

SEASONAL TEMPERATURE VARIATION IN THE PAINTED TURTLE (*CHRYSEMYS PICTA*)

KRISTINE L. GRAYSON AND MICHAEL E. DORCAS¹

Department of Biology, Davidson College, Davidson, NC 28035, USA

ABSTRACT: We measured temperature variation in a free-ranging ectotherm by attaching micro-dataloggers to the carapaces of 34 painted turtles (*Chrysemys picta*) in a farm pond located in Davidson, NC. Water and mud temperatures (T_w) were simultaneously monitored. We successfully recorded external shell temperature (T_s) in 18 turtles from September 2001–April 2002 and 23 turtles from April 2002–October 2002. Turtle temperatures steadily decreased through the fall and basking continued until the middle of December. Minimum yearly T_s (1–3 C) occurred during the same week (2–7 January 2002) for all turtles. Turtle temperatures then steadily rose and basking resumed in February. More basking events took place during February and March than during other months of the year when *C. picta* used basking to reach T_s 5–16 C above the maximum water temperature. During the summer, turtle T_s reached values similar to those achieved via basking during cooler months, apparently without leaving the water. The number of basking events per month was significantly different between consecutive months for seven of eleven consecutive month pairs. Contrary to our predictions, more basking events were recorded for male turtles than for females overall for the year. Monthly basking profiles were also significantly different for male and female turtles, with males basking earlier in spring than females. Mean maximum weekly T_s were significantly higher for males than for females. Our research documents seasonal variation in temperature and basking behavior in *C. picta*, as well as the importance of basking for achieving high temperatures during cooler months. We demonstrate the effectiveness of microdatalogger technology for measuring temperature variation in small reptiles and we contribute to a more complete understanding of the thermal biology of *C. picta*.

Key words: Basking; Body temperature; *Chrysemys picta*; Datalogger; Over-wintering; Painted turtle; Seasonal temperature variation; Shell temperature; Thermochron iButton

BODY temperature (T_b) plays important roles in many aspects of the ecology of ectotherms, such as reptiles. Body temperature directly affects activity, metabolism, and growth (Congdon, 1989; Cossins and Bowler, 1987; Huey, 1982). By affecting many behavioral, physiological, and developmental variables, T_b also influences ecological and fitness variables such as susceptibility to predation, reproductive effort, energy balance, survivorship, habitat utilization, and patterns of distribution (Peterson et al., 1993; Zimmerman et al., 1994). Thus, understanding how T_b varies in free-ranging reptiles is a key component to understanding the causes and consequences of their body temperature variation (Peterson et al., 1993; Manning and Grigg, 1997). Unfortunately, continually measuring T_b in the field for extended periods of time can be difficult and has only been recorded for a limited number of species.

Measuring body temperature variation in free-ranging reptiles has been limited by the

lack of inexpensive and reliable data collection methods. Many studies of T_b variation in free-ranging reptiles have relied on spot temperature measurements of active animals, despite the fact that reptiles are inactive much of the time (Avery, 1982; Dall'Antonia et al., 2001; Dorcas and Peterson, 1998; Peterson et al., 1993). Temperature-sensitive radio transmitters have been used extensively in squamates (e.g., Blouin-Demers and Weatherhead, 2001; Christian and Weavers, 1996; Pearson et al., 2003; Whitaker and Shine, 2002) and to a limited degree in turtles (Brown et al., 1990; Manning and Grigg, 1997; Zimmerman et al., 1994). However, to obtain continual temperature readings using radio transmitters, a rather elaborate and potentially expensive automated monitoring system is required (Beaupre and Beaupre, 1994; Dorcas and Peterson, 1998; Peterson et al., 1993). Miniaturized dataloggers provide an alternative method for recording temperature in free-ranging animals. Dataloggers have been used in several studies to measure temperatures of turtles, nests, and hibernacula (Dall'Antonia et al., 2001; Litzgus et al., 1999; Mueller and

¹ CORRESPONDENCE: e-mail, midorcas@davidson.edu

Rakestraw, 1995; Nussear et al., 2002; Sajwaj and Lang, 2000). Recent further miniaturization of dataloggers provides the potential to study a wider range of organisms (Angilletta and Krochmal, 2003; Roberts and Thompson, 2003).

In this study we describe seasonal temperature changes in a southern population of painted turtles (*Chrysemys picta*) and test the effectiveness of micro-datalogger technology for measuring temperature variation in free-ranging reptiles. *Chrysemys picta* have been used as model organisms for many ecological and evolutionary studies of ectotherms; however, little is known about their thermal biology in the field (Packard and Packard, 2001). Most studies have focused on survivorship of over-wintering hatchlings (e.g., DePari, 1996; Lindeman, 1991; Nagle et al., 2000) and few studies have focused on temperature variation in adult *C. picta*. Peterson (1987) demonstrated that hibernating *C. picta* do not exhibit endothermy or physiological temperature control, clarifying earlier studies that suggested submerged turtles may be able to maintain elevated T_b when surrounded by low ambient temperatures (Ernst, 1972). Active *C. picta* have been observed at low temperatures and even under ice in the northern part of their range (Gibbons, 1967; Peterson, 1987).

Like many other semi-aquatic turtles, *C. picta* often elevate their T_b above water temperature by basking (Avery, 1982). Schwarzkopf and Brooks (1995) examined environmental variables that affect basking behavior in a northern population of *C. picta* and agreed with Boyer (1965) that turtles are most likely to bask when the difference between water and air temperature was the greatest. Obtaining high T_b by basking can have many benefits for turtles, such as enhanced digestive rates, increased ability to fight parasites and infections, and reproductive benefits such as increased fat mobilization and rates of follicle development (Avery, 1982; Congdon, 1989; Gatten, 1974). Food intake and assimilation efficiency, as well as overall metabolic rate, are also thermally dependent factors in *C. picta* (Kepenik and McManus, 1974). Koper and Brooks (2000) found that growth of *C. picta* in the laboratory was positively correlated with basking frequency and not with the amount of food provided.

We hypothesize that basking as a thermoregulatory method will be utilized by our population to raise body temperature above water temperature.

Given the potential reproductive benefits of obtaining elevated T_b by basking, many researchers have suggested that female turtles may exhibit more basking behavior than male turtles (Ernst, 1982; Lefevre and Brooks, 1995). In *C. picta*, Schwarzkopf and Brooks (1995) found an effect of body size on basking behavior; larger females basked for longer periods of time from May through August. This effect was not seen in Lefevre and Brooks (1995), where the males and females did not differ in basking time or duration during July. Krawchuk and Brooks (1998) observed more frequent and longer basking events in female *C. picta*, but only in the days just prior to and during nesting and not in early May nor the two months following nesting. These three studies were all conducted in Ontario, Canada, close to the northern range limit of *C. picta*. Based on these studies, we predict that females in our southern population will bask more often than males, particularly in early spring.

MATERIALS AND METHODS

Our study was conducted at a 5-ha farm pond 2 km east of Davidson, in the western Piedmont of North Carolina (Mecklenburg County; WGS-84—UTM E: 0516008, N: 3928872). Turtles at this pond have been intensively trapped during fall, spring, and summer since June 1999. The trapping seasons used for our study were fall 2001, spring 2002, and fall 2002. *Chrysemys picta* were captured more frequently than other species (snapping turtles, *Chelydra serpentina* and eastern mud turtles, *Kinosternon subrubrum*) and we typically obtained high recapture rates (80–90%) of the marked population each season (Lindsay and Dorcas, 2001). The high recapture rates allowed retrieval of individual turtles with high reliability, thus providing a good opportunity for monitoring seasonal temperature variation using micro-dataloggers, without the need for radiotelemetry. We trapped turtles with hoop-net traps baited with sardines. Each turtle was individually marked by filing notches in the marginal scutes or recorded as a recapture.

Sex, mass (to the nearest g), and straight-line carapace and plastron length (to the nearest mm) were recorded for each turtle. For more detailed description of trapping and marking techniques see Lindsay and Dorcas (2001).

We used four miniature dataloggers (Tidbit Stowaways, Onset Computer Inc., part no. TBI32-20+50, Pocasset, MA; size = 33 mm × 53 mm, 28 g) placed in the water and mud in four different locations (depth ranged from 0.25–2 m) to measure temperatures available to the turtles while submerged. Some of the water and mud temperature data were excluded due to small mammals (e.g., raccoons) and cattle pulling dataloggers out of the water and onto the bank. Air temperature was also monitored using a HOBO datalogger (Onset Computer Inc., part no. H08-032-08, Pocasset, MA). To estimate T_b , we measured shell temperature (T_s) using micro-dataloggers (Thermochron iButtons, product DS1921L-F51, Dallas Semiconductor, Dallas, TX; 5.9 mm × 17.4 mm, 3.12 g; Angilletta and Krochmal, 2003).

During September and October 2001, we attached dataloggers to the carapaces of adult male ($n = 10$; mean carapace length = 126.5 mm ± 8.4 SD; mean mass = 245.2 g ± 42.4 SD) and female ($n = 9$; mean carapace length = 144.7 mm ± 8.3 SD; mean mass = 379.2 g ± 45.6 SD) *C. picta*. The mass of the dataloggers equaled 1.6% of the body mass of the smallest turtle (mean percentage of turtle mass was 0.99%). Dataloggers were programmed, using the standard 32-Bit iButton-TMEX Runtime Environment software (Dallas Semiconductor, Dallas, TX), with a sample rate of 180 min, which allowed readings to be collected for 256 days before the memory of the datalogger filled (Thermochron iButton dataloggers can hold 2048 time and date-stamped temperature readings and have a resolution of 0.5 C). The start time and thus, the subsequent measuring times, were programmed arbitrarily so that temperature measurements for each turtle were taken at different points in the day (i.e., temperature measurements were asynchronous among turtles). Programmed dataloggers were sealed in plastic tool dip (Plasti Dip International, Circle Pines, MN; a fast-drying liquid plastic traditionally used to coat the grips of hand tools) and attached to small, UV-resistant plastic

cable ties with a small amount of silicon. Once dry, they were dipped once more in black plastic tool dip. To attach the dataloggers to the turtles, two small holes were drilled in the posterior marginal scutes on one side. We chose to drill holes for attachment, a method which has been used previously in turtles (e.g., Buhlmann and Vaughan, 1991; Schwarzkopf and Brooks, 1985), as opposed to gluing dataloggers directly to the carapaces to minimize datalogger loss due to shedding of the scutes. The cable ties were fastened through the holes with the datalogger positioned on the dorsal side of the carapace so that movement of the hind leg was not impeded. An additional coat of plastic tool dip was applied to each datalogger to reduce the amount of debris that might accumulate between the carapace and the attached datalogger. After a short drying time (20–30 min), turtles were returned to the pond.

From 24 March until 10 May 2002, we trapped the population to recover the turtles and dataloggers. Dataloggers were removed and replaced using the same procedures described above. An additional 16 dataloggers were attached to increase the sample size for the summer months ($n = 7$ additional males, carapace length = 128.2 mm ± 10.7 SD, mean mass = 216.6 g ± 32.8 SD; $n = 9$ additional females, carapace length = 149.7 mm ± 6.7 SD, mean mass = 417.5 g ± 54.6 SD). From 31 August until 27 October 2002, we again trapped the population to recover turtles with dataloggers.

To examine temperature trends among seasons, we compared the mean maximum and minimum water temperature (T_w) and T_s by week. The maximum and minimum temperature per week was determined for each environmental datalogger and for each turtle and then the grand mean of each was taken. Sample sizes of the turtles for calculating the weekly T_s grand mean were 18 turtles for the first trapping period (September 2001–mid-April 2002) and 23 for the second trapping period (mid-April 2002–September 2002), due to different recapture rates, and varied from 6–21 turtles for the initial, final, and mid-point weeks due to variation in datalogger attachment and removal times (Table 1). The sample size of the environmental dataloggers for calculating the weekly T_w grand mean was

TABLE 1.—Sample sizes and recapture rates of *Chrysemys picta* with dataloggers for each trapping season. “New” refers to turtles that did not have dataloggers attached over the winter, but had dataloggers affixed for summer to increase the sample size. Parenthetical numbers refer to the number of turtles recaptured that had dataloggers during winter and the number of turtles that were new in spring 2002, respectively.

Season	Females	Males	Total
Attached fall 2001	9	10	19
Recaptured spring 2002	8	10	18
Attached spring 2002	8 + 9 new	10 + 7 new	34
Recaptured fall 2002	6 (4, 2)	8 (5, 3)	14
Recaptured spring 2003	5 (1, 4)	4 (2, 2)	9
<i>n</i> for entire year	5	7	12
<i>n</i> for winter only	3	3	6
<i>n</i> for summer only	6	5	11

four, except during brief periods where data were excluded due to environmental dataloggers being out of the water (see above).

To investigate the effects of season on basking behavior, we quantified the number of basking events per turtle for each month. The sample sizes for each month were the same as above for calculating the weekly T_s . A basking event was defined for the purposes of our study as a T_s measurement >6 C above the maximum T_w measurement at the time of the T_s measurement (Fig. 1). The value of 6 C above maximum T_w was selected as the

criterion because it was the smallest whole value that accounted for the variation within T_w at any given time (i.e., points selected represented temperatures that could not be obtained by the turtle changing location within the water). By using this method and having a 3-h datalogger measuring interval, our estimation of number of basking events was less than the actual number of basking events, because turtles often bask for durations of <1 h or may bask and not reach temperatures >6 C above the maximum water temperature (Schwarzkopf and Brooks, 1985; K. Grayson, personal observation). However, our criteria equally excluded basking events where 6 C above T_w was not reached among turtles. Our underestimation of the number of basking events should be uniform over time and among turtles because the probability of recording a particular basking period is distributed evenly among the turtles. Thus, although we cannot quantify the absolute number of basking events for individual turtles, our data allow us to infer and compare behavioral patterns at broad temporal scales (i.e., seasonal patterns).

We compared the differences in the mean number of basking events per month between consecutive months using individual paired-sample *t*-tests. We performed a Bonferroni adjustment for these comparisons (adjusted

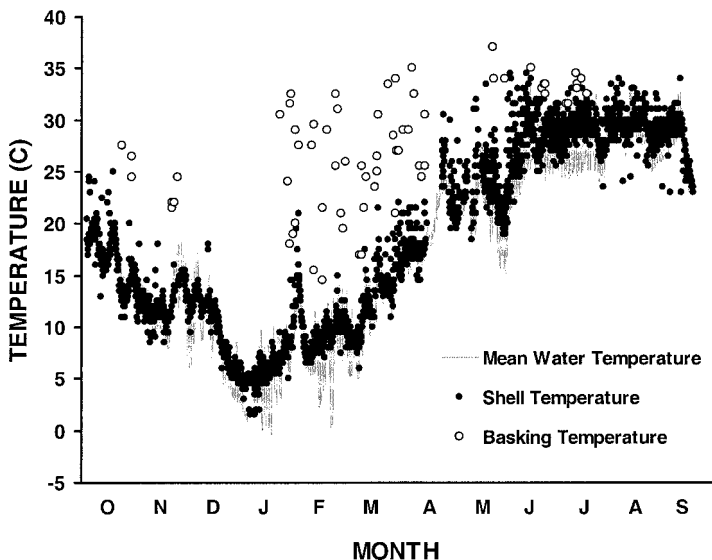


FIG. 1.—Seasonal temperature variation of one male *Chrysemys picta* over 1 yr. Basking temperature points are shell temperatures >6 C above maximum T_w .

$\alpha = 0.005$). We compared the total number of basking events recorded for the entire year between male and female turtles using a single-factor ANOVA. For this analysis, we only used data from the male and female turtles for which we had an entire year of temperature records ($n = 5$ females and 7 males). We examined the effects of sex and month on the number of basking events using a repeated-measures ANOVA with month as the repeated factor. To balance sample sizes for this analysis, two male turtles were randomly selected for exclusion from the analysis. To compare seasonal temperature differences between sexes, the weekly maximum and minimum T_s for female turtles was subtracted from the weekly maximum and minimum T_s for male turtles. We used a repeated-measures ANOVA with week as the repeated factor to compare minimum and maximum weekly temperatures between the sexes. We used the same sample sizes as the previous repeated-measures ANOVA. Statistical tests were performed using Microsoft Excel, Minitab (Minitab Inc., State College, PA), or JMP (SAS Institute, Cary, NC). Alpha level was set at 0.05 for all tests unless otherwise noted.

To evaluate the effectiveness of externally attached dataloggers for approximating T_b , we compared the readings of attached dataloggers to measurements of turtle cloacal temperatures in a controlled setting. Cloacal temperatures were measured using a thermocouple thermometer (Oakton, model 90600-300, Chicago, IL) and a 20-gauge, type-T thermocouple inserted approximately 5 cm into the cloaca. Four dataloggers were programmed to record at 1-min intervals synchronized with a stopwatch. These were attached to two typically sized females (carapace length = 138 and 153 mm) and two typically sized males (carapace length = 118 and 125 mm) captured from the study site that did not previously have dataloggers attached. These turtles were held in a plastic wading pool during a warm, sunny afternoon in May 2002 (air temperature = 30–32 C; 1400–1700 h). We began the experiment with water in the pool (approximately 20 cm deep) and provided a cover object (70 × 70 cm piece of plywood) under which turtles could hide. After a 30-min period of acclimation, cloacal temperatures were recorded every 15 min. The cover object was removed after the

first measurement. After four more readings, the water was removed, and the turtles were forced to warm in the sun. Water was replaced after two measurements (i.e., 30 min), and measurements were taken for three more 15-min intervals. Data from the dataloggers were downloaded and matched with the corresponding cloacal temperature to estimate the difference between cloacal temperature and externally attached dataloggers.

RESULTS

We found the dataloggers and our attachment technique to be reliable in the field. Observations of turtles swimming (at the surface and underwater) in the pond after attachment of the dataloggers indicated no interference with normal swimming activity. Dataloggers apparently did not interfere with reproductive behavior. A female turtle with a datalogger was observed nesting on 17 May 2002 with no sign of difficulty. Of the 18 turtles recaptured after the winter season, none had lost their dataloggers nor did any of the dataloggers suffer any physical damage (Table 1). Of the 17 turtles recaptured after the summer season, three dataloggers were lost (Table 1). One loss was due to a failure of the cable tie and two cases were due to the holes being drilled too close to the edge of the scutes and opening, creating gaps where the cable ties slipped off. Nine turtles not recaptured during fall 2002 were captured during the spring of 2003 with their dataloggers still attached and with summer 2002 data retained. All 41 recovered dataloggers were successfully downloaded upon recovery and no data were missing or appeared to be erroneous. Altogether, we collected T_s data for 7100 turtle days (56,800 time and date stamped temperature readings).

Patterns of T_s variation were relatively consistent among turtles throughout the year (see Fig. 1 for an example of T_s variation over 1 yr for one turtle) and were correlated with seasonal changes in environmental temperature. Minimum yearly T_s (1–3 C) occurred during the same week (first week of January) for all turtles, with most yearly minimum T_s occurring on 3 January 2002 (Fig. 2). No datalogger recorded a temperature below 0 C. No environmental datalogger located at

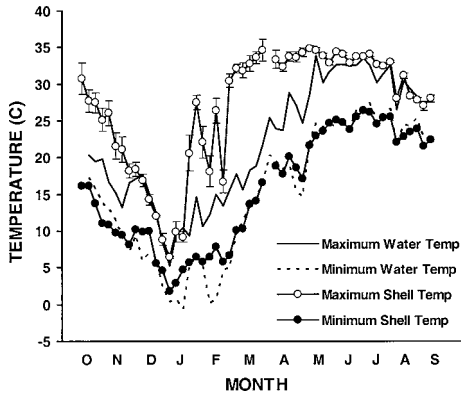


FIG. 2.—Mean weekly minimum and maximum T_s and T_w for *Chrysemys picta* over 1 yr. See methods for explanation of sample sizes. Error bars on T_s means are ± 1 SE.

depths >1.5 m recorded a T_w below 0 C. However, dataloggers recording T_w at shallower depths recorded minimum temperatures ranging from -4.4 C to -3.4 C. The coldest air temperature of the year was -11.7 C on 4 January 2002.

We found a significant positive linear relationship between mean minimum weekly T_s for all turtles and minimum weekly T_w for the entire year ($P < 0.001$; Fig. 3). Differences between mean minimum T_s and mean minimum T_w were greatest during January and February (minimum T_s 2.9 C ± 1.1 SE warmer than minimum T_w for weekly temperatures in January and February; Fig. 2). The largest difference occurred during the last week in February when mean minimum T_s was 7.3 C warmer than the minimum T_w .

We found large differences between mean maximum and minimum T_s during the fall months (mean difference = 12.8 C ± 0.6 SE for weekly temperatures in October and November). Mean maximum and minimum T_s were closest during December and the first 3 wk of January (mean difference = 5.8 C ± 0.6 SE, Fig. 2). Large differences between mean maximum weekly T_s and minimum weekly T_s began again in February (mean difference = 16.9 C ± 2.0 SE for weekly temperatures in February) and continued through May (mean difference = 17.5 C ± 1.1 SE for weekly temperatures in March, April, and May). Differences between maximum and minimum weekly T_s were smaller

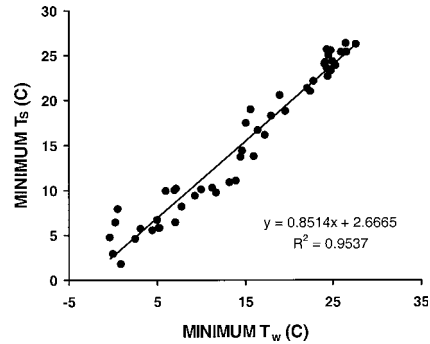


FIG. 3.—The relationship between mean weekly minimum T_s for all turtles and weekly minimum T_w over the entire year. Each data point represents one week.

during June, July, and August (mean difference = 8.6 C ± 0.4 SE).

Differences between mean maximum T_s and T_w followed the same pattern as the differences between maximum and minimum T_s (Fig. 2). Mean maximum T_s and T_w were similar during cold winter months (mean difference = 1.2 C ± 1.5 SE for weekly temperatures in December and January) and hot summer months (mean difference = 1.3 C ± 0.3 SE for weekly temperatures in June, July, and August). However, large differences were observed in October and November (mean difference = 6.6 C ± 0.9 SE) and during spring (mean difference = 10.7 C ± 1.0 SE for weekly temperatures in February, March, April, and May).

We observed differences in the overall number of basking events by time of year. Over the winter, the number of basking events decreased at the end of November and only a few turtles continued to bask during the first week of December. A single basking event was detected both on 15 and 28 December 2001, and sporadic basking events were again recorded on 9, 10, and 12 January 2002. These basking events were very close to the dates of the yearly minimum temperature for each turtle (2–7 January). Large numbers of basking events were recorded again at the end of January and beginning of February and continued through August when basking decreased. Individual comparisons between consecutive months showed significant differences in the number of basking events between all consecutive months, except for October–November, December–January, June–July,

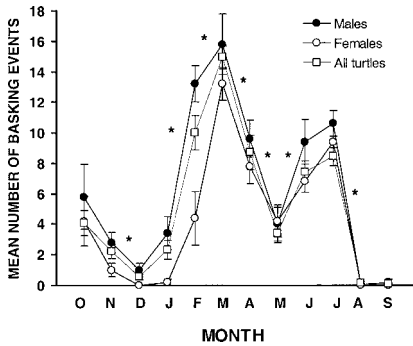


FIG. 4.—The mean number of basking events per month for male, female, and all *Chrysemys picta*. The “*” denotes a significance difference in the number of basking events between consecutive months for all turtles. Male and female data are those used in the statistical analyses ($n = 5$; see methods). All turtles includes data where the number of basking events was recorded for the entire month ($n = 14$ –23). Error bars represent ± 1 SE.

and August–September (Oct–Nov $P = 0.03$, Dec–Jan $P = 0.008$, Jun–Jul $P = 0.24$, Aug–Sept $P = 0.43$, $P < 0.005$ for all other month pairs; Fig. 4). The highest numbers of basking events were observed during February and March and few or no basking events were recorded during the fall, early winter, and late summer (October–December, August, and September, Fig. 4).

Overall for the year, more basking events were recorded for male turtles (mean total number of basking events = 70.9 ± 5.4 SE, $n = 7$) than for female turtles (mean total number of basking events = 51.2 ± 3.5 SE, $n = 5$; ANOVA, $F = 7.8$, $df = 1, 10$, $P = 0.02$; Fig. 4). The results of a repeated-measures ANOVA with month as the repeated variable indicated significant differences in basking behavior among months ($F = 41.01$, $df = 11, 48$, $P < 0.001$), between sexes ($F = 20.54$, $df = 1, 48$, $P < 0.001$), and a significant sex by month interaction effect ($F = 2.31$, $df = 11, 48$, $P = 0.02$; Fig. 4). The largest differences between sexes were recorded in January and February when males basked more than females. The number of basking events reported in our study should not be interpreted as a measure of the actual amount of basking behavior in *C. picta*, but is used for comparison among seasons and between sexes.

The mean maximum weekly T_s measured for males was greater than the maximum T_s measured for females (mean male–female

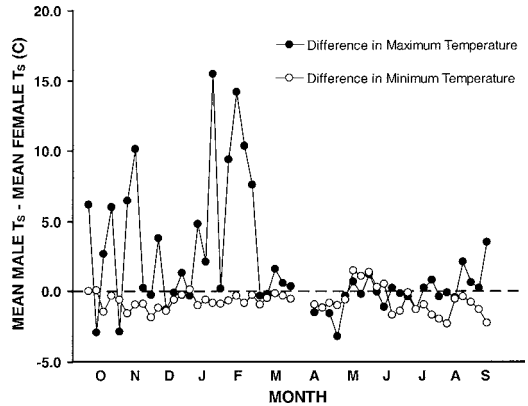


FIG. 5.—The difference between mean weekly maximum and minimum T_s for male and female *Chrysemys picta*.

difference = $1.8 \text{ C} \pm 0.6$ SE; repeated-measures ANOVA, sex [$F = 28.86$, $df = 1, 140$, $P < 0.001$], week [$F = 58.36$, $df = 34, 140$, $P < 0.001$], sex by week interaction [$F = 4.25$, $df = 34, 140$, $P < 0.001$]; Fig. 5). The mean minimum weekly T_s reached by male turtles was lower than the minimum T_s reached by female turtles (mean male–female difference = $-0.4 \text{ C} \pm 0.1 \text{ C SE}$), but this difference was only significant for week ($F = 366.48$, $df = 34, 140$, $P < 0.001$) and not significant for sex ($F = 2.02$, $df = 1, 140$, $P = 0.16$) or for the sex by week interaction ($F = 0.86$, $df = 34, 140$, $P = 0.69$). The difference in maximum T_s between males and females was greatest during October, November, February, and March (Fig. 5).

Comparisons between the temperatures recorded using externally attached dataloggers and cloacal temperatures revealed only small differences (mean difference = datalogger $0.26 \text{ C} \pm 0.24$ SE lower than cloacal temperature; Fig. 6). Mean differences were greatest during basking (datalogger readings 1.3 C warmer than cloacal temperature) and upon return to cooler water (datalogger readings 1.2 C lower than cloacal temperature).

DISCUSSION

We recorded seasonal temperature variation over an entire year in a southern population of *C. picta*. As expected, turtle temperatures were highly correlated with environmental temperatures. Based on T_s patterns, our population of *C. picta* continued activity

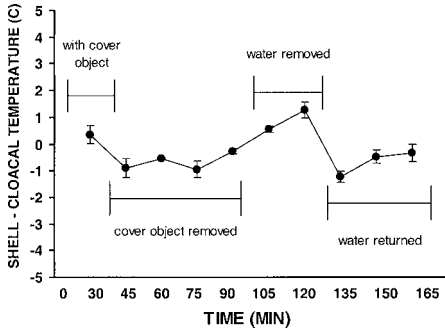


FIG. 6.—Comparison of cloacal and datalogger temperatures for four turtles over 3 h. Data are presented as the mean of the datalogger temperatures minus the cloacal temperatures ± 1 SE. Environmental manipulations are noted above data points and are explained in the text.

during much of winter. We recorded no subzero temperatures for any turtle. We found that *C. picta* used basking most frequently during spring to raise T_b substantially above T_w and apparently relied on basking less during summer, when water temperatures were warm enough to sustain high T_b without exposure. Differences in maximum and minimum temperature and basking behavior revealed seasonal changes in thermoregulatory behavior. Contrary to our predictions, more basking events were recorded for male turtles than female turtles and male maximum temperatures were consequently higher than female maximum temperatures. We found micro-dataloggers both effective and reliable in our study, not only for recording temperature but also for allowing strong inferences to be made about behavior over large temporal scales.

Our data suggest that hibernation (i.e., brumation) for *C. picta* can be a more active period than previously assumed, at least in southern portions of the range. During winter, *C. picta* have been found buried at depths as great as 45 cm in the mud substrate (Ernst, 1972) and may take advantage of thermal gradients available to them during winter to find the optimum between cold, oxygenated water and warmer anoxic mud (Peterson, 1987). Observations of activity in a Pennsylvania population of *Clemmys guttata* found turtles swimming in waters <10 C and even moving beneath ice cover (Ernst, 1982). *Chrysemys picta* have also been observed

swimming under ice cover and in shallow water at 4 C (Gibbons, 1967). Our results indicate that southern populations of *C. picta* have relatively high levels of activity during winter. Although air temperature and shallow water temperatures were below freezing during several winter days, neither T_s nor the mud or deep water temperatures fell below 0 C. By over-wintering in the mud and/or deep water, adult *C. picta* apparently did not face the same freezing risks as hatchlings in terrestrial nests (Nagle et al., 2000). Turtles may have utilized temperature gradients available to them during winter to avoid freezing. During the coldest weeks, minimum T_s was greater than minimum recorded T_w , indicating that turtles avoided areas of low temperature (i.e., the shallower water); maximum T_s was approximately equal to the maximum recorded T_w , indicating that turtles used the warmest areas (i.e., mud and deep water).

We found that *C. picta* use basking seasonally to obtain high temperatures. Our results indicate that turtles use basking to maximize their T_b predominately during the end of winter and during spring months and, to a lesser degree, in fall. We found low minimum T_s through February and March, correlating with low water temperatures, but turtles reached maximum T_s well above the maximum T_w by basking during times of high insolation (5–16 C above maximum T_w). By basking during cooler months, *C. picta* can be more active and obtain higher T_b for longer periods of time than if they remained in the water. Based on T_s patterns, it appears that turtles often moved from the mud or deep water to basking locations during winter and early spring.

Turtles apparently utilized basking much less during the coldest periods of winter or the hottest periods of summer. During these time periods, we found low numbers of basking events and similar maximum T_s and T_w , indicating that turtles did not leave the water. During the coldest months of the year we suspect turtles did not leave the water to bask because the environment provided no opportunities to raise T_b above T_w . In summer months, our data suggest that turtles did not leave the water because they could reach high T_b without basking. If turtles basked frequently or for long periods of time during

summer, they would likely reach lethal T_b (Ernst, 1972). During summer, lower numbers of basking events have also been observed in other studies. Ernst (1982) observed a decrease in activity in *C. guttata* during the warmest periods of summer. Spotila et al. (1984) found that turtles inhabiting ponds with artificially warmed water basked less than turtles in cooler ponds. The duration of basking events has been shown to be inversely proportional to air temperature in both *C. guttata* and *C. picta* (Ernst, 1982; Lefevre and Brooks, 1995). Sajwaj and Lang (2000) also observed a decrease in thermoregulating events in *Emydoidea blandingii* during summer and suggested increasing the amount of time in aquatic habitats could have benefits such as increased foraging time.

We found that both the overall amount of basking and monthly basking profiles differed for male and female *C. picta*. Surprisingly, we found more basking behavior in male turtles than female turtles. Males basked more than females, particularly in January and February, which may be related to mate searching behavior. A study of river cooters, *Pseudemys concinna*, found that male turtles basked more frequently than female turtles during August and September, but no differences were detected from April–July (Buhlmann and Vaughan, 1991). Although in both our study and in Buhlmann and Vaughan (1991), more basking was observed in males, the time periods are not comparable; we did not detect large differences in basking behavior in August and September. The difference in timing could be due to interspecific differences in seasonal basking behavior. We did not observe any patterns that might suggest females in our southern population basked more during periods of egg development or nesting. This finding does not imply that female turtles do not use basking to aid in egg development, merely that we did not detect more basking by females when compared to males during this time. Results of previous studies are inconclusive on whether a difference exists between male and female *C. picta* in regards to basking frequency and duration (Krawchuk and Brooks, 1998; Lefevre and Brooks, 1995). Although our data describe basking on a broader temporal scale, and we were not able to compare the duration of basking events, our

data do indicated that female *C. picta* do not bask more frequently than male turtles.

Maximum temperatures over the year also varied between sexes; males achieved higher maximum weekly T_s than females. We suspect that this may be due to differences in basking behavior. Higher temperatures were recorded for male turtles because males reached higher temperatures while basking. Perhaps males reached these higher temperatures because they basked for longer periods of time than females, although we could not measure the duration of basking in this study. It is notable that the greatest difference between male and female maximum T_s occurred during the same period as the greatest difference in the number of basking events.

Based on our results, we believe that Thermochron iButton dataloggers provide a reliable and accurate method for monitoring the temperatures of free-ranging, semi-aquatic turtles. We found that Thermochron iButton dataloggers circumvented many of the problems of larger, more expensive dataloggers (e.g., Tidbit Stowaway dataloggers, Onset Computer Inc., Pocasset, MA; 33 mm × 53 mm, 28 g, \$119 US per Tidbit Stowaway compared to 5.9 mm × 17.4 mm, 3.12 g, \$14 US per Thermochron iButton; Angilletta and Krochmal, 2003). We suspect the low recapture rate of individuals during the fall 2002 trapping season was partly due to low water levels that resulted from a 3-yr drought (recapture of marked turtles in the population that were not part of this study was also low). Increased precipitation in early 2003 and the consequent higher water levels resulted in a larger number of turtles recaptured the following spring, as well as eight additional turtles with dataloggers that had not been previously recaptured. Drought substantially increases rates of emigration in freshwater turtles (Gibbons et al., 1983), and we suspect that many of the turtles with dataloggers that were not recaptured moved to nearby ponds during the drought. Future studies with fewer animals could use radio-telemetry to insure the recovery of dataloggers.

Our data show that carapace attachment of dataloggers and measurements of T_s provided good estimates of T_b in most circumstances. Previous research has found that substrate temperature accurately predicts the T_b of

hibernating *C. picta*; thus, datalogger T_s measurements can be considered relatively equivalent to core T_b during hibernation (Peterson, 1987). For investigations of temperature variation during the active season, T_s should closely approximate turtle T_b in water. Measurements of turtles in tanks of water at varying temperatures and field measurements of turtles captured swimming in water indicated that turtles rarely have temperatures more than a few tenths of a degree above water temperature (Boyer, 1965; Brown and Brooks, 1991) and circulatory system effects (e.g., counter-current exchangers) would likely have minimal benefit to small- and medium-sized aquatic turtles (Boyer, 1965). Our results suggest that T_s differs most from T_b during basking and immediately after reentry into water (Fig. 6). The same conclusion was reached in two other studies that found variation between internal temperatures and those recorded by externally attached dataloggers to be greatest during periods of large environmental temperature fluctuation, such as warming (Nussear et al., 2002; Zimmerman et al., 1994). Thus, we conclude that T_s closely approximated T_b for all conditions in our study except during basking events, when turtle temperatures are dependent on a wider number of factors such as of insolation, air temperature, body size and posture, and the duration of the basking event. Carapace temperatures reached during basking were usually between 25 and 32 C, but the few highest basking temperatures recorded for each turtle ranged from 34.5–40.5 C (Fig. 2). As the thermal maximum for painted turtles is approximately 41.5–42.5 C (Brattstrom, 1965; Ernst, 1972), the dataloggers may have warmed faster than the turtles' core temperature. The reason a larger difference between T_s and cloacal temperature was not obvious in our controlled experiment may have been that the "forced" basking period was only 30 min. Although our measurements are reflective of T_b , all turtle temperatures recorded in the field in our study were measured from the carapace and should only be treated as estimates of T_b . We suspect, due to the small body size of *C. picta*, the differences between shell and internal temperature are minimal while in the water, but this difference could be magnified in larger species (e.g., *Pseudemys* or *Gopherus*

as in Nussear et al., 2002). Although core T_b was not measured in our study, examination of temperature plots allowed strong inferences to be made regarding behavior and activity patterns of the turtles (e.g., time of basking versus time spent in water), without the bias induced by or time required for direct observation. Future studies could use surgical implantation to more closely approximate core T_b , a method not used in our study due to the size of our animals.

Numerous studies have highlighted the ability of ectotherms to control their T_b behaviorally during periods of ambient temperature fluctuation. Our study demonstrates that southern populations of *C. picta* are active during much of winter and basking is utilized most by turtles during spring months. During spring, turtles can reach high T_b through basking, despite low T_w , which likely results in numerous energetic benefits (Congdon, 1989). During summer, turtles can apparently achieve the same high T_b without leaving the water, decreasing the risks of exposure and potentially increasing foraging time.

Due to the importance of basking in *C. picta*, human disturbance of turtles may represent an important conservation concern. Turtles are wary while basking and return to the water when disturbed. If basking is continually interrupted, turtles may not be able to reach high T_b during fall and spring months, which may have negative consequences for energy acquisition and reproduction (Avery, 1982; Congdon, 1989; Koper and Brooks, 2000; Krawchuk and Brooks, 1998). Human recreation has been documented as the cause of turtle declines even in protected areas (Garber and Burger, 1995). Sajwaj and Lang (2000) expressed concern over increasing human encroachment, such as fishing and boating, which caused frequent and large disturbances to basking in *E. blandingii*. An additional concern is the clearing of potential basking substrates, such as driftwood and edge habitat, which decreases the number of suitable locations to emerge from the water and leaves turtles more vulnerable while basking. Several studies have found significant correlations between turtle density and woody debris available for basking (reviewed in Bodie, 2001). Future research should consider T_b variation in ectotherms and the behaviors

required for thermoregulation as a potentially important component that should be considered when developing conservation plans.

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