

Heating and cooling rates of eastern diamondback rattlesnakes, *Crotalus adamanteus*

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Abstract

1. Establishing if and how organisms modulate temperature changes is an important component of understanding their thermal biology.
2. We used temperature-sensitive radio-transmitters to monitor heating and cooling rates between 5 and 35 °C of four *Crotalus adamanteus* in the laboratory.
3. We found no difference between heating and cooling rates in *C. adamanteus*. Additionally, rates of temperature change mirrored those of a biophysical model, further suggesting a lack of physiological thermoregulation.
4. Our findings contrast previously published studies that demonstrate active temperature control of similarly sized reptiles and demonstrate a need for more investigations of physiological thermoregulation in reptiles.

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1. Introduction

Growth, reproduction, times of activity, and prey capture are but a few important natural history characteristics affected by temperature (Daniels et al., 1987; O'Connor, 1999; Shine, 2005). Consequently, many ectotherms regulate their body temperatures (T_b) to optimize these important functions. By increasing heating rates and decreasing cooling rates, ectotherms can often increase the amount of time that they can spend within their preferred T_b range (Grigg et al., 1979). Therefore, most ectotherms behaviorally and/or physiologically regulate their rates of T_b change (Slip and Shine, 1988a, b; Carrascal et al., 1992; May et al., 1996).

Body size is a major factor affecting the ability of ectotherms to regulate the rate of their T_b change. Because of a high-surface area to volume ratio, many snakes employ behavioral mechanisms to regulate T_b , such as postural adjustments (e.g., tightly coiling or stretching out) (Johnson, 1972; Hammerson, 1979; Heatwole and Johnson, 1979; Lillywhite, 1980), or microhabitat selection (Slip and Shine, 1988b; Carrascal et al., 1992). Of the few taxa examined, large ectotherms physiologically regulate changes of their internal temperature by altering peripheral blood circulation or heart rate (Grigg et al., 1979; Smith et al., 1981; Els et al., 1988). Large ectotherms also have the advantage of high thermal inertias, which help buffer them from short-term fluctuations in environmental temperatures (Slip and Shine, 1988b; Spotila et al., 1991). Unfortunately, there are relatively few thermal biology studies of large reptiles, as most research has focused on smaller species which are often more conducive to study (Saint Girons and Bradshaw, 1981; Slip and Shine, 1988a, b). Further, the only snakes shown to physiologically thermoregulate have been pythons (e.g. Slip and Shine, 1988a, b), which raises the question whether large snakes other than pythons possess similar thermoregulatory abilities.

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The eastern diamondback rattlesnake (*Crotalus adamanteus*) is the largest species of rattlesnake (Klauber, 1956) and offers an excellent opportunity to examine control of heating and cooling rates in a relatively large snake from a lineage separate from pythons. *C. adamanteus* is native to the Coastal Plain of the southeastern United States from Florida to North Carolina and west to Louisiana (Klauber, 1956; Timmerman, 1995). *C. adamanteus* remains above ground most of the time during its active season (Timmerman, 1995) and thus would be expected to resist fluctuations in T_b over short periods of time (e.g., hours) using physiological and behavioral thermoregulation.

Our goal in this study was to examine the response of *C. adamanteus* to temperature changes during heating and cooling and examine this species' ability to control its heating and cooling rates. Second, we sought to evaluate the effects of body size on *C. adamanteus*' rates of heating and cooling. Based on previous research (Bartholomew and Lasiewski, 1965; Bakken, 1976; Shine and Madsen, 1996; Ayers and Shine, 1997; Shine et al., 2000), we predicted that *C. adamanteus* would physiologically regulate its T_b so that it heats faster than it cools.

2. Materials and methods

We subjected four long-term captive eastern diamondback rattlesnakes (4.8, 4.4, 1.8, 1.1 kg; approximately 0.8–1.8 m) to heating and cooling over temperature intervals of 5–35 °C and measured their T_b 's using radio-telemetry. Temperature-sensitive radio transmitters (model SB-2T; Holohil Systems Ltd. Carp, Ont., Canada) were used to measure T_b . Transmitters were calibrated in a circulating waterbath to the nearest 0.1 °C and then implanted into a dead rat or mouse. Implanted rodents were fed to each of the snakes (4.8, 3.0 kg were fed rats, 1.8, 1.1 kg were fed mice).

A sealed copper pipe (61 cm long, 7.6 cm diameter) was filled with water, and served as a biophysical model (Peterson et al., 1993). The internal temperature of the model was recorded every 15 min using a data logger (Stowaway XTI; Onset Computer Corporation, Bourne, MA, USA). The model approximated the mean surface area to volume ratio of the four snakes.

During the experiments, each snake was housed separately in a large plastic container (1.1, 1.8, and 4.4 kg snakes in 49.5 × 39 × 15 cm; 4.8 kg snake in 50.5 × 31 × 32 cm) where they could adjust their body posture freely, and placed into an environmental chamber (model no. EB30, Percival Scientific, Boone, IA, USA) set at 5 °C. We circulated air through the containers using a small air hose and an aquarium air pump to increase air circulation between the environmental chamber and snake containers. Air temperature within the containers (T_a) was monitored using a thermocouple placed in the container housing the snake (Dzialowski and O'Connor, 2001). Prior to temperature change experiments, snakes were placed inside the experimental chamber from 12–16 h to allow them to

equilibrate with T_a . After equilibration, a baseline temperature reading was taken and the containers and snakes were then moved to an adjacent environmental chamber set at 35 °C. The inter-pulse periods of the transmitters were measured every 15 min until the snake T_b 's matched the environmental chamber temperature. The snakes were left at 35 °C for 12 h and, after a baseline temperature measurement was recorded, the containers (with snakes) were moved to the environmental chamber set at 5 °C. Again, the snake T_b 's were recorded initially every 15 min until the T_b 's matched the chamber temperature. Heating and cooling experiments following the same parameters were repeated for all snakes.

Thermal time constants (τ) were calculated for each snake for each trial following the methodology of Dzialowski and O'Connor (2001). The final temperature of the environmental chamber (T_a) was subtracted from the T_b , and the natural log was determined: $\ln(T_b - T_a)$. Because the regression of the natural log of the difference in temperature over time is linear, the slope of this regression line is inversely proportional to the thermal time constant, τ . This method is a more analytically rigorous and consistent way of determining τ , compared to directly measuring the time at which body temperature reaches a midpoint (Spotila et al., 1973; Bakken, 1976; Grigg et al., 1979; Dzialowski and O'Connor, 2001). Thermal time constants for heating and cooling were statistically analyzed with a repeated-measures ANCOVA, with body mass as the covariate (*sensu* Dorcas et al., 2004) using the SAS statistical package (SAS v. 9.1, SAS Institute, Cary, NC, USA). An alpha of 0.05 was used.

3. Results

We found no difference in the rates of heating and cooling for *C. adamanteus* (ANCOVA; $F = 0.01$, $df = 3$, $p = 0.929$; Fig. 1(A)–(D)). The thermal constant (mean ± SE) for heating was 85.602 ± 3.841 min, and the thermal constant for cooling was 93.128 ± 5.761 min. Values for the slope of $\ln(T_b - T_e)$, τ , and the R^2 values for the regression for each individual snake are provided in Table 1. The copper model exhibited a similar pattern of temperature change for both heating and cooling (Fig. 1(E)).

Although not significant ($F = 9.66$, $df = 2$, $p = 0.0898$), mass did appear to play a role in the heating and cooling rates of the snakes: larger *C. adamanteus* heated and cooled more slowly than the smaller snakes. The rate of temperature change was inversely proportional to body size (Table 1; Fig. 1).

4. Discussion

We found that eastern diamondback rattlesnakes are apparently unable to physiologically thermoregulate to increase their heating and decrease their cooling rates. Two components of our experiment provide confirmation of this phenomenon: (1) the similarity in the heating and cooling

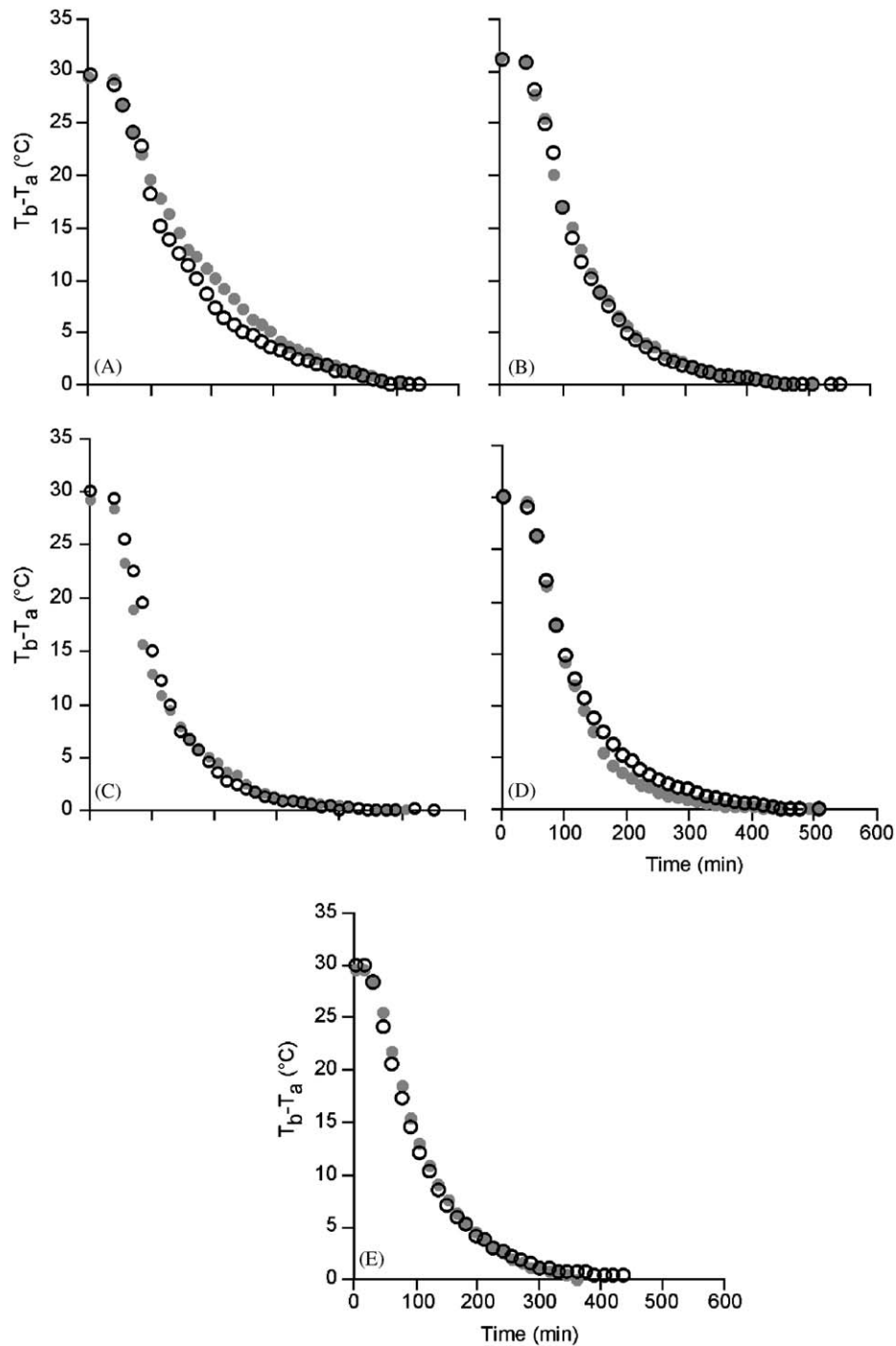


Fig. 1. Heating (black open circles) and cooling rates (gray filled circles), expressed as the difference between body temperature (T_b) and environmental temperature (T_a), of four *Crotalus adamanteus* between 5–35 °C: (A) 4.8 kg, (B) 4.4 kg, (C) 1.8 kg, (D) 1.1 kg, and (E) 7.6 cm diameter copper pipe model. The heating and cooling rates of snakes and the model are similar, indicating that *C. adamanteus* did not physiologically alter their heating and cooling rates.

rates between the snakes and the copper model, and (2) the lack of a difference between heating and cooling among individual snakes. Although not statistically significant due to our small sample size, larger snakes tended to heat and cool more slowly than smaller snakes.

We expected *C. adamanteus* to thermoregulate in a similar manner to other relatively heavy-bodied reptiles (Bartholomew and Lasiewski, 1965; Shine and Madsen,

1996; Ayers and Shine, 1997; Shine et al., 2000). Although our sample size was small, we believe our results represent a real biological phenomenon when one considers that other studies of heating and cooling rates in relatively large reptiles (Bartholomew and Lasiewski, 1965; Smith et al., 1981) have found large, easily detectable differences in heating and cooling time constants. The apparent lack of thermoregulatory abilities in *C. adamanteus* raises the

Table 1
Thermal constants (τ), slope of $\ln(T_b - T_e)$ vs. time regression (M), and corresponding R^2 values for *C. adamanteus* snakes during heating and cooling from 5–35 °C.

Snake	Mass (kg)	Treatment	M	τ	R^2
1	4.78	Cooling	-0.0083	120.155	0.967
1	4.78	Heating	-0.0109	92.067	0.987
1	4.78	Cooling	-0.0090	110.730	0.985
1	4.78	Heating	-0.0093	107.324	0.949
2	4.4	Cooling	-0.0110	91.123	0.979
2	4.4	Heating	-0.0126	79.659	0.977
2	4.4	Cooling	-0.0115	87.091	0.991
2	4.4	Heating	-0.0120	83.480	0.978
3	1.8	Cooling	-0.0110	91.261	0.943
3	1.8	Heating	-0.0122	81.764	0.958
3	1.8	Cooling	-0.0118	84.657	0.992
3	1.8	Heating	-0.0121	82.881	0.968
4	1.09	Cooling	-0.0114	87.941	0.942
4	1.09	Heating	-0.0136	73.552	0.950
4	1.09	Cooling	-0.0139	72.066	0.991
4	1.09	Heating	-0.0119	84.087	0.969
Model	3" diameter	Cooling	-0.011	88.5	0.976
Model	3" diameter	Heating	-0.011	93.8	0.985

possibility that the general paradigm of large reptiles being able to physiologically thermoregulate may not apply to all large snakes (Bartholomew and Lasiewski, 1965; Grigg et al., 1979; Slip and Shine, 1988a; Spotila et al., 1991).

For snakes living in tropical climates, thermoregulation may be unimportant because of a relatively constant temperature regime which allows many reptiles to remain within their preferred T_b range without physiological or behavioral thermoregulation (Shine and Madsen, 1996). However, snakes living in temperate areas often encounter large temperature fluctuations (Peterson, 1987), and thus many have evolved strategies to maintain a preferred T_b (Blouin-Demers and Weatherhead, 2001). *C. adamanteus* inhabits relatively warm, temperate climates, but these regions are still prone to dramatic temperature fluctuations. Temperature changes experienced by *C. adamanteus* in the environmental chambers are similar both in magnitude and time frame to those experienced by *C. adamanteus* during colder seasons (spring and fall) in the southeastern United States (Klauber, 1956; Timmerman, 1995). Therefore, given the characteristics of its environment, we found it surprising that *C. adamanteus* was apparently unable to alter its heating and cooling rates physiologically.

Body size profoundly impacts heating and cooling rates in reptiles, and therefore, the mechanisms they employ to regulate their T_b (Ayers and Shine, 1997; Shine, 2005). For small snakes, behavioral adaptations may be sufficient to facilitate effective thermoregulation (Webb and Shine, 1998; Blouin-Demers and Weatherhead, 2001, 2002; Whitaker and Shine, 2002; Ladyman et al., 2003; Isaac and Gregory, 2004). Large pythons are the only snakes that have been shown to exhibit substantial abilities to physiologically thermoregulate (Slip and Shine, 1988a, b).

Thus, further tests of heating and cooling rates in large snakes and other phylogenetic groups are necessary to fully understand the evolution of physiological thermoregulatory abilities of snakes.

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