

Response of western diamondback rattlesnakes *Crotalus atrox* to airborne sounds

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Summary

In order to test the hypothesis that snakes can not only perceive airborne sounds, but also respond to them, an acoustic isolation chamber was designed and constructed to perform best within the 150–450 Hz range in which snakes perceive sound. Suspended within this acoustic chamber was a steel mesh basket designed to minimize the potential for groundborne vibrations. A synthesized tone was created out of 20 different 150 ms sounds, each separated by a 50 ms period of silence; the acoustic energy of each of the 20 sounds was concentrated between 200–400 Hz, and each sound included frequency modulation. The trial stimuli were presented to western

diamondback rattlesnakes *Crotalus atrox* at a level 5–10 dB above their perception threshold. Four significant behavioural responses were observed upon stimulus presentation: cessation of body movements, reduction or cessation of tongue flicking, rapid jerks of the head and rattling. At least one significant behavioural response was observed in 92% of the behavioural trials. This study provides the first experimental evidence that snakes can respond behaviourally to airborne sounds.

Key words: acoustic, communication, reptilia, squamata, hearing, behaviour, western diamondback rattlesnake, *Crotalus atrox*.

Introduction

Recently there has been a growing appreciation of the complexity of the behavioural and sensory ecology of snakes (see Greene, 1997). The sensory ecology of snakes remains poorly known (for a review, see Ford and Burghardt, 1993), although studies have shown unexpected roles of tactile (Chiszar et al., 1987), visual (e.g. Garcia and Drummond, 1995), infra-red (e.g. Grace et al., 2001), and chemosensory (e.g. Smith et al., 2000) information. Despite the advances in some aspects of the sensory ecology of snakes, one area, sound perception, has received little attention. Many popular and some technical works continue to misrepresent the acoustic sense of snakes, particularly by claiming that snakes are either deaf or can hear only groundborne vibrations.

Wever conducted a series of experiments in which he recorded the cochlear potentials of snakes exposed to controlled tones (Wever and Vernon, 1960; Wever, 1978). These studies demonstrated that snakes can perceive airborne vibrations at a higher sensitivity than groundborne stimuli. Wever (1978) presented a series of auditory sensitivity curves, demonstrating that perception of airborne vibrations occurred within a rather narrow frequency range (approximately 200–400 Hz), with some species maintaining high sensitivity for approximately 100 Hz either side of this range. Wever's findings were confirmed by Hartline and Campbell (1969) and Hartline (1971a,b), who used intracellular recordings from auditory neurons to document the acoustic sensitivity of snakes exposed to airborne sounds. Though aspects of snake

bioacoustics remain poorly known (B. A. Young, manuscript submitted for publication), there is clear evidence that snakes can perceive airborne sounds.

Previous physiological studies of snake audition were performed on immobilized anesthetized snakes, and thus provided no evidence of a behavioural response to airborne sounds. Manning (1923) used a telephone receiver to present airborne stimuli to rattlesnakes. Few variables were controlled in this study and though Manning (1923) concluded that snakes are deaf, he reported that some rattlesnakes exhibited consistent responses to airborne stimuli. Other studies of airborne hearing in snakes have been more anecdotal and largely devoid of controls (e.g. Davenport, 1934; Klauber, 1956). Several studies (e.g. O'Reilly, 1894; Werner, 1999) have shown that snake 'charming' is not dependent on the snake hearing airborne sounds. Several recent studies have explored the behavioural response of snakes to groundborne vibrations (e.g. Randall and Matocq, 1997; Burger, 1998; Shivik et al., 2000; Young and Morain, 2002). The purpose of the present study was to explore the ability of snakes to respond behaviourally to airborne sounds presented within a controlled context.

Materials and methods

This study was conducted using eight specimens of *Crotalus atrox* Baird and Girard (snout–vent length, SVL, 72–98 cm) collected in western Texas. At Lafayette College the snakes

were housed in a venomous snake room in individual terraria under a 12 h:12 h L:D cycle. The room was heated to 26–31°C; the snakes were provided with water *ad libitum* and maintained on a diet of pre-killed mice.

An acoustic chamber was constructed out of an old environmental chamber. This chamber had internal dimensions of 91.5 cm wide \times 123 cm tall \times 46 cm deep and was constructed of an inner metal shell separated from the outer metal frame by a 5 cm layer of insulation. All electronic and movable parts were removed from the environmental chamber, then the inner surface was covered with acoustic dampening insulation. Auralex LENRD Bass trap (noise criteria, NC rating at 250 Hz=1.28) was installed in the corners, and all other inner surfaces were covered in Auralex 7.5 cm wedge foam (NC rating at 250 Hz=0.49). Three portals were made in the chamber. On one wall a fluorescent 40 W bulb was installed; given the low heat produced by this light, the bulb was recessed slightly into the acoustic foam. The socket for the bulb was located between the inner and outer shells of the chamber; the portal through which the cord penetrated the outer shell was packed with acoustic foam. An Optimus speaker (frequency response 50–15 000 Hz) was installed in the upper corner of the chamber opposite the light. The speaker was not hard-mounted to the chamber, but was held in position by the surrounding acoustic foam. The portal through which the speaker wire exited the outer shell of the chamber was packed with acoustic foam. A large portal was cut in the top of the chamber to accommodate a Sony Video8 videocamera. Only the lens of the video camera extended through the inner foam shell of the chamber where the adjacent acoustic foam was trimmed to provide a view of the interior of the chamber.

A 'hanging basket' was constructed using 1.25 cm steel mesh. The steel mesh was attached to a frame constructed of 2 cm-wide aluminum, which gave the hanging basket final dimensions of 46 cm wide \times 30 cm tall \times 25 cm deep. The top of the basket was attached using a long stiff hinge, which was the only movable part on the basket. The basket was designed to contain the rattlesnakes while providing minimal surface area for transmitting substratum vibrations. Eyebolts located on the upper corners of the basket and in the roof of the chamber were linked with plastic-coated steel cable to hang the basket within the chamber. When suspended, the bottom of the basket was approximately 90 cm from the top of the chamber and did not touch any of the acoustic insulation lining the inner surface of the chamber.

The entire outer surface of the chamber was covered in Auralex Sheetblok sound dampening insulation (sound transmission class, STC at 250 Hz=19). The chamber rested upon a layer of Auralex Platfoam acoustic platform designed to minimize vibration transmission between the floor and the chamber. The chamber was located within a laboratory designed for acoustic experiments. Wever (1978) used cochlear microphonics to generate acoustic sensitivity curves to airborne sounds from a number of snakes, including *Crotalus viridis*. We converted Wever's intensity data over to sound pressure level (SPL) with a reference of (dB re

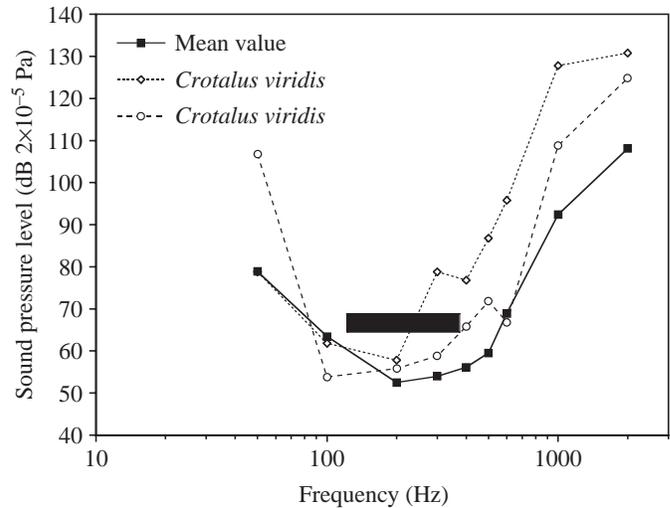


Fig. 1. Auditory sensitivity curve. The curve for mean value was calculated by averaging all the frequency response curves (to airborne stimuli) presented by Wever (1978); the two curves for *Crotalus viridis* are taken from Wever (1978). The black rectangle represents the frequency and intensity of the stimuli presented during these experiments.

2×10^{-5} Pa) and averaged all of the airborne sensitivity curves that he published (Fig. 1). 20 sounds were synthesized using SoundEdit 16 (MacroMedia) on a PowerBook G4 (Apple); each sound had a unique combination of frequencies and frequency modulation patterns, but all concentrated their acoustic energy within the range 150–450 Hz (Fig. 1). The amplitude of the 20 sounds was standardized. Each sound had a duration of 150 ms and was separated from the next sound by 50 ms of silence. The end product was a 4 s acoustic stimulus which was temporally patterned and included a variety of frequencies and frequency modulations.

The computer was coupled to a GRASS AM8 audio monitor that routed the stimulus to the speaker. A SPER 840029 sound meter was placed within the hanging basket. With the hamming filter window of the GRASS AM8 set at 30 and 1000 Hz, the amplitude of the stimulus was adjusted (using both the computer and the GRASS AM8) to a range of 65–75 dB (the variation in acoustic properties of the component sounds results in a slight variation in amplitudes). This acoustic intensity, measured at the bottom of the hanging basket, meant that the stimulus would be presented at 5–10 dB over the threshold determined by Wever (1978) (Fig. 1).

A GRASS SPA1 accelerometer was used to determine the resonance, and thus the likelihood of substrate transmission of the stimulus, of the hanging basket. The accelerometer was wedged into the steel mesh of the hanging basket (which contained a dead specimen with a SVL of 89 cm), in different directions, and connected to a GRASS P511 AC amplifier. The GRASS P511 was coupled to an Instrunet 100B A/D converter and ultimately to a G4 computer (Apple) running Instrunet data acquisition software (GW Instruments). Newly synthesized sounds (frequency range 50–2000 Hz) were presented at the

same amplitude range (65–75 dB) determined for the trial stimulus, but with no filtering from the GRASS AM8 audio monitor. With the GRASS P511 amplifier set to a gain of 50 000, clear resonance (signals over 1 V) was detected from the hanging basket upon presentation of the sound (Fig. 2). When the trial stimulus was presented, with the hamming filter set to 30 and 1000 Hz, no resonance signature was recorded (Fig. 2). Our analyses suggested that the hanging basket had a resonance frequency of approximately 600 Hz, which was well above the acoustic range of our trial stimulus.

For the behavioural trials the laboratory was heated, using portable electric heaters, to 28°C. The snakes were placed individually within the hanging basket and the acoustic chamber sealed. The florescent light and video camera remained switched on throughout the trials. The behaviour of the snake was monitored with the video camera until the snake was judged to have assumed a relaxed or investigative behaviour (defined by a lack of rattling, slow movement and no defensive tongue flicks; for suites of behaviours in *Crotalus*, see also Kardong, 1986; Hayes and Duvall, 1991; Young et al., 2002). Once a minimum of 30 continuous seconds of relaxed or investigative behaviours were observed the trial was initiated. For each trial we recorded 104 s of videotape consisting of an initial 30 s control period, the 4 s of stimulus presentation, and a final 30 s recovery period. Each specimen was used for three trials, with a minimum time of 90 min between trials.

For analysis, the videotape record of each trial was divided into a control period (the 10 s immediately prior to the presentation of the stimulus), a stimulus period (the 4 s of the stimulus and the subsequent 6 s), and a recovery period (10 s in duration, beginning 20 s following the onset of the stimulus). For each period we quantified the number of tongue flicks, the number of head jerks (rapid lateral movements of the head independent of directed movement of the body), and the number of seconds during which the snake was moving within

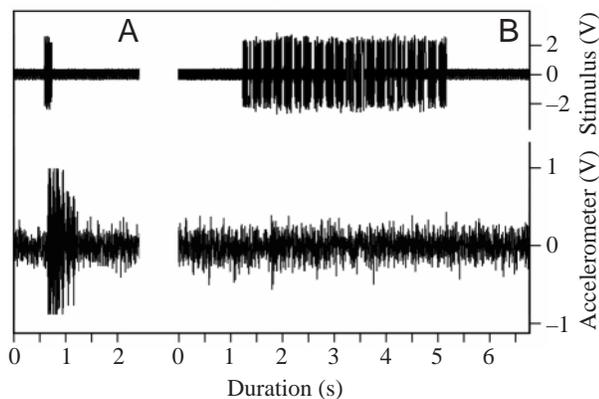


Fig. 2. Response of an accelerometer located in the hanging basket to airborne sounds. (A) Synthesized sound with frequencies near 650 Hz; note the prominent resonance within the hanging basket; (B) trial stimulus presented to the live specimens; note the absence of resonance vibration in the hanging basket.

the hanging basket. We determined (using both visual and audio information) whether or not the snake rattled. Quantitative data from the video records were processed using Systat 5.2.1 and analyzed using ANOVA.

The protocols used for this experiment conform to guidelines for research on reptiles and venomous snakes, and were approved by the Institutional Animal Care and Use Committee of Lafayette College.

Results

General behavioural reactions

Pooling the data for all three trials and every specimen provides a general view of the response observed in *Crotalus atrox* upon the presentation of airborne sound. The following quantitative data are based on three 10 s behavioural periods; the majority (6 s) of the trial period occurs after the termination of the stimulus. The total number of tongue flicks observed decreased upon presentation of the stimulus, and returned to the control level during the recovery period (Fig. 3A). The

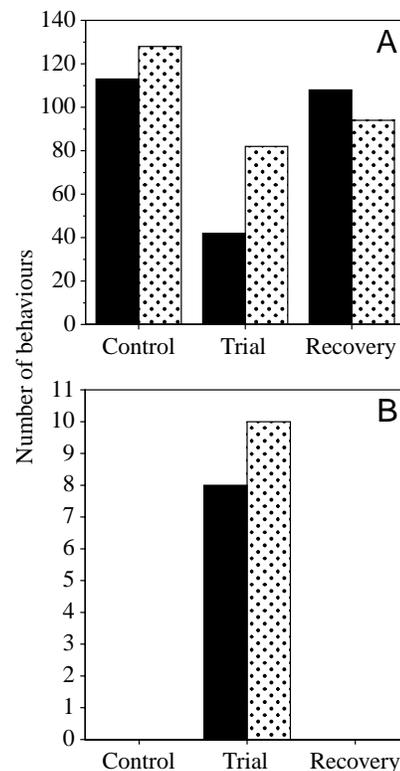


Fig. 3. Summary of behavioural responses to the trial stimulus; responses are summed over three trials, each of eight specimens. (A) Incidence of body movement (black) defined as number of seconds (out of 10) during which the snake was in motion during the three periods and tongue flicks (stippled). Note that the 'freeze' response produced a significant decline in movement during the trial period, and the significant decrease in tongue flicks. For an explanation, see text. (B) Incidence of head jerks (black) and rattling (stippled), note that both behaviours were only observed during the trial period leading to significant responses for both.

reduced number of tongue flicks during the trial period, as compared to either the control or recovery periods, was significant (F -ratio=3.46, P =0.037). Presentation of the stimulus commonly produced what we termed a 'freeze' behaviour; snakes that were actively moving about the hanging basket during the control period would become motionless upon introduction of the stimulus. This resulted in a significant (F -ratio=3.62, P =0.032) decrease in movement scores between the control and trial periods (Fig. 3A); the freezing behaviour was transitory, so that most of the snakes began to move again prior to the recovery period (Fig. 3A). Presentation of the stimulus produced a novel behaviour, the head jerk, in 8 (33%) of the trials. Head jerks were never observed during the control or recovery periods (Fig. 3B), making their distribution highly significant (F -ratio=6.60, P =0.002). Rattling was never observed during the control or recovery periods (Fig. 3B), but was observed in 42% (10 out of 24) of the trial periods (Fig. 3B), producing a significantly (F -ratio=16.07, P <0.0001) skewed distribution of this behaviour.

Total response

Presentation of the airborne stimulus resulted in a suite of four significant responses: decreased tongue flicking, a freeze behaviour, head jerks and rattling. At least one of these four behavioural responses was observed in 22 of the 24 trials (Fig. 4). Two of the four responses were observed in six of the trials, while three of the four responses were recorded from five trials (Fig. 4). The four behaviours were observed concurrently in only two of the trials (Fig. 4). At least one positive response was obtained from each specimen, and four of the eight specimens responded positively to sound during each trial.

Intraspecific variation

An examination of the distribution of positive responses for

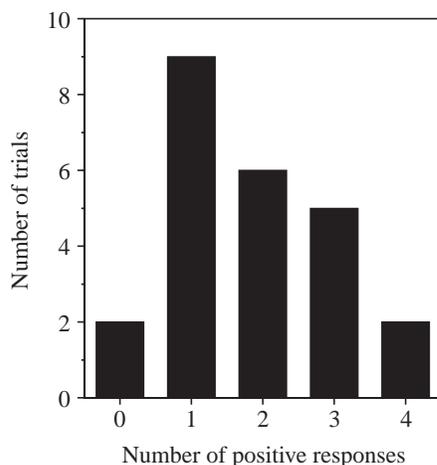


Fig. 4. Total responses observed. A positive response was defined as the presence, during the trial period, of either rattling behavior, a head jerk, a decrease in the tongue flick rate, or a decrease in body movement.

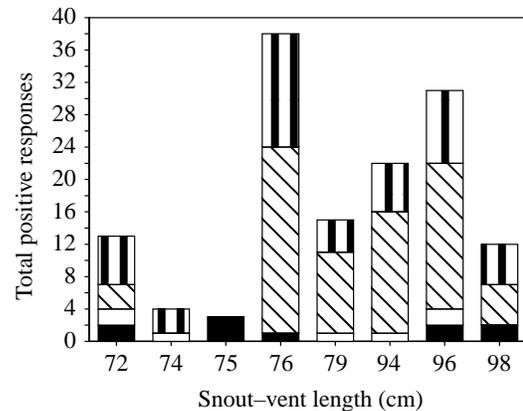


Fig. 5. Intraspecific variation in the response to airborne stimuli. The total number of positive responses are shown for each specimen (diagonal lines, body movement; vertical lines, tongue flicks; solid black, rattling; solid white, head jerks). Note the relationship between body movement and tongue flicks, the intraspecific variation in response, and the absence of a clear relationship between snake size and response.

each behavioural variable among the eight specimens reveals little evidence of trends with increasing body size (Fig. 5). Changes in tongue flick rates and body movement showed a similar pattern among the species. There is clearly interspecific variation in the responses, particularly with the 76 cm and 96 cm SVL specimens (Fig. 5).

Discussion

The level of positive response observed is almost certainly an underestimate of the behavioural response to airborne sounds by *Crotalus atrox*. One of the responses observed, the freeze behaviour, can only be recognized as behavioural change in a moving snake. The snake remained motionless throughout the control period in 42% of the trials (10 out of 24), which precluded the recognition of a freeze during the trial period and presumably led to a lower incidence of this response (Figs 3A, 5). The snakes appeared to revert to resting or investigative behaviours quickly following the termination of the stimulus. The cessation of the behavioural responses was rapid enough to be completed during the terminal portion of the trial period; as such the incidence of movement and tongue flicks during the trial period may underestimate the behavioural impact of the stimulus (Fig. 3A).

Crotalus atrox was used for this study due to its reputation as an irritable species (e.g. Ernst, 1992; Tennant and Bartlett, 2000) and the presence of overt suites of defensive and predatory behaviours found in *Crotalus* sp. Previous studies have characterized defensive behaviour in *Crotalus* sp. as including rattling, limited body movement (due to maintained elevated coiling), and a decrease in tongue-flick rate (Kardong, 1986; Hayes and Duvall, 1991; Young et al., 2002). This study relied exclusively on these overt behaviours to gauge the response to the stimulus; inclusion of more physiological

responses, such as heart rate or hormone levels (e.g. Moore et al., 2000; Secor et al., 2000; Mathies et al., 2001), would probably increase the number of positive responses. Lastly, though steps were taken to increase the potential information content of the stimulus tone (by using multiple unique tones with temporal patterning and frequency modulation), they remained artificial tones played to specimens in an isolation chamber. Presumably a biological sound, especially one coupled with other biological stimuli, would be more likely to evoke a behavioural response.

Wever (1978) and Hartline (1971a,b) both documented that snakes are capable of perceiving airborne vibrations, and that they are more sensitive to airborne than groundborne vibrations (see Young, 2002). Despite these findings, many works still describe snakes as hearing only groundborne or substratum vibrations (e.g. Bauchot, 1994). This study was designed to use unrestrained and unanesthetized snakes while restricting, if not eliminating, the potential for groundborne vibration detection. Combining the low frequency sound-dampening insulation with a freely suspended 'hanging basket' greatly reduced the likelihood that an acoustic bounce from the inside of the chamber would be absorbed by the hanging basket. The open mesh design of the hanging basket reduced the transmission of acoustic energy from the air to the basket. The data from the accelerometer trials indicate that transmission of sufficient acoustic energy to induce vibrations of the hanging basket was not occurring within the frequency range of the behavioural trials. Lastly, the airborne stimulus was designed to be 5–10 dB above the threshold response determined by Wever (1978). Given the necessary loss of energy if these vibrations were transmitted to the hanging basket, and the findings of both Wever (1978) and Hartline (1971a,b) that snakes are less sensitive to groundborne vibrations, it seems unlikely that our trial stimulus was of an amplitude sufficient to evoke a response as a groundborne vibration.

Few studies have attempted to place vibration detection in snakes within the context of behavioural ecology. Randall and Matocq (1997) showed that *Pituophis melanoleucus* was attracted to the sounds produced by a buried 'artificial thumper', which was used to represent the defensive foot drumming of kangaroo rats (*Dipodomys spectabilis*). Burger (1998) modeled the footfalls of a potential predator by dropping a rock (behind a screen) and reported that hatchling *P. melanoleucus* retreated when exposed to the resulting vibrations. Shivik et al. (2000) claimed that *Boiga irregularis* responded in a predatory fashion to vibrational stimuli (though in this study the snake may have been responding to motion). Young et al. (2000) used geophones to model the snake ear and recorded the groundborne vibrations produced by potential predators and prey; their results suggested that groundborne vibrations could prove an effective detection system against potential snake predators, but probably only valuable for predation under special circumstances (Young et al., 2000). Young and Morain (2002) documented that Saharan sand vipers (*Cerastes cerastes*) were capable of using groundborne

vibrations to target prey items. Though only anecdotal, there are additional claims for vibration detection being used for prey capture (e.g. Wharton, 1969) and defense (e.g. Klauber, 1956). The present study is the first evidence from controlled experimentation of a behavioural response to airborne sound in snakes.

The head jerks that were observed in 33% of the trials (Fig. 3B) appeared to be a startle response rather than an orientation behaviour, in that the head was not jerked in the direction of the speaker. Though we saw a positive response in 92% of the behavioural trials, we saw no evidence of acoustic orientation or even that the *Crotalus atrox* could spatially localize the sound source. In sharp contrast, Young and Morain (2002) found that *C. cerastes* could localize small, free-moving mice spatially using groundborne vibrations. No experimental work has been done on the ability of snakes to localize airborne sound stimuli spatially, and there are several reasons to suspect that this ability may differ from what is known in other reptiles (Young, 2002). The results of the recent study of *C. cerastes* (Young and Morain, 2002) audition, combined with those of the present study, suggest that snakes are capable of contextualizing vibratory information. Both *C. cerastes* and *Crotalus atrox* have distinct suites of predatory and defensive behaviours (e.g. Young et al., 1999, 2002). In these studies *C. cerastes* never exhibited defensive behaviour when presented with a small live mouse, and *Crotalus* never exhibited predatory behaviour when presented with synthesized tones.

As Hartline (1971b) discussed, there are effectively two different pathways for hearing in snakes: an auditory pathway, involving the stapes-cochlear complex, and a poorly understood somatic pathway, involving cutaneous vibration receptors. Both pathways can perceive both airborne and groundborne vibrations (Hartline 1971b). It seems unlikely that one pathway preferentially responds to groundborne vibrations through specific neural pathways that lead to predatory behaviour. Instead, we believe that snakes are able to extract enough information from the vibrational stimuli to contextualize the sounds accurately, though the mechanism for these contextualizations remains unknown. If snakes can extract information from vibrational stimuli, they could possibly recognize prey- or predator-specific signatures from these signals, which is the converse of the interesting system detailed by Rowe and colleagues (e.g. Rowe and Owings, 1990, 1996), in which ground squirrels were shown to extract biologically useful information from the sound produced by rattling rattlesnakes. Whatever the extent of contextualization of the perceived vibrations, the results of the present study indicate that the sensory ecology of rattlesnakes, and presumably all snakes, is more complex than previously realized.

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References

- Bauchot, R.** (1994). *Snakes: A Natural History*. New York: Sterling Publishing Co.
- Burger, J.** (1998). Antipredator behaviour of hatchling snakes: Effects of incubation temperature and simulated predators. *Anim. Behav.* **56**, 547-553.
- Chiszar, D., Radcliffe, C. W., Boyer, T. and Behler, J. L.** (1987). Cover-seeking behavior in red spitting cobras (*Naja mossambica pallida*): Effects of tactile cues and darkness. *Zoo. Biol.* **6**, 161-167.
- Davenport, J. W.** (1934). *Field Book of the Snakes of Bexar County, Texas and Vicinity*. Texas: White Memorial Museum.
- Ernst, C. H.** (1992). *Venomous Reptiles of North America*. Washington, DC: Smithsonian Institution Press.
- Ford, N. B. and Burghardt, G. M.** (1993). Perceptual mechanisms and the behavioral ecology of snakes. In *Snakes: Ecology and Behavior* (ed. R. A. Seigel and J. T. Collins), pp. 117-164. New York: McGraw Hill.
- Garcia, C. M. and Drummond, H.** (1995). Components of visual prey recognition by the Mexican aquatic garter snake *Thamnophis melanogaster*. *Ethology* **101**, 101-111.
- Grace, M. S., Woodward, O. M., Church, D. R. and Calish, G.** (2001). Prey targeting by the infrared-imaging snake *Python*: Effects of experimental and congenital visual deprivation. *Behav. Brain Res.* **119**, 23-31.
- Greene, H.** (1997). *Snakes: The Evolution of Mystery in Nature*. Berkeley: University of California Press.
- Hartline, P.** (1971a). Physiological basis for detection of sound and vibration in snakes. *J. Exp. Biol.* **54**, 349-371.
- Hartline, P.** (1971b). Midbrain responses to the auditory and somatic vibration system in snakes. *J. Exp. Biol.* **54**, 373-390.
- Hartline, P. and Campbell, H.** (1969). Auditory and vibratory responses in the midbrain of snakes. *Science* **163**, 1221-1223.
- Hayes, W. and Duvall, D.** (1991). A field study of prairie rattlesnake predatory strike. *Herpetologica* **47**, 78-81.
- Kardong, K. V.** (1986). The rattlesnake strike: When things go amiss. *Copeia* **1986**, 816-820.
- Klauber, L. M.** (1956). *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. Two volumes. Berkeley: University of California Press.
- Manning, F. B.** (1923). Hearing in rattlesnakes. *J. Comp. Psychol.* **3**, 241-247.
- Mathies, T., Felix, T. A. and Lance, V. A.** (2001). Effects of trapping and subsequent short-term confinement stress on plasma corticosterone in the brown treesnake (*Boiga irregularis*) on Guam. *Gen. Comp. Endocrinol.* **124**, 106-114.
- Moore, I. T., Lemaster, M. P. and Mason, R. T.** (2000). Behavioral and hormonal responses to capture stress in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. *Anim. Behav.* **59**, 529-534.
- O'Reilly, G. R.** (1894). The cobra and other serpents. *Pop. Sci. Monthly* **46**, 67-78.
- Randall, J. A. and Matocq, M. D.** (1997). Why do kangaroo rats (*Dipodomys spectabilis*) footdrum at snakes? *Behav. Ecol.* **8**, 404-413.
- Rowe, M. P. and Owings, D. H.** (1990). Probing, assessment, and management during interactions between ground-squirrels and rattlesnakes. 1. Risks related to rattlesnake size and body-temperature. *Ethology* **86**, 237-249.
- Rowe, M. P. and Owings, D. H.** (1996). Probing, assessment, and management during interactions between ground-squirrels and rattlesnakes. 2. Cues afforded by rattlesnake rattling. *Ethology* **102**, 856-874.
- Secor, S. M., Hicks, J. W. and Bennett, A. F.** (2000). Ventilatory and cardiovascular responses of a python (*Python molurus*) to exercise and digestion. *J. Exp. Biol.* **203**, 2447-2454.
- Shivik, J. A., Bourassa, J. and Donnigan, S. N.** (2000). Elicitation of brown treesnake predatory behavior using polymodal stimuli. *J. Wild. Mgmt* **64**, 969-975.
- Smith, T. L., Kardong, K. V. and Lavin-Murcio, P. A.** (2000). Persistence of trailing behavior: Cues involved in poststrike behavior by the rattlesnake (*Crotalus viridis oreganus*). *Behavior* **137**, 691-703.
- Tennant, A. and Bartlett, R. D.** (2000). *Snakes of North America: Eastern and Central regions*. Houston: Gulf Publishing.
- Werner, Y. L.** (1999). Does the cobra obey the snake charmer's flute? *Hamadryad* **24**, 23-28.
- Wever, E. G.** (1978). *The Reptile Ear: Its Structure and Function*. Princeton: Princeton University Press.
- Wever, E. and Vernon, J.** (1960). The problem of hearing in snakes. *J. Aud. Res.* **1**, 77-83.
- Wharton, C. H.** (1969). The cottonmouth moccasin on Sea Horse Key, Florida. *Bull. Florida State Mus.* **14**, 227-272.
- Young, B. A., Meltzer, K. and Marsit, C.** (1999). Scratching the surface of mimicry: Sound production through scale abrasion in snakes. *Hamadryad* **24**, 29-38.
- Young, B. A., Marvin, J. and Marosi, K.** (2000). The potential significance of ground-borne vibration to predator-prey relationships in snakes. *Hamadryad* **25**, 164-174.
- Young, B. A. and Morain, M.** (2002). The use of ground-borne vibrations for prey localization in the Saharan sand vipers (*Cerastes*). *J. Exp. Biol.* **205**, 661-665.
- Young, B. A., Phelan, M., Jagers, J. and Nejman, N.** (2002). Kinematic modulation of the strike of the western diamondback rattlesnakes (*Crotalus atrox*). *Hamadryad* **26**, 316-349.