

Do thermal cues influence the defensive strike of cottonmouths (*Agkistrodon piscivorus*)?

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Crotaline snakes (family Viperidae, subfamily Crotalinae) are unique among snakes in the possession of facial pits situated on each side of the head between the nostril and the eye (Klauber, 1972). These organs are depressions with highly innervated membranes at their bases that have a heat-sensing function and that transmit information to the part of the brain that receives visual data (Desmoulins, 1824; Bullock and Diecke, 1956; Barrett, 1970; Hartline et al., 1978). Thus, pitvipers can detect temperatures through the radiant heat energy emitted by objects and/or organisms relative to the background temperature. This thermoreceptive sense is not specific to crotalines: some booids also have the capacity to detect temperature variation but the thermal receptors are situated on the labial scales, and hence are called labial pits.

The significance of this thermoreceptive organ on the predatory strike of booid and viperid snakes has been established (De Cock Buning, 1983; Kardong and Mackessy, 1991; Shine and Sun, 2003). However, no evidence has been provided on alternative functional roles played by thermal pits (Greene, 1992), specifically on defense. It has been suggested that thermal pits might help snakes in detecting predators (De Cock Buning, 1983), in finding optimal basking sites for thermoregulation (Goris and Nomoto, 1967; Herbert and Hayes, 1992), and in locating winter dens (Sexton et al., 1992).

Because we lack empirical studies on the role of these pits in a non-predatory context, this study provides further understanding on

the function of thermal pits. We conducted a simple experiment to test the influence of warm thermal cues on the defensive strike of a pitviper species, the cottonmouth (*Agkistrodon piscivorus*). Visual cues are of paramount importance in releasing a defensive strike (Scudder and Chiszar, 1977). In addition, cottonmouths are preyed upon by predators with different thermal profiles (e.g., ectotherms, endotherms). Thus, we predicted that there would be no difference in the striking response of cottonmouths tested with a warmed versus a non-warmed artificial arm.

We collected 21 cottonmouths, 14 females and 7 males ($\bar{x} \pm \sigma$; SVL = 74.25 ± 3.33 cm), on the Savannah River Site, South Carolina, USA, during spring 2003. After capture, we fasted each snake for 7 days to eliminate the effect of recent feeding on defensive behavior (Herzog and Bailey, 1987). The snakes were individually housed in identical polyethylene containers (Rubbermaid™ [58 × 42 × 14-cm high]) within an environmental chamber (12L:12D, 26°C) with water dish (provided ad-libitum) and bark mulch as a substrate. We did not disturb snakes prior to the experiment. Snout-vent length of the specimens was within a range of 60 to 100 cm SVL, and all were mature individuals (Blem, 1997).

We performed all trials in the individual housing container that we previously placed in a larger plastic-walled arena (82 × 52 × 34-cm). All trials were performed between 1200 and 1600 hrs. The experimental stimulus consisted in tapping on the snake mid-body three successive times at 1-sec intervals with a pair of snake tongs (Midwest Productions™) customized to look like a human arm (Gibbons and

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Dorcas, 2002). We wrapped a piece of heating tape (Flexwatt™) around the arm. To insure the diffusion of heat, we wrapped aluminum foil around the length of the arm. We then covered the artificial arm wrapped in aluminum foil with a shirtsleeve. We randomly assigned two treatments to each snake. We used a repeated measure design because of the high individual variation in defensive behavior (Brodie III, 1993). In the control treatment, the temperature of the arm was within a range of 22–26°C (T°C; $\bar{x} = 24.87 \pm 0.22^\circ\text{C}$). In the experimental treatment, we heated the arm to a temperature of 32–36°C (T°C = $33.75 \pm 0.25^\circ\text{C}$). We monitored the temperature of the arm with an infrared thermometer (Raytek MiniTemp™). Cottonmouths would have been unable to react to infrared radiation emanating from the tester's body because thermal receptivity is limited to 35 to 70 cm (Noble and Schmidt, 1937; Greene, 1997), and the artificial arm was approximately 1-m long. We covered the anterior part of the arm with polyethylene and replaced it between each trial so that chemical cues left on the arm did not influence the response of the subsequent snake. Because snakes could habituate to handling when tested over consecutive days (Glaudas, in press), we performed the second trial four days after the first test. The tester wore the same shade of clothing throughout the experiment so that his appearance did not influence the snake's behavior (Whitaker and Shine, 1999). We recorded the following variables: whether the snake struck, the number of strikes, and latency to strike. We recorded latency to strike with a stopwatch using the first tap as the point of reference (time 0).

We analyzed data on the occurrence of striking using *Z* sign-test. To investigate whether strike numbers differed among treatments, we used a non-parametric repeated measure analysis, the Friedman test. We used Wilcoxon matched pairs test to test for differences in latency to strike between treatments.

We found no difference in the occurrence of striking (Sign Test, $Z = .000$, $P = 1.0$). Four-

teen of 21 control snakes (62%) struck whereas 13 (58%) of 21 struck in the experimental treatment. Only five individual snakes exhibited a change in striking behavior: three of them struck in the control experiment only and the other two did so in the experimental treatment only. We found no difference in strike numbers directed at the stimulus (Friedman test, $\chi_r^2 = .20$, $df = 1$, $P < 0.65$): 12 of them struck once, and two struck twice in the control treatment. In the experimental treatment, 10 snakes struck once and three snakes had two strikes. We recorded time to strike for only 8 of them (out of 11) since the videotapes did not allow us to accurately record latency to strike. Time to strike did not differ among treatments (Wilcoxon matched pairs test, $Z = 0.50$, $P < 0.62$).

As we predicted, thermal cues did not influence the propensity of a snake to strike or not strike, the number of strikes, or latency to strike between the control and the experimental treatments. We do not find it surprising that the thermal detection capabilities of the facial pits would not be used in predator evaluation even in close terrestrial encounters. Predators of cottonmouths range from reptiles (e.g., conspecifics) whose temperatures could vary widely, to a variety of mammals and birds that have consistently higher body temperatures. For a generalized prey species, relying on the body temperature of a threat to determine its defensive response would be ill adapted.

However, because we only had 8 snakes that struck in both treatments and for which latency to strike was recordable from the tapes, we make no conclusion on the issue of latency to strike. Possibly, an increase in sample size would reveal an effect on this response variable.

Visual cues are of primary importance in releasing a defensive strike (Scudder and Chiszar, 1977). However, in situations of low visibility an alternative sensory organ may be advantageous (De Cock Buning, 1983). For example, our experiment was conducted in a well-lit environment where snakes could rely solely on visual information. It is possible that in a noctur-

nal setting, thermal cues may be a useful substitute to visual cues, specifically for a species like the cottonmouth, which develops nocturnal habits during late spring and summer (Ernst, 1992). Also, thermal cues may be useful during ecdysis, a period at which snakes are vulnerable partially because of a loss of visual acuity (King and Turmo, 1997). These two hypotheses could easily be tested in a controlled environment.

Previous studies have shown that thermal cues affect predatory strikes. For example, red diamondback rattlesnakes (*Crotalus ruber*) with closed nostrils and amputated tongue tips effectively struck at live mice but did not strike when thermal pits were covered (Dullemeijer, 1961). A congenitally blind northern Pacific rattlesnake (*Crotalus oreganus*) was as effective at striking live mice, as were control subjects with full sensory capacities. However, the same blind rattlesnake lost its efficiency when thermal pits were covered (Kardong and Mackessy, 1991).

To our knowledge, prey detection is the only demonstrated role of thermal pits even though other functional significance has been proposed. For example, Sexton et al. (1992) suggested that thermal pits might help rattlesnakes in detecting winter dens at varying distances because of the intense infrared radiation of rock outcrops. This is unlikely since the thermal organ is only useful at very close range.

Greene (1992) suggested that facial pits originated as defense mechanisms, and Barrett (1970) stated that thermal pits serve the same function in all crotalines. Yet crotaline species may differ in their reactivity to thermal cues because different behavioral traits could potentially lead to different micro-evolutionary pathways (e.g., sensory hierarchy). For example, many *Crotalus* species feed exclusively on endothermic prey (Rubio, 1998), and one may expect strong selection to operate on this thermoreceptive organ. In contrast, our study organism, the cottonmouth is an opportunistic feeder and eats, ectothermic and endothermic prey, as well as carrion (Ernst et al., 2003). Therefore, selection for thermal sensitivity may be de-

creased in the cottonmouth. Future studies are needed to investigate potential interspecific differences to infrared receptivity in a defensive context in crotalines.

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References

- Barrett, R. (1970): The pit organ of snakes. In: *Biology of the Reptilia*, Vol. 2, p. 277-300. Gans, C., Huey, R.B., Eds, New York, Alan R. Liss.
- Blem, C.R. (1997): Lipid reserves of the eastern cottonmouth (*Agkistrodon piscivorus*) at the northern edge of its range. *Copeia* **1997**: 53-59.
- Breidenbach, C.H. (1990): Thermal cues influence strikes in pitless vipers. *J. Herpetol.* **24**: 448-450.
- Brodie, E.D., III (1993): Consistency of individual differences in anti-predator behavior and colour pattern in the garter snake, *Thamnophis ordinoides*. *Anim. Behav.* **45**: 851-861.
- Bullock, T.H., Diecke, F.P.J. (1956): Properties of an infrared receptor. *J. Physiol.* **134**: 47-87.
- De Cock Buning, T. (1983): Thermal sensitivity as a specialization for prey capture and feeding in snakes. *Amer. Zool.* **23**: 363-375.
- Desmoulins, A. (1824): Mémoire sur le système nerveux et l'appareil lacrymal des serpents à sonnettes, des trigonocéphales, et de quelques autres serpents. *Magendie J. Phys. Exp. Path.* **4**: 264-284.
- Dullemeijer, P. (1961): Some remarks on the feeding behavior of rattlesnakes. *Proc. Acad. Wetensch. Amsterdam, Serie C* **64**: 383-396.
- Ernst, C.H. (1992): *Venomous reptiles of North America*. Washington, DC, Smithsonian Institution Press.
- Ernst, C.H., Ernst, E.M., Corker, R.M. (2003): *Snakes of the United States and Canada*. Washington, DC, Smithsonian Institution Press.
- Gibbons, J.W., Dorcas, M.E. (2002): Defensive behavior of cottonmouths (*Agkistrodon piscivorus*) toward humans. *Copeia* **2002**: 195-198.
- Glaudas, X. In press. Do cottonmouths (*Agkistrodon piscivorus*) habituate to human confrontations? *Southeastern Naturalist*.

- Goris, R.C., Nomoto, M. (1967): Infrared reception in oriental crotaline snakes. *Comp. Biochem. Physiol.* **23**: 879-892.
- Greene, H.W. (1992): The ecological and behavioral context for pit viper evolution. In: *Biology of the Pit vipers*, p. 107-117. Campbell, J.A., Brodie, Jr., E.D., Eds, Tyler, TX, Selva.
- Greene, H.W. (1997): *Snakes: The Evolution of Mystery in Nature*. Berkeley, CA, University of California Press.
- Hartline, P.H., Kass, L., Loop, M.S. (1978): Merging of modalities in the optic tectum: Infrared and visual integration in rattlesnakes. *Science* **199**: 1225-1229.
- Herbert, S.S., Hayes, W.K. (1992): The role of facial pits in the thermoregulatory behavior of pitvipers. *J. Tenn. Acad. Sci.* **67**: 19.
- Herzog, H.A., Jr., Bailey, B.D. (1987): Development of antipredator responses in snakes: II. Effects of recent feeding on defensive behaviors of juvenile garter snakes (*Thamnophis sirtalis*). *J. Comp. Psych.* **100**: 233-242.
- Kardong, K.V., MacKessy, S.P. (1991): The strike behavior of a congenitally blind rattlesnake. *J. Herpetol.* **25**: 208-211.
- King, R.B., Turmo, J.R. (1997): The effects of ecdysis on feeding frequency and behavior of the common garter snake (*Thamnophis sirtalis*). *J. Herpetol.* **31**: 310-312.
- Klauber, L.M. (1972): *Rattlesnakes: Their habits, life histories, and influence on mankind*, Vols. 1, 2. Berkeley, CA, University of California Press.
- Noble, G.K., Schmidt, A. (1937): Structure and function of the facial and labial pits of snakes. *Proc. Amer. Phil. Soc.* **77**: 263-288.
- Rubio, M. (1998): *Rattlesnake: Portrait of a predator*. Washington, DC, Smithsonian Institution Press.
- Scudder, K.M., Chiszar, D. (1977): Effects of six visual stimulus conditions on defensive and exploratory behavior in two species of rattlesnakes. *Psych. Rec.* **27**: 519-526.
- Sexton, O.J., Jacobson, P., Bramble, J.E. (1992): Geographic variation in some activities associated with hibernation in nearctic pitvipers. In: *Biology of the Pit vipers*, p. 337-346. Campbell, J.A., Brodie, Jr., E.D., Eds, Tyler, TX, Selva.
- Shine, R., Sun, L.-X. (2003): Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper's strike? *Funct. Ecol.* **17**: 340-348.
- Smith, T.L., Kardong, K.V. (1999): The role of radiation receptors in the predatory behavior of anacondas. *Amer. Zool.* **39**: 18A.
- Whitaker, P.B., Shine, R. (1999): Responses of free-ranging brownsnakes (*Pseudonaja textilis*: Elapidae) to encounters with humans. *Wildl. Res.* **26**: 689-704.

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