Thermal biology and temperature-based habitat selection in a large aquatic ectotherm, the alligator snapping turtle, *Macroclemys temminckii*

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ABSTRACT

Ectotherms in water experience rates of heat transfer at least two orders of magnitude greater than in air, seriously constraining their thermoregulatory capabilities. Yet, even in water, individuals may exert control over body temperature (T_b) via behaviors such as selecting thermally favorable microhabitats. The interactions among body size, physiology, and behavior on the thermal biology of large, entirely aquatic, ectotherms is poorly understood. We tested the hypothesis that alligator snapping turtles (*Macroclemmys temminckii*) selected microhabitats based on temperature by comparing temperatures at sites used by turtles to temperatures at randomly selected sites. These large turtles selected a narrow range of microhabitats that were significantly warmer and less variable in temperature than random sites. Cooling trials in the laboratory indicated larger turtles equilibrated more slowly to ambient temperature (T_a) than smaller turtles. We recorded T_a and body temperature (T_b) of turtles in the field continuously throughout the year. The T_b generally conformed to T_a but there were periods when $T_b - T_a$ differences were great. These results suggest that while physiology and size of aquatic turtles can affect T_b transiently, microhabitat selection may be the only meaningful mechanism for large, entirely aquatic, turtles to control T_b.

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1. Introduction

Early studies of the role of temperature in ectotherm biology emphasized the precision of thermoregulation (*e.g.* Cowles and Bogert, 1944). However, later studies showed many ectotherms lacked thermoregulatory precision and conformed to ambient temperatures (Rand, 1964; Brattstrom, 1965). Regardless, temperature is central to the lives of both thermoregulators and thermoconformers, influencing every aspect of their biology including performance, growth, reproduction, and metabolism (Huey, 1982). Ectotherms achieve body temperature via physiological mechanisms and behavioral interactions with their environment (Hertz et al., 1993; Huey, 1991). An accurate picture of an organism's thermal biology can therefore be gained by disentangling the interactions between physiology, behavior, and environment.

Body size influences an organism's thermal inertia by increasing time required for T_b to equilibrate to T_a (Terpin et al., 1979; Schmidt-Nielsen, 1984; Stevenson, 1985; Turner and Tracy, 1985; Seebacher et al., 1999). McNab and Auffenburg (1976) demonstrated thermal inertia associated with large body sizes ("giganteothermy" Spotila et al., 1991) in Komodo dragons (*Varanus komodoensis*). Large

individuals' T_b was greater than T_a throughout the night due to effects of thermal inertia. There are fewer examples of aquatic ectotherms maintaining a $T_b - T_a$ differential. A very large species, the leatherback turtle (*Dermochelys coriacea*), maintained T_b 18 °C warmer than T_a (Frair et al., 1972). The ability of leatherback turtles to achieve large temperature differentials was attributed to a combination of thermal inertia and locomotor thermogenesis (Neill and Stevens, 1974).

Although body size plays a large role in determining T_b, individuals may also exert control over T_b via behaviors such as basking and microhabitat selection (Stevenson, 1985). Galápagos land iguanas (*Conolophus pallidus*), for example, selected microhabitats that allowed them to minimize variation in T_b during activity and inactivity (Christian et al., 1983, 1984).

Physiological mechanisms enable ectotherms to exert control over T_b by altering rates of heating and cooling. It is well known from laboratory studies that reptiles heat faster than they cool (Bartholomew, 1982), and changes in circulation account for variation in heating and cooling rates (Turner, 1987). By altering blood flow to extremities and lungs, reptiles increase or retard heat loss or gain. Some aquatic turtles gain heat 25% faster than they lose heat (Weathers and White, 1971).

Rapid rates of heat transfer in the aquatic environment seriously constrain thermoregulatory capabilities of aquatic ectotherms. Ectotherms in water experience convective heat loss at least two

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orders of magnitude greater than in air (Porter and Gates, 1969; Turner, 1987). Not surprisingly, most studies have shown body temperature (T_b) of aquatic ectotherms conforms to ambient temperature (T_a). Basking emydid turtles raised T_b well above T_a but, when submerged, quickly equilibrated to water temperatures (Avery, 1982; Crawford et al., 1983). Shine and Lambeck (1985) found T_b of the aquatic Arafura filesnake (*Acrochordus arafurae*) was closely correlated to ambient water temperature.

These studies raise questions about the role of temperature in the ecology of aquatic ectotherms. Faced with high rates of heat transfer are physiological and behavioral mechanisms of temperature control important to an aquatic ectotherm? How important is body size to thermal biology of relatively inactive aquatic ectotherms? We hypothesized large body size, in conjunction with behavior and physiological control of heating and cooling rates, would retard heat loss and play a role in thermal biology of *Macroclemmys temminckii* in the field. Although we expected these aquatic ectotherms would largely conform to ambient temperatures (Brown et al., 1990), we predicted body size and physiology would play a role in thermal biology of *M. temminckii* and the turtles would select microhabitats based on T_a. We used 3 approaches to examine effects of habitat selection, physiology, and size on thermal biology of a large aquatic ectotherm, *M. temminckii*, Troost, (alligator snapping turtle). We measured habitat selection based on temperature in a sample of *M. temminckii*. We also continuously monitored T_b and T_a in a separate, replicated sample of individuals in the field. In the lab, we measured cooling rates of an ontogenetic series of *M. temminckii* to quantify effects of body size on thermal inertia.

2. Materials and methods

2.1. Study area

The study site was an oxbow lake of the Neches River, Tyler Co., Texas (N 30° 39′ 09″; W 94° 05′ 39″; 18 m asl). The lake is a natural oxbow that became completely isolated from the river by an earthen dam constructed in the mid 20th century. The lake is 3.4 km long and ranges in width from 10 to 76 m with sharply sloped banks, a mean depth of 2.4 m, and a maximum depth of 5.4 m. Water level of the lake fluctuated < 1.5 m during the study. The lake was acidic, stained, and turbid because of large amounts of leaves and vegetation accumulated on the lake bottom. Herbaceous vegetation was sparse and consisted of duckweed (*Lemna sp.*), mosquito fern (*Azolla caroliniana*), water-milfoil (*Myriophyllum spicatum*) and occasional mats of water lily (*Nuphar sp.*). Woody vegetation included bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), river birch (*Betula nigra*), and wax myrtle (*Myrica cerifera*).

2.2. Animal capture, telemetry, temperature logging

M. temminckii were captured through the use of large (1.2 m diameter) hoop nets baited with fresh fish. Once captured, turtles were individually marked using stainless steel pan-head screws placed in the rear marginals of the carapace. Eleven turtles were fitted with external radio transmitters (16 M, Advanced Telemetry Systems, Isanti, MN, weight=29 g). Four of these turtles were fitted with an externally mounted temperature datalogger (Stoway® Tidbit™, Onset Computer Corporation, Pocasset, MA, weight=14 g) and a temperature data logger surgically implanted inside the body cavity 2 cm posterior to the plastron and anterior to the right hind limb. The data loggers recorded T_a and T_b (± 0.2 °C) every 24 min for 132 days . Turtles were released at the point of capture and then recaptured to retrieve recorded data.

Two individuals were monitored from 2 August 1997 until 12 December 1997, 1 from 18 October 1997 until 27 February 1998, and for 1 individual from 12 June 1998 until 3 October 1998.

2.3. Habitat selection

Radio-tagged individuals were relocated at least six times per month. We tested the null hypothesis that turtles did not select microhabitat sites based on temperature by comparing water temperatures at locations the turtles were using to water temperatures at paired, random sites available to them. For each measured occupied site (OS) we chose a paired random site (RS). This method randomly chooses sites that were available to the individual turtle at the same time, but that were not occupied. Random sites were chosen using two random numbers generated from the uniform distribution. The first random number dictated linear stream distance (m) from OS, while the second dictated the percentage of distance across the oxbow. The distance from OS to RS was constrained to between 4 and 100 m. Distances < 4 m were eliminated because in some cases, such as when turtles were beneath large submerged logs, short distances to RS may not have represented distinct microhabitat sites. Distances > 100 m were eliminated because distant sites may not have been available to the individual turtle at the time it selected its current position. Whether distance was measured upstream or downstream was determined by the toss of a coin. At OS and RS, we simultaneously measured water temperature (0.1 °C) using a Type T thermocouple thermometer (TH-65, WesCor, Logan, UT).

The paired approach inherent in the OS and RS method increased our power to detect differences between selected and available habitats over methods that compare unpaired means of habitat use and availability (Waldschmidt and Tracy, 1983; Beck and Jennings, 2003). Adequate sample size insured that the universe of potentially occupied microhabitats was included in the randomly chosen paired sites. Each pair of OS and RS was independent among individuals. Alternative methods to test for temperature selection would have required measuring the temperature of the entire lake independently each time we examined an occupied microhabitat site. Use of the OS and RS method eliminated these pitfalls.

2.4. Heating and cooling trials

To ascertain the effects of size on cooling rates, we subjected five *M. temminckii* to cooling trials in the lab. Turtles ranged in size from 0.7 to 26.25 kg. Turtles were maintained in the laboratory in metal tanks (115×60 cm^2) filled with water at 23–25 °C for at least two weeks and fed fresh fish biweekly. No food was offered for two days before each trial. Type T thermocouples were passed through a 16 Ga hypodermic needle and inserted into the body cavity at the same location, where miniature data loggers were implanted in turtles in the field. The thermocouple was held in place with a suture and attached to a temperature datalogger (CR10, Campbell Scientific, Logan, UT) programmed to measure and store the temperature of the body cavity every 15 s. Water in the tanks was stirred with a small submersible pump to prevent thermal stratification. We confirmed that T_a was held to ± 1.0 °C by logging tank temperature on the bottom, mid-level, and near the surface and inspecting temperatures after the trial. Ambient temperature was adjusted as needed by adding hot water or ice. Trials consisted of placing the subject at room temperature into a tank at 32 °C. Once T_b reached 31.5 °C, we transferred the subject to a tank at 18 °C and logged T_b until it reached 18.5 °C. We then calculated cooling rates from the resulting cooling curves.

2.5. Analyses

We used a paired t-test to test for differences in temperature between OS and RS at locations for the radio-tagged turtles. Unbalanced numbers of repeated measures among the radio-tagged individuals presented problems for paired analyses. We minimized lack of independence in the habitat selection dataset by analyzing means for each individual's OS and RS temperatures. This approach was statistically valid (Hurlbert, 1984), but reduced our sample size from 158 observations of habitat use to 11 (the number of telemetered turtles for the habitat selection study). Moreover, averaging the data may mask some important variation. Therefore, we also used resampling statistics to evaluate the robustness of the habitat selection test (Hood, 1999). The randomization routine reshuffled the OS and RS temperature data for each individual and recalculated the paired t-test. We obtained the frequency distribution of simulated t-values with a Monte Carlo analysis (5000 replicates), and calculated the probability that the critical t-value, ($t_{0.05,\ 10} = 2.228$), was exceeded in the randomized tests. Low probability (< 0.05) of obtaining significant results in the randomized replicates would indicate the real test result was not spurious.

To determine the relationship between T_a and T_b of turtles in the field, we calculated linear regressions for each of the four turtles that were monitored with data loggers, using T_a as the independent variable and T_b as the dependent variable, and compared the variances of T_a and T_b for each turtle with paired t-tests. We applied a square-root transformation to variances to correct skewness in the dataset. Once transformed, the values were unimodal and approximately normally distributed. To examine the extent and frequency that T_b differed from T_a, we subtracted T_a from T_b for the 4 paired time series, pooled. We calculated the frequency distribution of $T_b - T_a$ differentials and tested for skewness and kurtosis to reveal patterns of differences between T_a and T_b. We examined daily patterns of T_b by computing and plotting pooled means for each of the 60, 24 min, time periods each day.

We also examined patterns in the time series of $T_b - T_a$ differentials to gain insight to turtle movements between areas with different ambient temperatures. A turtle whose T_b was not in equilibrium with T_a should exhibit periods when differences between T_b and T_a were independent through time. This could occur in a turtle moving through water of different temperatures, especially if long lag times were required for T_b to equilibrate with T_a, which is the case in large ectotherms. Conversely, if a turtle remained at equilibrium with T_a, differences between T_b and T_a would be close to zero through time, indicating the turtle was stationary or moved quickly to another place with similar ambient temperature.

Problems measuring operative temperature (T_e) are avoided for animals like M. temminckii that are entirely aquatic, remain in relatively deep (> 1 m), dark water, and never bask (Sloan and Taylor, 1987; Ernst et al., 1994; Harrel et al., 1996). Factors other than temperature have low probability of affecting T_e because the high heat capacity of water results in very rapid integration of all influences on water temperature. The water at our study site was stained and turbid, minimizing probability of solar and reflected radiation to directly influence T_b. There were no measurable currents in the lake, cold or hot springs, or any detectable temperature gradients at scales relevant to measurement of T_e for M. temminckii (e.g., vertical stratification 0.5 m off the bottom) that could create variability in water temperature at different points on the surface of even a large M. temminckii. Therefore we assumed the single temperature measured by the datalogger positioned on the carapace of the turtle adequately represented the temperature of the water surrounding the turtle.

These characteristics of the study system coupled with fast rates of heat transfer in water allowed us to assume $T_e = T_a$, and that turtles equilibrated to ambient water temperatures when stationary for several hours.

Differences between heating and cooling rates of turtles in the field were calculated, and heating and cooling time constants (τ) were calculated for each 24 min interval for each turtle from the field. In all calculations of τ from field data the water temperature was constant. Tau (the time constant) is a mathematically derived constant equal to the time necessary for an organism's T_b to increase or decrease 63% of the difference between T_a and T_b. It is expressed in minutes and is independent of the magnitude of difference between T_a and T_b. Tau was calculated by regressing time on natural logs of differences between T_b and final temperature ($\ln(T_b - T_f)$). The slope of the regression is $-1/\tau$ (Bakken, 1976; Neill and Stevens, 1974; Turner, 1987). We assumed study animals were not absorbing solar radiation. The values of τ for each 24-min period were sorted according to whether the turtle was heating or cooling. We tested the null hypothesis that mean heating and cooling rates (τ) were equal using a paired t-test on differences between heating and cooling time constants from the field data.

3. Results

3.1. Microhabitat selection based on temperature

M. temminckii occupied microhabitat sites that were warmer on average than randomly chosen unoccupied sites. Mean microhabitat temperatures at 158 sites where turtles were found (mean = 19.25 °C) were significantly warmer than at paired RS locations (18.11 °C; $t = 2.91$, df = 10, $p = 0.015$; Table 1). We used a randomization test to evaluate the robustness of this result (Hood, 1999). The test randomized observed OS and RS data and

Table 1
Descriptive statistics for water temperature at microhabitat sites occupied (OS) by individual M. temminckii and randomly chosen sites (RS).

Subject ID no.	Mass	n	Occupied sites min−(mean)−max variance	Random sites min−(mean)−max variance
21	15.25	14	10.3−(15.94)−24.4 34.21	10.4−(16.29)−27.5 47.88
26	8.20	18	10.6−(17.56)−29.0 45.03	10.2−(16.72)−26.4 40.43
28	17.50	18	9.9−(18.59)−28.2 53.87	10.1−(16.45)−30.0 38.26
30	11.25	14	20.3−(26.64)−29.6 4.89	17.2−(22.87)−32.2 20.93
36	10.50	10	10.4−(11.17)−12.7 0.70	10.2−(11.31)−14.0 1.34
37	27.50	5	10.4−(11.34)−13.6 1.78	10.0−(10.36)−10.9 0.11
39	17.75	18	20.6−(24.86)−29.5 8.61	16.7−(22.32)−29.4 15.64
47	21.50	13	20.6−(24.95)−28.9 8.62	18.4−(25.32)−35.4 13.22
51	21.50	10	10.2−(11.29)−12.6 0.88	10.0−(10.97)−13.9 1.41
74	17.25	15	21.5−(25.32)−28.7 4.39	19.1−(24.06)−30.9 16.78
77	15.00	20	19.2−(24.15)−27.5 6.51	16.2−(22.51)−33.4 25.45
Pooled		158	9.9−(20.37)−29.6 45.91	10.0−(19.06)−35.4 46.20
Averaged			14.9−(19.26)−24.1 15.41	13.5−(18.11)−25.8 21.95

recalculated the paired *t*-test (5000 replicates). The critical *t*-value, ($t_{0.05, \ 10}=2.228$), was never exceeded in the randomized test, yielding a very low probability ($P < 0.0001$) the result was spurious. We also calculated a paired *t*-test on the pseudoreplicated data (all 158 observations pooled) and this result was also significant ($t=3.69$, df=10, and $p < 0.0004$).

In addition to warmer average OS, there were significant differences in the variance between OS and RS (Table 1). The mean of variances at RS (mean RS variance=21.95°) was significantly greater than temperature variance at OS (mean OS variance=15.41°; paired *t*-test, $t=-2.11$, df=10, and $p=0.002$), indicating narrower range of temperature regimes at occupied microhabitat sites.

3.2. Seasonal and daily patterns of T_b and T_a

Data loggers recorded T_a and T_b simultaneously from four turtles in the field, providing replicated measures of $T_b - T_a$ differentials over long time series. The highest T_b experienced by any turtle was 32.62 °C while the lowest was 8.97 °C. Maximum and minimum water temperatures recorded from the datalogger on the carapace of the turtles were 38.17 and 8.60 °C, respectively (Table 2). Monthly mean T_b for the months sampled was highest in July (mean=27.76 °C) and lowest in December (12.21 °C).

Body temperature was less extreme and more constant than T_a in all subjects. Mean monthly T_a closely matched mean monthly T_b, but T_a was more variable (Table 2). Daily patterns of T_a and T_b also showed strong correspondence, with greater fluctuations in daily T_a (Fig. 1). The warm temperature pulses presumably were recorded when a turtle moved to a warmer spot. Maximum T_a was higher than maximum T_b and minimum T_a was lower than minimum T_b in every month (Table 2). Differences between minimum and maximum T_a and T_b were highest in summer months (July: T_b min$-T_a$ min=3.3 °C, T_a max$-T_b$ max=6.9 °C; August: T_b min$-T_a$ min=5.7 °C, T_a max$-T_b$ max=5.45 °C) and gradually decreased with onset of winter, with smallest differences between minimum and maximum T_a and T_b occurring in January (January: T_b min$-T_a$ min=0.38 °C, T_a max$-T_b$ max=0.27 °C).

While there was a diel cycle of difference between T_b and T_a, there was no daily pattern of T_b. Monthly mean temperatures of the 60, 24 min, periods of each day differed in most cases by less than 1 °C and never more than 2 °C (Fig. 2). Hence, turtles' T_b was relatively stable throughout the day, even though they were moving through waters of different temperatures.

3.3. Thermoregulatory patterns

M. temminckii were largely thermoconformers with T_b closely matching T_a (Fig. 3). Slopes of the regression lines formed by T_b and T_a for three turtles were very close to 1 (Slopes=0.977, 0.992, 0.992) with R^2 values ranging between 0.955 and 0.985. One subject (#30) differed from the rest in that its slope (0.837) and associated R^2 (0.701) were slightly lower. There was more opportunity for variation between T_b and T_a for this individual because it was monitored only in summer and early fall when T_a was more variable.

Differences between T_b and T_a for all turtles pooled were approximately normally distributed but clustered around the mean (kurtosis=14.66) and slightly skewed to the left (skewness=-0.136; Fig. 4). Mean $T_b - T_a$ differentials equaled 0.32 °C. Minimum and maximum values were -9.33 °C and 7.62 °C, respectively, and 90% of values fell between -0.84 and 1.24 °C indicating T_b was within 1.5 °C of T_a most of the time.
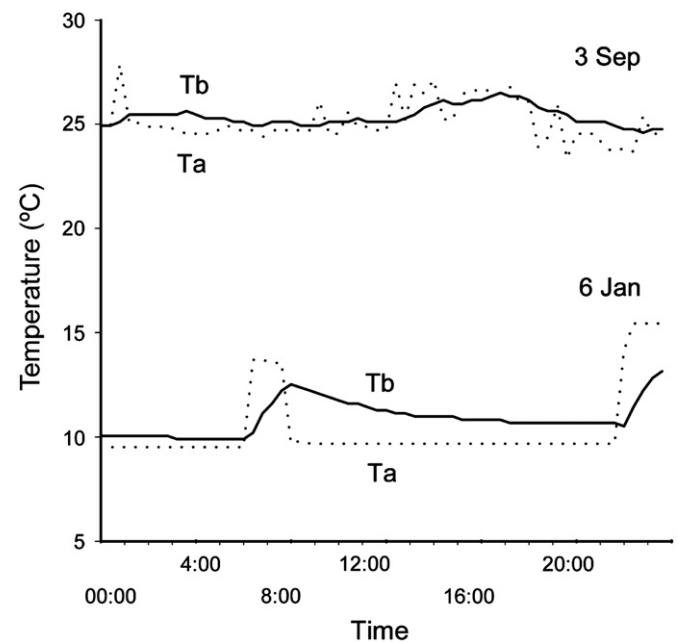

Fig. 1. Examples of T_b and T_a from two *Macroclemys temminckii* in the field. Solid lines represent T_b and dashed lines represent T_a.

Table 2
Descriptive statistics of monthly T_b and T_a (°C) logged continuously from 4 *Macroclemys temminckii* in the field.

|	Month								Total
	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	
Body temperature (T$_b$)									
Mean	27.76	27.37	25.16	20.71	14.67	12.21	12.24	13.13	19.96
Min	24.07	22.38	21.04	15.17	11.57	8.97	9.44	11.45	8.97
Max	31.27	32.62	30.13	25.63	20.43	16.12	16.59	17.39	32.62
Variance	1.78	1.96	2.39	5.41	3.12	2.91	2.72	1.66	39.22
n (turtles)	1	3	3	4	3	3	1	1	4
n (measurements)	960	5400	5400	4710	5400	3260	1860	1614	28,604
Ambient temperature (T$_a$)									
Mean	27.76	27.12	24.93	20.36	14.25	11.69	11.89	12.82	19.63
Min	20.74	16.67	17.79	14.8	11.38	8.60	9.06	11.23	8.60
Max	38.17	38.07	30.8	25.87	21.02	15.91	16.86	18.31	38.17
Variance	4.35	3.21	3.17	5.69	3.36	3.30	3.51	2.17	41.01
n (turtles)	1	3	3	4	3	3	1	1	4
n (measurements)	960	5400	5400	4710	5400	3260	1860	1614	28604
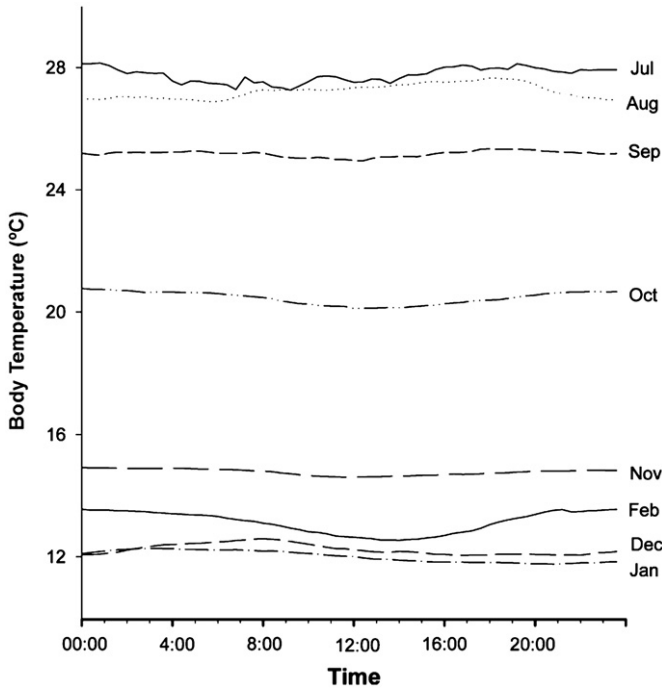
Fig. 2. Mean daily body temperatures of *Macroclemys temminckii* for each month.

Body temperature increased rapidly when the turtle was in a relatively warm environment and decreased slowly when the turtle moved to a cooler site (Fig. 1). Heating and cooling constants were also smaller when the *M. temminckii* were heating than when they were cooling (Table 3), and despite small sample size, the difference was significant (paired *t*, $t = 3.18$, df = 3, $p < 0.02$). Additionally, variances in T_b were significantly smaller than variances in T_a (paired *t*, $t = -6.82$, df = 4, $p = 0.016$; Table 3).

3.4. Cooling rates and body size

Cooling trials in the lab clearly demonstrated thermal inertia in *M. temminckii*. Largeer individuals cooled much more slowly than smaller individuals (Table 4). The largest turtle (26.25 kg) took 326 min to cool from 32 to 18 °C, whereas the smallest individual (0.7 kg) cooled from 32 to 18 °C in 27.75 min. Log τ and log mass scaled linearly [log $\tau = 0.803$ log mass -1.52 ($r^2 = 0.947$)] (Fig. 5).

4. Discussion

M. temminckii T_b's generally conformed to environmental temperatures in the field. Turtles that were warmer or cooler than their surroundings eventually equilibrated to ambient temperature presumably because of high rates of heat exchange in the aquatic medium. Although T_b rarely differed from T_a by more
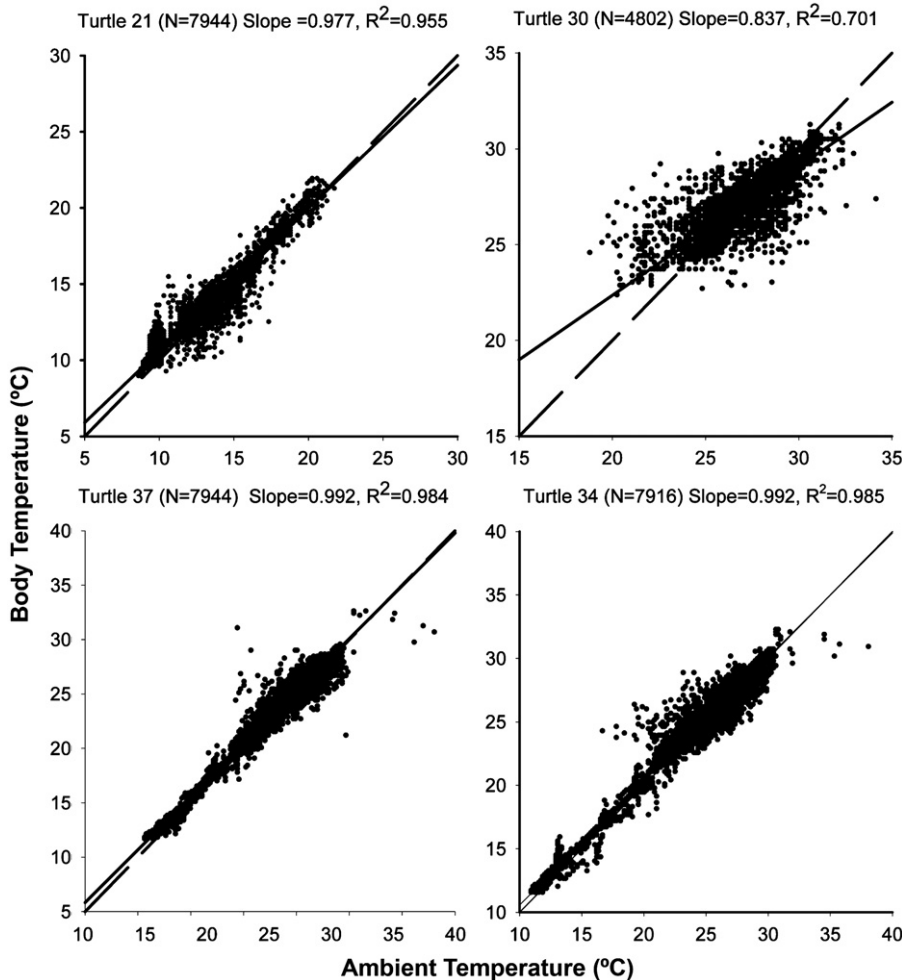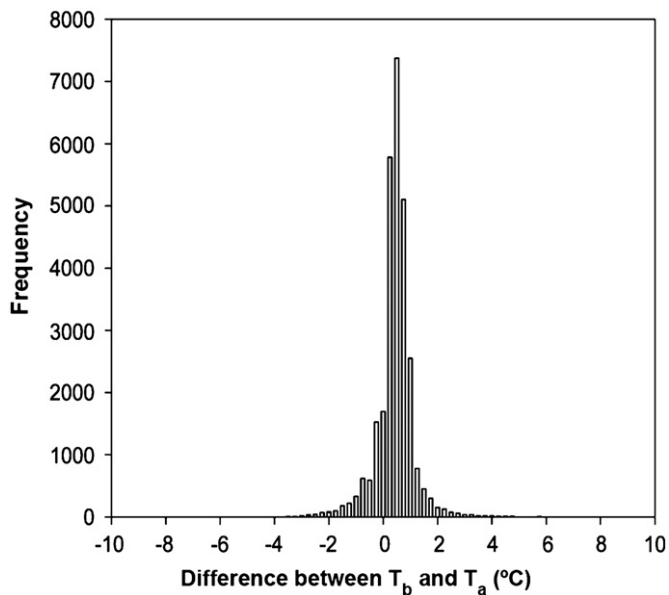

Fig. 3. Scattergrams of T_b versus T_a for four *Macroclemys temminckii* in the field. Regression lines are solid. Dashed lines show a slope of 1 ($T_b = T_a$).

Fig. 4. Frequency histogram of differences between T_b and T_a for four *Macroclemys temminckii* in the field. Positive values indicated $T_b > T_a$; negative values indicated $T_a > T_b$.

Table 3
Means, variances, and heating and cooling rates (τ) for subjects in the field.

Turtle ID	Mass	Mean T_b	Mean T_a	T_b variance	T_a variance	Heating τ	Cooling τ
37	27.50	20.98	20.62	26.01	27.14	52.56	139.2
34	10.50	21.27	20.96	32.26	33.29	47.15	119.92
30	11.25	26.93	26.81	2.65	4.12	62.56	86.94
21	15.25	13.41	13.00	6.45	6.97	66.20	128.77
Summary	16.13	20.65	20.34	16.84	17.88	57.12	118.70

Table 4
Cooling rates (τ) for 5 *Macroclemys temminckii* subjected to a 14 °C change from 32 to 18 °C during cooling trials in the laboratory.

Turtle ID	Mass (kg)	Minutes	Thermal time constant (τ)
101	0.70	27.75	7.26
24	3.50	89.00	13.51
22	4.25	91.50	28.65
52	7.00	175.00	37.45
33	26.25	326.00	111.11
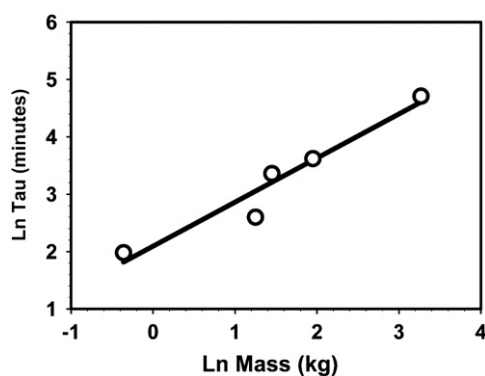
Fig. 5. The relationship between cooling time constants (τ) and turtle mass.

than 1.5 °C, there were periods when differences between T_b and T_a were great, leaving the potential for some control of T_b through behavioral and physiological mechanisms.

Shine and Madsen (1996) suggested thermoregulatory behaviors may be unimportant to large reptiles. They found water pythons (*Liasis fuscus*) maintained stable T_b without overt thermoregulatory behavior and found no evidence of temperature-based microhabitat selection. They attributed lack of thermoregulation in this species to abundance of suitable T_as and thermal inertia. For *M. temminckii*, not all microhabitats were thermally equivalent. We showed *M. temminckii* did select relatively warmer microhabitat sites based on their availability in the environment and occupied sites that were less variable in temperature than random sites. A study of microhabitat use by M. temminckii also showed that individuals used significantly deeper water during the warmest and coolest months (Riedle et al. 2006). Hence, turtles selected a surprisingly narrow range of microhabitats that were relatively warm. Large saltwater crocodiles (*Crocodylus porosus*) controlled T_b via basking and shuttling between warm and cool microhabitats (Seebacher et al., 1999). Unlike crocodilians, however, *M. temminckii* do not bask and we suggest temperature selection was probably the only mechanism whereby *M. temminckii* could exert control of T_b for long periods when T_b would eventually reach equilibrium with T_a. Selection of microhabitats based on temperature was apparent for *M. temminckii*, and we suggest it was important for their thermoregulation.

Daily average T_b during each month was surprisingly stable (Fig. 2) and T_b was tightly correlated with T_a (Fig. 3), because *M. temminckii* remaining in one spot equilibrated to T_a. However, the distribution of $T_b - T_a$ differentials showed T_b was different from T_a in many cases, no doubt reflecting movements of turtles into cooler or warmer water. Turtles move for many reasons, and we do not suggest turtles were only moving in order to thermoregulate.

Our results suggest *M. temminckii* exhibited some physiological control over body temperatures. Turtles in the field had smaller heating time constants than cooling time constants. *M. temminckii* heated more rapidly than they cooled presumably because of physiological phenomena such as changes in heart rate, blood shunting, and blood flow to extremities that are well known in turtles and other large reptiles (Weathers and White, 1971; Pough et al., 1998). In addition to the physiological controls *M. temminckii* presumably exerted over rates of heat loss, we confirmed thermal inertia in *M. temminckii* and described the relationship between cooling rate and body size.

5. Conclusions

We demonstrated that *M. temmincki* selected microhabitat sites based at least in part on those sites having warmer and less variable temperatures than nearby random sites. Individuals select resting sites based on multiple features such as habitat structure, suitable refuge, and ambush sites; we did not attempt to disentangle the relative importance of all factors in behavioral decisions exhibited by these turtles. However, we can conclude that effects of thermal inertia, due to the large size of these turtles, coupled with physiological control over rates of heat transfer resulted in less extreme and less variable values of T_b than T_a. Taken together, behavior, thermal inertia, and physiology apparently created the potential for *M. temminckii* to extend the range of habitats exploited and the amount of time spent there before reaching equilibrium with T_a.

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