



# Factors affecting temperature variation and habitat use in free-ranging diamondback terrapins



C.D. Akins<sup>a</sup>, C.D. Ruder<sup>a</sup>, S.J. Price<sup>b</sup>, L.A. Harden<sup>a,\*</sup>, J.W. Gibbons<sup>c</sup>, M.E. Dorcas<sup>a</sup>

<sup>a</sup> Department of Biology, Davidson College, Davidson, NC 28035, USA

<sup>b</sup> Department of Forestry, University of Kentucky, Lexington, KY 40546, USA

<sup>c</sup> Savannah River Ecology Laboratory, University of Georgia, Aiken, SC 29802, USA

## ARTICLE INFO

### Article history:

Received 4 April 2014

Received in revised form

25 June 2014

Accepted 30 June 2014

Available online 4 July 2014

### Keywords:

Temperature

Semi-aquatic turtle

Habitat use

Datalogger

Estuarine

Diamondback terrapin

## ABSTRACT

Measuring the thermal conditions of aquatic reptiles with temperature dataloggers is a cost-effective way to study their behavior and habitat use. Temperature dataloggers are a particularly useful and informative approach to studying organisms such as the estuarine diamondback terrapin (*Malaclemys terrapin*) that inhabits a dynamic environment often inaccessible to researchers. We used carapace-mounted dataloggers to measure hourly carapace temperature ( $T_c$ ) of free-ranging terrapins in South Carolina from October 2007 to 2008 to examine the effects of month, sex, creek site, and tide on  $T_c$  and to determine the effects of month, sex, and time of day on terrapin basking frequency. Simultaneous measurements of environmental temperatures ( $T_e$ ; shallow mud, deep mud, water) allowed us to make inferences about terrapin microhabitat use. Terrapin  $T_c$  differed significantly among months and creek and between sexes. Terrapin microhabitat use also varied monthly, with shallow mud temperature being the best predictor of  $T_c$  November–March and water temperature being the best predictor of  $T_c$  April–October. Terrapins basked most frequently in spring and fall and males basked more frequently than females. Our study contributes to a fuller understanding of terrapin thermal biology and provides support for using dataloggers to investigate behavior and habitat use of aquatic ectotherms inhabiting dynamic environments.

© 2014 Elsevier Ltd. All rights reserved.

## 1. Introduction

Changes in temperature have profound effects on the rates of many physiological processes, particularly those of ectotherms whose body temperatures ( $T_b$ ) are directly influenced by temperatures of their environment ( $T_e$ ; [Beitinger and Fitzpatrick, 1979](#); [Huey, 1982](#); [Fitzgerald and Nelson, 2011](#)). Ectotherms produce little metabolic heat, and must employ thermoregulatory behaviors such as basking and microhabitat selection to promote optimal physiological performance for locomotion, energy acquisition, reproduction, and other processes ([Stevenson, 1985](#); [Rowe and Dalgarn, 2009](#); [Bulte and Blouin-Demers, 2010](#)). Semi-aquatic ectotherms (e.g. many reptiles) rely on a combination of solar radiation and available  $T_e$ , such as water and substrate temperature, to regulate  $T_b$ . The effectiveness of a particular environment for thermoregulation may change seasonally, daily, or even hourly depending on specific properties of the microhabitats ([Heatwole and Taylor, 1987](#)). Thus, examining  $T_e$  in conjunction with temperatures of free-ranging, semi-aquatic reptiles is critical to

understanding the nuances of individual thermal variation, and may provide insights into behaviors (e.g. basking, burrowing, swimming) and habitat use ([Peterson et al., 1993](#)).

The semi-aquatic diamondback terrapin (*Malaclemys terrapin*) provides a reptilian model for investigating thermal variation and temperature-inferred habitat use because of the dynamic coastal ecosystem in which it lives. Terrapins inhabit salt marsh estuaries along the Eastern and Gulf coasts of the United States and they experience the dramatic variations in environmental factors associated with tidal and seasonal fluctuations (e.g., temperature, water level, salinity and oxygen availability; [Ernst and Lovich, 2009](#); [Largier, 2010](#)). Salinity can change from nearly fresh to nearly marine within a single tidal cycle ([NOAA, 2005](#)) and tidal amplitude can be up to two meters ([Kana et al., 1984](#)). Furthermore, water temperatures within many coastal estuaries can range from near freezing to above 30 °C ([Dame et al., 2000](#)), depending on the season and latitude. Terrapins also experience dramatic temperature fluctuations as a result of season or time of day. [Williard and Harden \(2011\)](#) documented terrapins experiencing 7 °C summer temperature variations and 9 °C winter temperature variations (including sub-zero temperatures), both within 24-h time periods.

\* Corresponding author. Tel.: +1 704 894 3096.

E-mail address: [leharden@davidson.edu](mailto:leharden@davidson.edu) (L.A. Harden).

Environmental fluctuations within estuaries likely have strong effects on terrapin  $T_b$  and various physiological processes, and may result in subsequent changes in habitat use. Previous studies have investigated thermal biology and habitat use of other semi-aquatic turtles by recording  $T_b$  or  $T_c$  (carapace temperature) and  $T_e$  with microdataloggers (Grayson and Dorcas, 2004; Harden et al., 2007; Dubois et al., 2009; Pittman and Dorcas, 2009; Rowe and Dalgarn, 2009; Bulte and Blouin-Demers, 2010), however, few studies have used this affordable and remote monitoring technique to measure thermal variation and assess temperature-inferred habitat use of diamondback terrapins in their uniquely dynamic environment (but see Harden et al. (2007) and Williard and Harden (2011)). We used temperature microdataloggers to measure environmental temperatures ( $T_e$ ; water, deep mud, shallow mud) and terrapin carapace temperatures ( $T_c$ , used as a proxy for  $T_b$ , see Section 2.4 for more detail) for 1 year in two salt marsh tidal creeks to address the following study objectives: 1) investigate the effects of month, sex, creek site, and tide level on terrapin  $T_c$ , 2) evaluate the relationships between  $T_e$  and  $T_c$  to infer seasonal variation in habitat use, and 3) examine the effects of month, sex, and time of day on basking behavior.

## 2. Materials and methods

### 2.1. Study area

This study was conducted in conjunction with long-term mark-recapture sampling of terrapins, initiated in 1983 (Lovich and Gibbons, 1990). We executed this study in two tidal creek tributaries, known as Fiddler creek and Oyster creek, of the Kiawah River adjacent to Kiawah Island, Charleston County, South Carolina, USA. Both tidal creeks were bordered by salt marsh dominated by *Spartina alterniflora* (for more information on the study site see Materials and Methods of Dorcas et al. (2007) and citations within).

### 2.2. Turtle capture and datalogger attachment

During 2007 and 2008, we captured terrapins using trammel nets and seines, primarily during low tides (Lovich and Gibbons, 1990) within the two aforementioned tributaries. Upon capture, any unmarked terrapins were uniquely marked by filing notches into their marginal scutes (Sexton, 1959). Measurements taken on each turtle included straight-line carapace length (SCL), plastron length, width, depth and mass (Tucker et al., 2001). Body mass was measured to the nearest gram using a digital scale. We determined sex via tail length and other secondary sex characteristics (Dorcas et al., 2007). All terrapins were returned to their location of capture within three days.

Prior to release, we attached temperature microdataloggers (iButton Thermochrons, Dallas Semiconductor, Dallas, TX; accuracy  $\pm 0.5$  °C; Grayson and Dorcas, 2004; Pittman and Dorcas, 2009) to the posterior carapace of each terrapin using marine-grade epoxy (Loctite Five Minute Marine Grade Epoxy, Avon, OH). We selected individuals for datalogger attachment based on previous capture frequency, which we believed would increase the probability of retrieving the dataloggers at the next sampling period. Before attachment, dataloggers were programmed following the protocols of Grayson and Dorcas (2004) to record  $T_c$  at 60-min intervals and were then covered in plastic tool dip (Plasti-Dip International, Circle Pines, MN) to prevent water damage. The amount of epoxy used for attachment was limited to reduce the weight carried by the turtle ( $\leq 6\%$  of the smallest turtle's mass). Previous investigations have shown that carapace temperature is strongly correlated with body temperature (Grayson and Dorcas,

2004; Chen and Lue, 2008). However, we did not directly compare body temperature and carapace temperature of terrapins in this study. Consequently, carapace temperatures may differ slightly from actual body temperature, especially during basking. Dataloggers recorded temperatures hourly from 16 October 2007 through 12 October 2008 with the exception of 17–23 May 2008 while they were being replaced. Overall, we recovered dataloggers and were able to evaluate  $T_c$  from 17 individual terrapins (males=12, females=5) during 2007 and 2008, although the duration of data collection varied among individual terrapins: 16 Oct. 2007–17 May 2008 ( $n=4$ ), 16 Oct. 2007–29 May 2008 ( $n=5$ ), 16 Oct. 2007–15 Sept. 2008 ( $n=2$ ), 12 May 2008–10 Oct. 2008 ( $n=4$ ), and 28 June 2008–12 Oct. 2008 ( $n=2$ ).

### 2.3. Environmental data collection

We measured environmental temperatures ( $T_e$ ) by placing the same model of microdataloggers used to measure  $T_c$  in each of three possible microhabitats used by terrapins: water (15 cm below the water surface;  $n=2$ ), shallow mud (10 cm mud depth;  $n=2$ ) and deep mud (45 cm mud depth;  $n=2$ ). The water habitat microdatalogger was secured 15 cm below a buoy tied to a rope and weighted by a small anchor. The two mud habitat microdataloggers were secured to a wooden stake using duct tape at the two designated mud depths (10 and 45 cm) and placed in the intertidal creekbank marsh of their respective creek site. One water datalogger and one wooden stake with two mud dataloggers were deployed at each field site, Fiddler and Oyster creek. Because tide level may influence both  $T_e$  and  $T_c$ , we obtained 2007–2008 tide information from a National Oceanic and Atmospheric Administration tidal station  $\sim 45$  km from Kiawah Island in Charleston, SC (NOAA National Data Buoy Center, Station CHTS1-8665530).

### 2.4. Data analysis

To evaluate the effects of month ( $n=12$ ), sex ( $n=2$ ), and creek ( $n=2$ ) on terrapin  $T_c$ , we performed a generalized linear model (GLM; SAS v. 9.2). To avoid auto-correlation among our  $T_c$  data, we randomly selected 30 daytime time-stamped  $T_c$  (decided by examining the average time of sunrise and set within each month) from both tidal creeks for each week, resulting in a total of 1560 data points over the course of the year-long study. To evaluate the effects of tide level (low, high;  $n=2$ ) on male and female terrapin  $T_c$ , we matched the available tide data to our time-stamped  $T_c$  data in order to identify the time points closest to both high and low tides for each day. Because each high or low tide time point was roughly 12 h removed from the previous tide time point, auto-correlation within this dataset was not an issue. Prior to analysis, all  $T_c$  data were separated by sex and log transformed to conform to the assumptions of parametric statistical analysis and then analyzed using a GLM to examine month, sex, creek, and tide as predictors of terrapin  $T_c$ . Significance of these independent variables was assessed using an  $\alpha=0.05$ . Finally, we used a Duncan's multiple-range test to investigate significant differences in mean terrapin  $T_c$  among our independent variables, which allowed us to determine if monthly differences in mean  $T_c$  differed, and whether mean  $T_c$  was different between sites, between sexes, and between high and low tide.

To evaluate the relationships between  $T_e$  and  $T_c$  and infer monthly habitat use, we used a corresponding subset of 30 weekly, daytime, time-stamped  $T_c$  from both tidal creeks and corresponding  $T_e$  (water, shallow mud, deep mud). All  $T_c$  and  $T_e$  data were log transformed to conform to the assumptions of parametric statistical analysis. We used linear regression to assess the effectiveness of each environmental predictor on terrapin  $T_c$ . We used an

information-theoretic approach to compare three models (water, shallow mud, deep mud) for each month and distinguished among competing models with Akaike's Information Criterion, corrected for small sample size ( $AIC_c$ ), and corresponding  $AIC_c$  weights (Burnham and Anderson, 2002).

To examine the effects of month and sex on basking frequency we used our full dataset and compared each terrapin's  $T_c$  at each recorded daytime time point to the warmest available  $T_e$  for that point. We inferred basking if  $T_c$  was recorded at 5 °C above  $T_e$  (Grayson and Dorcas, 2004). This basking criterion was established by Grayson and Dorcas (2004) because it was the smallest value that accounted for variation within  $T_e$  at a given time, where recorded  $T_c$  could not have been obtained by the turtle changing its habitat. Although this criterion likely results in an underestimation of basking events, the estimation will be uniform over time among terrapins and allowed us to infer and compare basking behavioral trends spatially and temporally. We used logistic regression and an information-theoretic approach to determine the probability of basking, with potential predictors being month, sex, time of day, month\*sex, month\*time of day, sex\*time of day, and month\*sex\*time of day.

### 3. Results

Mass for female terrapins used in our analysis ranged from 1073 to 1236 g (mean =  $1163 \pm 65$  g,  $n=5$ ) and SCL ranged from 186 to 202 mm (mean =  $191 \pm 6.3$  mm). Mass for male terrapins used in our analysis ranged from 228 to 334 g (mean =  $285 \pm 37$  g,  $n=12$ ) and SCL ranged from 111 to 133 mm (mean =  $123 \pm 6.0$  mm). Water temperature ranged from 3.7 to 34.1 °C (SD = 6.92,  $n=8538$ ), shallow mud temperature ranged from 3.3 to 32.3 °C (SD = 6.71,  $n=8538$ ), and deep mud temperature ranged from 12.4 to 31.1 °C (SD = 4.88,  $n=8538$ ). All three microhabitats followed similar temperature profiles, with deep mud fluctuating to a lesser degree.

We found considerable variation in terrapin  $T_c$  among months ( $F=677.43$ ,  $df=11$ ;  $p<0.001$ ), between sexes ( $F=36.82$ ,  $df=1$ ;  $p<0.001$ ), and creeks (GLM;  $F=5.77$ ;  $df=1$ ;  $p=0.02$ ), though mean  $T_c$  between sexes (males =  $21.1 \text{ °C} \pm 0.23$ , females =  $21.9 \text{ °C} \pm 0.30$ ) and creeks (Oyster =  $21.3 \text{ °C} \pm 0.26$ , Fiddler =  $21.5 \text{ °C} \pm 0.26$ ) were similar. Mean  $T_c$  differed among months, with the exception of the summer months (June–August), which did not differ from one another, and November and March, which also did

not differ (Fig. 1). Finally, we found no difference in mean  $T_c$  between high and low tides (GLM;  $F=0.43$ ,  $df=1$ ;  $p=0.51$ ).

The best  $T_e$  predictor for  $T_c$  varied seasonally and among microhabitats. Specifically, from November to March,  $T_e$  of shallow mud was the best-supported predictor of terrapin  $T_c$  ( $AIC w_i \geq 0.97$ ), whereas from April to October,  $T_e$  of the water was the best predictor of  $T_c$  ( $AIC w_i \geq 0.92$ ), with the exception of June when  $T_e$  of the shallow mud was the best predictor of terrapin  $T_c$  ( $AIC w_i \geq 0.99$ , Table 1). We found no support for terrapin  $T_c$  to be predicted by  $T_e$  of the deep mud.

To investigate their relationship with relative basking probability, sex, month, time of day, and each combination thereof were examined as predictors of relative basking probability. We detected 650 basking events throughout our study from all 17 terrapins. We found that the model that included sex and month best predicted relative basking probability ( $AIC w_i=0.69$ ), followed by the model that included sex, month, and time of day ( $w_i=0.31$ , Table 2). Across all months, males had a higher mean basking probability than females. We found that the probability of basking for both sexes was greatest during early spring (March–May), with April exhibiting the highest probability of basking for both males (0.038) and females (0.033). Compared to spring, both male and female terrapins had a relatively lower mean probability of basking ( $\leq 0.020$ ) during summer (June–August) and fall months (September–November). The winter months (December–February) had the lowest relative basking probability for both sexes (0.001, Fig. 2).

### 4. Discussion

Our results suggest that, like many ectotherms, terrapins are subject to environmental factors including surface, substrate and water temperatures, and rely on behavioral adaptations to thermoregulate (Helmuth et al., 2006). We observed that terrapin  $T_c$  closely followed  $T_e$  fluctuations throughout the year. By comparing  $T_c$  with available  $T_e$  we inferred a shift in microhabitat selection across the year, from shallow mud (November–March) to open water (April–October, with the exception of June). Additionally, in examining basking probabilities we found evidence that terrapins bask most frequently in the spring and fall months, and that adult males may bask more frequently than adult females. Finally, we found no evidence to support the idea that daily tidal fluctuations have an effect on terrapin basking or thermoregulatory behavior.

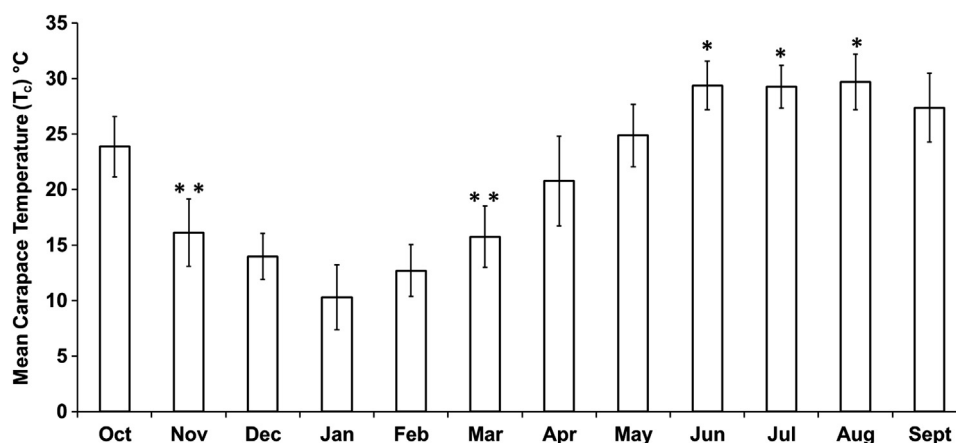


Fig. 1. Average  $T_c$  by month through one calendar year  $\pm$  SD. A warming trend is seen through the spring and summer months, followed by a cool down in late fall and early winter. Columns with matching numbers of asterisks were shown to be similar by a Duncan's Grouping.

**Table 1**  
Monthly microhabitat use inferred by using environmental temperatures ( $T_e$ ) as predictors of terrapin carapace temperature ( $T_c$ ). A generalized linear model and  $AIC_c$  inference was used to determine candidate microhabitat models that best predicted  $T_c$ , and thus, terrapin habitat use. The best supported predictor microhabitat model for each month is in bold. Number of parameters ( $K$ )=2 for every model.

Month	Microhabitat model ( $T_e$ )	$AIC_c$	$\Delta AIC_c$	Akaike weight ( $w_i$ )
October	<b>Water</b>	<b>-696.92</b>	<b>0.000</b>	<b>1.00</b>
	Deep mud	-539.72	157.207	0.00
	Shallow mud	-615.39	81.537	0.00
November	Water	-568.80	51.753	0.00
	Deep mud	-481.17	139.385	0.00
	<b>Shallow mud</b>	<b>-620.55</b>	<b>0.000</b>	<b>1.00</b>
December	Water	-611.90	70.112	0.00
	Deep mud	-477.19	204.819	0.00
	<b>Shallow mud</b>	<b>-682.01</b>	<b>0.000</b>	<b>1.00</b>
January	Water	-434.54	52.184	0.00
	Deep mud	-291.75	194.979	0.00
	<b>Shallow mud</b>	<b>-486.73</b>	<b>0.000</b>	<b>1.00</b>
February	Water	-596.97	6.678	0.03
	Deep mud	-436.84	166.808	0.00
	<b>Shallow mud</b>	<b>-603.65</b>	<b>0.000</b>	<b>0.97</b>
March	Water	-521.37	21.208	0.00
	Deep mud	-440.10	102.490	0.00
	<b>Shallow mud</b>	<b>-542.57</b>	<b>0.000</b>	<b>1.00</b>
April	<b>Water</b>	<b>-564.38</b>	<b>0.000</b>	<b>0.92</b>
	Deep mud	-535.16	129.218	0.00
	Shallow mud	-559.61	4.770	0.08
May	<b>Water</b>	<b>-742.99</b>	<b>0.000</b>	<b>0.99</b>
	Deep mud	-625.10	117.893	0.00
	Shallow mud	-734.01	8.983	0.01
June	Water	-733.52	9.509	0.01
	Deep mud	-661.35	81.676	0.00
	<b>Shallow mud</b>	<b>-743.02</b>	<b>0.000</b>	<b>0.99</b>
July	<b>Water</b>	<b>-811.55</b>	<b>0.000</b>	<b>1.00</b>
	Deep mud	-740.23	71.316	0.00
	Shallow mud	-778.86	32.686	0.00
August	<b>Water</b>	<b>-723.47</b>	<b>0.000</b>	<b>1.00</b>
	Deep mud	-646.83	76.641	0.00
	Shallow mud	-682.69	40.772	0.00
September	<b>Water</b>	<b>-719.82</b>	<b>0.000</b>	<b>1.00</b>
	Deep mud	-582.50	137.316	0.00
	Shallow mud	-687.58	32.238	0.00

**Table 2**  
Predictive power of month, sex, time of day, and combinations thereof on relative basking probability.  $AIC_c$  inference was used to determine which models best predicted relative basking probability. The best supported predictor models are in bold.

Model	$K$ (# of parameters)	$AIC_c$	$\Delta AIC_c$	Akaike weight ( $w_i$ )
<b>Sex and month</b>	<b>3</b>	<b>6337.02</b>	<b>0.00</b>	<b>0.69</b>
<b>Sex, month, and time of day</b>	<b>4</b>	<b>6338.59</b>	<b>1.56</b>	<b>0.31</b>
Sex and time of day	3	6845.89	508.86	0.00
Month and time of day	3	6384.92	47.89	0.00
Sex	2	6843.43	506.40	0.00
Month	2	6383.65	46.62	0.00
Time of day	2	6891.73	554.69	0.00

Previous studies of thermal biology of freshwater turtles have also shown a strong correlation between turtle temperature and  $T_e$ . For example, Grayson and Dorcas (2004) noted that  $T_b$  (measured as  $T_c$ ) of eastern painted turtles (*Chrysemys picta*) was correlated with  $T_e$  and Rowe and Dalgarn (2009) showed that *C. picta* behaviors correspond with daily fluctuations in ambient

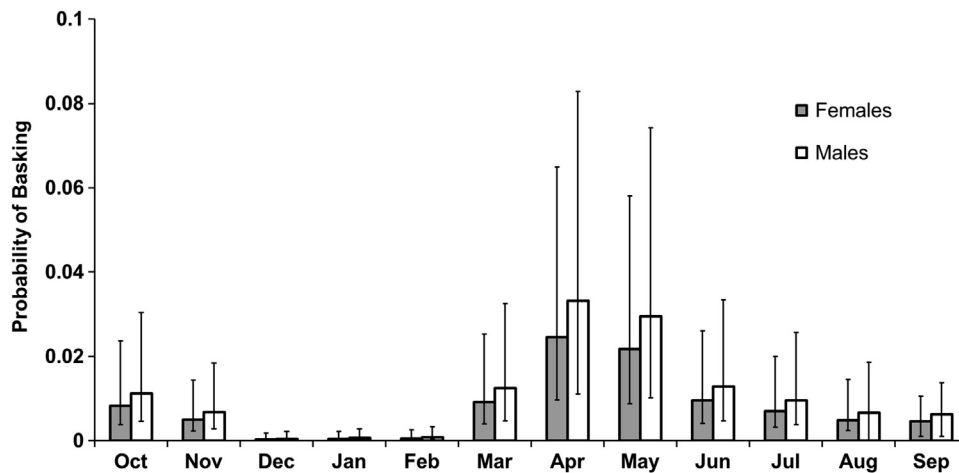
temperatures. Although  $T_c$  is likely not identical to internal  $T_b$ , particularly with larger aquatic turtles (e.g. *Chelydra serpentina*; Brown et al., 1990), previous studies have found  $T_c$  to be strong indicators of  $T_b$  of small to medium-sized turtles (*C. picta*: Grayson and Dorcas, 2004; *Cuora flavomarginata*: Chen and Lue, 2008; *Platysternon megacephalum*: Shen et al., 2013). Moreover, due to the relatively small body size of terrapins (mass range=228–1236 g, this study), thermal inertia between  $T_e$  and  $T_b$  is likely negligible (Lutterschmidt and Reinert, 2012), particularly on the hourly time interval we used.

The simultaneous measurements of  $T_c$  and  $T_e$  of estuarine microhabitats allowed us to document clear shifts in terrapin microhabitat use throughout the year. Our data suggest that terrapins at Kiawah Island use shallow mud from November to March and open water during most other months of the year, with the exception of June. During June, terrapins may have been in a transition zone between microhabitats, nesting, or visiting a habitat that we did not monitor with a similar temperature profile as the shallow mud. We found no support of deep mud as a predictor of terrapin  $T_c$  and thus conclude that terrapins rarely, if ever, bury themselves in deep mud (45 cm). Our results suggest that terrapins in South Carolina overwinter in the shallow intertidal mud of the salt marsh, and emerge from dormancy and enter the water column in/around April. Habitat predictions in this study are consistent with studies in southeastern North Carolina where terrapins were observed to hibernate in shallow intertidal mud (4–5 cm) from October to April (Williard and Harden, 2011; Harden and Williard, 2012). Although we found strong support for the use of two microhabitats, terrapins may occasionally use additional microhabitats, including dunes near estuarine areas, sandy mounds within marshes, natural sand levees, diked areas, and other coastal elevations above normal high tides (Palmer and Cordes, 1988). However, the focus of this particular study was to document monthly temporal shifts in frequented microhabitat used and activity (basking, swimming, burrowing) throughout a year and thus, we did not measure temperatures of all microhabitats available to terrapins within the marsh ecosystem.

Terrapins exhibited the highest probability of basking during the spring months and exhibited a second, smaller peak in the fall. Spring and fall are transitional periods during which the energy gained through solar radiation offsets the loss of energy through conduction while exposed to cooler environments (Heatwole and Taylor, 1987). During the summer months, we observed a decline in basking behavior, likely because in warmer months basking is not required to achieve an optimal body temperature (Harden et al., 2007). Grayson and Dorcas (2004) documented similar patterns of basking in *C. picta*, in which basking was used to obtain higher  $T_c$  predominately during the late winter, spring and fall months, and less often during summer months.

Throughout our study, adult males consistently had higher mean basking probabilities than adult females, which is corroborated with results from Grayson and Dorcas (2004) who recorded more basking events for males, particularly during the winter months of January and February. These findings may be explained by the dramatic sexual dimorphism of terrapins in which males have a higher surface area to volume (SA/V) ratio, potentially causing males to lose heat to their environment more rapidly than females. As a result, males may exhibit higher basking rates in order to maintain  $T_b$  above that of  $T_e$ . However, other studies have shown that female turtles bask more frequently than males, particularly when they are ovigerous and have elevated energy requirements for egg production (Carriere et al., 2008; Rowe and Dalgarn, 2009).

Adult male terrapins may also exhibit higher basking frequencies than adult females in order to maintain osmotic balance of body fluids, which likely poses more of a challenge for males due



**Fig. 2.** Relative basking probabilities of males and females each month  $\pm$  SE. The probability of recording a basking event in a given month by a given sex was calculated by dividing the total basking events recorded for a given sex in a month by the total daytime data points for individuals of that sex in that month.

to their larger SA/V ratio. Integument (skin and shell) permeability is generally low in reptiles, minimizing the passive exchange of water and salts between reptiles and their environment (Lillywhite, 2006). Documented rates of water efflux and salt influx across terrapin integument is also low, however, prolonged exposure to salt water results in a gradual, yet substantial, increase in plasma  $\text{Na}^+$  and  $\text{Cl}^-$  concentration and weight loss suggestive of dehydration (i.e. osmotic stress; Robinson and Dunson, 1976). Therefore, by leaving the water, terrapins are able to minimize salt and water exchange between their body fluids and their estuarine environment and thus reduce hyperosmotic stress, particularly during times when fresh water is not available. A study conducted on captive terrapins in seawater found that terrapins engage in emersion more often when deprived of freshwater, even when doing so results in a non-optimal  $T_b$  (when air temperature is markedly lower than water temperature and light source is absent; Davenport and Magill, 1996). Davenport and Magill (1996) also postulated that larger terrapins lose less water when immersed in seawater than smaller terrapins under similar conditions (due to differences in SA/V ratio for water and salt exchange), suggesting that larger terrapins can immerse for a shorter period to achieve osmotic balance of body fluids. Although evaporative water loss may be enhanced via basking, it is possible that the reduced salt intake from seawater and the elevated excretion of salt via the cloaca and salt glands that occurs while basking on land may provide a more efficient means of osmoregulation than might be possible in seawater (Davenport and Magill, 1996).

Shifts between aquatic and terrestrial habitats may play an important role in water and salt balance for this species (Coker, 1906; Yearicks et al., 1981; Spivey, 1998; Butler, 2002; Harden et al., 2007; Haramis et al., 2011; Williard and Harden, 2011; Harden and Williard, 2012). Thus, in addition to osmoregulation via increased basking frequency, terrapins may also be exploiting shallow mud habitats with high humidity levels and lower salinity of interstitial water in estuarine sediments to decrease rates of water exchange and further enhance the terrapin's ability to conserve water stores during periods of osmotic stress (Nestler, 1977; Davenport and Magill, 1996).

Inhabiting an estuarine environment means that terrapins must experience continuous fluctuations in tide. The daily tidal magnitude varies to a degree that it results in substantial habitat changes which may influence feeding ecology, predator interactions and basking opportunities (Ernst and Lovich, 2009). However, we found no correlation between  $T_c$  and tidal cycle. Even

during low tide, when we would expect to see elevated water temperatures correlated with a decrease in volume without a comparable decrease in surface area, there seems to be little to no effect on water temperatures. Harden et al. (2007) reported elevated  $T_c$  as a result of basking events rather than the daily tidal fluctuations. In a study on Florida terrapins, tide was not found to affect counts of terrapins (Butler, 2002), but Harden et al. (2009) found more terrapins in the water during head counts surveys at low tide than at high tide. Our data suggests that thermoregulation, and potentially behavior, are unaffected by tidal variations, but more study on the topic is needed to clarify the potential effects of tidal fluctuation on terrapin behavior.

Future studies to clarify our findings and support our explanations are required. Radio-telemetry in conjunction with temperature dataloggers could be especially effective in investigating microhabitat usage by allowing for comparisons between visual observations and thermal recordings. Additionally, understanding more about the seasonal osmotic and metabolic status of terrapins could help to elucidate the patterns in habitat use shifts and behavioral thermoregulation we documented in our study, particularly between sexes and months. Currently, terrapins face a suite of mainly anthropogenically-induced threats that suggest an uncertain future for their populations throughout much of their range, including Kiawah Island, SC. Knowledge of habitat use, behaviors, and thermal biology of terrapins can be used to establish and improve conservation and management measures. For example, knowledge of seasonal shifts in habitat use, as provided by our thermal profiles, can be important information for blue crab fishermen when they are deciding when and where to deploy crab pots that will minimize terrapin–crab pot interactions and potential bycatch.

### Acknowledgments

We thank Annette Baker and Wyndham Vacation Rentals for arranging and providing lodging. Marilyn Blizard, Sophia McCallister, and Sidi Limehouse have been instrumental in facilitating our long-term terrapin research project on Kiawah Island and improving terrapin conservation measures and awareness. We also thank the students, technicians, research coordinators, and volunteers for assistance in the field and the UGA-SREL and Davidson College personnel who have helped sample and process terrapins over the years. In particular we thank Andrea Drayer, Jackie Guzy, Judy Greene, Kristen Cecala, Shannon Pittman, Tom Luhring, Tony

Tucker, Cris Hagen, and J.D. Willson. We also thank the numerous Kiawah Island Nature Center Naturalists for their assistance, particularly Liz King, Jennifer Barbour, Nicholas Boehm, Mike Frees, and Jake Feary. Funding was provided by the University of Georgia, Davidson College Faculty Research Grants to MED, the Department of Biology at Davidson College, the Pittman Foundation, and EarthWatch Institute. Research was conducted under SCDNR Scientific Terrapin Collection Permit numbers SCI13-0100 and SCI11-0492 under the auspices of the Davidson College Animal Care and Use Committee.

## References

- Beitinger, T.L., Fitzpatrick, L.C., 1979. Physiological and ecological correlates of preferred temperature in fish. *Am. Zool.* 19, 319–329.
- Brown, G.P., Brooks, R.J., Layfield, J.A., 1990. Radiotelemetry of body temperatures of free-ranging snapping turtles (*Chelydra serpentina*) during summer. *Can. J. Zool.* 68, 1659–1663.
- Bulte, G., Blouin-Demers, G., 2010. Estimating the energetic significance of basking behaviour in a temperate-zone turtle. *Ecoscience* 17, 387–393.
- Burnham, K., Anderson, D., 2002. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, second ed. Springer, New York.
- Butler, J., 2002. Population ecology, home range, and seasonal movements of the Carolina diamondback terrapin, *Malaclemys terrapin centrata*, in Northeastern Florida. Final report, Florida Fish and Wildlife Conservation Commission, Project NG96-007, 620 South Meridian Street, Tallahassee, Florida 32399-1600, USA.
- Carriere, M., Rollinson, N., Suley, A., Brooks, R., 2008. Thermoregulation when the growing season is short: sex-biased patterns in a northern population of painted turtles (*Chrysemys picta*). *J. Herpetol.* 42, 206–209.
- Chen, T., Lue, K., 2008. Thermal preference of the yellow-margined box turtle (*Cuora flavomarginata*) (Testudines: Geoemydidae) inhabiting a mesic lowland, northern Taiwan. *Amphib.-Rept.* 29, 513–522.
- Coker, R.E., 1906. The natural history and cultivation of the diamondback terrapin. *North Carolina Geol. Surv.* 14, 3–69.
- Dame, R., Alber, M., Allen, D., Mallin, M., Montague, C., Lewitus, A., Chalmers, A., Gardner, R., Gilman, C., Kjerfve, B., Pinckney, J., Smith, N., 2000. Estuaries of the South Atlantic Coast of North America: their geographical signatures. *Estuaries* 23, 793–819.
- Davenport, J., Magill, S., 1996. Thermoregulation of or osmotic control? Some preliminary observations on the function of emersion in the diamondback terrapin *Malaclemys terrapin* (Latreille). *Herpetol. J.* 6, 26–29.
- Dorcas, M.E., Willson, J.D., Gibbons, J.W., 2007. Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. *Biol. Conserv.* 137, 334–340.
- Dubois, Y., Blouin-Demers, G., Shipley, B., Thomas, D., 2009. Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. *J. Anim. Ecol.* 78, 1023–1032.
- Ernst, C., Lovich, J.E., 2009. Turtles of the United States and Canada. Diamond-Backed Terrapins, second ed. Johns Hopkins University Press, MD.
- Fitzgerald, L., Nelson, R., 2011. Thermal biology and temperature-based habitat selection in a large aquatic ectotherm, the alligator snapping turtle, *Macrolemys temminckii*. *J. Therm. Biol.* 36, 160–166.
- Grayson, K.L., Dorcas, M.E., 2004. Seasonal temperature variation in the painted turtle (*Chrysemys picta*). *Herpetologica* 60, 325–336.
- Haramis, G.M., Henry, P.P.F., Day, D.D., 2011. Using scrape fishing to document diamondback terrapins in hibernacula in Chesapeake Bay. *Herpetol. Rev.* 42, 170–177.
- Harden, L.A., Pittman, S.E., Gibbons, J.W., Dorcas, M.E., 2009. Development of a rapid assessment technique for diamondback terrapin (*Malaclemys terrapin*) populations using head-count surveys. *App. Herpetol.* 6, 237–245.
- Harden, L.A., DiLuzio, N.A., Dorcas, M.E., Gibbons, J.W., 2007. The spatial ecology and thermal ecology of diamondback terrapins (*Malaclemys terrapin*) in a South Carolina salt marsh. *J. N. Carol. Acad. Sci.* 123, 154–162.
- Harden, L.A., Williard, A.S., 2012. Using spatial and behavioral data to evaluate the seasonal bycatch risk of diamondback terrapins (*Malaclemys terrapin*) in crab pots. *Mar. Ecol. Prog. Ser.* 467, 207–217.
- Heatwole, H., Taylor, J., 1987. Ecology of Reptiles. Surrey Beatty and Sons Pty Limited, New South Wales.
- Helmuth, B., Broitman, B., Blanchette, C., Gilman, S., Halpin, P., Harley, C., O'Donnell, M., Hofmann, G., Menge, B., Strickland, D., 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol. Monogr.* 76, 461–479.
- Huey, R., 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*. Academic Press, New York, pp. 25–67.
- Kana, T., Michel, J., Hayes, M., Jensen, J., 1984. The physical impact of sea level rise in the area of Charleston, South Carolina. In: Barth, M., Titus, J. (Eds.), *Greenhouse Effect and Sea Level Rise: A Challenge for This Generation*. Van Nostrand Reinhold Company, New York, pp. 105–150.
- Largier, J., 2010. Low-inflow estuaries: hypersaline, inverse, and thermal scenarios. In: Valle-Levinson, A. (Ed.), *Contemporary Issues in Estuarine Physics*. Cambridge University Press, Cambridge, pp. 247–272.
- Lillywhite, H.B., 2006. Water relations of tetrapod skin. *J. Exp. Biol.* 209, 202–226.
- Lovich, J.E., Gibbons, J.W., 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. *Oikos* 59, 126–134.
- Lutterschmidt, W., Reinert, H., 2012. Modeling body temperature and thermal inertia of large-bodied reptiles: support for water-filled biophysical models in radio telemetric studies. *J. Therm. Biol. Ecol.* 37, 282–285.
- Nestler, J., 1977. Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuar. Coast. Mar. Sci.* 5, 707–714.
- NOAA, 2005. NOAA's National Ocean Service: Estuaries [online] [accessed: 1.5.12]. ([http://oceanservice.noaa.gov/education/tutorial\\_estuaries/lessons/estuaries\\_tutorial.pdf](http://oceanservice.noaa.gov/education/tutorial_estuaries/lessons/estuaries_tutorial.pdf)).
- Palmer, W., Cordes, C., 1988. Habitat Suitability Index Models: Diamondback Terrapin (Nesting)-Atlantic Coast. National Wetlands Research Center, U.S. Fish and Wildlife Service, Lafayette, LA, pp. 1–18. (U.S. Fish Wildlife Services Biological Report 82(10.151).
- Peterson, C., Gibson, A., Dorcas, M.E., 1993. Snake thermal ecology: the causes and consequences of body temperature variation. In: Seigel, R.A., Collins, J.T. (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill Publishing Company, New York, pp. 241–314.
- Pittman, S.E., Dorcas, M.E., 2009. Movements, habitat use, and thermal ecology of an isolated population of bog turtles (*Glyptemys muhlenbergii*). *Copeia* 4, 781–790.
- Robinson, G.D., Dunson, W.A., 1976. Water and sodium balance in the estuarine diamondback terrapin (*Malaclemys*). *J. Comp. Physiol.* 105, 129–152.
- Rowe, J., Dalgarn, S., 2009. Effects of sex and microhabitat use on diel body temperature variation in midland painted turtles (*Chrysemys picta marginata*). *Copeia* 1, 85–92.
- Sexton, O., 1959. A method of estimating the age of painted turtles for use in demographic studies. *Ecology* 40, 716–718.
- Shen, J.W., Meng, F.W., Zhang, Y.P., Du, W.G., 2013. Field body temperature and thermal preference of the big-headed turtle *Platysternon megacephalum*. *Curr. Zool.* 59, 626–632.
- Spivey, P.B., 1998. Home Range, Habitat Selection, and Diet of the Diamondback Terrapin (*Malaclemys terrapin*) in a North Carolina Estuary. Department of Wildlife Ecology and Management, University of Georgia, Athens, G.A. (M.Sc. thesis).
- Stevenson, R., 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* 126, 362–386.
- Tucker, A., Gibbons, J.W., Greene, J., 2001. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. *Can. J. Zool.* 79, 2199–2209.
- Williard, A.S., Harden, L.A., 2011. Seasonal changes in thermal environment and metabolic enzyme activity in diamondback terrapin (*Malaclemys terrapin*). *Comp. Biochem. Physiol. Part A* 158, 477–484.
- Yearicks, E.F., Wood, C.R., Johnson, W.S., 1981. Hibernation of the northern diamondback terrapin, *Malaclemys terrapin terrapin*. *Estuaries* 4, 78–81.



**Christiana Akins** is a Member of the class of 2014 at Davidson College, Davidson, NC, where she graduated with a degree in Environmental Studies in May. She became a Member of Dr. Mike Dorcas' Herpetology Lab in Fall 2011, after a chance encounter at the lab's annual "Reptile Day." She is a member of the Association of Southeastern Biologists, The Billfish Foundation, and the Turtle Survival Alliance. She has given scientific presentations at Davidson College, The University of Georgia, and Seabrook Island, SC. Through the lab, she has studied numerous North Carolina native and nonnative reptile and amphibian species.



**Chance Ruder** originally hails from San Antonio, Texas, and is currently an undergraduate student at Davidson College, on track to receive a B.S. in Biology and a B.A. in Theatre in May of 2015. His past research interests have centered around easing conflicts between wildlife and human populations, and he hopes to continue his career in the field of international science communication.



**Steven J. Price** is an Assistant Professor of Stream and Riparian Ecology in the Department of Forestry at the University of Kentucky. He completed his Ph.D. in the Biology Department at Wake Forest University (2011), and obtained a B.S. (2000) and M.S. (2003) from the University of Wisconsin-Green Bay. Prior to moving to Kentucky, Steve was researcher coordinator, visiting faculty, and post-doctoral fellow in the Biology Department at Davidson College, Davidson, NC. Steve's research centers on the population biology, conservation and management of reptiles and amphibians. Steve has authored or co-authored over 50 articles and book chapters.



**Whit Gibbons** is Professor Emeritus of Ecology at the University of Georgia's Savannah River Ecology Laboratory. Whit is author or editor of 20 books, including two on thermal ecology, and has published more than 250 articles in scientific journals. He has had numerous ecological commentaries on National Public Radio and popular articles in magazines and newspapers, including a weekly environmental column. He has also written encyclopedia articles on ecology that have appeared in *World Book*, *Compton's*, and *Encyclopedia Britannica*.



**Leigh Anne** is an Adjunct Assistant Professor of Biology and a Postdoctoral Researcher at Davidson College in Davidson, North Carolina teaching Introductory Biology and coordinating undergraduate research in the Davidson College Herpetology Laboratory. She received her Ph.D. in Marine Biology from the University of North Carolina Wilmington in 2013 and her B.S. in Biology from Davidson College, NC in 2007. Leigh Anne was a National Science Foundation Graduate Research Fellow at UNCW, where her research focused on the physiological ecology of the estuarine diamondback terrapin. Leigh Anne's primary research interests include the behavioral and physiological ecology of reptiles with applications to conservation.



**Mike Dorcas** is a Professor in the Department of Biology at Davidson College, Davidson, NC. He received a B.S. (1986) and M.S. (1990) from the University of Texas at Arlington and a Ph.D. from Idaho State University in 1995. Mike is a Fellow of the American Association for the Advancement of Science and recently received the Senior Research Award from the Association of Southeastern Biologists and the Meritorious Teaching Award at the World Congress of Herpetology. Mike's student-centered research program focuses on the ecology, physiology, and conservation of amphibians and reptiles. Mike has published seven books, numerous book chapters and over 100 journal articles.