Physiological and behavioral control of heating and cooling rates in rubber boas, *Charina bottae*

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Abstract

1. We examined the ability of rubber boas (*Charina bottae*) to physiologically and behaviorally control their heating and cooling rates between 5 and 35 °C with constrained and unconstrained postural treatments.

2. In both the unconstrained and constrained treatments, heating rates were faster than cooling rates (ANOVA; $F = 52.25$; df $= 22$; $p < 0.001$), suggesting that rubber boas can physiologically slow their cooling rates and/or accelerate their heating rates.

3. Our findings provide a greater understanding of physiological thermoregulation in rubber boas and insight into mechanisms of reptilian thermoregulation.

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1. Introduction

Body temperature greatly impacts the ecology, behavior, and physiology of reptiles (Huey, 1982; Peterson, 1987; Peterson et al., 1993). Consequently, many species of reptiles thermoregulate to maintain body temperatures within a narrow, or preferred, temperature range (Hammerson, 1979; Girons and Bradshaw, 1981; Peterson, 1987). A reptile's ability to slow its cooling rate and accelerate its heating rate can increase the amount of time spent within its preferred temperature range, thus increasing physiological performance (Grigg et al., 1979).

Many reptiles have the ability to control their heating and cooling rates through behavioral and physiological thermoregulation (Lillywhite, 1980; Slip and Shine, 1988; Blouin-Demers and Weatherhead, 2001). Behaviors that reptiles employ to control body temperatures include postural adjustments, microhabitat selection, and basking (Brattstrom, 1965). In snakes, coiling reduces body surface area-to-volume ratio, which lowers the amount of surface area exposed to the environment and possibly slows

cooling rates (Ayers and Shine, 1997; Rice et al., 2006). Reptiles also have physiological responses to ambient temperature changes, which include evaporative cooling, redirecting blood flow, and in some species, limited metabolic heat production (Brattstrom, 1965). To date, only a limited number of studies on the behavioral and physiological control of heating and cooling rates have been conducted. Most studies have concluded that many reptiles have the ability to behaviorally and/or physiologically control their heating and cooling rates (Brattstrom, 1965; Lillywhite, 1980; Slip and Shine, 1988). These studies were conducted on relatively large reptiles because their lower surface area-to-volume ratio facilitates physiological thermoregulation. However, a recent investigation by Rice et al. (2006) found that eastern diamondback rattlesnakes (*Crotalus adamanteus*) apparently lack the ability to physiologically alter heating and cooling rates. Consequently, to develop a more complete understanding of the ability of reptiles to control their heating and cooling rates, examination of species that differ ecologically and phylogenetically from those studied thus far is needed.

In this study, we examine the control of heating and cooling rates in rubber boas (*Charina bottae*), nocturnal predators that are often active at low temperatures (Dorcas

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and Peterson, 1998). Previous studies have shown that rubber boas have the ability to physiologically maintain head temperature within narrower limits than their body temperature, even during nocturnal activity (Dorcas and Peterson, 1997). In this paper, we test the hypothesis that rubber boas employ both physiological and behavioral mechanisms to slow their cooling rates and accelerate their heating rates in order to maintain the body temperature within preferred temperature ranges.

2. Methods

Snakes were collected in southeastern Idaho and were housed at 23–25 °C in 38 L glass aquaria and regularly fed laboratory mice. The snakes (three females and five males) were implanted with temperature-sensitive PIT tags (Passive Integrative Transponder, Biomedic Data Systems, Seaford, DE; 14 mm long and 2.2 mm in diameter; Roark and Dorcas, 2000). Prior to implantation, we calibrated PIT tags to within 0.2 °C (Roark and Dorcas, 2000). To examine the effects of behavioral and physiological processes on heating and cooling rates, we conducted two experimental heating and cooling procedures, with one procedure allowing snakes to assume any body position (hereafter referred to as the "unconstrained treatment") and another procedure that physically constrained the snakes in elongated body postures ("constrained treatment").

We heated and cooled snakes in environmental chambers set at 5 and 35 °C (with subdued fluorescent lighting). For heating, we first placed all eight snakes in the 5 °C chamber, allowed them to equilibrate with the chamber temperature for a period of 4 h, and then transferred them to the 35 °C chamber. After transferring the snakes, we measured their core body temperatures every 5 min by reading the PIT tags through the bottom of each snake's container until their temperatures were equilibrated with the new environmental chamber temperature (Roark and Dorcas, 2000). We followed the same procedure for cooling, except that we equilibrated the snakes in the 35 °C chamber first and then transferred them to the 5 °C chamber. We waited 3 days between each heating and cooling procedure and conducted the treatments in the following order: unconstrained heating, unconstrained cooling, constrained heating, and constrained cooling.

During heating and cooling, we placed snakes in either an unconstrained posture or a constrained posture. For the unconstrained treatment, we placed each snake in its own plastic container (Ziploc®; 30 cm × 20 cm × 10 cm) punctured with numerous circular holes (3.14 mm diameter). These containers were large enough to allow the snakes to assume an extended posture (i.e., completely uncoiled) and the holes facilitated high rates of air exchange between the chamber and each snake's container. At each temperature measurement, we observed and recorded the postures of the snakes using a standardized rating system to describe the degree of coiling (1 = completely uncoiled,

2 = partially coiled with 1–35% of body surface overlapping, 3 = coiled with 35–65% of body surface overlapping, 4 = tightly coiled with greater than 65% of body surface overlapping). For the constrained treatment, we placed each snake in a plastic mesh tube (1.5 mm × 1.5 mm holes) slightly larger than the diameter of each snake, which allowed for airflow around the snake but eliminated the snakes' ability to coil.

We calculated thermal time constants (τ) for warming and cooling rates following the methods of Dzialowski and O'Conner (2001) and Rice et al. (2006). We determined the natural log of the difference between the body temperature of each snake (T_b) and the temperature of the environmental chamber (T_a). Plotting $\ln(T_b - T_a)$ versus time yielded a linear relationship. We used the inverse of the slope to determine each thermal time constant (τ). We performed a repeated-measures ANOVA with snake as the repeated factor, postural treatment (constrained vs. unconstrained) and temperature treatment (heat vs. cool) as the independent factors, and thermal time constant as the dependent factor (Minitab ver. 12.1, State College, PA). To analyze the effects of mass on heating and cooling rates, we performed a linear regression for each of the four treatments. To analyze the effects of treatment on posture in the unconstrained treatments, we performed a one-tailed Wilcoxon signed ranks test to test the hypothesis that snakes should coil more during cooling than during heating. A value for each snake was obtained by summing the postural scores during the first 30 min (= 6 scores) of unconstrained heating and cooling trials. This time period (i.e., 30 min) was chosen because the difference between body temperatures and environmental temperature was greatest during that period; hence, postural impact was predicted to have the greatest effect on cooling or heating rates during this time. We used an α of 0.05 to determine significance for all tests.

3. Results

Rubber boas always heated faster than they cooled (ANOVA; $F = 52.25$; df = 22; $p < 0.001$; Fig. 1). During the unconstrained treatment, the mean heating rate (mean $\tau = 18.65 \pm 3.06$ min) was faster than the mean cooling rate (mean $\tau = 41.81 \pm 6.54$ min). Similarly, with the constrained heating and cooling treatments, the mean heating rate (mean $\tau = 18.287 \pm 2.29$ min.) was faster than the mean cooling rate ($\tau = 57.308 \pm 0.47$ min).

The thermal constants for the unconstrained heating and cooling treatments were not significantly different from the thermal time constants for the constrained heating and cooling treatments (ANOVA; $F = 3.09$; df = 1; p = 0.093; Table 1; Fig. 1).

In the unconstrained heating treatment, mass significantly affected the rate of heating ($p = 0.009$; $R^2 = 0.704$; $y = 0.0892x + 8.778$; Fig. 2). However, in the other three treatments (unconstrained cooling, constrained heating, and constrained cooling), mass did not affect the heating or
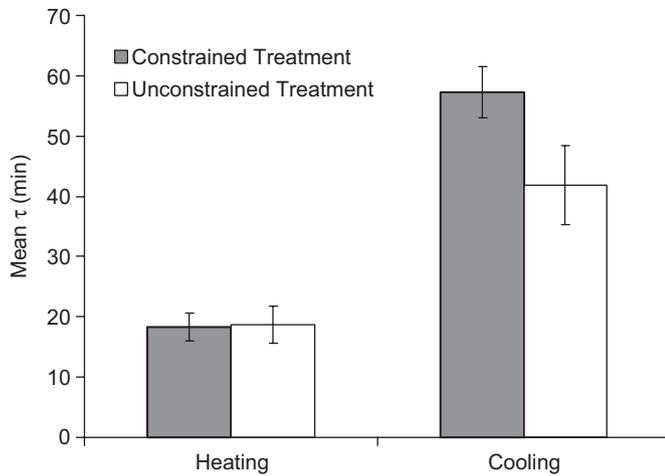
Fig. 1. Average thermal time constant for *C. bottae* ($n = 8$) for each treatment. Regardless of postural treatment, rubber boas heated faster than they cooled (ANOVA; $F = 52.25$; df $= 22$; $p < 0.001$).
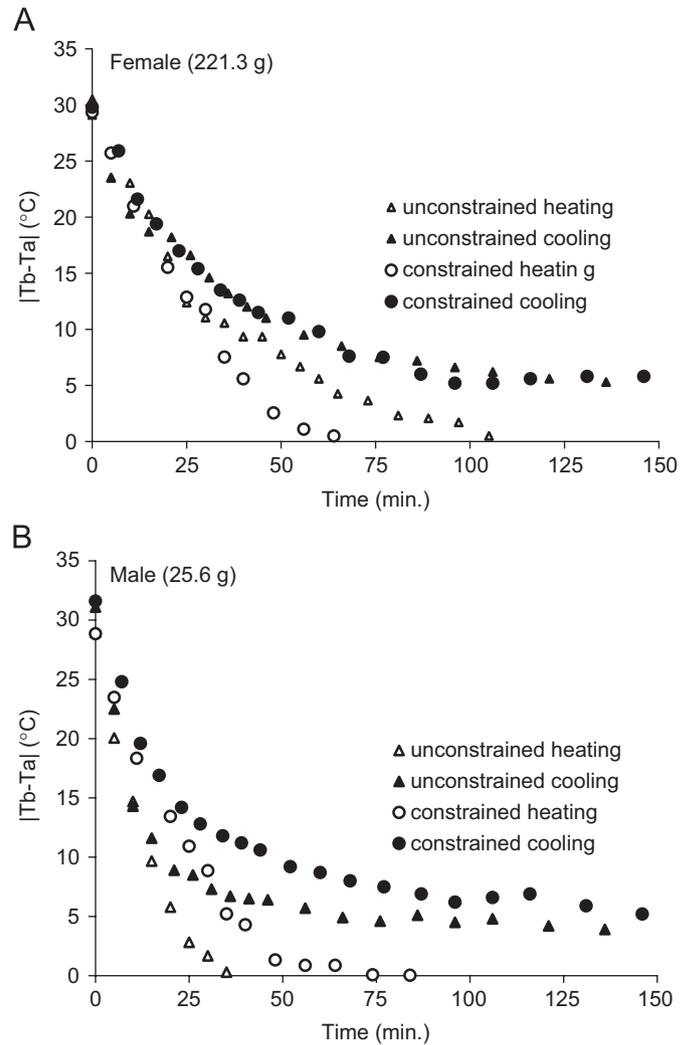

Fig. 2. Heating and cooling rates for (A) a large female (snake ID: 31) and (B) a small male (snake ID: 51), expressed as the difference between body temperature (T_b) and environmental chamber temperature (T_a). Both male and female snakes had faster heating rates than cooling rates. The small male equilibrated with its environmental temperature at a faster rate than the large female.

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

Snake	Mass (g)	Treatment	M	τ	R^2
1	176.7	UH	−0.033	30.03	0.995
1	–	UC	−0.015	67.57	0.956
1	–	CH	−0.038	26.18	0.981
1	–	CC	−0.0167	59.880	0.944
6	48.2	UH	−0.083	12.06	0.986
6	–	UC	−0.018	56.82	0.816
6	–	CH	−0.037	27.17	0.851
6	–	CC	−0.0179	55.866	0.956
7	37.4	UH	−0.085	11.82	0.983
7	–	UC	−0.050	20.00	0.973
7	–	CH	−0.068	14.73	0.988
7	–	CC	−0.0175	57.143	0.881
31	221.3	UH	−0.033	30.68	0.953
31	–	UC	−0.020	50.00	0.986
31	–	CH	−0.062	16.16	0.927
31	–	CC	−0.0271	36.900	0.987
51	25.6	UH	−0.096	10.44	0.981
51	–	UC	−0.039	25.58	0.880
51	–	CH	−0.061	16.47	0.953
51	–	CC	−0.0187	53.476	0.938
58	223.1	UH	−0.046	21.79	0.936
58	–	UC	−0.025	39.84	0.990
58	–	CH	−0.047	21.28	0.951
58	–	CC	−0.0128	78.125	0.945
61	72.0	UH	−0.045	22.27	0.924
61	–	UC	−0.052	19.19	0.988
61	–	CH	−0.059	17.09	0.959
61	–	CC	−0.0195	51.282	0.943
68	60.5	UH	−0.098	10.16	0.891
68	–	UC	−0.018	55.56	0.864
68	–	CH	−0.139	7.22	0.989
68	–	CC	−0.0152	65.789	0.929

UH = unconstrained heating; UC = unconstrained cooling; CH = constrained heating; CC = constrained cooling.

cooling rates of rubber boas (all p values $\geqslant 0.321$). In the unconstrained treatments, although we observed that snakes tended to move around more in their containers at higher temperatures, we found that treatment (heating or cooling) apparently had no effect on posture of the snakes (Wilcoxon signed ranks test; $T = 13$, $N = 8$, $p > 0.05$).

4. Discussion

Our data suggest that rubber boas are able to control their rates of heating and cooling. In both constrained and unconstrained postural treatments, snakes heated faster than they cooled. Snakes in the constrained posture did not cool or heat faster than they did in the unconstrained treatment, which indicates that physiological mechanisms (i.e., directing blood flow to different parts of the body) appear to play a more important role in rubber boa

thermoregulation than do postural adjustments. Although we found no significant effect of mass on heating and cooling rates in three of the treatments, we observed a trend for smaller (male) rubber boas to heat faster than larger (female) rubber boas in the unconstrained heating treatment.

Physiological factors (i.e., heart rate adjustments and redirection of blood flow) likely play a role in rubber boa thermoregulation. Studies on Galápagos marine iguanas (*Amblyrhynchus cristatus*) have shown that differences in heating and cooling rates can be attributed to changes in skin circulation (Bartholomew and Lasiewski, 1965). Soft-shell turtles (*Apalone spinifera*) increase heart rate during heating to increase circulation and heat gain and decrease heart rate during cooling to reduce circulation and heat loss (Smith et al., 1981). Although we did not measure heart rate or blood flow in our experiment, these physiological changes are the most likely mechanisms by which rubber boas alter their heating and cooling rates. Furthermore, one study has suggested that rubber boas can physiologically shunt blood to different regions of the body, thus supporting the hypothesis that these snakes may be able to physiologically control whole-body temperatures (Dorcas and Peterson, 1997).

In addition to physiological thermoregulation, snakes and other reptiles use behavioral mechanisms for thermo-regulatory purposes (Brattstrom, 1965; Lillywhite, 1980; Slip and Shine, 1988; Peterson et al., 1993). Many reptiles achieve body temperature control by basking in the sun, shuttling between different thermal environments, and adjusting their postures (Brattstrom, 1965; Hammel et al., 1967; Lillywhite, 1980; Slip and Shine, 1988). In our experiment, we focused on examining only the effects of postural adjustment (i.e., coiling) on the heating and cooling rates of rubber boas. The ability of snakes to coil largely influences their ability to alter surface area-to-volume ratios, which plays an important role in the thermoregulation of some large snakes (Lillywhite, 1980). Although we observed a tendency for rubber boas to coil more tightly when cooling, we did not find a statistically significant relationship between degree of coiling and the heating and cooling treatments, suggesting that, in the absence of solar radiation, postural adjustment may have negligible impacts on the regulation of heating and cooling rates. Rubber boas are smaller and have larger surface area-to-volume ratios than other snakes for which this phenomenon has been studied, thus reducing the potential benefits of postural adjustment (Ayers and Shine, 1997). However, it is also possible that the artificial nature of the experiment (i.e., plastic containers, environmental chambers) may have resulted in the snakes moving around within the containers rather than coiling as they might do in more natural settings.

Although physiological thermoregulation has been well documented in large reptiles, our study shows that smaller reptiles, such as rubber boas, also have the ability to thermoregulate by physiologically increasing heating rates and lowering cooling rates (Brattstrom, 1965; Blouin-Demers and Weatherhead, 2001). The ability to physiologically thermoregulate may be especially important for rubber boas because of their frequent nocturnal activity in relatively cool environments (Dorcas and Peterson, 1998).

This study provides us with a greater understanding of the thermoregulatory processes of reptiles in relation to environmental pressures (i.e., cold temperatures) that they may experience (Dorcas and Peterson, 1997). The extent to which accelerating heating rates and slowing cooling rates affect the amount of time rubber boas spend within their preferred temperature range is unknown. Future studies examining the ecological consequences of physiological thermoregulation in rubber boas and other small reptiles would be particularly enlightening.

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