

# The use of ground-borne vibrations for prey localization in the Saharan sand vipers (*Cerastes*)

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## Summary

Sand vipers of the genus *Cerastes* are specialized semi-fossorial snakes that launch predatory strikes at rodents and lizards while partially buried in the soft sand of the Saharan desert. This study attempted to document which environmental stimuli are used by these snakes as a trigger for the ambush behavior. Denervating the olfactory and vomeronasal organs produced no changes in prey capture behavior in *Cerastes cerastes*. Occluding the eyes of the denervated specimens resulted in significant decreases in strike distance, diversity of strike angle and strike accuracy, demonstrating the importance of visual stimuli for target acquisition in this species. Nevertheless, every olfactory-denervated, temporarily blinded specimen succeeded in capturing free-ranging mice in every trial.

Presentation of chemosensory-neutral targets to the olfactory-denervated, temporarily blinded specimens resulted in similar predatory behaviors, whether the target was isothermic to the environment or heated to mammalian body temperature. Collectively, these results provide evidence for the importance of visual stimuli during foraging in *C. cerastes*, the first experimental evidence for foraging by vibration detection in snakes and the strongest evidence to date that snakes are capable of 'hearing' vibrational stimuli.

Key words: feeding, prey capture, Reptilia, squamata, audition, behaviour, Saharan sand viper, *Cerastes cerastes*.

## Introduction

Snakes use a variety of environmental stimuli mediated through special sense organs to localize their prey (Ford and Burghardt, 1993). Previous work has shown the importance of chemosensory, visual and thermal stimuli, often in species-specific combinations (Austin and Gregory, 1998). Deprivation or enhancement of dominant stimuli produces a wide range of behavioral responses from disruption of predatory behavior (e.g. Haverly and Kardong, 1996), through no apparent effect (e.g. Bonnett et al., 1999) to exaggerated prey capture responses (e.g. Shivik et al., 2000).

Haverly and Kardong (1996) found that presenting motionless prey to rattlesnakes deprived of infrared and visual stimuli increased the duration to approach/strike fourfold, but this difference was not significant, and the authors concluded that vibration reception was not important for rattlesnake predation. The experimental design of most other studies on the sensory bases of snake predation have ignored vibrational stimuli (either ground-borne or airborne), perhaps reflecting the common view that snakes are incapable of responding to vibrations. Wever (1978) provided physiological evidence that snakes could perceive airborne and ground-borne vibrations, and Hartline (1971a,b) confirmed these findings and demonstrated that snakes can perceive vibrations both through their inner ears and from the body surface (termed somatic hearing). Although a fundamental frequency imbalance

between vibrational sensitivity and sound production appears to minimize the potential for intraspecific acoustic communication in snakes (Young, 1998), vibration detection may be an important aspect of interspecific interactions. A recent study attempted to quantify the distance over which snakes could detect prey items and identified particular habitats, including fossoriality, where vibration detection would be particularly important (Young et al., 2000).

The genus *Cerastes* consists of two species which inhabit the loose sand of the Saharan desert. These snakes are ambush predators that capture small rodents and lizards while fully or partially submerged in the sand (e.g. Schleich et al., 1996). The purpose of this paper was to determine whether *Cerastes* could use vibrational stimuli to locate its potential prey; if so, this would represent the first experimental evidence for vibration detection leading to an ecologically important behavioral response in snakes.

## Materials and methods

We examined the sensory basis of prey localization in four adult specimens of *Cerastes cerastes* (snout–vent length 39–60 cm), which were obtained commercially. The snakes were kept in a venomous snake room in individual terraria on a bedding of 5 cm of clean dry sand, at 30–33 °C, with a 12 h:12 h

light:dark cycle. Additional observations of prey capture were made on four specimens of *C. vipera* (snout-vent length 15–22 cm).

A 2 m×2 m×0.5 m high filming base was constructed of plywood. The filming base was elevated off the floor with wood beams 10 cm<sup>2</sup> in cross section; the joints between the beams and the floor and between the beams and the filming base were filled with vibration-dampening pads (Fisher). The filming base was filled to a depth of approximately 20 cm with clean dry sand. In the center of this filming base, on the surface of the sand, was positioned a 1 m×1 m×0.1 m filming cage constructed of Plexiglas. The filming cage had no bottom (it rested on the sand of the filming base), but it had a hinged Plexiglas top. Directly above the filming base, suspended from the ceiling of the laboratory, was a two-dimensional camera dolley which supported a 1000S high-speed digital video camera (Redlake Instruments). Using a series of pulleys and cables, the video camera could be positioned directly over the snake. The filming cage and the snake within it were heated with two 250 W infrared heat lamps.

#### Experiment 1

The first experiment involved three phases. In the first phase, the control, specimens of *C. cerastes* were placed individually in the filming chamber for a period of at least 12 h; the heat lamps came on automatically for the last 7 h and heated the sand surface of the filming chamber to a temperature of 28.5–31 °C (measured with a probe buried in the center of the filming cage). Immediately prior to the trial, the heat lamps were turned off and the filming cage was illuminated with a Northstar photographic light (Photographic Analysis). A single live mouse (mass 10.05±0.86 g, mean ± S.E.M.) was released into the filming cage at the furthest point from the head of the specimen. The mouse was allowed to move unrestrained until prey capture occurred. The prey capture strike was filmed at 500 frames s<sup>-1</sup> with a shutter speed of 1/20 000 s. The digital record was streamed to a PowerMac 8500 (Apple) and saved using Premiere 4.0 (Adobe). Using Image 1.6.2 (N.I.H.), the distance from the snake's snout to the mid-body of the mouse was quantified, as was the angle between the long axis of the snake's head and the mid-body of the mouse and the terminal velocity of the strike (defined as the mean velocity over the last 8 ms of the strike before contact). Each snake was filmed at most once every 7 days; at times, the interval between predation bouts exceeded 2 weeks. In total, 18 strikes were recorded, roughly evenly divided among the four specimens.

For the second phase of the experiment, the snakes were anesthetized by exposure to Isoflurane. Once fully anesthetized, the snakes were placed on a heated surgical table (VSSI) and prepared for sterile surgery. An incision was made near the naso-frontal joint, and the nasal and vomeronasal nerves were isolated, severed and mechanically disrupted. The specimens were given 2 weeks to recover and then presented with mice (mass 9.38±0.65 g; mean ± S.E.M.) as described above for the control trials. In total, 18 strikes, roughly evenly

divided between the four snakes, were analyzed during the second phase of the experiment.

For the third phase of the experiment, the same four snakes were briefly anesthetized with Isoflurane, and small pieces of surgical tape were placed over each eye. The outer surface of the surgical tape was painted with a non-toxic black paint (RoseArt). A third series of trials was performed as described above, except that, before each trial, the snake was lightly restrained and a fresh coat of black paint was applied over the eyes. Functional blindness of the snake was assayed before each trial by the visual appearance of the eye and the failure of the snake to respond to movements of the researchers. In total, 16 strikes, roughly evenly divided among the specimens, were recorded at live mice with a mass of 8.78±0.71 g (mean ± S.E.M.).

#### Experiment 2

The second experiment was performed using the four denervated, temporarily blinded *Cerastes cerastes* (described above). The targets for these experiments were Styrofoam balls with a diameter of 3.8 cm. The balls were rinsed in distilled water and only handled with surgical gloves. One ball was placed in the center of the filming cage, the other was placed in front of a radiant heater. The heat lamps were used to heat the sand in the filming cage and the target ball to approximately 29.5 °C; the radiant heater warmed the surface of the second target ball to approximately 37.8 °C (determined using the surface probe of a 100A digital thermometer; VWR). Individual snakes were placed in the cage and allowed to adopt the typical predatory posture (see below), and a 2 min control period was then recorded using a standard video camera (Handycam, Sony). The target ball was manipulated using a tack attached to the end of a 1 m long balsa-wood dowel (diameter of 4 mm); the target ball was used to tap the surface of the sand gently in the region of the snake's head. Care was taken not to touch the snake with the target ball. The target ball was presented for 30 s, and the snake's response was video-recorded. The snake was given 5 min to recover, and the second target ball was then presented in the same fashion. The order of presentation of the two target balls (isothermic and heated) was alternated, and four trials were recorded from each snake. From the video recordings of each trial (containing two control and two experimental periods), the total number of tongue flicks, head movements and strikes was quantified. Any struck target was replaced prior to the next trial.

All experimental procedures were conducted in accordance with established procedures for research on ectothermic vertebrates and venomous snakes. The experimental procedures were approved by the Institutional Animal Care and Use Committee of Lafayette College.

Results are presented as means ± S.E.M.

### Results

*Cerastes* is a specialized ambush hunter with rather consistent predatory behavior. The specimens lie in loose coils

buried in the sand and exhibit little overt behavior when the prey are introduced: they neither tongue-flick nor reposition their head, but do regularly caudal lure. The prey are captured, and held, through rapid strikes. The predatory strikes of *Cerastes* frequently involve dramatic changes in direction, with the long axis of the head rotating by up to 180° (i.e. the head starts forward but then loops around to strike backwards). The high-speed digital recordings reveal that the head and fore-body are turned in mid-strike; these changes in direction occur smoothly, with no evidence of changing velocity or the integration of multiple strikes. There was interspecific variation in the predatory behavior; *C. vipera* buries completely into the sand with, at most, just the eyes exposed at the surface. Burying depth is more variable in *C. cerastes*, although normally at least half the head is positioned below the surface of the sand.

#### Experiment 1

The analysis of the control strikes revealed the diversity of strike angle in *Cerastes cerastes* (Fig. 1A). Control strikes had a mean distance to target of  $5.27 \pm 0.69$  cm ( $N=18$ ) and a mean strike velocity of  $116.2 \pm 7.6$  cm s<sup>-1</sup>. Predatory encounters recorded following recovery from the denervation surgery revealed no behavioral changes (the snakes still waited in ambush with the head partially buried and little or no tongue-flicking). The strikes still exhibited considerable angular variation (Fig. 1B), the distance to target ( $7.02 \pm 0.95$  cm,  $N=18$ ) and velocity of the strike ( $125.84 \pm 6.91$  cm s<sup>-1</sup>) were greater than in the controls, but not significantly so.

During predatory trials, the denervated, temporarily blinded snakes exhibited unusual predatory behaviors. Tongue flicks were frequently observed, although not when in close proximity to the prey and, rather than remaining immobile, the snakes often pursued the prey in short, jerky movements. Examination of the video recordings revealed that immobile prey were never struck; instead, strikes were launched immediately following a footfall (particularly following a jump or similar large-scale movement). These behaviors combined to produce short strikes directed primarily straight ahead (Fig. 1C). The distance to target ( $3.12 \pm 0.40$  cm,  $N=16$ ) and velocity of the strike ( $101.2 \pm 10.8$  cm s<sup>-1</sup>) were lower than in the controls, but only significantly so ( $t=2.84$ , d.f.=2,  $P=0.012$ ) in the case of target distance.

The angular distributions of the strikes were divided into 30° intervals (defined from the long axis of the head) with strikes pooled from the left and right sides of the snake. The results reveal the prevalence of 'straight' (0–30°) strikes in the denervated, temporarily blinded specimens, and the scarcity of strikes with angular deflections over 90° during these same trials (Fig. 2). The prey targets used were fairly small to prevent satiation and defensive behaviors. The accuracy of the strike was gauged by determining the number of strikes from each trial in which the snake hit the mouse with both fangs (bilateral strike), only one fang (unilateral strike) or no fangs (missed strike). In both the control and denervated trials, bilateral strikes were the most common, followed by unilateral, then missed

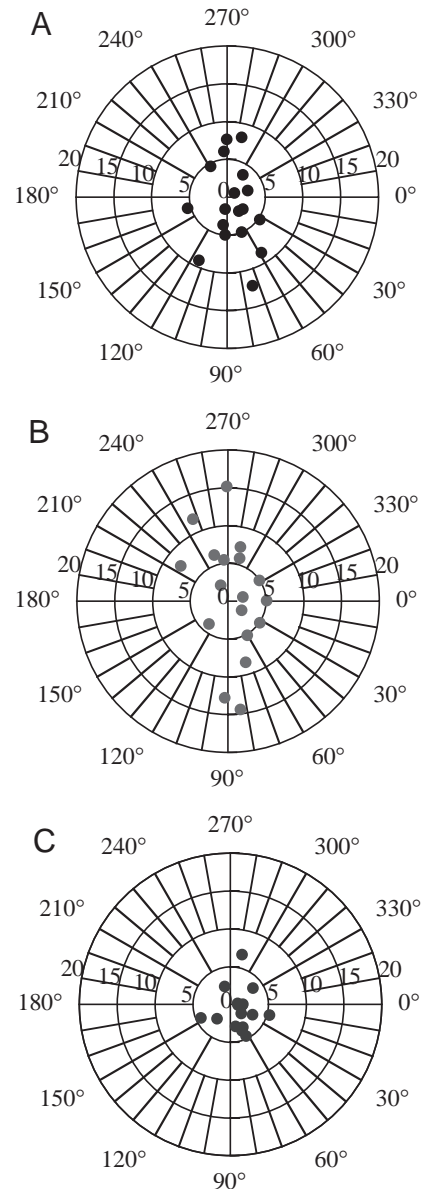


Fig. 1. Polar coordinate plots of the predatory strike of *Cerastes cerastes*. In each plot, the strike angle was measured between the long axis of the snake's head and the midpoint of the prey's body (with 0° defined as directly in front of the snake); distance (in cm) was measured from the tip of the snake's snout to the midpoint of the prey. (A) Control strikes; (B) strikes following denervation of the olfactory and vomeronasal nerves; (C) strikes following denervation and bilateral occlusion of the eyes. Note the similarity between the control and denervated strikes and the marked decrease in distance and strike angle following occlusion of the eyes.

strikes; in contrast, in the denervated, temporarily blinded trials, there were nearly equal number of bilateral, unilateral and missed strikes (Fig. 3). Pooling the data from the three trials revealed a significant relationship between increasing prey mass and increasing distance to target at strike ( $b=0.53$ ,  $t=11$ ,  $P<0.001$ ,  $r^2=0.72$ ) as well as between increasing distance to target and strike velocity ( $b=16.06$ ,  $t=11$ ,  $P<0.001$ ,  $r^2=0.69$ ).

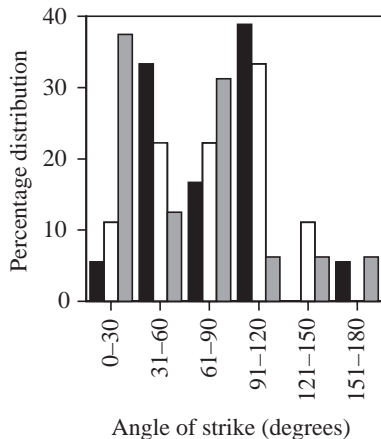


Fig. 2. Distribution of strikes by angle. Significantly greater strike angles were recorded from control (black columns) and denervated (white columns) specimens than from the denervated specimens following visual occlusion (grey columns).

### Experiment 2

Presentation of an inanimate target to the denervated, functionally blind snakes evoked a pronounced reaction (Fig. 4). The numbers of tongue flicks, target-directed head movements and strikes were all significantly greater following presentation of the target. Analysis of the videotape revealed that target-directed head movements and strikes were always launched immediately following contact of the target ball with the substratum. No significant difference in response was observed between isothermic and heated artificial targets.

### Discussion

There was little evidence for a primary role of chemosensory information in prey localization by *Cerastes*. These snakes frequently launched the strike while both their mouth and nostrils were under the sand and did not tongue-flick prior to striking. Denervating the vomeronasal and olfactory nerve had no significant effect on prey capture (Figs 1–3). In contrast, the results suggest that visual information was important in prey targeting. When vision was obscured, the snakes struck over a significantly shorter distance, with significantly reduced diversity of strike angles and with reduced accuracy (Figs 1–3). Previous studies suggest that there is considerable diversity in the relative importance of visual stimuli in snake predation: Bonnett et al. (1999) and Kardong and Mackessy (1991) describe successful predation in congenitally blind snakes; Grace et al. (2001) found that occluding the eyes of *Python molurus* produced decreases in predatory success similar to those described herein; Mullin and Cooper (1998) and Shivik (1998) both document the importance of visual stimuli among arboreal species. Although most previous studies use simple visual stimuli or tests (i.e. motion *versus* no motion), Garcia and Drummond (1995) have documented behavioral responses to different types of visual stimuli in the garter snake *Thamnophis melanogaster*. The results of the

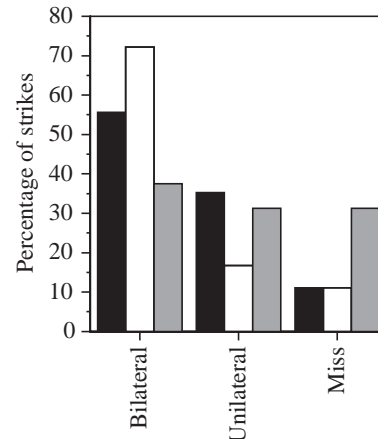


Fig. 3. Accuracy of the strike following experimental manipulation. Bilateral strikes (in which both fangs contact the prey) were most common in the control (black columns) and denervated (white columns) trials, with decreasing levels of unilateral and missed strikes. Strikes recorded following denervation and visual occlusion (grey columns) showed reduced accuracy, with roughly equal numbers of bilateral, unilateral and missed strikes.

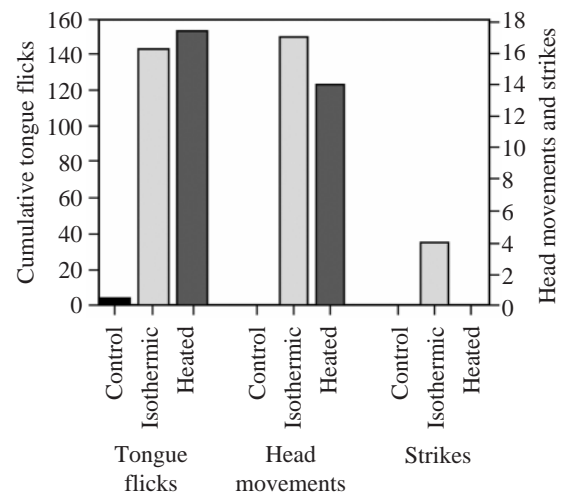


Fig. 4. Response of the denervated and visually occluded specimens to artificial vibrational stimuli. Data are cumulative scores from 16 trials; each trial included 4 min of control and 30 s of each experimental condition. The strong response to the vibrational stimuli (including strikes in one-quarter of the trials) is evident in a comparison of the control (black column) and experimental data. The similar responses to isothermic targets (light grey columns) and those heated to mammalian body temperature (dark grey columns) suggest that the specimens were using vibrational, rather than thermal, cues.

current study are somewhat surprising in that viperid snakes, such as *Cerastes*, are generally viewed as relying on chemosensory, not visual, stimuli for foraging.

While deprived of chemosensory information and temporarily blinded, every snake was able to locate freely mobile prey in every trial. Even in cases where the strike missed, the error was not pronounced (normally the snake struck just to the side of the mouse) and the prey was captured

in a subsequent strike. Larger prey, which presumably generated higher-amplitude ground-borne vibrations, evoked strikes from greater distances than did smaller prey. Previous studies have suggested that snakes, even taxa such as *Cerastes* that lack the prominent infrared receptive 'pits' on the cephalic scalation, may respond to the body heat of prey items (Dickman et al., 1987; Austin and Gregory, 1998). Analysis of the predatory strikes, particularly the observations that strikes were always launched after footfalls, suggested that vibration reception, rather than thermal stimuli, was being used to locate the prey.

The second experiment was designed to separate these two stimulus sources. Presentation of the artificial stimulus was associated with significant increases in tongue-flicks, head movements and strikes (Fig. 4) despite the fact that the control periods were four times the duration of the experimental periods. The presentation of a chemosensory-free target that was isothermic to the surrounding environment still elicited a strong response, including successful strikes, from the specimens. Furthermore, the video recordings suggest that these behavioral responses were temporally linked to impact of the artificial target with the substratum. No significant differences in response were observed between the two targets, despite the fact that one was approximately 8 ° warmer (approximating mammalian body temperature).

Previous studies have documented the importance of chemosensory (e.g. Chiszar et al., 1999; Miller and Gutzke, 1999), visual (e.g. Mullin and Cooper, 1998) and thermal (e.g. Grace et al., 2001) stimuli in ophidian behavior; however, most previous studies on the sensory bases of snake behavior have explicitly, or implicitly, ignored vibrational stimuli. Early workers (e.g. Klauber, 1956; Wharton, 1969) speculated about vibration-based behavioral responses in snakes, but this is the first study to link ground-borne vibration to a behavior as ecologically important as prey localization.

An earlier theoretical study (Young et al., 2000) suggested that fossorial snakes, such as *Cerastes*, would be more likely to use vibration detection during foraging. The results of the current study are similar to those of Hetherington (1992), who demonstrated that *Scincus scincus*, a fossorial sand-dwelling lizard, uses ground-borne vibrations to locate insect prey. Our observations of foraging behavior in snakes suggest that other species, particularly fossorial forms such as *Xenopeltis unicolor* and *Loxocemus bicolor*, may rely, at least in part, on vibration detection for prey localization and possibly as a stimulus for other behavioral responses.

There is an important distinction to be made between perception (the apprehension of vibrational stimuli through the sensory system) and hearing (the subjective appreciation of external sounds). Earlier physiological studies (Hartline, 1971a,b; Wever, 1978) demonstrated the ability of snakes to perceive air-borne and ground-borne vibrations. In the present study, we document a suite of subjective responses, tongue-flicking, head movements and striking, to vibrations caused by

both live prey and artificial targets. The present study provides evidence that snakes are capable of hearing, albeit, perhaps, in a unique sense of that term.

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