With these actions we insure that the name *Crotalus durissus* will continue to be used for the majority of populations referred to by that name since 1941 and that *Crotalus simus* will be associated unambiguously with a Mexico-Central American species of Neotropical rattlesnake.

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Body Temperatures of Free-Ranging Softshell Turtles (*Apalone spinifera*) in a Small Stream

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The thermal ecology of freshwater turtles is based largely on studies of a relatively few species in which, typically, body temperatures are highly variable, average approximately 24–28°C, and commonly track water temperatures. Basking is a common, but not universal (e.g., *Chelydra*, Brown et al. 1990; *Pseudemydura*, King et al. 1998) behavior associated with elevating body temperature. However, even for the many species that do in fact bask, whether heat gained from basking uncouples body temperatures from water temperatures long enough to be biologically significant in thermoregulation has long been debated and likely varies with species and locality (e.g., Auth 1975; Boyer 1965; Crawford et al. 1983; Di Tranni and Zuffi 1997; Manning and Grigg 1997; Moll and Legler 1971; Schwarzkopf and Brooks 1985; Spotila et al. 1990).

Compared to the various semi-aquatic turtles for which thermal biology has been studied (mostly emydids), it would seem that certain features of the highly aquatic trionychid turtles might impact their thermal ecology. For example, highly aquatic turtles, such as trionychids, (1) have a lower critical thermal maximum (CTM) than semi-aquatic species, such as emydids (Hutchison et al. 1966, 1979); (2) the flat shell of softshells enhances the rate of radiant heat exchange (Boyer 1965); (3) the cutaneous surface area of softshells is the highest known among turtle species (Stone and Iverson 1999); and (4) softshells have the highest rate of evaporative water loss of any known reptile, 3–4 times that of the emydid *Trachemys* (Robertson and Smith 1982). High evaporative water loss causes trionychids, unlike emydids, to cool faster than they heat in air (Smith et al. 1981) and can depress surface and core body temperatures, at least in the laboratory (Khosatzky 1981; Robertson and Smith 1982).

Although the physiology related to various thermal characteristics of trionychid turtles has been studied in the laboratory (Boyer 1965; Hutchison et al. 1966, 1979; Khosatzky 1981; Nebeker and Bury 2001; Robertson and Smith 1982; Smith et al. 1981), field thermal data are extremely sparse. The only available thermal data for free-living trionychid turtles include a few ambient water temperatures measured opportunistically for *A. mutica* and *A. spinifera* (Graham and Graham 1991; Plummer 1977; Williams and Christiansen 1981) and body and ambient water temperatures of hibernating *A. spinifera* measured with temperature-sensitive radiotransmitters (Plummer and Burnley 1997). Body tempera-

tures have not been reported for any free-living trionychid species during their active season. The purpose of this paper is to provide basic field information on softshell thermal ecology by describing body temperatures of free-living A. spinifera in a small stream.

Materials and Methods

We have studied a population of Apalone spinifera by mark-recapture in Gin Creek, a first-order tributary (average width = 4–5 m, depth = ~35 cm) of the Little Red River in White County, Arkansas since 1994 (unpubl. data). A detailed description of the study area is given by Plummer et al. (1997). Softshells were captured by hand or in funnel traps. Of the approximate 300 marked turtles (50 adults) in the population, only adult females were used in the present study because, compared to males, their larger body size facilitated implantation of transmitters and data loggers. Similar body sizes of the selected females (200–240 mm plastron lengths) reduced possible size-related differences in heating and cooling rates. For each softshell, plastron length (PL) and body weight were measured, a unique mark was provided, and a transmitter (Model SM-1, AVM Instrument Co., Livermore, California) was attached to the posterior part of the carapace prior to its release at its site of capture. Beyond these common methods, data were collected differently in 1995 and 2000.

In addition to the attached transmitter, in 1995 a second temperature-sensitive transmitter (Model CHP-2P, Telonics, Inc., Mesa, Arizona) was surgically implanted in each of four adult females. Implanted transmitters (6 x 12 x 30 mm, 6–7 g) were inserted into the body cavity through a small incision made in the body wall anterior to the hind legs near the bridge. The incision was closed with nylon sutures. Combined mass of the attached and implanted transmitters was <1% of turtle mass.

In 1995, each softshell was located each day during their activity season (15 Mar–29 Oct). At each location, the pulse rate of the temperature-sensitive transmitter, water temperature, and air temperature were recorded. We also attempted to determine the turtle's behavior (active, inactive, buried, basking). Transmitter pulse rates were later converted to temperatures from calibration curves constructed previously for each transmitter. At the end of the study period, turtles were recaptured and taken to the lab where implanted transmitters were removed and the incision closed. Turtles were then released at the site of their last capture.

In 2000, a TidBit® temperature data logger (Onset Computer Corp., Pocasset, Massachusetts) was surgically implanted in the body cavities of two adult females using the surgical procedures outlined above. The combined mass of TidBits (17 x 21 mm, 21 g) and attached transmitters was <3% of turtle mass. TidBits were programmed to record temperatures at 5 min. intervals. After implantation, turtles were released into the field. From 11 May to 17 August 2000, we infrequently and irregularly located turtles and attempted to determine their behavior (active, inactive, buried, basking). At the end of the study period, turtles were recaptured and taken to the lab where implanted data loggers were removed for downloading and the incision was closed. Turtles were then released into the field at the site of their last capture.

Basking events were indirectly identified in 2000 by comparing body temperature traces with concurrent water temperatures. Sharp increases (at least 4°C within 60 min.) in sequential body tem-

peratures relative to water temperatures were assumed to represent aerial basking events (Fig. 1). This technique was highly conservative as basking events not resulting in sharp increases in body temperatures could not be identified. For example, brief basking events and basking events occurring in the shade, late in the season when water temperatures were warm, or early in the morning on overcast days may not have been detected on the temperature traces.

To obtain concurrent minimum environmental temperatures available to softshells in 2000, a TidBit data logger was suspended in a pool at a shaded 25 cm depth about 30 m upstream of a low water dam. The pool maintained an approximate constant water level during the course of data collection. To obtain concurrent maximum environmental temperatures available to aerially basking softshells, we constructed a metal softshell model painted medium flat gray and containing a TidBit data logger. At non-lethal temperatures (<35°C) produced in the laboratory with radiant heat, equilibrium temperatures of a tethered softshell and the model were similar. In the field, the model was placed near a known softshell basking site on the stream bank that was exposed to full sunlight throughout the day.

Statistical analyses were conducted with SYSTAT (SYSTAT, 2002). For data that were normally distributed and had homogeneous variances, paired-samples t-tests with Bonferroni probabilities were used to compare body temperatures between buried/basking and early/late season for individual turtles. A nonparametric Wilcoxon test was used to compare body temperatures between active/inactive individual turtles because the data did not meet parametric assumptions. Coefficients of determination (r^2) were used to describe the relative amount of variation in body temperature that was explained by water and air temperatures. Unless otherwise stated, means are accompanied by one standard error.
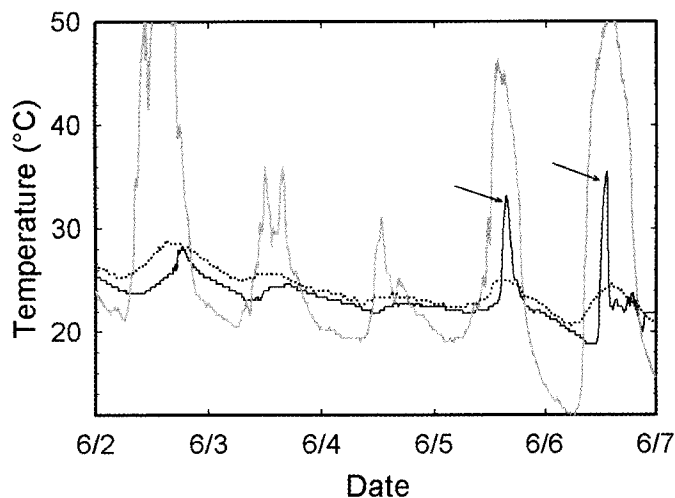

Fig. 1. Water temperatures (dotted line), model temperatures (gray line), and body temperatures (solid line) of an Apalone spinifera on representative days in 2000. Model temperatures were relatively high on 2, 5, and 6 June, but basking occurred only on 5 and 6 June. Arrows indicate spikes in body temperature that were assumed to result from aerial basking on 5 and 6 June. On 3 and 4 June, model temperatures were relatively low; apparently no basking occurred as body temperatures tracked water temperatures with little variance throughout the day.

TABLE 1. Times monitored and body temperatures (°C) of active (moving), inactive (nonmoving), buried in stream substrate, and aerially basking *Apalone spinifera* in 1995. Shown are mean, standard error, and sample size (in parentheses).

	Turtle Number			
Category	4	16	63	80
time	15 Mar–27 Sep	15 Mar–24 Oct	21 Jul–24 Oct	21 Jun–24 Oct
active	25.5 ± 0.42 (76)	25.5 ± 0.42 (95)	27.0 ± 0.65 (39)	27.6 ± 0.6 (39)
inactive	24.0 ± 0.60 (95)	23.0 ± 0.65 (85)	24.3 ± 0.66 (51)	25.7 ± 0.56 (60)
buried	19.9 ± 1.26 (3)	29.3 ± 1.25 (11)	28.5 (1)	28.4 ± 0.98 (15)
basking	25.4 ± 1.78 (9)	28.9 ± 0.82 (12)	(0)	26.3 ± 1.59 (4)

RESULTS

For 1995, a total of 677 body temperatures were measured on four *A. spinifera* throughout their activity season. Categories of body temperatures that could be associated with concurrent turtle behavior were generally similar among the four turtles (Table 1). Body temperatures, pooled from all four turtles, averaged 25.2 ± 0.20°C (range 12.8–34.0°C). Pooled body temperatures of active turtles averaged 26.1 ± 0.25°C (15.2–33.2°C, N = 249) and those of inactive turtles averaged 24.1 ± 0.32°C (21.8–33.4°C, N = 291). Variation in water temperature explained more variation in body temperature among the four turtles (73–89%; mean 81%) than did air temperature (60–63%; mean 62%). Water temperature explained more variation in body temperatures of inactive turtles (78–97%; mean 89%) than active turtles (62–87%; mean 74%). Body temperatures were statistically higher when turtles were active than when inactive for three of the four turtles (Table 1; Wilcoxon, no. 4, Z = -6.05, P < 0.001; no. 16, Z = -5.14, P < 0.001; no. 63, Z = -2.21, P < 0.05; no. 80, Z = 1.02, P > 0.30). For inactive turtles, body temperatures when buried (27.9 ± 0.82°C, 18.0–34.0°C, N = 30) did not differ from basking turtles (27.2 ± 0.84°C, 17.0–32.9°C, N = 25; Table 1; no. 4, t = -6.50, P > 0.30; no. 16, t = 0.65, P > 0.60; no. 80, t = 1.03, P > 0.50). This lack of significance could have resulted from the small sample size or because softshells often buried in very warm water. On several occasions in 1995, we captured softshells buried in substrates that exceeded 33°C.

For 2000, a total of 40,287 body temperature measurements were recorded. Overall body temperature averaged 25.0 ± 0.05°C (17.9 –37.9°C) and the distributions of body temperatures were similar

TABLE 2. Body temperatures (°C) of two *Apalone spinifera* in 2000. Shown are mean, standard error, and minimum-maximum (in parentheses).

Turtle No.	Entire Season (May–August)	Early Season (May–June)	Late Season (July–August)
15	25.7 ± 0.02 (17.9–37.9)	24.2 ± 0.02 (17.9–35.5)	27.6 ± 0.02 (21.9–37.9)
189	25.1 ± 0.02 (18.8–35.9)	24.5 ± 0.02 (18.8–35.9)	28.5 ± 0.04 (25.0–32.8)

between turtles (Fig. 2A). Water temperature explained 65–67% of the variation in body temperature in two turtles. At night (2200–0600 h), water temperature explained 78–84% of the variation in body temperatures compared to 60–63% in the day (0600–2200 h). Body temperatures in late season averaged 2–4°C higher than in early season (t = 115.31, P < 0.001; Table 2; Fig. 2B). Higher seasonal body temperatures were associated with an average 3.5°C higher water temperature and 4.5°C higher model temperature in July and August in 2000.

Opportunities for aerial basking to raise body temperature were rarely constrained by low environmental temperatures as maxi-
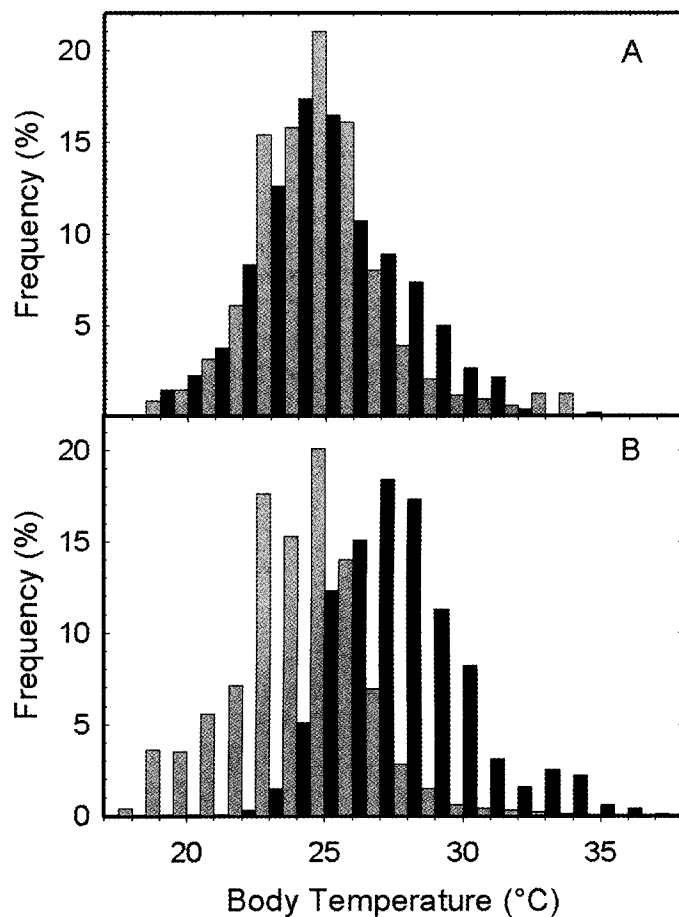

FIG. 2. A. Histogram of body temperatures for two *Apalone spinifera* during the same time period in 2000 (20 May – 6 July; N = 13,680 each turtle). During this period, mean body temperature for turtle no. 15 (dark bars) was 25.1 ± 0.023°C and that for no. 189 (gray bars) was 25.0 ± 0.023°C. B. Histogram of body temperatures for *Apalone spinifera* no. 15 in early season (May–June; gray bars) and late season (July–August; dark bars) in 2000. Mean early season body temperature was 24.2 ± 0.02°C (N = 14,678) and that for late season was 27.6 ± 0.02°C (N = 11,631).

TABLE 3. Statistics of basking in two *Apalone spinifera* as determined from a comparison of body temperature and water temperature tracings in 2000. Shown are turtle number, number of days monitored, number and percent of days that included a basking event, total number of basking events, average number of basking events per day, average number of basking events per day for days that included a basking event, and length in minutes of basking events (mean, SD, min.–max.).

Turtle No.	No. Days	No. Basking Days (%)	No. Basking Events	No. Events/ Day	No. Events/ Basking Day	Length of Basking Event (min)
189	49	25 (51.0)	42	0.86	1.7	104 ± 95 (10–415)
15	96	45 (46.8)	80	0.83	1.8	122 ± 91 (16–560)

mum model temperature exceeded 35°C on 90 of 94 days during the study period. Results from our highly conservative method of identifying aerial basking suggested that each turtle basked about 1.5–2 times per day on at least half of the days it was monitored (Table 3). Basking events averaged 1.5–2 h in length and were highly variable (CVs ~75–90%). We visually observed a total of seven aerial basking events in the field, six of which were later independently identified from the downloaded body temperature data.

DISCUSSION

The few temperature data available for softshells include preferred ambient temperatures for *T. sinensis* in the laboratory (20–25°C; Khosatzky 1981), ambient water temperatures for free-living *A. mutica* early and late in the activity season (13.5–25.5°C; Plummer 1977), preferences of juvenile *A. mutica* in a laboratory thermal gradient (~27°C; Nebeker and Bury 2001), body temperatures of basking *A. ferox* in the laboratory (26.5–35.2°C, mean = 32.7°C; Boyer 1965), and for *A. spinifera*, ambient water temperatures of buried turtles (Graham and Graham 1991) and a telemetered free-living individual (~30°C; Williams and Christiansen 1981), and the preferred (32.7°C), voluntary maximum (35.7°C), and CTM (41°C) determined from individuals in the laboratory (Hutchison et al. 1966). Our estimates of average field body temperatures for *A. spinifera* are toward the low end of the range of body temperatures reported for trionychids in the literature, and were remarkably similar using different methods in two different years (25.2°C in 1995 and 25.0°C in 2000). Highly aquatic turtles, such as softshells, often have lower CTMs than semi-aquatic or terrestrial turtles (Hutchison et al. 1966) and a lower CTM often indicates lower optimum body temperatures during activity for some reptiles (Huey 1982). Nebeker and Bury (2001) found a lower thermal preference for hatchlings of the highly aquatic *A. mutica* compared to the semi-aquatic emydid *Pseudemys nelsoni*.

Softshells appear to function as thermoconformers much of the time, with body temperature tracking water temperature. The higher r^2 values for body and water temperatures for nighttime periods and for inactive turtles reflect basic softshell natural history, i.e., diurnal turtles that spend large amounts of time burrowed in the substrate under water (Ernst et al. 1994). The difference also suggests that daytime-active softshells thermoregulate to some degree. Comparison of early-season and late-season data from both 1995 (Table 1) and 2000 (Table 2; Fig. 2) further emphasizes the large effect that water temperature has on body temperature. Peri-

ods of elevated body temperatures resulting from aerial basking occur commonly, but generally are of brief duration and do not result in a "plateau" of regulated body temperature over an extended period as often occurs in terrestrial reptiles and in some semi-aquatic turtles that shuttle between land and water (e.g., *Emydoidea*, Sajwaj and Lang 2000). Our observations suggest that, despite fundamental differences in behavior (highly aquatic), body shape (flattened), and physiology (high cutaneous surface area and evaporative water loss), field body temperatures of trionychids are similar to that of other freshwater turtles in levels of preference and variation and that softshells appear to most often function as thermoconformers as do many other freshwater turtle species.

The assumption that body temperature spikes indicated aerial basking events was supported by the fact that six of seven basking events directly observed in the field were independently identified on the temperature traces. Aerial basking is a common occurrence for *A. spinifera* in Gin Creek (~50% of days; ~2/d/turtle) and can result in elevated body temperatures. These results compare favorably with Auth's (1975) direct observations of basking in *Pseudemys scripta* (44% of days; 2–3/d/turtle, up to 5/d in favorable weather) especially given that our highly conservative indirect method likely failed to detect every basking event. In addition to aerial basking, we observed *A. spinifera* practicing partial aerial basking (i.e., body partially submerged; N = 5 observations), as did Graham and Graham (1997) and Plummer and Burnley (1997).

Basking may have several functions in turtles (summarized in Boyer 1965; Moll and Legler 1971). For some species, thermoregulatory heat gain is primary (e.g., Crawford et al. 1983; Spotila et al. 1990) whereas other turtles commonly bask without raising body temperature (e.g., Manning and Grigg 1997). Aerial basking coupled with terrestrial behavior may be important in the daily and seasonal thermal strategy of semi-aquatic turtles such as *Emydoidea* (Sajwaj and Lang 2000) and *Clemmys* (Litzgus and Brooks 2000), but *Apalone* species are highly aquatic and typically leave water only briefly to nest and bask (Ernst et al. 1994; MVP pers. obs. 1975, 2003). We do not deny the importance of basking in *Apalone* spp. as it apparently is a widespread, commonly occurring behavior the specifics of which differ among sympatric *Apalone* species (Lindeman 2001) and possibly between the sexes (Plummer 1977). Nevertheless, considering the behavior of softshells and a morphology/physiology that promotes rapid environmental heat exchange, we doubt whether body temperatures of basking *Apalone* are uncoupled from water temperatures long enough to be of thermoregulatory significance in their over-

all thermal strategy (Congdon 1989).

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Sources of Larval Identities for Amphibians from Borneo

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At present, 160 species of amphibians (composed exclusively of Anura and Gymnophiona) are known from Borneo (Das 2005; Das and Haas 2005; Inger and Stuebing 2005). The last summary of knowledge on their larval forms, compiled by Inger (1985), revealed that 45–60% of the fauna then described (63 larval forms), had known larval stages. An additional 14 larval forms could not be assigned to the parent species at the time. Some progress has been made in the two decades that has now elapsed, through the