

Respiratory cooling in rattlesnakes

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Abstract

We used infrared thermography to study respiratory cooling in the rattlesnakes (Viperidae: Crotalinae) and to partition the effects of air temperature, humidity, and activity levels on head–body temperature differences. We observed a single, cooled region centered around the mouth and nasal capsule that extended across the pit membrane at air temperatures above 20 °C. Both head and body temperatures of rattlesnakes increased linearly with air temperature. Head–body temperature differentials also increased with air temperature, but declined significantly at higher relative humidities. Rattling rattlesnakes exhibited significantly greater head–body temperature differentials than did resting rattlesnakes. We suggest that respiratory cooling may provide a thermal buffer for the thermoreceptive pit organs at high air temperatures, but caution that this adaptive hypothesis must be tested with direct neural or behavioral assays.

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1. Introduction

Because the nervous system exhibits a remarkable sensitivity to fluctuations in temperature, organisms have evolved elaborate means of thermoregulating brain and sensory tissue (Schmidt-Nielsen, 1993). Certain ocean fishes utilize modified eye musculature to elevate eye and brain temperature well above water temperature (Carey, 1982; Block and Franzini-Armstrong, 1988). Harbour seals can elevate the surface temperatures of their mystacial and supraorbital vibrissal pads as much as 25 °C above water temperature, and exhibit high tactile sensitivity in waters as cool as 0 °C (Mauck et al., 2000).

Head–body temperature differences in reptiles have often been taken as evidence for the precision by which these ectotherm animals regulate temperatures. By differentially exposing certain body parts to impinging solar

radiation, many reptiles elevate head temperatures relative to their bodies upon emergence from burrows (Heath, 1964; Hammerson, 1977; Gregory, 1990). They maintain these thermal gradients during activity via countercurrent heat exchangers (Heath, 1966). Localized cooling of nervous tissue may occur during exposure to heat stress or bouts of intense metabolic activity and is primarily controlled by the rate of water evaporation from respiratory passageways. When exposed to heat stress, many lizards and crocodylians increase their rate of ventilation and breathe with an open mouth (Crawford et al., 1977; Spotila et al., 1977). Panting has a marginal influence on the overall heat balance of these reptiles, but, in the desert-dwelling chuckwalla, brain temperature is stabilized at nearly 3 °C below air temperature through evaporative cooling (Crawford, 1972). Localized cooling in reptiles may be further facilitated by ancillary adaptations such as blood shunts and countercurrent heat exchangers (Heath, 1966; Webb and Heatwole, 1971), but these circulatory mechanisms alter only the distribution of cooled blood within the body.

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Evaporative cooling and associated brain cooling are dominated by one environmental variable (humidity) and one physiological variable (respiratory rate; McLean, 1974). Past researchers have only examined head–body temperatures of reptiles in relation to air temperature alone (Heath, 1964; Webb and Heatwole, 1971; Crawford, 1972; Johnson, 1972, 1973, 1975; Hammerson, 1977; Spotila et al., 1977; Dorcas and Peterson, 1997). Here, we use infrared thermography to examine head–body temperature differences in three species of rattlesnakes (the western diamondback rattlesnake, *Crotalus atrox*; the rock rattlesnake, *Crotalus lepidus*; and the black-tailed rattlesnake, *Crotalus molossus*) as a function of air temperature, humidity, and activity levels. Head–body temperature differences in rattlesnakes are of particular interest because rattlesnakes, like all vipers in the subfamily Crotalinae, possess specialized sensory organs known as facial pit organs. Pit organs are thermoreceptive organs derived from tactile receptors, and, like other sensory organs, must be maintained within a narrow temperature range (Molenaar, 1992). Because these receptors are critical during activities ranging from prey capture to microhabitat selection (Krochmal and Bakken, 2003), understanding the thermal environment in which they operate is a primary goal of this study.

2. Materials and methods

2.1. Study organism

The western diamondback rattlesnake (*C. atrox*) is a habitat generalist commonly found throughout much of the American Southwest. Twelve western diamondbacks from Texas were collected between June 1998 and October 1999. Three black-tailed rattlesnakes (*C. molossus*) and two rock rattlesnakes (*C. lepidus*) from Texas were also used in this study. (Texas Parks and Wildlife Permits #SPR-029-19 to J. Johnson, UT-El Paso; #SPR-1017-912 to T. LaDuc).

Rattlesnakes were maintained in two isolated reptile rooms at the University of Texas at Austin. All snakes were kept in a 12 h:12 h L:D cycle at 27–30 °C. Each animal was housed individually in either 38 or 76 L glass aquaria. Water was provided ad libitum. Snakes were fed mice, both alive and dead, on regular 2-week intervals. All snakes were held in captivity for at least 6 months prior to filming (UT Animal Welfare Committee #99031201).

2.2. Thermographic measurements

Individual experimental animals were placed in a filming chamber that consisted of a 38 L glass aquarium modified to allow either the insertion of the lens of an AVIO Handy Thermo TVS-110 camera (temperature resolution of 0.2 °C; filming rate of 10 frames/s), or a

Sony CCD-TRV16 camcorder. The interior of the aquarium was lined with cardboard panels that tapered away from the camera, thus serving to constrain the snake within the camera's field of view approximately 30 cm from the lens. Lighting for the camcorder was provided via overhead fluorescent bulbs, which yield a negligible amount of radiant heat energy. A digital thermometer/hygrometer (Mannix LAM880D) was placed inside the filming chamber to simultaneously monitor air temperature and relative humidity (RH). Air temperature (T_a) was controlled by placing the filming chamber in a HotPoint environmental room.

Snakes were allowed to acclimatize in the filming chamber for 30–60 min, and only thermograms in which body temperature was within 2.5 °C of air temperature were used. In only 7 out of 101 thermograms used in this study did this deviation exceed 2 °C, and body temperature was elevated on average 0.19 °C (± 0.11 S.E.M.) above air (not significantly different from zero; two-sided t -test, $t_{100}=1.74$, $p>0.05$).

To examine the effects of humidity on head–body temperature differences, thermographic images were recorded at air temperatures within 2 °C of 15, 20, 25, 30, 35, and 40 °C. Humidity was modified by misting water in the aquarium. The initial temperature of the chamber was selected randomly, and the direction of temperature cycling was varied to reduce possible biases due to thermal history of the animal. Emissivity of rattlesnakes was assumed to be 95%, the value reported for human skin (Çengel, 1997). Because of the difficulty in identifying anatomical features in thermograms, body temperatures (T_b) were derived from up to three measurements along the body, whereas head temperatures (T_h) were taken from the center of cooling on the rostrum. Values of T_{diff} , the maximum head–body temperature difference, were calculated as $T_b - T_h$.

To examine the effects of activity level on head–body temperatures, the same 12 western diamondback rattlesnakes used in the above experiment were examined both at rest and during rattling subsequent to visual or tactile stimulation. Thermograms were recorded at 15, 20, 25, and 30 °C. Thermograms from each snake at each temperature were recorded within 3% RH of one other, and humidity levels between thermograms of a given snake at rest or rattling did not significantly differ (repeated measures ANOVA, $F_{1,11}=0.02$, $p=0.8939$).

2.3. Statistics

Interspecific differences in T_{diff} were tested with an analysis of covariance (ANCOVA), with T_a , RH, and species identity as independent variables. A multiple regression was used to examine the relationship between T_{diff} , T_a , and RH. In order to test the effects of rattling in *C. atrox*, a repeated-measures ANOVA was used modeling stimulus and temperature class as within-subject sources of

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