

Thermoregulation is the pits: use of thermal radiation for retreat site selection by rattlesnakes

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Summary

Pitvipers (*Viperidae*: *Crotalinae*) possess unique sensory organs, the facial pits, capable of sensing subtle fluctuations in thermal radiation. Prey acquisition has long been regarded as the sole function of the facial pits. However, the ability to sense thermal radiation could also direct thermoregulatory behavior by remotely sensing nearby surface temperatures. Using a series of behavioral arenas of varying spatial complexity and ecological relevance, we surveyed the ability of the western diamondback rattlesnake *Crotalus atrox* to direct successful thermoregulatory movements with either

functional or disabled facial pits. We found that western diamondback rattlesnakes could base thermoregulatory decisions on thermal radiation cues when their pits were functional, but not when blocked. Our results indicate that the facial pit is part of a generalized sense, and suggest thermoregulation as an alternative hypothesis to prey acquisition for the origin of facial pits.

Key words: *Crotalus atrox*, facial pit, behavioral thermoregulation, rattlesnake, prey acquisition, thermal detection.

Introduction

Like many other ectotherms, pitvipers regulate their body temperature by adjusting activity patterns to utilize the heterogeneity of the thermal environment. Behavioral thermoregulation optimizes temperature-dependent physiological processes (Huey, 1982; Angilletta et al., 2002) but limits the time and place of activity and thus constrains other essential behaviors, including courtship (e.g. Navas and Bevier, 2001), foraging (e.g. Gvozdik, 2002), and predator avoidance (e.g. Mori and Burghardt, 2001). The ability to locate favorable microsites efficiently minimizes these constraints while maximizing time spent at optimal body temperatures (Huey, 1991). For example, the thermoregulatory precision of lizards exposed to a novel environment can improve after a learning period (Heath, 1965).

Little work has been devoted to investigating the sensory information by which ectotherms locate favorable microsites from a distance. As sunlight is the common cause of both visual illumination and solar heating, a few studies have tested the use of light intensity as a visual cue to the temperature of a microsite (e.g. Hertz et al., 1994; Sievert and Hutchinson, 1988). Under many circumstances, this may be adequate for successful thermoregulation (e.g. Hertz et al., 1994). However, visual illumination gives no direct information about temperature and can be misleading during the day (e.g. a dark rock in the sun would be hot though visually dark). Further, visual illumination is a largely ineffective cue at night, when residual temperature variations caused by solar heating are no longer associated with illumination cues.

In contrast, emitted thermal radiation is a direct cue that gives reliable information about nearby surface temperatures. Natural surfaces emit thermal radiation in direct proportion to their surface temperatures. Accordingly, emitted thermal radiation is a reliable and efficient means for distinguishing among microsites of varying thermal quality.

The pitvipers (*Viperidae*: *Crotalinae*) are named for their paired, thermally sensitive facial pits located midway between the eye and nostril on either side of the head. These organs are responsive to emitted thermal radiation and can detect variations in surrounding surface temperature (Bullock and Diecke, 1956; Cock Buning, 1983). Facial pits have been repeatedly shown to aid in orienting and striking towards prey (Noble and Schmidt, 1937; Bullock and Diecke, 1956; Cock Buning, 1983; Kardong and Mackessy, 1991; Kardong and Berkhoudt, 1999). Although no other behavioral roles have been demonstrated for facial pits, they could, in principle, be a part of a generalized sense used to examine any temperature variations in the local environment (Goris and Nomoto, 1967; Greene, 1997). For example, this ability to sense thermal radiation could be used to cue behavioral thermoregulation. This possibility has been summarily dismissed on neurological grounds (Bullock and Barrett, 1968; Barrett et al., 1970; Newman and Hartline, 1982) but has never been empirically tested in behavioral studies.

Neuroanatomical and behavioral evidence suggest that the eyes and facial pits are functionally integrated into a generalized multispectral visual sense. Neural output from the

facial pits is combined with visual information in the optic tectum (e.g. Hartline et al., 1978). Behaviorally, one sense can compensate for deficiencies in the other. Kardong and Berkhoudt (1999) report that the predatory performance of rattlesnakes deprived of either visual or thermal stimuli did not differ from each other or from that of unimpaired animals, while animals deprived of both visual and thermal stimuli exhibited drastically hampered performances. Furthermore, Kardong and Mackessy (1991) report that the predatory performance of a congenitally blind rattlesnake did not differ from that of healthy conspecifics.

As the ability to sense temperature from a distance could greatly improve behavioral thermoregulation, it provides a good test of whether facial pits function as a generalized sense. The hypothesis that the facial pits aid thermoregulation makes two testable predictions. (1) Pitvipers can locate thermally favorable microhabitats in the absence of obvious cues (e.g. difference in visual illumination, temperature gradients and landmarks). (2) Pitvipers will subsequently lose this ability when their facial pits are temporarily disabled.

We tested these predictions by performing a series of behavioral experiments on western diamondback rattlesnakes *Crotalus atrox*, in which we presented snakes with a sequentially smaller target under conditions of increasing spatial complexity and ecological relevance. The western diamondback rattlesnake is a representative North American pitviper that inhabits desert and grassland areas. There, it escapes extreme temperatures by locating and moving towards thermal refugia (e.g. rodent burrows, rock crevices). We exploited this natural escape behavior to compare the ability of rattlesnakes with either functional or disabled facial pits to locate a thermal refuge within a stressful environment.

Materials and methods

Experimental animals

We obtained 18 wild-caught western diamondback rattlesnakes *Crotalus atrox* Baird and Givaud 1853 (mean snout–vent length 77 cm) from a commercial supplier (Glades Herp, Inc., Fort Myers, FL, USA). Snakes were individually housed in 50 cm×27 cm×30 cm aquaria with newspaper substrates and supplied with water and shelter. All snakes were in captivity for a minimum of 1 year on a 12 h:12 h L:D cycle and 30°C:23.5°C temperature cycle before testing began.

Experimental temperatures

Snakes are not easily trained (e.g. Wolfe and Brown, 1940; Holtzman et al., 1999), and consequently the experiments were designed to exploit innate responses. We encouraged active behavioral thermoregulation in our study animals by subjecting them to a high, but sublethal, heat stress and providing a thermal refuge that they had to identify from a distance. Different temperatures thus provided both the motivation and the reward.

We held all thermal refugia at 30°C. Western diamondbacks regularly select a body temperature near 30°C under natural

conditions (e.g. Cowles and Bogert, 1944; Beck, 1995, 1996). The appropriate ambient heat stress temperature to motivate escape behavior was less obvious, however. Few, if any, reliable data exist regarding upper temperature tolerance in *C. atrox* (Cowles and Bogert, 1944). We therefore conducted preliminary experiments in which we placed snakes in an arena held at a temperature typical of the upper selected limits for desert reptiles, 40–42°C. We used a thermal imager (ThermaCam® PM575, FLIR, North Billerica, MA, USA) to monitor body temperature (Jones and Avery, 1989) and observed behavior using closed-circuit video. When held at 40°C, animals displayed normal behavioral patterns for up to 1 h, and though body temperature approached 40°C, we never observed gaping, immobility, loss of righting responses, escape behavior or other indication of potentially injurious heat stress. Accordingly, we selected 40°C as the stressful environmental temperature.

Facial pit blocking

We temporarily disabled facial pits by first lightly anesthetizing snakes with isoflurane (Abbott Laboratories, North Chicago, IL, USA). When the snake was immobile, we placed a small polystyrene foam ball inside the facial pit cavity and glued a piece of aluminum foil over the facial pit opening using a latex adhesive (Skin Bond®, Smith-Nephew Inc., Fort Largo, FL, USA). The aluminum foil served to reflect incoming thermal radiation and retain the polystyrene foam ball, which acted as a piece of physical insulation against pit membrane heating by the aluminum. This modification of an existing technique (Kardong, 1992; Haverly and Kardong, 1996) provided a semi-permanent, reliable blockage that could easily be removed with mineral oil. Snakes received a sham procedure when dictated by experimental design. This consisted of anesthetizing snakes, inserting and removing a polystyrene foam ball from the facial pit cavity, and holding a glue-laden aluminum patch ca. 1 mm from the facial pit for 20 s.

Experimental arenas

The overall design consisted of three experiments, in which we presented snakes with sequentially smaller infrared targets (Fig. 1) in increasingly complex and ecologically relevant experimental arenas. The details of each arena are described below.

Experiment I

We first tested the ability of rattlesnakes to locate a favorable microsite in a simple Y-maze experiment. We constructed Y-mazes using transparent polycarbonate tube (8.9 cm o.d., 8.2 cm i.d.) and polyvinylchloride (PVC) plumbing components. The maze consisted of four main parts. The center section was a three-branch PVC Y shape with the base and two side branches fitted with open-ended 35 cm sections of polycarbonate tube. An acrylic window in the center branch allowed behavior to be videotaped as the snake emerged from the base and went down either of the branches. The base of the

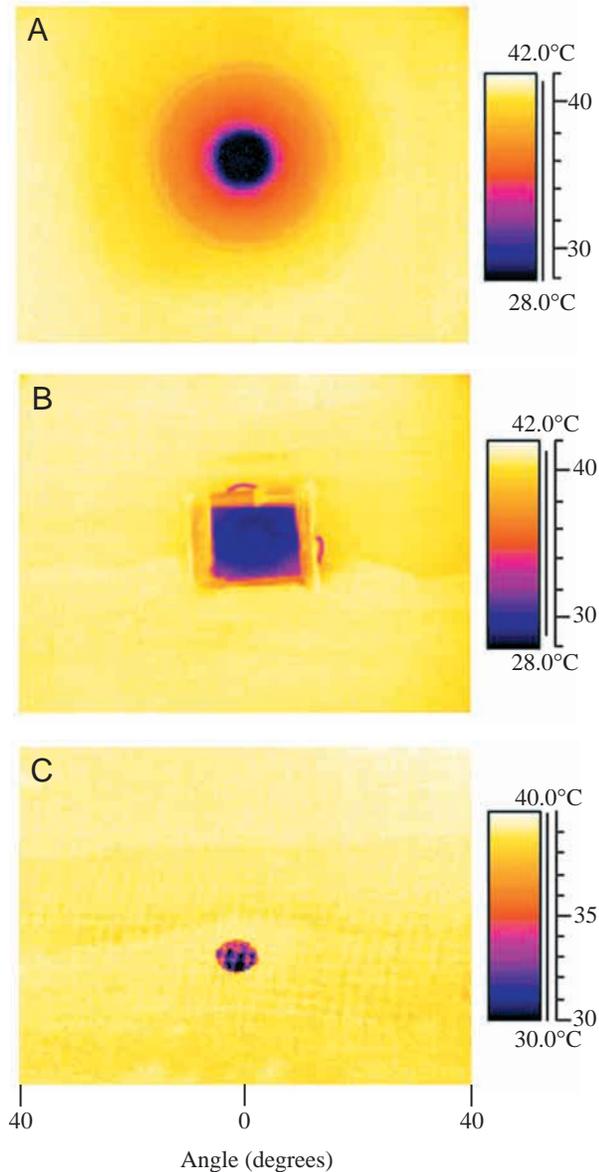


Fig. 1. Thermal images of the refuges in the Y-maze (A), hide-box (B) and artificial burrow (C) experiments. All images were taken at a distance of 1 m from the radiating surface. The horizontal field of view subtended at an angle of 80°.

Y consisted of a removable snake carrier composed of a 45 cm long polycarbonate tube with a PVC cap on the distal end. The proximal end was fitted with a PVC coupling slotted to accommodate a sliding door. The two terminal ends of the maze branch (the 'goals') consisted of similar carriers wrapped with copper heat exchange coils and covered with insulation. We attached the carrier and goals to the maze by slipping the coupling over the open-end tubes and tightening a nylon set screw.

To regulate the main part of the maze at a uniform and stressful level, the entire maze was placed in a walk-in environmental chamber (model 08083, Hotpack Corporation, Philadelphia, PA) set at 40°C. We regulated one goal at the

same 40°C and the other (the 'refuge') at 30°C by circulating water from two temperature-controlled water baths through the copper coils. During trials, water lines from the baths were attached to the goals using quick-connects.

To minimize unintentional cues, we randomized the association between a particular goal and its temperature, and we circulated water around both goals at the same rate. Also, we randomized refuge location (right- or left-maze branch) and the overall maze orientation within the environmental chamber (three-way rotational symmetry of Y-maze); this resulted in six unique maze configurations under which each snake was tested twice, once with functional and once with disabled facial pits. We thoroughly cleaned the maze with bleach solution between trials to remove odor trails. We verified the absence of air and surface temperature gradients near the branch point of the assembly using fine thermocouples in the air space and glued to the substrate, as well as thermography imaging of external maze surface temperature. Note that the appearance of a temperature gradient in Fig. 1A is an artifact caused by small-angle reflection of thermal radiation from the polished tubing surface. It is not seen when the maze is imaged at right angles to the surface.

At the start of each experiment, the carrier was covered with a black cloth and attached to a fitting on the side of a plastic tub. We moved each snake from its cage to the tub with a snake hook, whereupon the snake would attempt to hide by entering the carrier, which resembled a dark burrow. When it did, we closed the sliding door, removed the carrier, and attached it to the base of the maze. We began the experiment by raising the sliding door on the carrier and leaving the environmental chamber. All behavioral data were recorded with normal room illumination using closed-circuit video cameras. At the end of the experiment, we closed the sliding door in the goal containing the snake, removed the goal, and returned the snake to its cage.

We tested 12 wild-caught *C. atrox* (mean snout-vent length 68 cm) under a control-treatment-control design. First, all 12 snakes were tested with functional facial pits. These snakes then had their facial pits blocked and were retested. Finally, the same snakes had the blockages removed and were once again tested with functional pits. This experimental design enabled us to investigate the role of facial pits in thermoregulatory behavior while simultaneously detecting any learning or temporal (e.g. seasonal) effects or any lasting effects of facial pit blocking. The null hypothesis was that each snake would initially move toward the refuge in 50% of the trials. We scored each snake as having selected a branch when its head was 5 cm from the branch point and 60 cm from the opening of the refuge.

Experiment II

For this experiment, we presented snakes with a more complex thermoregulatory decision. We tested $N=16$ snakes (12 from the previous experiment; mean snout-vent length=74 cm) in a 1.8 m diameter circular metal stock tank painted flat gray (to prevent thermal radiation reflections and

thus provide a uniform thermal radiation background) and filled with sand to a depth of 10 cm. The arena was housed in a walk-in environmental chamber held at 40°C. We placed four 18 cm×18 cm×18 cm hide boxes about the perimeter at 90° intervals. The inside of all hide boxes was painted flat black to provide a uniform visual signal contrasting with the gray background. The temperature of the back wall of each box was regulated by water circulated in copper coils soldered to the copper back wall. One of the four boxes was held 30°C, while the other hide boxes were regulated at 40°C. This arrangement allowed us to test snakes under conditions of greater spatial complexity using a more statistically powerful design.

We randomized the location of the 30°C refuge across the four possible locations, generating four orthogonal arena configurations. Snakes were tested twice under each configuration, once when facial pits were functional and once when they were blocked. We removed association between temperature and a specific hide box, and we used the same rate of water flow through the coils on all hide boxes. We mixed the sand thoroughly between trials to eliminate directional odor trails, and we verified the absence of air and surface temperature gradients with thermocouples and thermal imaging.

Snakes were initially held in a circular wire cage that allowed them to view and approach within 69 cm of the hide boxes. The upper part of the cage was covered with a black cloth so that the snakes could not observe the investigator leaving the environmental chamber. Otherwise, the snakes would assume a defensive coil and face the door indefinitely. After a pre-determined amount of time based on individual heating curve data (A. R. Krochmal and G. S. Bakken, unpublished data; mean time=4 min), we released the snakes by remotely lifting the cage a few cm. We scored the snake as having selected a particular refuge when it was moving toward a hide box and its head crossed a circle 64 cm from the hide boxes.

Analysis of experiment 1 did not demonstrate any lasting effects of blocking facial pits. Therefore, we simplified our experimental design. At the start of experimentation, half of the experimental animals had their facial pits blocked, while the other half underwent a sham procedure and maintained functional pits. Midway through experimentation, those with functional pits had their pits blocked, while those with blocked pits had the blockages removed. The null hypothesis was that each snake would initially move toward the refuge in 25% of the trials.

Experiment III

For the third experiment, we surveyed the ability of the same 16 snakes to distinguish among quasi-natural retreat sites of varying thermal quality. We simulated natural retreat sites by burying four temperature-controlled artificial burrows beneath the sand substrate of the same circular arena used in the previous experiment. The artificial burrows were polycarbonate tube assemblies similar to those used as Y-maze goals. Each was wrapped with copper tubing and insulation,

inserted into a 20.3 cm diameter PVC sleeve, and buried in the sand with the opening facing the arena center. We regulated the arena at 40°C, and we maintained one burrow at 30°C and the others at the ambient 40°C by circulating water from regulated water baths through the copper coils. All other procedures, randomizations and parameters followed those used in the hide box trials.

Statistical analysis

During each of our three experiments, we tested snakes multiple times, corresponding to the number of orthogonal experimental configurations used to randomize potential confounding variables. For each snake and treatment we divided the number of initial movements toward the thermal refuge by the total number of trials to obtain a proportion of success. We arcsine transformed these proportions, calculated the mean proportion of success for each snake-treatment combination, and pooled means across snakes within a treatment (functional or disabled pits). In each experiment, the null hypothesis proportion of success was taken as (number of favorable refuges)/(number of potential refuges). We compared the observed result (mean for all snakes within each treatment group) to the null hypothesis using one-sample *t*-tests. To be conservative, we report two-tailed *P* values, even though the hypothesis is strictly one-tailed.

Results

Experiment I

The presence of functional pits clearly allowed snakes to identify the cool refuge from a distance (Fig. 2A). When initially tested with functional pits, snakes located the thermally favorable (30°C) side of the maze far more often than predicted by chance ($t=3.89$, d.f.=11, $P=0.003$). When retested with blocked pits, the same individuals subsequently lost this ability ($t=0.42$, d.f.=11, $P=0.68$) but regained it when again tested with functional pits ($t=4.00$, d.f.=11, $P=0.002$).

We gathered no evidence for any detrimental impact of the facial pit blocking procedure, as snakes with open pits performed equally well whether or not the facial pit had been blocked and unblocked previously (two-sample *t*-test, $t=-0.097$, d.f.=1,10 $P=0.92$). Experimental snakes showed no side preference after removing the effect of temperature difference ($\chi^2=1.39$, $P>0.1$).

Experiment II

Functional pits allowed snakes to identify the cool refuge from a distance, even given the greater spatial complexity (Fig. 2B). Snakes with functional pits moved toward the thermal refuge significantly more often than predicted by chance ($t=4.82$, d.f.=15, $P<0.001$). Temporarily disabling the facial pits eliminated this ability ($t=-0.085$, d.f.=15, $P>0.9$). Pooled across all trials, snakes showed no preference for physical hide box locations ($\chi^2=0.80$, d.f.=3, $P>0.75$). In the trials where animals with functional pits did not move toward the refuge, movements were distributed

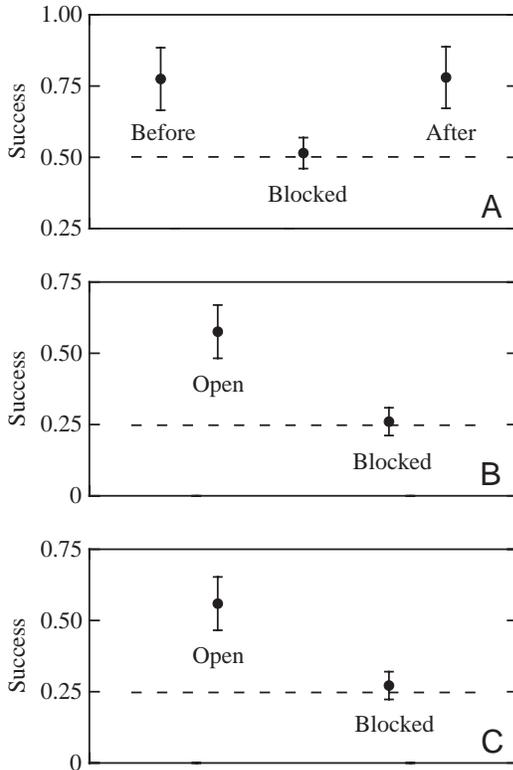


Fig. 2. Western diamondback rattlesnakes can rely on their facial pits to mediate thermoregulatory behavior. The plot compares means and 95% confidence intervals for rattlesnakes with either open or blocked facial pits in (A) the Y-maze, (B) the circular arena with hide boxes or (C) the circular arena fitted with artificial burrows. The dashed lines represent the experiment-specific null-hypothesis prediction.

evenly among the remaining hide boxes ($\chi^2=0.35$, d.f.=2, $P>0.75$).

Experiment III

When presented with a natural thermoregulatory target signal, experimental snakes relied on information from their facial pits to direct thermoregulatory movements (Fig. 2C). Animals with functional pits chose the 30°C burrow ($t=4.0641$, d.f.=5, $P=0.002$), while those with disabled pits selected burrows at random ($t=-0.078$, d.f.=15, $P=0.951$). Overall, snakes did not favor any physical burrow position ($\chi^2=0.99$, d.f.=3, $P>0.75$). In the trials where animals with functional pits did not move toward the refuge, movements were distributed evenly among the remaining burrows ($\chi^2=2.05$, d.f.=2, $P>0.1$).

Discussion

Our experimental results clearly demonstrate that *C. atrox* can and do use their facial pits to direct thermoregulatory behavior, contradicting published assertions to the contrary, which were based on extrapolations from neurological data (Bullock and Barrett, 1968; Barrett et al., 1970). This previously undocumented behavior might be a significant

component of behavioral thermoregulation in this species. This seems especially likely considering that experimental animals performed well under spatially complex and ecologically relevant conditions.

Though snakes with functional pits performed significantly better than predicted by chance, they did not perform perfectly. We conclude that performance was limited by motivation rather than by ability. This is, at least in part, a consequence of factors inherent in the experimental designs. First, the 40°C ambient temperature, while stressful, allowed snakes to explore the arenas indefinitely rather than seek immediate shelter. Indeed, several individuals displayed normal exploratory behavior in the arenas for as long as 60 min, and for much of this time the snakes had a thermographic body temperature near 40°C. Second, average performance in locating the cool refuge was unaffected by increased spatial complexity, while we would expect that performance would have been degraded if snakes had difficulty using thermal radiation cues.

We conclude that thermal radiation was the only cue available to the snakes to direct their movement toward the refuge. By eliminating or randomizing all non-thermal cues within our arenas (e.g. fluctuations in ambient light intensity, features of the physical environment), we potentially removed additional key sensory information with which snakes might mediate natural behavior. While minute thermal gradients existed very close to the cool refuge, we scored behavior on the basis of the direction of movement well before snakes would have encountered such gradients.

Our results give further support to the hypothesis that facial pits are general sense organs used to survey the environment, and that information derived from visual and thermal radiation is well integrated, perhaps even functioning as a single multispectral sense. Neuroanatomically, the neural output from the facial pits is integrated with visual information in the optic tectum, the area of the brain in which spatiotopic maps of the senses are formed (Hartline et al., 1978; Newman and Hartline, 1981). Moreover, more than half of the receptive units within the optic tectum exhibit cross-modality interactions (i.e. respond better to both facial pit and visual stimuli than to either stimulus alone), further emphasizing the functional integration of visual and thermal signals (Newman and Hartline, 1981). Behaviorally, the compensatory nature of visual and thermal information has already been established. For example, Kardong and Mackessy (1991) and Kardong and Berkhoudt (1999) showed that rattlesnakes strike as well when using only thermal or visual information as when using both senses, demonstrating parallel behavioral uses of these two senses.

Previously, prey acquisition was the sole documented role of facial pits and was therefore considered the adaptive function that drove their evolution (e.g. Greene, 1997). Other proposed uses of the facial pit included predator detection, den site selection and behavioral thermoregulation (e.g. Greene, 1997). While all these hypotheses are plausible, behavioral thermoregulation currently stands as the only documented role of facial pits aside from prey acquisition, and therefore

suggests a viable alternative hypothesis for explaining their evolution.

The merits of three possible scenarios must be considered when pondering the adaptive forces that drove the evolution of facial pits. (1) Facial pits might have initially evolved as an aid in behavioral thermoregulation and were then recruited to assist in prey acquisition; (2) facial pits could have arisen as prey acquisition aids, with the ability to direct thermoregulatory movements arising later; (3) some as-yet-undocumented behavioral role (e.g. predator detection) was the adaptive force that drove the evolution of facial pits, with the currently demonstrated roles evolving subsequently. While other uses of the facial pit are likely to exist, they do not currently represent functional alternative hypotheses for comparative analysis, as they have not undergone empirical testing. The relative merits of the remaining two scenarios can be determined by considering the possible behavioral uses of the progenitor to the facial pit.

The precursor of the facial pit was probably relatively insensitive to emitted thermal radiation. Prey items at ecologically relevant distances give off weak thermal signals. Alternatively, environmental features subtend far larger solid angles and possess relatively larger temperature differences than do prey items, and they would therefore present a larger total thermal signal than would prey items. This would make environmental features more easily sensed than prey items by animals with a limited form of thermal detection. An ancestral, comparatively limited, ability to sense thermal radiation might therefore have been more useful for thermoregulation than for prey acquisition. Accordingly, we propose that the facial pit might have arisen as a thermoregulatory aid and was subsequently co-opted to acquire prey. Once established, the persistence of specialized thermal detection in pitvipers can be maintained by a variety of functions, including enhanced thermoregulation, prey acquisition and other proposed, but currently undocumented, behaviors.

Whether predation or thermoregulation was the original utility function driving the evolution of facial pits might be clarified by a combination of ecological and phylogenetic studies. First, the ability to direct thermoregulatory movement *via* the facial pits has only been documented in *C. atrox* subjected to high heat stress, and therefore might reflect recent ecological history. *C. atrox* is a xeric-adapted denizen of the American Southwest, where high daytime surface temperatures (50°C or higher) and high daily fluctuations in temperature make behavioral thermoregulation a constant care. Such habitats present both strong thermal infrared signals and clear and immediate benefits from efficient thermoregulatory decisions. Consequently, thermoregulatory use of the facial pit might be a recent ecological adaptation. It is less clear whether similar signals and selective pressures would be present in more stable, benign situations. A survey of the presence or absence of this behavior in pitvipers found in a variety of thermal regimes is a possible test of this hypothesis. Should only animals from thermally stressful environments use

facial pits to mediate behavioral thermoregulation, it would appear to be a response to recent selection by local conditions. Thermoregulation is then less likely to be the original selective force that drove facial pit evolution. If, however, thermoregulatory use of the facial pits is found in species occupying a range of habitat types, then the case for a thermoregulatory origin is strengthened.

Further insight could come from a broad phylogenetic survey of the presence or absence of thermoregulatory behavior cued by thermal radiation across ophidian taxa. For example, true vipers, a closely related subfamily within the family Viperidae, possess supranasal sacs. These organs neurologically and histologically resemble a thermal detector (York et al., 1998). Additionally, some true viper species (Russell's viper *Daboia russelli* and puff adder *Bitis arietans*) are reportedly able to incorporate thermal information into their behavioral patterns (Breidenbach, 1990), further supporting the notion that they possess a thermal sensor. While quantitative neurophysiological data comparing the thermal sensitivity of true vipers and pitvipers are lacking, the structure of the facial pits suggests that they are likely to be more sensitive to emitted thermal radiation than supranasal sacs. Therefore, whether homologous with the facial pit or not, the supranasal sac might provide a model for the early radiation sensor.

The ability of the western diamondback rattlesnakes to mediate thermoregulatory decisions *via* the facial pit may play a substantial role in their natural thermoregulation, as animals exhibited this behavior under spatially complex and ecologically relevant conditions. Investigating the ability of snakes to rely on radiative cues to mediate thermoregulatory decisions within an ecological and phylogenetic framework will allow for tests of key functional and adaptive hypotheses regarding the use and evolution of the organ. Together, such studies may identify the phylogenetic root of this behavior and perhaps clarify the origins of this novel sense organ.

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References

- Angilletta, M. J., Jr, Niewiarowski, P. H. and Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* **27**, 249-268.
- Barrett, R., Maderson, P. F. A. and Meszler, R. M. (1970). The pit organs of snakes. In *Biology of the Reptilia*, vol. 2 (ed. C. Gans and T. S. Parsons), pp. 277-300. London: Academic Press.
- Beck, D. D. (1995). Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *J. Herpetol.* **29**, 211-223.
- Beck, D. D. (1996). Effects of feeding on body temperatures of rattlesnakes: a field experiment. *Physiol. Zool.* **69**, 1442-1455.

- Breidenbach, C. H.** (1990). Thermal cues influence strikes in pitless vipers. *J. Herpetol.* **24**, 448-450.
- Bullock, T. H. and Barrett, R.** (1968). Radiant heat receptors in snakes. *Commun. Behav. Biol. A* **1**, 19-29.
- Bullock, T. H. and Diecke, F. P. J.** (1956). Properties of an infra-red receptor. *J. Physiol. (Lond.)* **134**, 47-87.
- Cowles, R. B. and Bogert, C. M.** (1944). A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Museum Nat. Hist.* **83**, 265-296.
- de Cock Buning, T.** (1983). Thermal sensitivity as a specialization for prey capture and feeding in snakes. *Amer. Zool.* **23**, 363-375.
- Goris, R. C. and Nomoto, M.** (1967). Infrared reception in oriental crotaline snakes. *Comp. Biochem. Physiol.* **23**, 879-892.
- Greene, H. W.** (1997). *Snakes: The Evolution of Mystery in Nature*. Princeton, NJ: Princeton University Press.
- Gvozdik, L.** (2002). To heat or save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. *Can. J. Zool.* **80**, 479-492.
- Hartline, P. H., Kass, L. and Loop, M. S.** (1978). Merging of modalities in the optic tectum: infrared and visual integration in rattlesnakes. *Science* **199**, 1225-1229.
- Haverly, J. E. and Kardong, K. V.** (1996). Sensory deprivation effects on the predatory behavior of the rattlesnake, *Crotalus viridis oreganus*. *Copeia* **1996**, 419-428.
- Heath, J. E.** (1965). Temperature regulation and diurnal activity in horned lizards. *Univ. Calif. Pub. Zool.* **64**, 97-136.
- Hertz, P. E., Fleishman, L. J. and Armsby, C.** (1994). The influence of light intensity and temperature on microhabitat selection in two *Anolis* lizards. *Func. Ecol.* **8**, 720-729.
- Holtzman, D. A., Harris, T. W., Aranguren, G. and Bostock, E.** (1999). Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Anim. Behav.* **57**, 51-60.
- Huey, R. B.** (1991). Physiological consequences of habitat selection. *Amer. Nat.* **137**, S91-S115.
- Huey, R. B.** (1982). Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia*, vol. 12 (ed. C. Gans and F. H. Pough), pp. 25-91. London: Academic Press.
- Jones, S. M. and Avery, R. A.** (1989). The use of a pyroelectric vidicon infra-red camera to monitor the body temperatures of small terrestrial vertebrates. *Func. Ecol.* **3**, 373-377.
- Kardong, K. V.** (1992). Proximate factors affecting guidance of the rattlesnake strike. *Zool. Jb. Anat.* **122**, 233-244.
- Kardong, K. V. and Berkhoudt, H.** (1999). Rattlesnake hunting behavior: correlations between plasticity of predatory performance and neuroanatomy. *Brain Behav. Evol.* **53**, 20-28.
- Kardong, K. V. and Mackessy, S. P.** (1991). The strike behavior of a congenitally blind rattlesnake. *J. Herpetol.* **25**, 208-211.
- Mori, A. and Burghardt, G. M.** (2001). Temperature effects on anti-predator behavior in *Rhabdophis tigrinus*, a snake with toxic nuchal glands. *Ethology* **107**, 795-811.
- Navas, C. A. and Bevier, C. R.** (2001). Thermal dependency of calling performance in the eurythermic frog *Colostethus subpunctatus*. *Herpetologica* **57**, 384-395.
- Newman, E. A. and Hartline, P. H.** (1981). Integration of visual and infrared information in bimodal neurons of the rattlesnake optic tectum. *Science* **213**, 789-791.
- Newman, E. A. and Hartline, P. H.** (1982). The infrared 'vision' of snakes. *Sci. Amer.* **246**, 116-127.
- Noble, G. K. and Schmidt, A.** (1937). The structure and function of the facial and labial pits of snakes. *Proc. Am. Phil. Soc.* **77**, 263-288.
- Sievert, L. M. and Hutchison, V. H.** (1988). Light versus heat: Thermoregulatory behavior in nocturnal lizard (*Gekko gekko*). *Herpetologica* **44**, 266-273.
- Wolfe, D. L. and Brown, C. S.** (1940). A learning experiment with snakes. *Copeia* **1940**, 134.
- York, D. S., Silver, T. M., and Smith, A. A.** (1998). Innervation of the supranasal sac of the puff adder. *Anat. Rec.* **251**, 221-225.