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Source: *Herpetologica*, Vol. 35, No. 3 (Sep., 1979), pp. 234-239

Published by: [Herpetologists' League](#)

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BODY HEATING AND COOLING IN THE MUDPUPPY, *NECTURUS MACULOSUS*

KEITH A. ANDERSON AND THOMAS L. BEITINGER

ABSTRACT: Body temperatures of 26 mudpuppies, *Necturus maculosus*, weighing 59.6–221.8 g were monitored following reciprocal exposures to 22 and 28 C. Temperature change halftimes ($T_{1/2}$) for heating and cooling were significantly correlated to body weight in a double logarithmic fashion. Best fit regression equations were: $\log T_{1/2} = -0.64 + 0.47 \log \text{wt}$ and $\log T_{1/2} = -0.35 + 0.35 \log \text{wt}$ for heating and cooling, respectively. Mean heating-cooling ratios were less than unity in both live (0.926) and dead (0.960) animals. The similarity in heating and cooling times is related to the physiological ecology of this species.

Key words: Amphibia; Caudata; Proteidae; *Necturus*; Heating; Cooling

IN addition to behavioral responses, numerous ectothermic vertebrates possess limited physiological control over their body temperatures. Physiological intervention appears as temperature induced adjustments in cardiovascular processes and/or endogenous heat production which influence rates of change of body temperatures in animals relative to the direction of change in environmental temperature (Bartholomew et al., 1965; Morgareidge and White, 1969; Weathers, 1971). Inequalities in rates of body heating and cooling (i.e., heating-cooling hysteresis) were first observed in lizards of the families Agamidae, Varanidae, Scincidae, and Iguanidae (Bartholomew and Tucker, 1963, 1964; Bartholomew and Lasiewski, 1965; Bartholomew et al., 1965; Bartholomew, 1966). The direction of hysteresis (whether body heating or cooling rates are faster) appears to be dependent on the relationship between an individual's ecritic or preferred temperature and environmental temperatures particularly during foraging. In the majority of species, heating rates exceed cooling when environmental temperatures are lower than ecritic temperature. Examples are numerous among lizards (see references above) and also include turtles (Weathers and White, 1971; Spray and May, 1972), crocodilians (Smith, 1976; Grigg and Alchin, 1976), 1 snake (Dmi'el and Borut, 1972) and fishes (Crawshaw, 1976; Spigarelli et al., 1977;

Beitinger et al., 1977). However, in at least 3 species of turtles more rapid cooling has been reported (*Terrapene ornata*—Betha, 1972; *Terrapene carolina* and *Gopherus polyphemus*—Spray and May, 1972).

Body temperature relations and rates of heat exchange have been examined in a variety of fishes, and semiaquatic and terrestrial reptiles. However, few data exist for amphibians, particularly aquatic salamanders (Brattstrom, 1963; 1970). Among the giant aquatic salamanders of North America (*Siren*, *Amphiuma*, *Cryptobranchus*, *Necturus*), physiological ecology of the mudpuppy, *Necturus maculosus*, has received the most attention with the majority of the research conducted by V. H. Hutchison and his colleagues. *Necturus maculosus* exhibits trimodal gas exchange (Guimond and Hutchison, 1972), has a critical thermal maximum of approximately 35.7 C which is influenced by acclimation (Hutchison and Rowlan, 1975), and behaviorally selects temperature in laboratory thermal gradients (Hutchison and Hill, 1976).

The objective of this study was to characterize the kinetics of body temperature in the mudpuppy and relate this information to the physiological ecology of the species.

MATERIALS AND METHODS

Trials consisted of monitoring the body temperatures of 26 *N. maculosus* (59.6–

221.8 g, $\bar{x} = 122.9$ g) exposed to an instantaneous change of ± 6.0 C in water temperature by reciprocal transfer between constant temperature baths set at 22.0 and 28.0 C. Each bath consisted of a 40-liter aquarium (animal chamber) placed within a 200-liter fiberglass tank. Temperatures in the inner chambers were maintained within ± 0.1 C by circulating thermoregulators mounted in the outer tanks. A single airstone provided gentle aeration in the animal chamber. Mudpuppies were obtained from a Wisconsin supplier and maintained in the laboratory at 22 C for 2–4 weeks. During trials mudpuppies were in a postabsorptive condition. A thermistor (1-s time constant) was inserted ≈ 5 cm into the intestine via the cloaca and was secured with sutures. Each mudpuppy was placed into a $25 \times 25 \times 15$ cm mesh box and completely submerged in the cooler (22.0 C) bath. Mudpuppies were able to move during trials but could not contact the sides or bottom of the bath. Following thermal equilibration, the mesh box with enclosed mudpuppy was rapidly transferred to the warmer (28.0 C) bath. Body and bath temperatures were monitored with a multichannel digital thermometer and the body temperature at each 15-s interval was recorded until the mudpuppy's body temperature restabilized to the higher temperature. Then a cooling trial was initiated by return of the mesh box and mudpuppy to the cooler bath.

Temperature change halftimes ($T_{1/2}$) adopted from radioactive decay theory by Spigarelli et al. (1974) were employed to characterize heating and cooling responses. The $T_{1/2}$ represents the time for an animal to gain or lose 50% of the existing ΔT between body and equilibration temperatures. As mudpuppies were unable to maintain measurable excess (= above ambient body temperatures), the equilibration temperature equalled the bath temperature. Halftimes, similar to time constants (see Smith, 1976), are not dependent on the magnitude of the ΔT unlike heating and cooling rates. Newton's Law of Cooling states that the instantaneous temperature (T_t) of an object

at any exposure time (t) equals $T_b + (T_o - T_b)e^{-kt}$ where T_o = original body temperature, T_b = bath temperature, and k = rate coefficient (i.e., slope). Solving for k yields $-\ln [(T_t - T_b)/(T_o - T_b)]/t$. Temperatures from each trial were linearized by the above equation, plotted, and regressed against time by least squares to obtain the best fit. Because half-time and rate coefficient are inversely related ($T_{1/2} = -\ln 0.5/k$ or $0.693/k$), the half-time for each was determined as the time (abscissa) corresponding to a change of 0.693 units on the ordinate (Fig. 1). The T_t values at the beginning and near stabilization of each trial were excluded from regression analyses to compensate for delays in initiation of heat transfer and to eliminate possible low ΔT measurement errors, respectively. Detailed treatments of rationale underlying use of halftimes are given by Spigarelli et al. (1977) and Beiting et al. (1977).

RESULTS AND DISCUSSION

Fig. 1 presents the body temperature response curve (lower panel) and logarithmically linearized data (upper panel) from a heating trial of a representative mudpuppy (137.7 g). A highly significant fit between transformed body temperature and time is demonstrated by a .9994 coefficient of determination. The half-time for this trial, determined as the time corresponding to a change of 0.693 units on the ordinate (panel B), equals 2.47 min. Halftimes ($T_{1/2}$) are easily converted to time constants T_c , ($T_c = 1.44 T_{1/2}$) and rate coefficients k , ($0.693/T_{1/2}$). Consequently a $T_{1/2}$ of 2.47 min is equivalent to a T_c of 3.54 min and k of $0.28 \text{ C min}^{-1} \text{ C}^{-1}$.

Heat exchange halftimes of mudpuppies were significantly correlated ($P < .01$) with body weight in a double logarithmic fashion. Log half-time equalled $-0.64 + 0.47 \log \text{ weight}$ for heating ($r^2 = .61$) and $-0.35 + 0.35 \log \text{ weight}$ for cooling ($r^2 = .42$). Standard errors for slopes of regression equations equalled 0.077 and 0.085 for heating and cooling, respectively. Slopes (= exponents) relating weight and heat exchange times fall nearer to the low end of

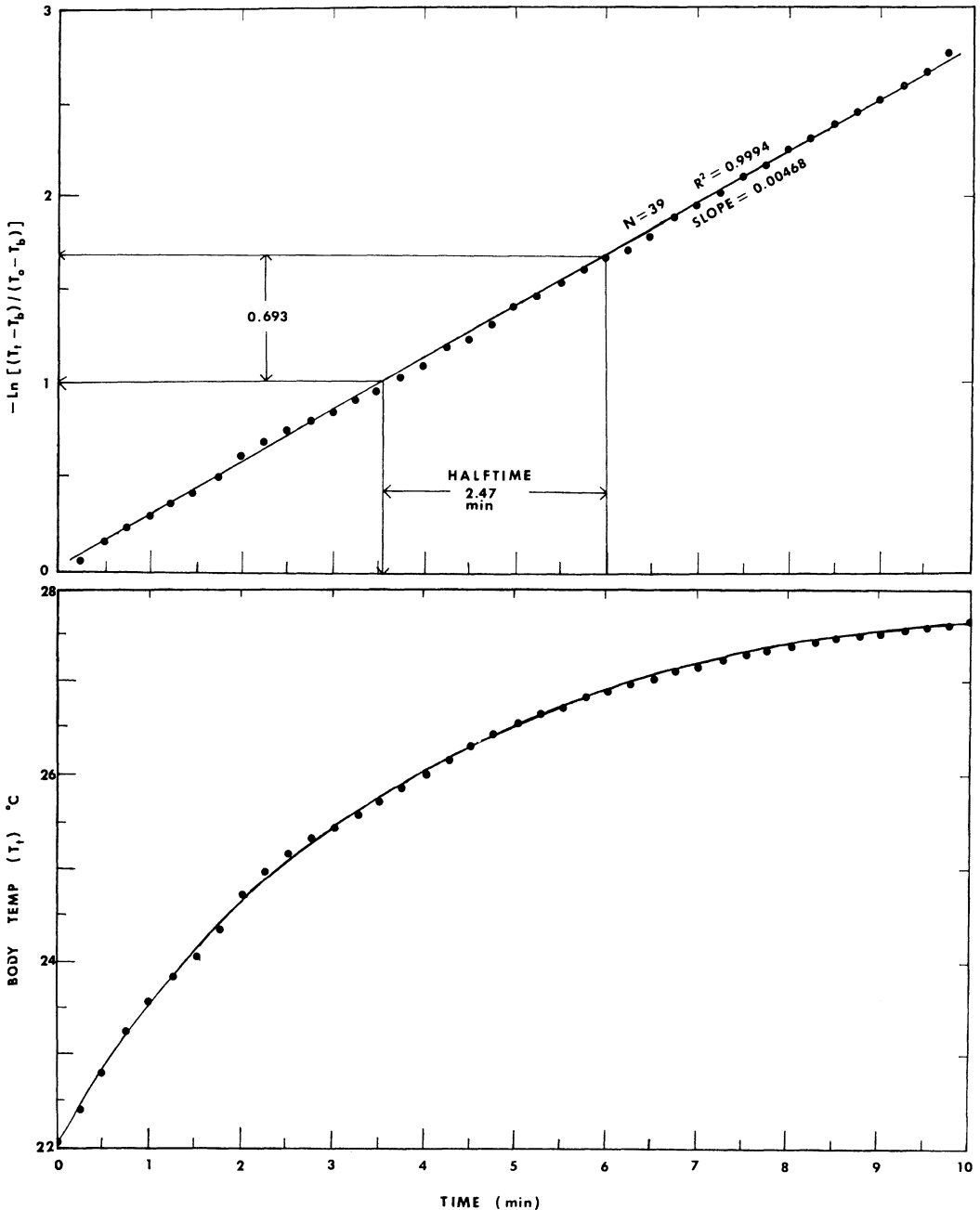


FIG. 1.—Actual (lower panel) and logarithmically transformed (upper panel) body temperatures of a 137.7 g mudpuppy during a heating trial.

the range of slopes for other species tested in water. Published slopes from double logarithmic regressions of weight and heat exchange rates (or times) range 0.33–0.74

for fishes and reptiles tested in water (Bartholomew and Lasiewski, 1965; Stevens and Fry, 1970, 1974; Weathers and White, 1971; Smith, 1976; Spigarelli et al., 1977; Beitingger

et al., 1977). We believe the relatively small slopes and coefficients of determination computed from heat exchange data of mudpuppies result from a relatively small range in weight. The largest mudpuppy was only 3.72 times heavier than the smallest; in addition, 22 of the 26 individuals weighed between 93–150 g.

The heating-cooling ratio for the 26 mudpuppies equalled 0.926 ± 0.12 ($\bar{x} \pm s$, Table 1). Since ratios equal to unity reflect equity in heating and cooling halftimes, our data suggest that on the average, mudpuppies heat 7.4% more rapidly than they cool. Unexpectedly, statistical analyses (paired-*t* and Wilcoxon matched pairs, signed ranks) indicated a significant difference ($P < .01$) between heating and cooling times. This slight heating-cooling hysteresis if real, may be explained by increased circulation (or activity) during heating and the opposite during cooling. These responses would tend to accelerate heating relative to cooling rates. We anesthetized (tricaine methane sulfonate, MS-222) electrocuted and repeated heating and cooling trials on 10 randomly selected mudpuppies to check for possible bias in our experimental approach. Halftimes for dead mudpuppies were approximately 1.6 times greater than those of live mudpuppies. Unexpectedly, the mean heating-cooling ratio for dead mudpuppies was also less than unity, 0.960 ± 0.06 (Table 1). Although most investigators assume a priori that heating and cooling rates are equal in dead animals, few data have been published. Heating and cooling ratios have been reported for a total of 26 dead fish representing 3 species (*Lepomis macrochirus*—Stauffer et al., 1975; *Micropterus salmoides*—Reynolds, 1977; *Dorsoma cepedianum*—Beitinger et al., 1977) and 16 dead reptiles of 7 species (*Amphibolurus barbatus*—Bartholomew and Tucker, 1963; *Dipsosaurus dorsalis*—Weathers, 1970; *Chrysemys picta*, *Gopherus polyphemus*, and *Terrepenne carolina*—Spray and May, 1972; *Crocodylus johnstoni*—Grigg and Alchin, 1976; *Alligator mississippiensis*—Smith, 1976). Fourteen of the dead reptiles

TABLE 1.—Heating:cooling ratios (mean \pm 1 standard deviation) computed from individual ratios of 26 live and 10 dead mudpuppies.

Status	n	Weight (g)	Heat:cool ratio
Alive	26	122.9 \pm 34.6	0.926 \pm 0.120
Dead	10	132.7 \pm 26.3	0.960 \pm 0.060

were tested in air under a variety of wind velocities and 2 were tested in water. The mean heating and cooling ratio for the combined data ($n = 44$) equals 0.976 with a range of individual ratios of 0.81–1.28. Heating-cooling ratios for dead animals which vary from unity may be related to randomness in small sample sizes or experimental bias.

Correcting heating-cooling ratios for live mudpuppies by subtracting the 4% mean difference observed in the dead specimen suggests the difference between heating and cooling is minor. Even without correction, the difference between heating and cooling was only 3.6–12.6 sec over the weight range examined and is probably ecologically unimportant to the mudpuppy.

Hysteresis in body heating and cooling is attributed to temperature induced responses of the cardiovascular system (heart rate, blood distribution and flow) and endogenous heat production relative to the direction of change in ambient temperature. Within this framework, the absence of a large hysteresis in the mudpuppy is not surprising. First, the mudpuppy is an obligate aquatic animal owing to its reliance on gills as primary sites and skin as secondary sites of external respiration (Guimond and Hutchison, 1972). Because heat diffusion proceeds about 1 order of magnitude more rapidly than molecular diffusion, peripheral vasomotor responses influencing rates of heat gain or loss would simultaneously jeopardize rates of O_2 extraction. Also, large heat capacity of water relative to air accelerates heat exchange (Bartholomew and Lasiewski, 1965; Smith, 1976). Consequently, water breathing animals have difficulty in not only generating large excess

(= above ambient) body temperatures but also differentially influencing heating and cooling rates. Second, since metabolic rates of the mudpuppy are extremely low (Guimond and Hutchison, 1972, 1976), temperature induced changes in rates of endogenous heat production are prevented from greatly augmenting rates of heating and decreasing rates of cooling.

Large hysteresis in which heating rates are 2 or more times faster than cooling has been observed in heliothermic reptiles such as the Galápagos marine iguana (Bartholomew and Lasiewski, 1965) and American alligator (Smith, 1976). The ability to physiologically alter rates of heating and cooling has ecological significance in heliothermic ectotherms. Increased rates of heating relative to cooling allows these animals to rapidly increase and maintain body temperatures at ecritic or preferred levels when foraging in cooler microhabitats. It should be noted that both above mentioned heliothermic species are semiaquatic animals which bask to elevate body temperatures and forage primarily in aquatic environments (Bartholomew, 1966; Smith, 1976). Large hysteresis would be difficult to achieve in an exclusively nonbasking aquatic species such as the mudpuppy. Mudpuppies can only exert behavioral control over their body temperature.

Acknowledgments.—We thank R. Cain for help in data analysis, L. Gulick for assistance in preparation of the MS. and J. Glidewell, B. Dial, D. Huey, and J. Stanford for reviewing the MS. Equipment and animals were purchased with funds provided by the Department of Biological Sciences and a North Texas State University faculty research grant to the junior author.

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Accepted: 29 October 1978

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Herpetologica, 35(3), 1979, 239-244
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TAXONOMIC RELATIONS AMONG SEA TURTLES ELUCIDATED BY SEROLOGICAL TESTS

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ABSTRACT: Quantitative turbidimetric immunoprecipitation tests indicate a close affinity for the five types of marine turtles, with *Caretta*, *Eretmochelys*, and *Lepidochelys* being more closely related to each other than to *Chelonia*, and these four types being distinct from *Dermochelys*. There is evidence that *Lepidochelys* is closest to a sea turtle ancestry. Among non-marine turtles, the emydid *Terrapene* appears to be most like marine turtles.

Key words: Reptilia; Testudines; Sea turtles; Serology; Taxonomy

THE five types of living sea turtles generally recognized are *Caretta* (loggerhead), *Chelonia* (green turtle), *Dermochelys* (leatherback), *Eretmochelys* (hawksbill), and *Lepidochelys* (ridley). The most diverse member of this group is *Dermochelys*, which lacks a hard shell and which has been distinguished taxonomically from other sea turtles at the rank of suborder (Carr, 1952; Deraniyagala, 1971), superfamily (Mlynarski, 1969; Romer, 1956; Williams, 1950), or family (Gaffney, 1975; Wermuth and Mertens, 1961, 1977; Zangerl, 1969). Most authorities currently place the four

hardshelled sea turtles in a monotypic family (for exceptions see Deraniyagala, 1939, 1971).

An affinity between *Caretta* and *Lepidochelys* is widely recognized, and *Chelonia* and *Eretmochelys* generally are believed to be closely related (but a question was raised about the latter pairing by Carr [1942]). Most questions in taxonomy of marine turtles have not been subjected to biochemical evaluation, and earlier serological studies included very limited quantities of protein solutions from sea turtles (Frair, 1964, 1969; Frair and Prol, 1978).