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Ambient Temperature Activity of Horned Adders, *Bitis caudalis*: How Cold Is Too Cold?

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Most physiological processes are greatly affected by temperature; therefore animals thermoregulate to maintain a body temperature (T_b) that approximates that which is optimal for physiological performance (reviews by Avery, 1982; Huey, 1982; but see Webb and Shine, 1998). As an ectotherm, a snake relies on external heat sources to maintain its preferred T_b. Although heat sources are readily available during the day, the nocturnal environment has few, if any, heat sources. Even though the nocturnal environment poses a significant thermal handicap, numerous snakes species are nocturnal (Greene, 1997). Because of the lack of heat sources, activity of nocturnal species should be sensitive to ambient temperature (T_a).

The physiological and behavioral means by which snakes adapt to thermal challenges associated with nocturnality has not received extensive study. Many performance measures including locomotion, digestion rate, tongue flick, and strike velocity are maximized at relatively high T_b (e.g., Stevenson et al., 1985; Ayers and Shine, 1997; Dorcas et al., 1997; Webb and Shine, 1998). These body functions are near maximum levels during the day but are significantly reduced at night (Stevenson et al., 1985). Activity at night would not only require a snake to use physiological processes associated with foraging (e.g., locomotion, tongue-flick rate, strike velocity) when they are suboptimal but could also negatively impact temperature-sensitive physiological processes, which are not associated with activity (e.g., digestion). Nocturnal activity of rubber boas, *Charina bottae*, led to a T_b below that which would occur if the snake remained in a nighttime refugium (an inverted T_b pattern; Dorcas and Peterson, 1998).

A nocturnally active snake typically has a T_b that approximates T_a (Dorcas and Peterson, 1998); therefore, T_a may be more critical to performance of nocturnal species than of diurnal species, where radiation and conductance can lead to a T_b much greater than T_a (Peterson, 1987). Because of the thermosensitivity of processes critical to foraging, thermal factors might constrain the timing, place, and duration of predatory bouts (Ayers and Shine, 1997). Such constraints can lead to seasonal differences in activity period. For example, copperheads, *Agkistrodon contortrix*, are diurnal during cool seasons (spring and fall) but are nocturnal during the warm summer months (Sanders and Jacob, 1981). Thermal constraints can also lead to ontogenetic differences in activity period. Adult diamond pythons, *Morelia spilota spilota*, forage nocturnally, whereas juveniles are diurnal (Ayers and Shine, 1997). We used a controlled laboratory environment to test the thermosensitivity of activity in a small nocturnal snake. We hypothesize that activity by a nocturnal snake will decrease as nocturnal T_a decreases.

Four male horned adders, *Bitis caudalis*, were collected in October, 1996, in the vicinity of Keetmanshoop, Namibia. *Bitis caudalis* is a small viper distributed throughout southern Africa. Snout–vent length of males ranges from 190 to 400 mm (Shine et al., 1998). Males used in this study ranged in mass from 40 to 77 g. *Bitis caudalis* feeds on small mammals and lizards, using a sit-and-wait foraging mode by day but actively foraging at night. In more xeric environments, such as the Keetmanshoop area, *B. caudalis* is considered nocturnal and saurophagus (Shine et al., 1998).

Snakes were housed individually in standard 40-liter glass aquaria containing a substrate of utility sand, a water bowl, and a refuge. Mylar heat tape (Flex Watt, West Wareham, MA) was placed under one end of each aquarium to provide subsurface heat and therefore a thermogradient. Room lighting and supplemental heat were set to a 12:12 cycle. Room temperature was a constant 25°C. The snakes were offered a diet of lizards or small mice approximately every two weeks. At this frequency, meals were routinely consumed unless the animal was in preecdysis.

Behavioral testing was conducted in an environmental chamber set at the desired test temperature (5, 10, 15, 20, or 25°C). The test arena consisted of an approximately 76 cm × 92 cm fiberglass tub containing utility sand at a depth of approximately 1.5 cm. Four equal-sized quadrants were created by stringing yarn across the top of the arena, connecting the midpoints of opposite walls. Supplemental heat sources (subsurface mylar heat strip and one or more flood lamps) were provided at one end of the arena (quadrants 1 and 2). The wattage of the bulbs in the lamps varied with varying experimental room temperature, so as to attain a surface temperature of 38 ± 1°C when the lights were on. The lights and the mylar heat strip were on a 12:12 cycle (lights and heat on from 0600–1800 h). When the heat sources went off, surface temperature under the lamps gradually cooled to test temperature. Test runs using temperature dataloggers (Stowaway XTI, Onset Computer Corporation, Bourne, MA) verified that the rate of cooling increased with lower test temperatures. The time it took for surface temperature to decrease from 38°C to 2°C above room temperature ranged from 95 min at 5°C to 147 min at 25°C. A red light was suspended high above the arena to allow for videotaping during the scotophase but made a negligible heat contribution to the arena. A piece of driftwood was placed in the center of the arena to serve as a potential refuge.

Experimental trials were conducted from March to December 1998. A snake that had not been offered food for two weeks was placed in the test arena at least 24 h prior to the experimental trial to allow it to adjust to the new environment. Twenty minutes prior to the time the lights and subsurface heating went off on the day of the trial, a circular tray was placed in the middle of each quadrant. Trays in quadrants 1 and 2 (those associated with the supplemental heat sources) were empty. The third tray contained fresh artificial bedding material (CareFRESH, International Absorbents, Inc., Bellingham, WA), whereas the fourth tray contained artificial bedding which had been soiled with feces, urine, and pieces of shed skin from a gecko (*Coleonyx variegates* or *Diplodactylus stenodactylus*). The quadrant location of each of the latter two

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