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ORIGINAL RESEARCH

Here comes the sun: Thermoregulatory behavior in ectotherms illuminated by light-level geolocators

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Abstract

Daily activity patterns of free-ranging wildlife affect a wide range of ecological and physiological processes and, in turn are affected by anthropogenic disturbances to the environment. However, obtaining a continuous record of activity without disturbing wild animals is logistically challenging. We used commercially available, multi-purpose light-level geolocator dataloggers to continuously record light environment and time spent out of water during 5-months (1 May to 9 September 2021) in an ectothermic freshwater turtle species, the northern map turtle (*Graptemys geographica*). We used these data to compare time of year and sex differences in thermoregulatory behavior in an ectothermic species in its natural habitat. We recorded >500 000 data points from 17 individual turtles (nine males and eight females). We found no differences in the mean light levels, or proportion of time spent out of the water, between males and females. However, there was a significant effect of both time of year and sex by time of year interaction in both light level, proportion of time spent dry, and number of state changes (i.e., shuttling behavior, wet to dry or dry to wet), suggesting that turtles alter their aerial basking behavior over the course of the season and that the changes in patterns of aerial basking behavior differ between the sexes throughout the year. In general, the proportion of time spent dry decreased over the active season, with an increase during the last week of June and the first week of July, while the number of state changes increased in females during late May/early June before decreasing, while males remained relatively constant. These changes may reflect the different energetic demands associated with reproduction between the two sexes. The overall downward trend in aerial basking likely reflects the role of increasing environmental temperatures, particularly water temperature, in the maintenance of body temperature in this largely aquatic species.

Introduction

The distribution of an animal's activity throughout the daily cycle is a key feature of behavior with important implications for a wide range of ecological and physiological processes (Daan, 1981; Gallo et al., 2022; Refinetti & Menaker, 1992). Environmental variability has led to species developing diel activity patterns to match behavior to current environmental conditions, reflecting a complex interaction between foraging, mating, resting, basking, predator avoidance, inter- and intra-species competition, and environmental constraints that determine fitness (Halle & Stenseth, 2012; Kronfeld-Schor et al., 2013). Diel activity patterns may shift in response to differences in requirements between sexes (e.g., nesting behavior, egg production, mate guarding, etc.), seasonal variation in environmental conditions, or varying climatic conditions such as temperature (Fraser et al., 1993) and water availability (Lockard, 1978).

In most terrestrial animals, daily activity is regulated by the endogenous circadian clock and a more direct response to available light levels (Sánchez-Vázquez et al., 2019). For example, the relative position of the sun and available light levels have been used to explain the onset of activity in ectothermic lizards (Díaz, 1997), butterflies (Pivnick & McNeil, 1987), and endothermic marmots (Semenov et al., 2001). Ectothermic species such as reptiles behaviorally regulate body temperature within a range that maximizes physiology and performance (i.e., optimum body temperature; Huey & Kingsolver, 1989), but such behavioral thermoregulation can also be energetically costly

(Huey & Slatkin, 1976). While optimum body temperatures allow for increased performance in individuals, energy and time are expended seeking thermoregulatory opportunities, often placing individuals in situations where they may be more visible to predators (Huey & Slatkin, 1976).

In aquatic turtle species, behavioral thermoregulation occurs primarily through aerial basking. Basking in turtles increases digestion and metabolic rates (Bulté & Blouin-Demers, 2010; Moll & Legler, 1971; Polo-Cavia et al., 2012), speeds follicular development and egg production (Carrière et al., 2008; Janzen et al., 2018; Krawchuk & Brooks, 1998), fights infection (Monagas & Gatten Jr., 1983), and helps remove ectoparasites (McKnight et al., 2021). Despite basking being one of the most conspicuous behaviors of turtles and one of the most important diel activities, studies directly quantifying aerial basking behavior are rare.

We used a commercially available, light-level geolocator datalogger (hereafter, datalogger; Intigeo® series geolocator; Migrate Technology Ltd., Cambridge, United Kingdom) to continually record light level and wet/dry state during a 5-month period (May–September) of an aquatic turtle's active season (~April–October). These dataloggers collect individuals' time spent basking out of the water and the intensity of light exposure, which would be prohibitively labor-intensive if direct human observations were required. Originally developed to track migration pathways in birds (Bridge et al., 2013; Shaffer et al., 2005; Streby et al., 2015; Stutchbury et al., 2009), these dataloggers have been used to address a variety of other biological questions. For example, they have been used to evaluate activity patterns in Nearctic mammals (Anders et al., 2017) and compare behavioral plasticity in lizards (Refsnider et al., 2018). Dataloggers are ideal for remote field conditions, are relatively inexpensive (~120–180 USD), waterproof, self-powered, small (12 × 5 × 4 mm to 17 × 19 × 8 mm), and lightweight (0.32 to 3.3 g). They can be affixed directly to a turtle's carapace for periodic data downloads while still attached to the animal, or they can be attached to a radio transmitter affixed to an animal, which allows for easy removal and retrieval.

Here, our objective was to compare the aerial basking behavior of male and female northern map turtles (*Graptemys geographica*) to characterize patterns as they relate to environmental variables. Because males and females differ in energetic demands throughout the active season, we hypothesized that aerial basking patterns would change throughout the year as environmental conditions changed and vary between the sexes as reproductive activities changed. We predicted that both males and females would bask less later in the year as environmental temperatures increased. We also predicted that females would bask more frequently than males, particularly early in the active season, due to the higher energetic costs associated with egg production prior to nesting.

Materials and methods

Study species

We used northern map turtles as a model species as they are widespread inhabitants of rivers, small streams, lakes, and impoundments in the eastern and upper Midwest of North America, from Georgia into Canada. They exhibit pronounced sexual dimorphism, with adult females growing nearly twice the length of males (Fig. 1). Males reach sexual maturity at 3–5 years (Iverson, 1988) while females mature after at least 10 years (Nagle & Congdon, 2016). Both sexes bask daily on deadfall, rocks, banks, at the water surface, or on floating vegetative mats. Adult females travel overland in June to upland nesting habitats, typically on exposed riverbanks (Otten, 2022). Northern map turtles at the study site are generally active from April through October and enter brumation or winter dormancy when air and water temperatures approach 10.0° C (Otten, personal observation). Brumation locations are usually deeper pools or in burrows in the riverbank below the waterline (Crocker et al., 2000; Robichaud et al., 2022).

Study site

We conducted our research in 8.2 km of the Kalamazoo River in Calhoun County, Michigan, USA (Fig. 2). Within the study site, the Kalamazoo River ranges from 9.0–40.0 m wide, 0.2–3.5 m deep, at 255–260 m in elevation, and contains

Figure 1 (a) Light-level geolocator datalogger (and radio transmitter attached to a female northern map turtle (*Graptemys geographica*) with marine epoxy. (b) Typical adult male (left) and female (right) northern map turtle exhibiting sexual dimorphism. (c) Dataloggers (Migrate Tech model C330 [3.3 g]) used in this study, shown from three different angles.

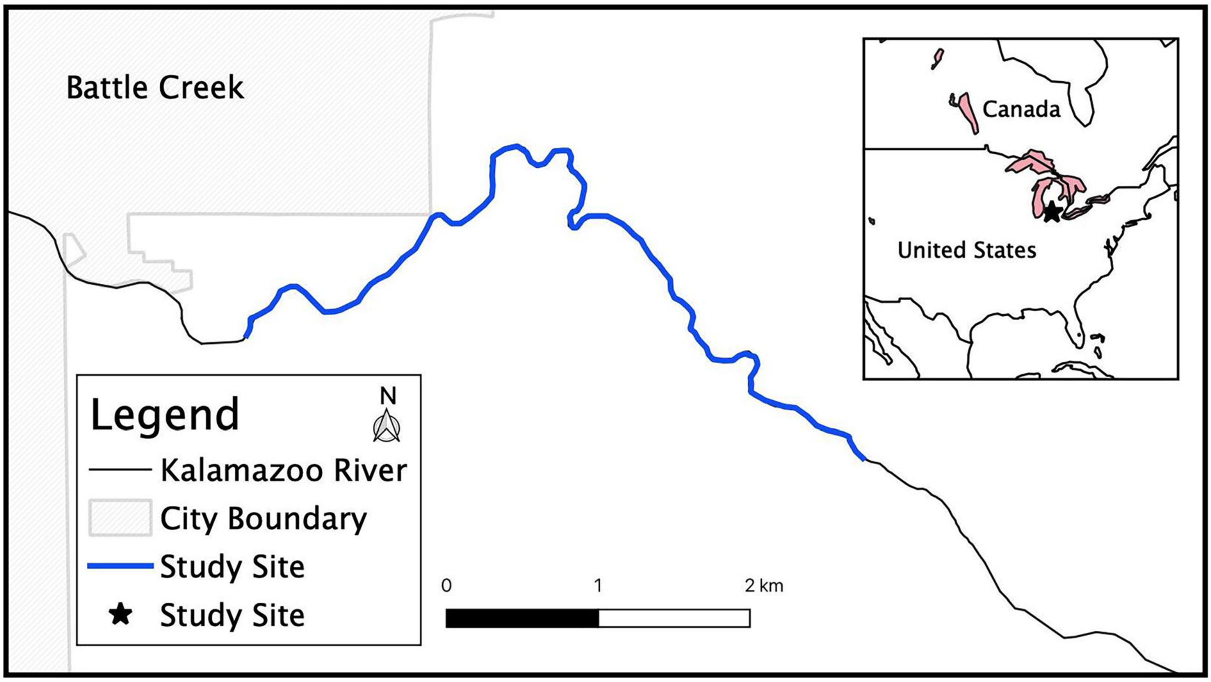

Figure 2 Location of study site where light-level geolocator dataloggers were attached to 10 male and 10 female northern map turtles (*Graptemys geographica*) in 2021. Turtles were captured within an 8.2-km length of the Kalamazoo River in Calhoun County, Michigan, USA.

substantial woody debris and exposed riverbank throughout (Fongers, 2008), providing ample basking structures for northern map turtles to use (Otten et al., 2022).

Data collection

We captured turtles from late April to May 2021, using dipnets from a kayak (Lagler, 1943) or by hand while snorkeling (Marchand, 1945). All turtles were identified by sex using secondary sex characteristics (i.e., cloaca placement in relation to shell, shell length, and tail size), and a unique combination of notches was filed in the marginal scutes for identification (Cagle, 1939). We recorded each turtle's capture location with a handheld GPS unit (Garmin International Inc.) with an accuracy of <3 m. We recorded the straight carapace length (SCL) along the midline with calipers to the nearest mm and mass using a digital scale to the nearest 0.1 g. Only turtles identifiable as adult males (>5 years [>8.5 cm SCL]) with a mass >145 g and adult females (>14 years [>17.5 cm SCL]) were used for datalogger and radio transmitter attachment.

We affixed radio transmitters (Advanced Telemetry Solutions model RI-2B [5 g]) and dataloggers (Migrate Tech model C65 [1.0 g] or C330 [3.3 g]) to 10 female and 10 male northern map turtles with marine epoxy to the posterior costal scutes where they would not impede feeding, swimming, mating, or nesting movements (Fig. 1). The transmitter, datalogger, and epoxy mass never exceeded 5.0% of a turtle's body mass. We held turtles up to 24 h following transmitter attachment to allow epoxy to cure and ensure dataloggers were recording, and turtles were then released at their point of capture. We programmed dataloggers to record the maximum light level measured over a five-min interval and any change in wet/dry state, with total time spent in each state recorded to the nearest 6 s interval. The wet/dry logging mode records whether conductivity between conduct pegs (used for programming and data download) is made through submersion in freshwater. Logging is continuous, with time recorded in a state (i.e., wet or dry) recorded when connection between conducts changes, either no longer connected via freshwater (i.e., dry) or connected via freshwater (wet). Time in a state is recorded in 6 s intervals. Periodically, we relocated turtles using radio telemetry to download data from the dataloggers and check transmitter and datalogger attachment. Transmitters and dataloggers were removed from some turtles before they entered brumation in August and September 2021, and the remaining transmitters and dataloggers were removed from turtles in June 2022.

We calculated environmental conditions from data collected at the nearest National Oceanic and Atmospheric Administration (NOAA) weather station (Battle Creek Executive Airport [KBTL]; 282 m elevation), approximately 32 km from the study site, and the United States Geological Survey river station (USGS 04108660 Kalamazoo River at New Richmond, MI; 180 m elevation), approximately 86 km from the study site. We determined the mean weekly air and water temperatures from daily summary data from 1 May to 9 September 2021.

Data analysis

Data aggregation for individuals with multiple downloads was conducted in Python (version 3.11.1), and the code is available on github (https://github.com/donfbecker/Intigeo-data-logger-parser-and-aggregator). Further data processing and analysis were conducted in R (version 4.2.1). All code is available on github (https://github.com/itclifton/Turtle-Light.git). To minimize bias due to handling turtles, we filtered the data for each individual to begin at sunrise the day following its release, and to conclude at sunset on 9 September 2021. For each individual turtle, we created a "full daytime" dataset by excluding all data recorded between sunset and sunrise throughout the entire recording period using the package "suncalc" in R (version 1.4–4; Thieurmel et al., 2019). We also created a "dry only" dataset for each individual to further parse aerial basking data from activity at the water surface, which could produce high light levels similar to but independent of basking behavior. To do this, we filtered the full daytime data to include only light measurements recorded during the dry state.

To account for potential wet/dry sampling errors that could occur due to rain or water droplets remaining on the datalogger after a turtle emerged from the water, which may keep the connection between the conduct pegs, we considered a state change as one in which the animal had been in the previous state for at least 60 s.

Variation in aerial basking behavior

We calculated the mean daily light level (lux) recorded for each turtle from the "full daytime" dataset (i.e., sunrise to sunset) and the "dry only" dataset. We also calculated the proportion of time each turtle spent dry each day (i.e., sum of dry state recordings/sum total of wet and dry states logged each day during daylight hours). Finally, we calculated the total daily number of state changes (i.e., wet to dry and vice versa) for each individual to estimate shuttling behavior from the "full daytime" dataset. We compared the mean daily light level, proportion of time spent dry, and mean number of state changes between the two sexes throughout the active season using linear mixed effects models with sex, week, and their interaction as fixed effects and individual identity as a random effect to account for repeated measures.

Results

We recovered dataloggers from 17 of the 20 northern map turtles (nine males, eight females). Data from one male and two females were not obtained, as these individuals could never be relocated through radio telemetry, likely due to leaving the study area or radio transmitter failure. The size of male turtles with dataloggers recovered ranged from 10.6 to 12.7 cm SCL ($\bar{x} = 11.5 \pm 0.7$ SD) with a mass ranging from 145 to 215 g ($\bar{x} = 172.7 \pm 22.9$ SD). The size of female turtles with dataloggers recovered ranged from 21.2 to 25.1 cm SCL ($\bar{x} = 23.3 \pm 1.2$ SD), with a mass ranging from 1254 to 2032 g ($\bar{x} = 1621.5 \pm 281.2$ SD).

From 1 May to 9 September 2021, we obtained 553 946 light-level data points, 313 473 of which were obtained during daylight hours. We also obtained 13 246 wet/dry state changes, which indicate shuttling behavior (e.g., wet to dry or dry to wet with a duration of >1 min). A summary of the datalogger recording duration and total data points recorded can be found in Table S1. The length of time dataloggers recorded varied across individuals, as some turtles could not be re-located due to radio transmitters falling off, loss of radio transmitter signal, or failure of dataloggers (i.e., the datalogger of one male stopped recording partway through the study). Dataloggers recorded data for 111.9 days (±6.6), ranging from 43 to 132 days.

Variation in aerial basking behavior

We found no differences in the mean light level or proportion of time spent dry between males and females during daylight hours (Table 1). We also observed no differences in the mean light levels recorded between males and females in the dry state (Table 1). However, for both metrics during both daylight hours and in the dry state, we found a significant effect of both week and the interaction between sex and week (Table 1; Fig. 3). That is, aerial basking behavior as measured by light level and time spent dry changed over the course of the active season, and those changes were not necessarily the same in both sexes. In July and August, the proportion of time spent in the dry state was nearly identical between sexes, but light levels were significantly higher for females (Figs 3 and 4).

We found no difference in the number of state changes (shuttling behavior) between males and females (Table 1). However, we found a significant effect of both week and the interaction between sex and week (Table 1; Fig. 4), changing over the course of the active season but not necessarily the same in both sexes. Northern map turtles changed state an average of 6.95 (±0.13 SD) times daily. This would equate to nearly 3.5 times an animal exhibited the following scenario in one day going from in the water to out of the water to bask, and then back in the water. Individual daily shuttling varied, with males ranging from 2.14 (±0.25) to 10.14 (±0.95) state changes and females ranging from 5.48 (±0.31) to 8.93 (±0.82).

Discussion

While previous ectotherm thermoregulatory studies have developed quantifiable indices to determine behavior (e.g., Edwards & Blouin-Demers, 2007; Paget et al., 2023; Picard et al., 2011), to our knowledge, this is the first study to utilize light-level dataloggers to continuously record light level and wet/dry state to estimate aerial basking and shuttling behavior in a wild turtle species. As we predicted, there was an overall downward trend in aerial basking activity throughout the season, such that individuals of both sexes spent the most time dry and experienced the highest light levels in May, and these parameters gradually decreased weekly, likely the result of increasing air and water temperatures leading into fall brumation (Fig. 4). While we found no differences between northern map turtle sexes in time employed in aerial basking, we found evidence of a significant interaction between these parameters and week, supporting our prediction that aerial basking behavior would vary between the two sexes throughout the active season and suggesting that while males and females spend a similar amount of time basking, there were alternating periods when individuals of one sex basked more than individuals of

Table 1 Statistical summary of northern map turtle (*Graptemys geographica*) basking metrics we compared in the full daytime dataset (i.e., every light level measured during daytime hours throughout the active season and the daily proportion of time spent dry) and dry only dataset (i.e., only the light level measurements recorded when the dataloggers were dry)

		Sex			Week			Sex*Week		
Metric	Mean ± SE	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Full daytime										
Mean light	18.2 ± 0.3	1, 15.67	2.64	0.12	19, 1851.91	48.61	<**0.001**	19, 1851.91	4.18	<**0.001**
Proportion dry	0.33 ± 0.005	1, 15.35	0.073	0.79	19, 1851.07	23.61	<**0.001**	19, 1851.07	4.33	<**0.001**
State changes	6.95 ± 0.13	1, 16.20	0.715	0.410	19, 1854.90	10.17	<**0.001**	19, 1854.9	6.83	<**0.001**
Dry only										
Mean light	39.4 ± 0.5	1, 15.27	3.41	0.084	19, 1693.97	35.34	<**0.001**	19, 1693.97	4.66	<**0.001**

The mean light levels are presented in kilolux (klx). Proportion dry is the proportion of daytime hours in which turtles spend basking out of the water. State changes refer to the number of times a turtle changed state (i.e., wet to dry or dry to wet). Bolded *P*-values indicate statistical significance at a significance level of $\alpha = 0.05$.

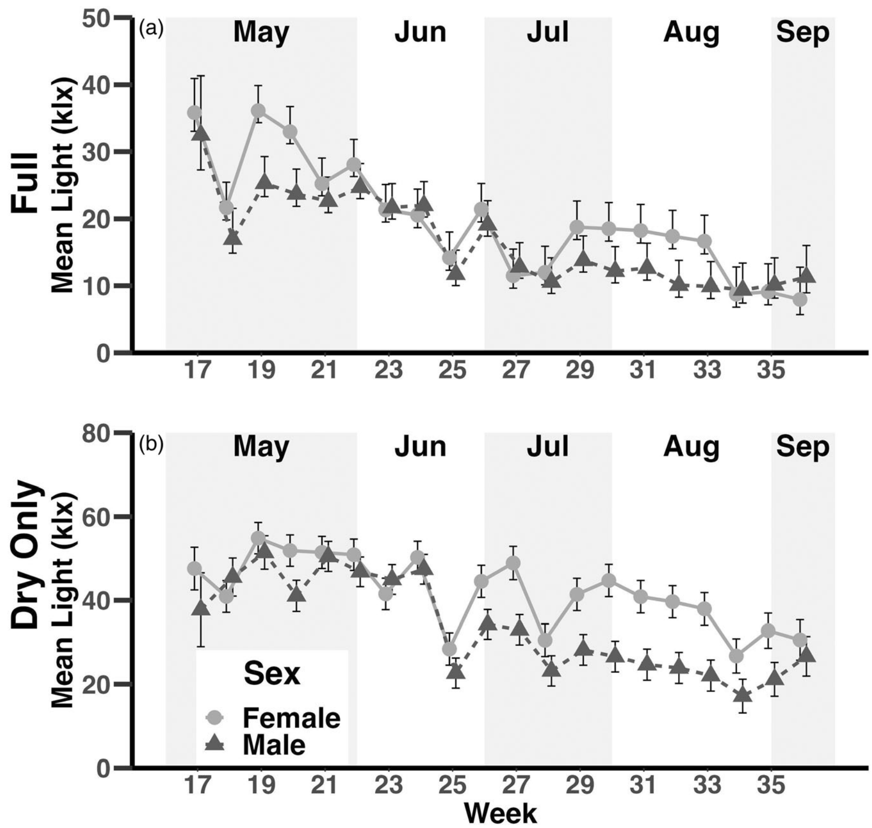

Figure 3 Weekly mean light levels recorded by light-level geolocator dataloggers on male and female northern map turtles (*Graptemys geographica*) during the 2021 active season using the full daytime dataset (a) and the measurements taken only during periods when the turtles were outside of the water (i.e., dry; b). All light levels are presented in kilolux (klx).

the other sex (Figs 3 and 4). However, contrary to our expectations, females appear to bask more than males later in the season and after nesting (late June).

The significant week effect and interaction between sex and week we observed suggests that northern map turtles alter their aerial basking behavior over the course of the active season and that these temporal changes in aerial basking behavior differ between the sexes. Sex-specific changes in aerial basking may reflect intersexual differences in life history demands throughout the season, as previous studies have indicated that basking in turtles' functions to enhance follicle development and egg production in females (Carrière et al., 2008; Janzen et al., 2018; Krawchuk & Brooks, 1998). Interestingly, although both sexes spent nearly double the time basking in late June (coinciding

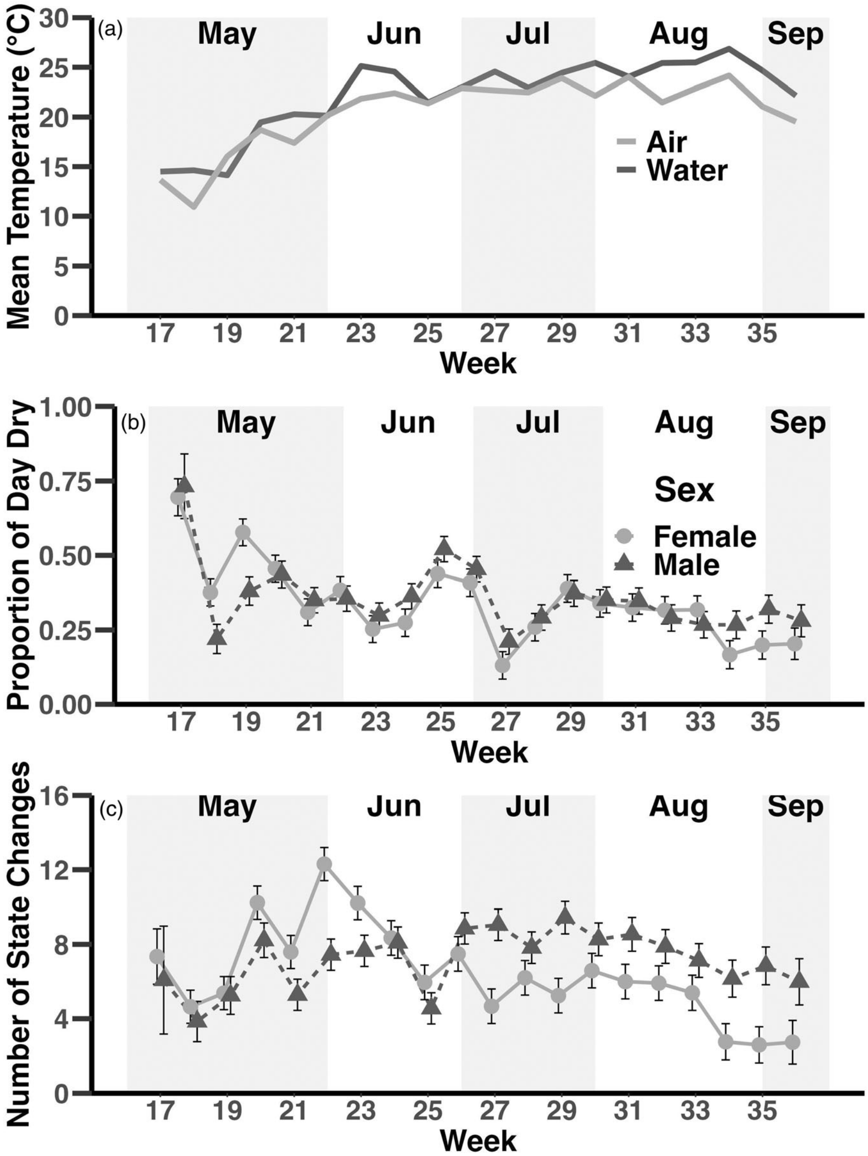

Figure 4 (a) Mean weekly air and water temperatures of the Kalamazoo River derived from daily summary data retrieved from the National Oceanic and Atmospheric Administration (NOAA) weather station (Battle Creek Executive Airport [KBTL]) and the United States Geological Survey river station (USGS 04108660 Kalamazoo River at New Richmond, MI) across the 2021 active season. (b) Weekly mean proportion of time male and female northern map turtles (*Graptemys geographica*) spent in the dry state (i.e., out of the water) during daylight hours of the 2021 active season. (c) Average number of state changes (i.e., shuttling, from wet to dry, or dry to wet) for male and female northern map turtles across the 2021 active season.

with the observed nesting period in this population) compared to late May and early June, the changes in time spent dry and in light levels between late May and late June were nearly identical for both sexes, suggesting that these temporal shifts in aerial basking behavior may not necessarily be related to egg production in females. Similar results for seasonality of aerial basking behavior have been observed in a different population of northern map turtles (Bulté & Blouin-Demers, 2010), as well as northern populations of painted turtles (*Chrysemys picta*; Edwards & Blouin-Demers, 2007). These results may be more a reflection of light availability and differences in lux strength due to changes in seasons.

Seasonality behavioral comparisons in turtle populations typically focus on timing of life events (i.e., post-brumation, pre-nesting, post-nesting, and pre-brumation) rather than seasons of the year (i.e., spring, summer, fall, and winter; Haxton & Berrill, 2001; James et al., 2005; Walde et al., 2007). Due to constraints in the current study, we were able to collect data on a full active season from only four individuals (two male and two female), which limited data from the pre- and post-brumation seasons. Therefore, the analysis focused on weekly comparisons rather than seasonal differences. In addition, females in this population have been found to nest throughout the month of June, with some individuals double-clutching, creating difficulty in assigning a pre- and post-nesting season (Otten, 2022; Otten & Refsnider, 2024). However, using dataloggers from this study would allow for seasonal behavioral comparisons in wildlife studies in which clearly defined seasons exist. Furthermore, we found that this type of datalogger could also be used as a low-cost, low-effort method to determine approximate dates and times at which turtles enter and exit brumation. Using the first and last time an individual exited and entered the water for the year could be used as a quantifiable metric for brumation.

Our data suggest that female northern map turtles seek out high-light environments later in the active season compared to males. This suggests that regardless of whether they were in or out of the water, females were in higher-light environments than males. This may be due to differences in size between the sexes and the resulting potential predation risk, as adult female northern map turtles have few natural predators within the study site compared to males (Otten, 2022). Aerial basking in less conspicuous locations (lower-light environments) in males may be the way of seeking spots less visible to predators compared to the larger females. This also coincides with what we found during the last week of August and first week of September males spent more time in the dry state (i.e., out of the water) than females, but females were recorded in higher-light environments. We also found that females shuttled significantly less than males during this time. This proclivity toward more intense aerial basking conditions in females later in the season may reflect their higher energetic demands due to egg production and nesting, potential differences in diet (i.e., males feed primarily on small gastropods while females feed on pleurocerid snails; Richards-Dimitrie et al., 2013), or energy requirement differences due to sexual dimorphism in the species. Alternatively, males may bask at times of the day when solar radiation is weaker, which could explain why males apparently use lower-light environments than females. Because male map turtles are substantially smaller than females, they may warm faster than females and may be better able to increase body temperature even in low-light environments, which could be beneficial by reducing the energetic needs of shuttling behavior. However, while we found no overall difference in shuttling behavior between sexes, females shuttled more often than males prior to the nesting season (late June), and males shuttled more often than females after the nesting season.

Further studies could be conducted to compare aerial basking behavior recorded from dataloggers to body temperature and observed basking behavior. For example, additional dataloggers or ibutton temperature loggers could be attached to record shell temperature, allowing for correlational comparisons between light level, basking time, and turtle body temperature. This may help explain differences in basking time and light level between weeks and sexes. Observational studies locating basking structures used by turtles may help determine if there are preferences in basking locations and structures, which could result in differences in light level and basking times recorded in the current study. We often observed adult males basking on deadfall near the shore, slightly wider than their shells, while females were typically found in deeper water locations further from the bank on deadfall that was typically large, downed trees. Near-shore locations could be shaded during a larger portion of the days compared to those open-water areas. Investigating differences in basking structure location and light level available at these locations (i.e., control dataloggers) would provide further insight into basking behavior variability.

Although outside of the scope of this study, we found that by using dataloggers to continuously record thermoregulatory behavior, we were able to compare diel activity patterns and detect unusual behavior. For example, the highest proportion of time spent out of the water occurred between 10:00 and 13:00. In addition, we detected more than half of the individuals (seven females and three males) leaving the water during the night, with some turtles remaining out of the water all night and others for only a few minutes. Such nocturnal "basking" has only recently been described in turtles (Barhadiya et al., 2020; Nordberg & McKnight, 2020), but it is unclear what drives aquatic turtles to make these moves (Toms et al., 2022). The dataloggers used in this study are likely an ideal method for studying this poorly understood behavior and may provide new insight into the drivers of this behavior, as they provide 24 hr/day datalogging capabilities for 12–36 months (depending on model of unit).

Adequate aerial basking opportunities are critical for maintaining and maximizing physiological function in many ectothermic species, including numerous aquatic turtle species (Huey, 1977; Picard et al., 2011; Shine & Madsen, 1996). However, this behavior can be both ecologically costly (e.g., increasing predation risk; Huey & Slatkin, 1976; Gregory et al., 1999) and physiologically costly (e.g., increased energetic demands from shuttling; Brewster et al., 2013). By continuously recording individual basking behavior, we were able to compare intersexual trends in basking activity related to different reproductive demands between the two sexes. We were also able to evaluate daily and weekly trends in aerial basking activity, likely related to changing temperatures and shifts in energetic demands. Here, we show that aerial basking in northern map turtles on the Kalamazoo River declines throughout the active season as environmental temperatures increase. We also provide evidence of sexually divergent aerial basking patterns across the active season. Future research should focus on parsing the underlying mechanisms that drive these divergent patterns. While the divergent patterns are likely related to temporal shifts in reproductive demands, it remains unclear precisely how changes in energetic demands affect basking in free-ranging species.

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Conflict of interest

The authors declare no competing interests.

Author contributions

J.G.O. and I.T.C. are considered co-first authors, equally conceiving the idea, designing methodology, and conducting all fieldwork and data collection. I.T.C. and D.F.B. compiled data. I.T.C. analyzed the data and created figs. J.G.O. received funding to purchase dataloggers. J.G.O. led the writing of the manuscript. All authors contributed critically and approved the publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of data collected from the retrieved light-level geolocator dataloggers for 17 individual northern map turtles (*Graptemys geographica*) from the Kalamazoo River, Calhoun County, Michigan, USA. SCL represents straight carapace length measured at first capture. The collection period represents the dates encompassing data collection for each individual. Light data points were recorded every 5 min, and state changes occurred every time a turtle changed from wet to dry or dry to wet for >60 s.