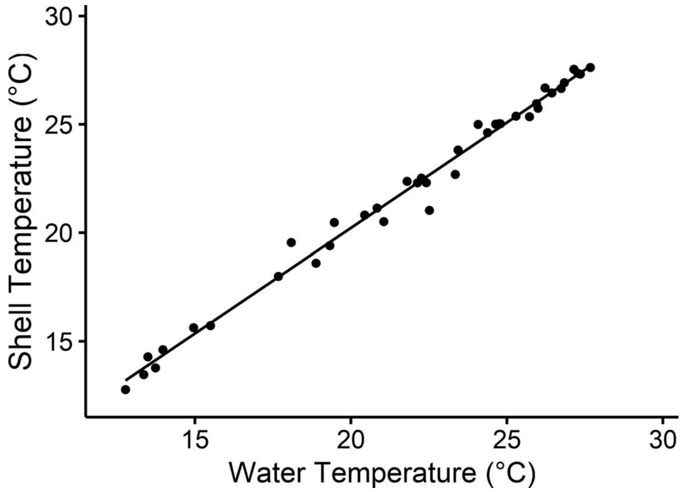

Fig. 2. Relationship between weekly mean water temperatures and weekly mean shell temperatures in a Spotted Turtle (*Clemmys guttata*) population from southeastern Georgia ($P < 0.0001$, $R^2 = 0.99$). Each point represents a single weekly mean value.

DISCUSSION

We found little evidence to indicate that Spotted Turtles at the southern end of their range spend a significant amount of time maintaining their body temperature above that of the surrounding environment. Mean T_s was highly correlated with mean T_w at Site 1 where water was available year-round. Thermoconformity occurs in ectotherms when the costs of thermoregulation outweigh the benefits or when the thermal habitat quality is high, reducing the need to actively thermoregulate (Huey and Slatkin, 1976; Blouin-Demers and Nadeau, 2005). In laboratory experiments, Spotted Turtles from an Ontario population had a preferred T_b ranging from 20–26°C (Yagi and Litzgus, 2013). Optimal or preferred temperatures have not been examined for any southern Spotted Turtle populations; however, temperatures observed in the two populations that we monitored fell within 20–26°C for much of the year. Spotted Turtles have an expansive range that covers a wide variety of habitat types and thermal environments (Ernst and Lovich, 2009), and the data reported for these and other populations indicate that individuals spend a majority of their time conforming to environmental temperatures (Ernst, 1982; Yagi and Litzgus, 2013).

There appear to be few times of the year when low temperatures prevent Georgia Spotted Turtles from being active. Spotted Turtles have been observed active in the water at temperatures below 5°C, can begin courtship activities at less than 10°C, and begin actively foraging at approximately 15°C (Ernst, 1982; Litzgus and Brooks, 2000; Rasmussen and Litzgus, 2010; Yagi and Litzgus, 2013). It is unlikely that winter temperatures in Georgia are ever cold enough to force Spotted Turtles into long periods of hibernation as is common in other parts of the range. Occurrence records from the state indicate that turtles can indeed be active across the entire year (Stevenson et al., 2015), and we documented turtles active in the water over the entire nine-month tracking period (Chandler et al., 2019).

In southern Spotted Turtle populations, high temperatures during the summer combined with wetland drying likely have a greater impact on populations than winter temperatures. Spotted Turtles may become less energetically efficient overall as temperatures climb above 30°C (Ernst, 1982). T_w in the summer months routinely approached 30°C, and T_a can exceed 30°C almost every day for approximately four months. Decreases in activity or aestivation during the hottest parts of the year have been documented in both Spotted Turtles (Litzgus and Brooks, 2000; Milam and Melvin, 2001; Litzgus and Mousseau, 2004; Yagi and Litzgus, 2012; Chandler et al., 2019) and other turtle species (Kennett and Christian, 1994). Periods of summer inactivity and aestivation could be related to drying wetlands and predator avoidance (Litzgus and Brooks, 2000; Rowe et al., 2013) and not necessarily just high temperatures. We observed almost complete wetland drying for an extended period at Site 2, and water levels at Site 1 were reduced during the late summer. The lack of water at Site 2 likely led to greater variation in T_s and lower mean minimum T_s because water can act as a buffer for turtles against T_a extremes (Litzgus et al., 1999; Jacobs et al., 2008). Contrary to our predictions, a lack of water did not lead to turtles experiencing higher T_s at Site 2. We documented turtles using areas of high canopy cover at both sites, potentially reducing exposures to high summer temperatures. Avoiding thermal limits can play an important role in ectotherm ecology (Cowles and Bogert, 1944; Lutterschmidt and Hutchison, 1997; Sunday et al., 2014), and the ability to shelter from environmental temperatures that can approach 40°C may play a role in the distribution of southern Spotted Turtle populations.

Despite general conformity to environmental temperatures, we documented occasions where individuals were potentially basking to raise T_s above the available T_w. Unsurprisingly, these behaviors were most common in the spring and the early fall when water temperatures were lowest. Spring basking is fairly common in Spotted Turtle populations as turtles emerge from winter retreats (Ernst, 1982; Lovich, 1998; Litzgus et al., 1999; Litzgus and Mousseau, 2004). This time period coincides with increased foraging, courtship, and mating activity, with some individuals traveling long distances to participate in mating aggregations (Ernst, 1970, 1976; Lovich, 1998; Litzgus and Mousseau, 2006). Female turtles basked more frequently in May than male turtles, and gravid females reached higher T_s than male turtles during the time period surrounding egg development (e.g., May). Female basking duration during the reproductive period can be longer in other turtle species (Carrière et al., 2008), and increased T_b could stimulate follicular growth (Sarkar et al., 1996) or aid in energy intake needed to produce eggs (Lefevre and Brooks, 1995). Basking activity during the fall was also common, but turtles generally did not obtain a T_s above 30°C, instead raising T_s into the preferred range (20–26°C; Yagi and Litzgus, 2013) from lower temperatures. Male turtles tended to bask more in the fall, and this is potentially related to mate searching during a fall courtship period that occurs in southern Spotted Turtle populations (Litzgus and Mousseau, 2006; Chandler et al., 2019). Overall, the number of basking events identified via temperature and the number of actual basking events observed during radio telemetry was small, especially when compared to some other aquatic turtle species (Lovich, 1988). Infrequent tracking likely contributed to a lack of actual basking observations, and it is possible that individuals were occasionally disturbed from basking positions during radio tracking before this behavior could be observed. However,

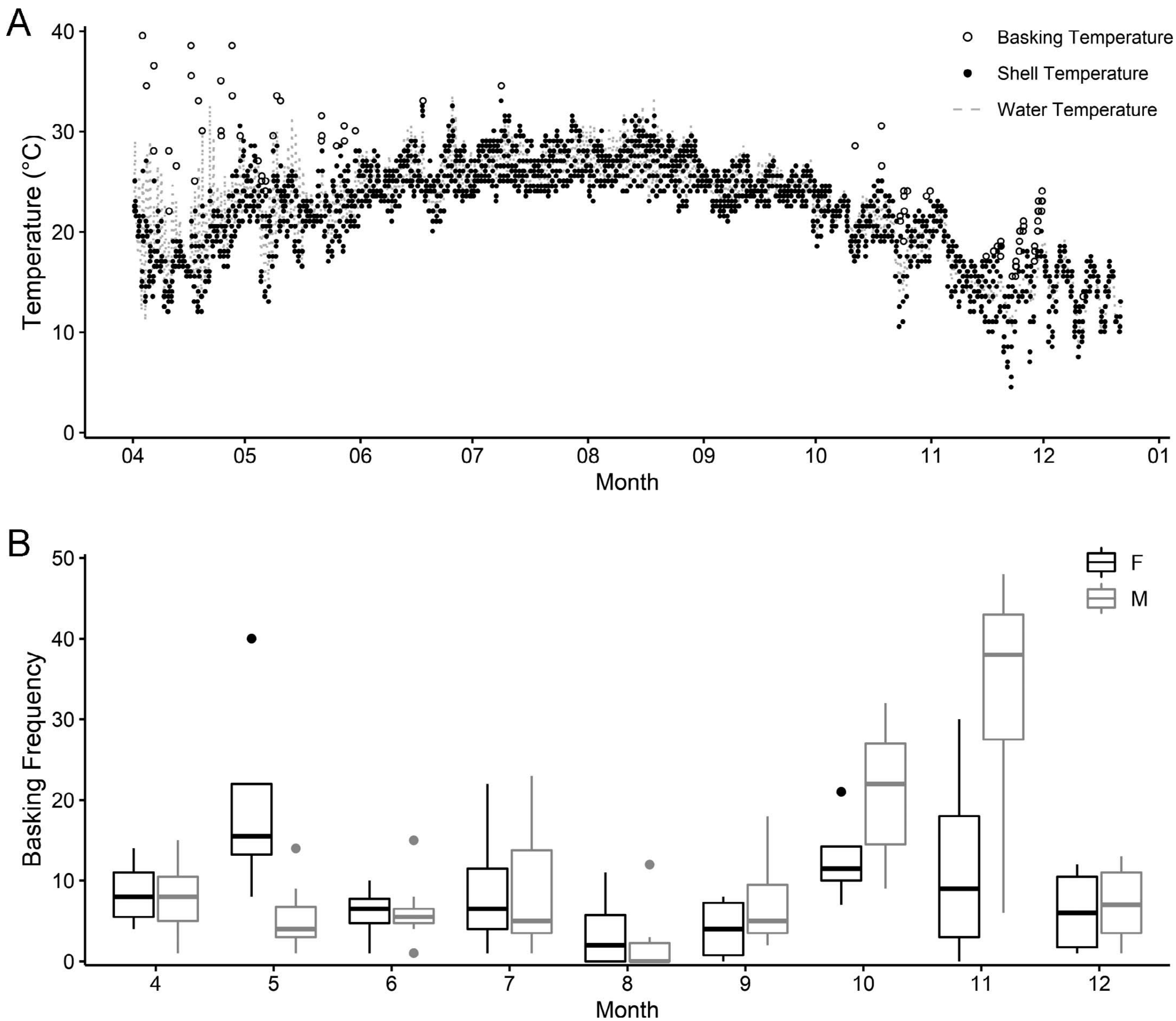

Fig. 3. Shell and water temperatures were measured every 90 minutes with temperature loggers and were used to identify potential basking events in a population of Spotted Turtles (*Clemmys guttata*) from southeastern Georgia. Potential basking events were defined as times when the shell temperature was 3°C above the maximum water temperature for that timestamp (A). The total number of potential basking events in the population was summed across time and by sex (B).

observed environmental temperatures suggest that during many times of the year, Spotted Turtles in these populations do not need to bask to reach preferred temperatures (Yagi and Litzgus, 2013). It is worth noting that basking behavior in turtles is not always associated with thermoregulation (Manning and Grigg, 1997), and there are other potential benefits of basking (e.g., limiting algal growth) in addition to any thermoregulatory advantages (Neil and Allen, 1954; Pritchard and Greenhood, 1968).

Several factors likely impacted our estimates of basking behavior. The timing of our study prevented us from recording temperatures during February and March as turtles were becoming more active after colder winter temperatures. Typical basking behavior is most commonly observed during this time of the year in these populations (Stevenson, unpubl. data). It is also possible that basking events lasted less than 90 minutes and would not have been identified via our methodology (Schwarzkopf and Brooks, 1985). Conversely, there were some observations of turtles out of the water, both in the open and in cover, and these time periods could have represented some of the higher temperature measurements. It is unclear why individuals were sometimes found out of the water when water was available, and it is likely that just spending time exposed to air temperatures during the late spring and summer is enough to increase T_b.

Spotted Turtle populations cover a broad latitudinal gradient that exposes individuals to a variety of thermal environments. At the southern end of this distribution, thermal environments appear to be suitable for activity for a much larger percentage of the year than those in northern populations. Environmental temperatures are generally warm enough that little thermoregulation is needed to

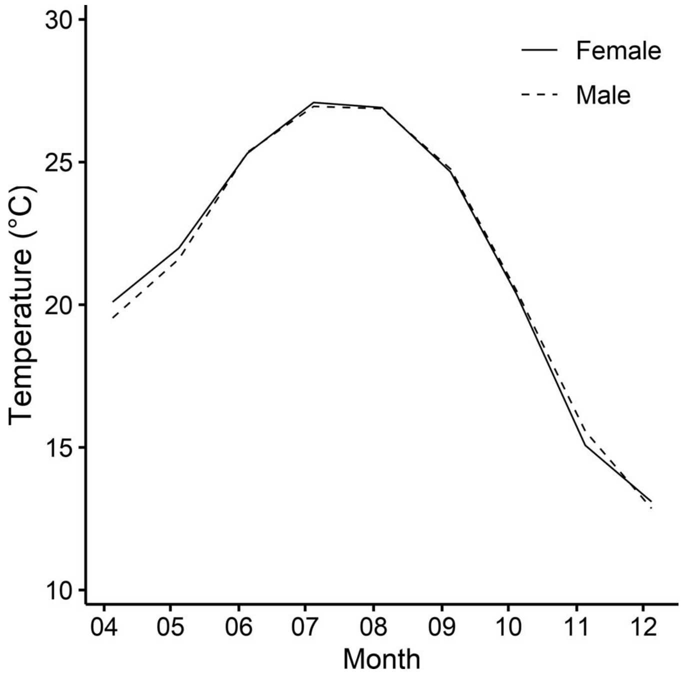

Fig. 4. Mean male and female shell temperatures observed in two Spotted Turtle (*Clemmys guttata*) populations from southeastern Georgia over a nine-month period.

maintain T_b within the preferred range for at least 6–8 months of the year. However, longer activity periods each year could also have negative consequences including more time spent avoiding predation and higher annual energy expenditure. Temperature's effects on behavior are likely mediated in these habitats by the availability of water (Yagi and Litzgus, 2012), especially at sites where wetlands are dry for months at a time. Further study is needed to better understand how the availability of water impacts behavior at both coarse and fine scales. Finally, the southeastern U.S. is predicted to experience higher temperatures and less predictable rainfall patterns as a result of ongoing climate change (Barros et al., 2014). These environmental changes have the potential to impact multiple aspects of Spotted Turtle behavior and biology (e.g., sex ratios via temperature-dependent sex determination; Schwanz and Janzen, 2008). There is already significant conservation concern for Spotted Turtles because of habitat loss and collection for the pet trade (Ernst and Lovich, 2009; van Dijk, 2011). Further environmental changes could exacerbate existing stressors, and individuals must be able to tolerate potentially less favorable conditions for populations to persist long-term.

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Table 2. Number of times each behavior was recorded for Spotted Turtles (*Clemmys guttata*) in two Georgia populations over a nine-month period (18 individuals at Site 1 and 11 individuals at Site 2). Turtles were defined as in cover if they were not visible to the observer. Turtles classified as in the open were visible and moving or stationary.

	Site 1	Site 2	Total
Basking	5	1	6
Courtship/Mating	4	2	6
Feeding	3	1	4
In cover			
Land	206	311	517
Water	389	60	449
In open			
Land	7	9	16
Water	201	46	247
Nesting	1	0	1

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