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SNAKE BIOACOUSTICS: TOWARD A RICHER UNDERSTANDING OF THE BEHAVIORAL ECOLOGY OF SNAKES

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ABSTRACT

Snakes are frequently described in both popular and technical literature as either deaf or able to perceive only groundborne vibrations. Physiological studies have shown that snakes are actually most sensitive to airborne vibrations. Snakes are able to detect both airborne and groundborne vibrations using their body surface (termed somatic hearing) as well as from their inner ears. The central auditory pathways for these two modes of "hearing" remain unknown. Recent experimental evidence has shown that snakes can respond behaviorally to both airborne and groundborne vibrations. The ability of snakes to contextualize the sounds and respond with consistent predatory or defensive behaviors suggests that auditory stimuli may play a larger role in the behavioral ecology of snakes than was previously realized. Snakes produce sounds in a variety of ways, and there appear to be multiple acoustic Batesian mimicry complexes among snakes. Analyses of the proclivity for sound production and the acoustics of the sounds produced within a habitat or phylogeny specific context may provide insights into the behavioral ecology of snakes. The relatively low information content in the sounds produced by snakes suggests that these sounds are not suitable for intraspecific communication. Nevertheless, given the diversity of habitats in which snakes are found, and their dual auditory pathways, some form of intraspecific acoustic communication may exist in some species.

IN RECENT YEARS a richer appreciation of snakes has begun to emerge; studies of topics such as social structure and parental care, both of which had been largely dismissed in snakes, have expanded our understanding of the behavioral ecology of serpents (for a good overview of this new perspective, see Greene 1997). This deeper understanding of snakes has largely neglected their bioacoustics; the bioacoustic literature on snakes is still dominated by older anecdotal accounts and persistent stereotypes. While most of vertebrate bioacoustics is moving into auditory scene analysis—the complex extraction of information from the acoustic environment (Hulse 2002)—there are still accounts published of cobras crowing like roosters (Shuker 1991). Even the more "technical" literature has tended to misrepresent the bioacoustics of snakes; for example, snakes are either described as deaf or as hearing vibrations from the substratum, even though the physiological studies show that they are most sensitive to airborne vibrations (Wever 1978). Here I review the current literature on the bioacoustics of snakes, with an attempt to show where additional studies might improve our understanding of not only the bioacous-

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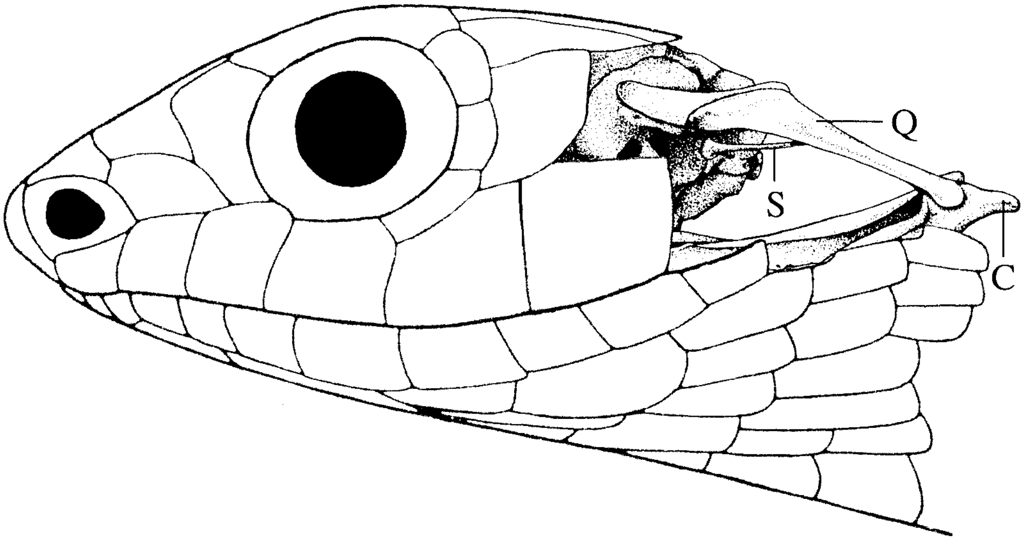

FIGURE 1. THE OPHIDIAN STAPES
This generalized view of a dissected boomslang (*Dispholidus typus*) illustrates the spatial relationship between the stapes (S), quadrate (Q), and the lower jaw (C).

tics but also the behavioral ecology and evolution of snakes.

SNAKE VIBRATION PERCEPTION AND HEARING

Prominent herpetologists and naturalists have expressed a wide range of opinions regarding the auditory abilities of snakes. Pope (1937) and Klauber (1956) argued that snakes are deaf, whereas Wall (1921), Smith (1943), and Taylor (1965) argued that they hear quite well; Gadow (1901) claimed that the conduction system of snakes would produce “thundering noise” (p 583) at the level of the inner ear. Generally, the more popular literature proclaimed snakes to be deaf.

ANATOMY OF THE SNAKE AUDITORY SYSTEM

The assumption that snakes are deaf was presumably based on their lack of an external ear. Though a similar morphology is found in other squamate taxa (e.g., *Aprasia, Holbrookia*), snakes are the largest group of vertebrates for which there is no external evidence of an auditory system. This is often cited as support of a fossorial ancestry for snakes (e.g., Walls 1942; Bellairs and Underwood 1951; Bellairs 1972), but the condition is not incompatible with an aquatic ancestry (Nopsca 1923; Lee 1998). The morphology of the ophidian ear has also been interpreted as a retained primitive condition (Tumarkin 1955), and as a necessity to increased cranial kinesis (Berman and Regal 1967). Further resolution of the evolutionary history of the ophidian ear must await a clearer understanding of the phylogeny of snakes.

The middle ear of snakes is highly modified (Figure 1); the eustachian tube is absent and there is a single middle ear ossicle, the stapes or columella auris (e.g., Baird 1970; Bellairs 1970). The stapes is in the immediate proximity of skeletal muscle and vascular elements. Wever (1978) described the middle ear cavity as reduced to a small membrane-bound space surrounding the stapes. The proximal end of the stapes supports an expanded footplate that rests in the vestibular window or fenestra ovalis (Figure 1). The stapes extends posterolaterally and terminates in a small cartilaginous element which articulates with the medial surface of the quadrate. The embryology and homology of this cartilaginous element—often referred to as the extrastapes (or extracolumella)—have

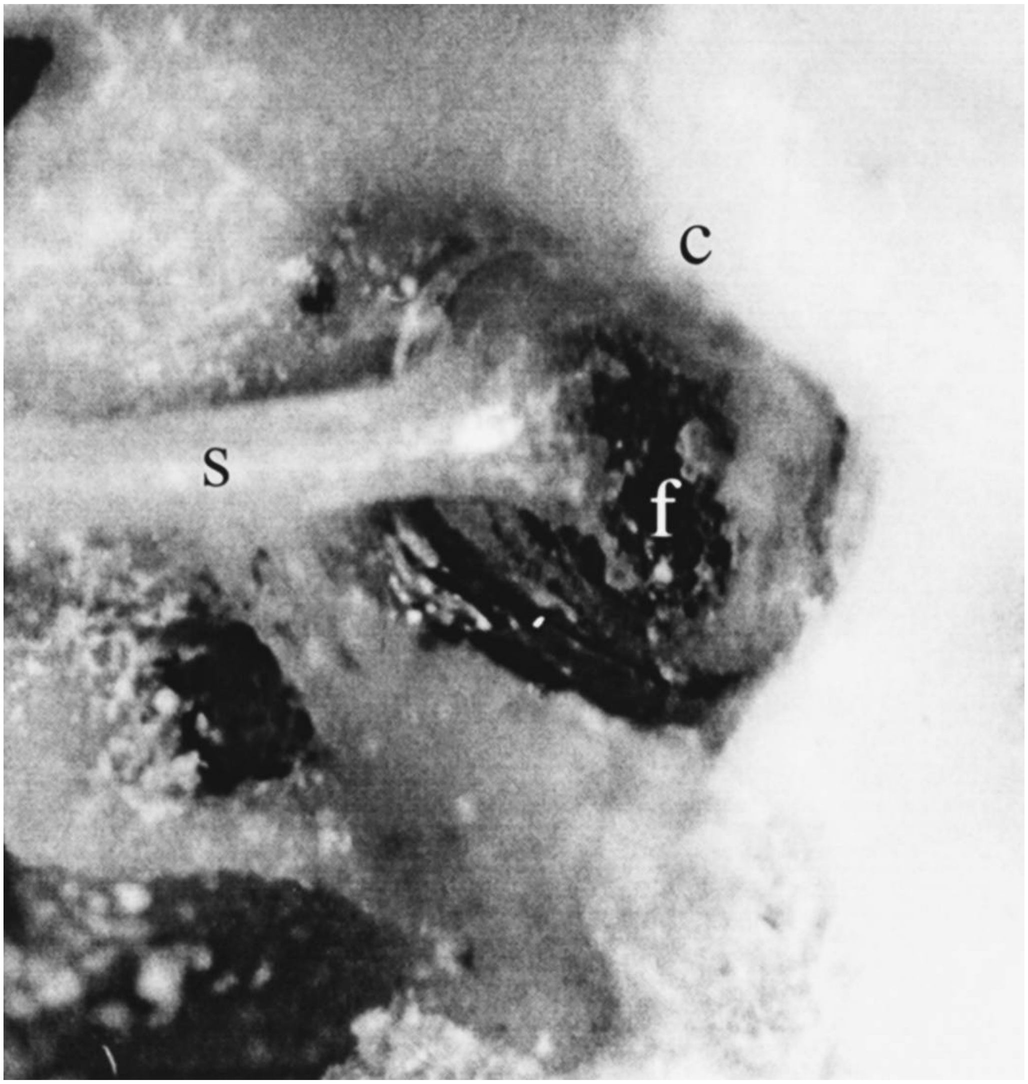

Figure 2. The Stapedial Footplate

Lateral view of the skull of *Thamnophis elegans* showing the stapes (s) and the expanded stapedial footplate (f) resting within the fenestra ovalis. Note the elevated crista circumfenestralis (c) surrounding the fenestra and demarcating the juxtastapedial sinus.

been frequently discussed (de Beer 1937; Kamal and Hammouda 1965; McDowell 1967; Ludicke 1978). Rieppel (1980) explored the morphological variation in this region, particularly the diversity of arthrologies between the stapes, the distal cartilaginous element, and the medial surface of the quadrate (see also Rieppel 1993).

Snakes are unique among squamates in having a ridge of bone, the crista circumfenestralis (Figure 2), which surrounds the fenestra ovalis and stapedial footplate to create a deep fossa (Baird 1960; Rieppel 1979). The juxtastapedial sinus fills this fossa and is covered laterally by the thick periotic membrane which is anchored to the proximal portion of the stapedial shaft (de Burlet 1934). There is considerable variation among snakes

FIGURE 3. ANATOMY OF THE VIBRATION CONDUCTING SYSTEM

Frontal sections through the head of the eastern hognose snake (*Heterodon platyrhinos*). **A.** Section through the inner ear showing the stapedial footplate (S) surrounded by juxtastapedial sinus (J) and the periotic membrane (P). The cochlear ducts (C) are visible within the inner ear. **B.** Section through the articulation between the extrastapes (E) and the medial surface of the quadrate (Q).

in the height of the crista circumfenestralis and in the size of the stapedial footplate relative to the fenestra ovalis (Baird 1970). While fossorial forms generally exhibit pronounced crista circumfenestralis and relatively large stapedial footplates, these variations do not show a strict correlation with either snake ecology or phylogeny.

Several workers have argued that the mechanical couplings of the snake middle ear were incapable of, or highly ineffective at, vibration transmission (e.g., Manning 1923; Pope 1937). Influencing the efficiency of this mechanical coupling is the interaction between the stapedial footplate and the perilymphatic fluid of the inner ear (Figure 3). The inner ear of snakes is surrounded by a cavity, the perilymphatic labryinth, which is filled with a perilymphatic fluid. In most terrestrial vertebrates, pressure waves within the perilymph, created by displacement of the stapedial footplate, are dissipated at the round window. In snakes and a few other reptilian taxa, the round window is absent and the perilymphatic pressure waves created by the stapedial footplate make a complete circuit through the perilymphatic labyrinth and return to the stapes. Wever termed this the reentrant fluid circuit, and noted that: “The system serves its purpose well at low vibratory frequencies, but a burden is imposed on the cochlear action at higher frequencies because of the considerable mass of fluid that must be moved and the friction encountered within the fluid itself and along its confining walls” (Wever 1978:91).

Experimental analyses of the mechanics and efficiency of vibratory transmission—performed through sequential removal of superficial tissue to isolate first the stapes-quadrate couple, then the stapes alone—have shown that the quadrate plays the key role in transmitting vibrations to the stapes (Wever and Vernon 1960; Wever and Strother, unpub-

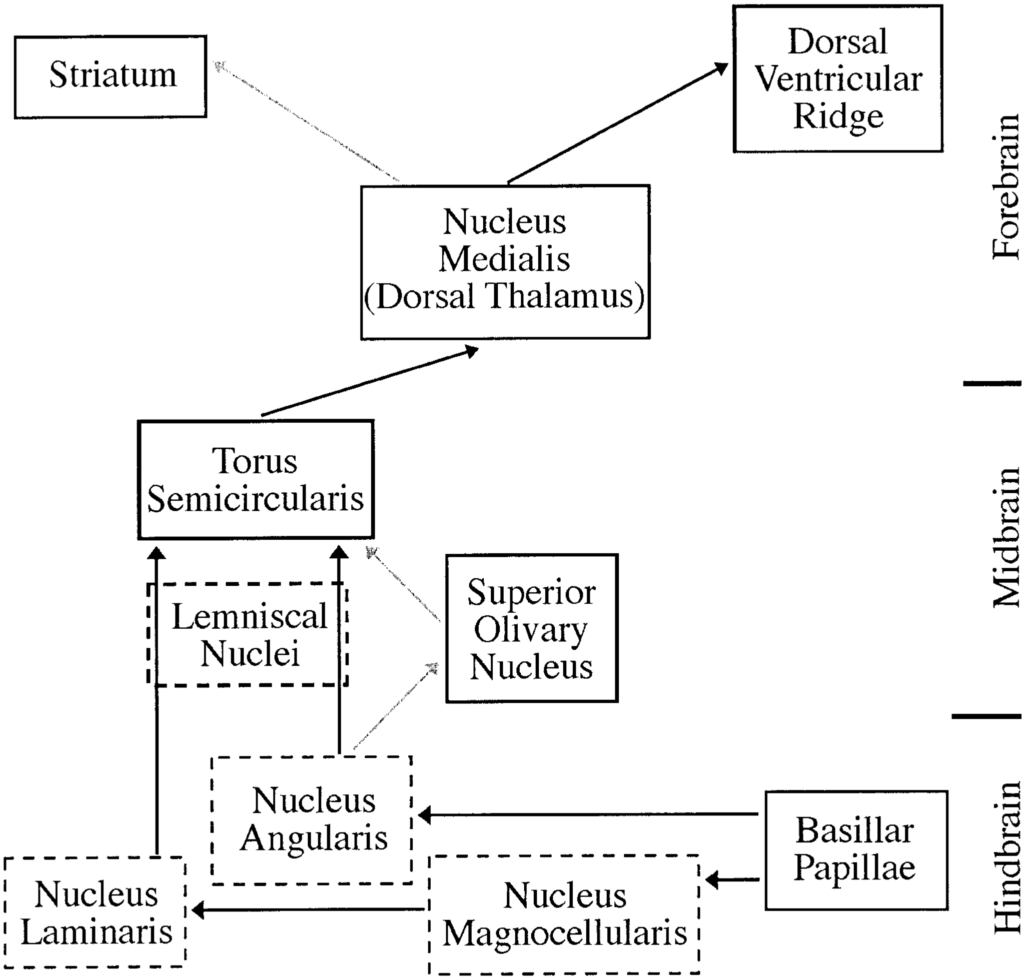

FIGURE 4. SCHEMATIC OF THE CENTRAL AUDITORY PATHWAY IN SNAKES

In this schematic, nuclei for which there is clear anatomical evidence are shown in solid boxes, other nuclei are indicated in dashed boxes. Established tracts are indicated by black arrows, hypothesized tracts are denoted with gray arrows. For the sake of clarity, no distinction is made between ipsilateral and contralateral tracts.

lished, detailed in Wever 1978). Wever (1978) discussed the impedance-matching problem in the snake middle ear, but little work has been done in this area. Though detailed experimental studies exist for other vertebrates with a single ear ossicle (e.g., for birds: Gummer et al. 1989a,b), our understanding of the vibratory mechanics of the snake ear remains incomplete.

The cochlear duct in snakes bears a constriction which divides it into a basal limbus and a terminal lagena (Miller 1966, 1968). The variations in the relative size of the two portions of the cochlea show no clear phylogenetic or ecological pattern (Miller 1968; Baird 1970). The lagena supports a small, poorly known sensory area, the macula lagenae; Bellairs (1970) believed this structure to be homologous to the original sensory macula of fish. The limbic region supports the principle sensory area, the basilar papilla, which is structurally similar to the sensory organs seen in other reptiles. Although there is considerable variation in the size and shape of the basilar papillae (Miller 1968; Baird 1970; Wever 1978), the variations show no clear phylogenetic or ecological patterns. An elongate basilar papilla could expand the potential frequency response range, but there is no evidence that this occurs in snakes. The basilar papilla is comprised of two populations of cells, supporting cells and hair cells (which react to the pressure waves). The supporting cells are relatively more numerous in snakes (as compared to lizards) and they have ultrastructural features that suggest that they are more specialized than those of other reptiles (Baird 1969). A mean of 245 hair cells were recorded in the basilar papillae of selected snakes by Wever (1978), fewer than in most lizards and far fewer than in mammals, which frequently have over 10,000 hair cells (Peterson 1966). An interesting exception was *Acrochordus javanicus* which had nearly 1,500 hair cells, roughly six times the average of the other snakes examined (Wever 1978).

Recent work has explored the phylogeny of the vertebrate cochlea, in particular suites of shared features and the incidence of parallel evolution and unique functional complexes (e.g., Manley and Koppl 1998; Manley 2000). One of these presumably ancestral features is cochlear amplification—the active alteration of the hair cells to increase sensitivity and expand the range of frequency response—which has been well documented in mammals (Dallos and Evans 1995; Martin and Hudspeth 1999) and reported in other vertebrates including lizards (Manley 2001; Manley et al. 2001). Cochlear amplification has not been investigated in snakes, nor have the ophidian cochlea and cochlear function been placed within a clear phylogenetic framework.

The afferent auditory pathway through the snake brain has received very little attention, and only Miller (1980) examined this system using modern tracing or marking techniques. Ludicke (1962) reviewed the older literature on snake neuroanatomy; most modern studies of reptilian neuroanatomy appear to assume that snakes and lizards are similar (snakes are discussed despite the absence of any literature citations on snake anatomy). The following description is based on complete serial sections through the brain of *Elaphe obsoleta* (produced in my laboratory) as well as reviews of the auditory pathway in lizards (Butler and Hodos 1996; Carr and Code 2000). In the generalized reptilian pattern there are three cochlear nuclei in the hindbrain; two primary nuclei, the nucleus magnocellularis and nucleus angularis, and a secondary nucleus, the nucleus laminaris, which is innervated by the nucleus magnocellularis (Figure 4). Both primary nuclei may be subdivided into medial and lateral portions (e.g., Leake 1974; Carr 1992). Previous studies of snakes have produced conflicting descriptions of these nuclei: Holmes (1903) and Schwab (1979) reported a single cochlear nuclei; Weston (1936) found no evidence of the nucleus laminaris; and Miller (1980) described a nucleus angularis, a divided nucleus magnocellularis, and a well-developed nucleus laminaris.

Axons from the nucleus angularis and either the nucleus laminaris or nucleus magnocellularis project bilaterally (as the lateral lemniscus) to reach the torus semicircularis in the roof of the midbrain (Figure 4). There are commonly two nuclei located within the lateral lemniscus (the dorsal and ventral nuclei) which receive afferents from the cochlear nuclei and send efferents to the torus semicircularis (e.g., ten Donkelaar et al. 1987). In some lizards, axons of the cochlear nuclei also contact the superior olivary nucleus (Carr and Code 2000); the ramifications of the auditory pathway between the cochlear nuclei and the torus semicircularis in snakes have not been detailed. The torus semicircularis of lizards consists of superficial, laminar, and central nuclei; the central nucleus is incorporated into the auditory pathway (Foster and Hall 1978; Kennedy and Brower 1981). The central nucleus has commissural fibers, as well as axons which project ipsilaterally to the nucleus medialis (also termed the nucleus reuniens pars compacta) of the dorsal thalamus (Figure 4) (Foster and Hall 1978; Butler 1995). The cytoarchitecture of the torus semicircularis of snakes and its connections with the nucleus medialis have been poorly studied. The nucleus medialis projects to the auditory telencephalon (located near the medial wall of the dorsal ventricular ridge) and may project to the striatum (Bruce and Butler 1984). Though variation in the size and location of the auditory telencephalon has been documented among reptiles (Pritz and Stritzel 1992; Andreu et al. 1996), little is known of the auditory telencephalon in snakes.

PHYSIOLOGICAL STUDIES OF SNAKE AUDITORY PERCEPTION

Adrian (1938) obtained no detectable response from an isolated preparation of the acoustic nerve of *Natrix*. Wever conducted a series of experiments in which he recorded the cochlear potential of snakes exposed to controlled tones (Wever and Vernon 1960; Wever 1978). The initial study examined six species of colubrids, while the later work examined 19 species representing 6 families. Through manipulation of the sound source, and the position and support of the snake's head, these studies demonstrated that snakes can perceive airborne vibrations and that an asymmetric source results in differential activity in the two ears (Wever and Vernon 1960; Wever 1978). Wever and Vernon (1960) and later Wever and Strother (unpublished work, detailed in Wever 1978) investigated the still popular hypothesis that all vibration detection in snakes involves the transmission of airborne vibrations into substrate vibrations which are then transmitted to the inner ear by the quadrate. After pointing out the theoretical difficulties with this scenario (airborne vibrations are strongly attenuated when transmitted to the substrate), localized vibratory stimuli and other experiments were used to demonstrate that direct perception of airborne sounds was not only possible, but physiologically superior. Though Wever (1978) dismissed the biological significance of groundborne stimuli, many sources still present snake hearing in terms of substrate-based vibrations.

Wever (1978) presented a series of auditory sensitivity curves, showing that vibration perception occurred within a rather narrow frequency range (200–400 Hz), with some species maintaining high sensitivity for roughly 100 Hertz on either side of this range (Figure 5). Wever (1978) found no clear phylogenetic or ecological correlates with the acoustic performance of the snakes he examined, although he tentatively noted a correlation between maximum auditory sensitivity and the number of hair cells in the basilar papilla. The use of cochlear potentials to estimate hearing sensitivity has been criticized (e.g., Manley 1990). Some of these criticisms are probably not applicable to the low frequency system of snakes, and the overall consistency of the data presented by Wever (1978), and its support by subsequent experimental techniques (see below), suggests that these sensitivity curves reasonably reflect biological performance.

Wever's work was extended by Hartline (Hartline and Campbell 1969; Hartline 1971a,b), who used intracellular recordings from neurons in the torus semicircularis, as opposed to the cochlear microphonics of Wever. The data presented by Hartline are in good agreement with those of Wever; Hartline documented the ability of snakes to perceive both airborne and groundborne vibrations, the same relatively restricted frequency range of response, and snake's greater sensitivity to airborne stimuli (Hartline and Campbell 1969; Hartline 1971a,b). Auditory neurons in the torus semicircularis had a mean latency of 40 msec and a mean refractory period of over 200 msec, values much greater than in other vertebrates (Hartline 1971b). The temporal performance of these neurons was slow enough that Hartline concluded, "Of relevance to the biology of snakes is the observation that snakes are not well suited, at the mid-brain level, for rapid analysis of sequential vibratory events" (Hartline 1971b:389). One of the most important findings of Hartline's studies was that snakes could perceive vibrations from their body surface (termed somatic hearing) as well as from their inner ear (Hartline and Campbell 1969; Hartline 1971a,b). The exact mechanism of somatic hearing is not understood, in part due to conflicting results in Hartline's studies concerning the potential role of the spinal nerves. Hartline (1971a,b) argued that peripheral cutaneous mechanoreceptors, similar, if not identical, to those previously described in snake skin by Proske (1969), could play an important role in somatic hearing.

Collectively the physiological data presented by Wever and Hartline clearly establish that not only are snakes not deaf, they are capable of perceiving airborne vibrations (in some species with sensitivities similar to those of other

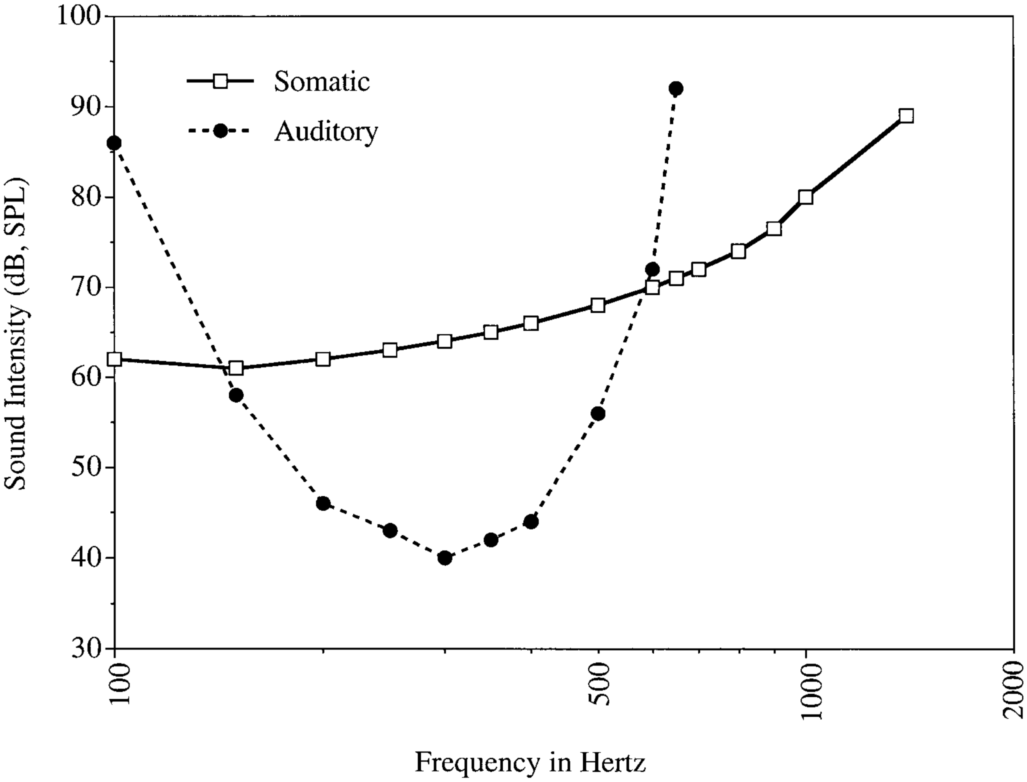

FIGURE 5. SUMMARY ACOUSTIC SENSITIVITY CURVE FOR SNAKES

This figure is based on data presented in the unpublished (1969) dissertation of Peter Hartline and in Wever (1978). The lower the values on the *y*-axis, the greater the acoustic sensitivity. Note that somatic hearing is characterized by lower sensitivity but a greater frequency range.

terrestrial vertebrates, including primates). Perhaps most intriguing are the differences between vibration detection through the inner ear (greater sensitivity but reduced frequency range) and somatic hearing (lower sensitivity but greater frequency range). Snakes essentially have two, at least peripherally distinct, auditory systems (Hartline 1971a). The neural pathways of these two systems have not been detailed for any species; it is possible that signals from these two pathways are processed differently in the brain. Whether or not these two systems are specialized for different behavioral contexts remains to be seen.

Hartline (1971a) proposed that the lung may play a role in transmitting vibrations from the snake's body to the brain. Other studies have explored the possible function of the lung in sound transmission in amphibians and reptiles (e.g., Hetherington 2001), but the underlying mechanism remains elusive. The ophidian lung does possess pulmonary stretch receptors (e.g., Sundin et al. 2001), but no known mechanical links analogous to a Webberian apparatus exists between the lung and the brain. The previous studies on the role of the lung in audition have not distinguished between the lung itself and the overlying body wall; since the snake's body expands furthest in the region of the lung, the adjacent body wall may have a higher density of receptors, or a unique class of receptors, than other regions. Specialized projections, interpreted as sensory organs, have been described from the scales of several snakes (e.g., Povel and Van der Kooij 1997;

Young and Wallach 1998). Similar scale projections could function in somatic hearing.

BEHAVIORAL STUDIES OF VIBRATION DETECTION BY SNAKES

The natural history literature contains numerous reports of workers interpreting snake behavior as indicative of differing degrees of hearing (e.g., Macht 1954; DeLisle 1977; Ahmad Yahya 1978; Trembling 1982). Corkill (1932) argued that snakes could hear high-frequency sounds, Elliot (1934) claimed they hear sounds through the costal cartilages of the ribs, and Brooking (1934) describes rattlesnakes being attracted to the sound of machinery. Wall (1921) blindfolded snakes and then made sounds around them, Davenport (1934) rattled cans filled with rocks near snakes, and Klauber (1956) described elaborate attempts to explore hearing in rattlesnakes. The response of the cobra to the snake charmer's music was investigated by O'Reily (1894) and more recently by Werner (1999); in both cases the studies revealed that the cobras were responding to tactile and visual, but not auditory, stimuli.

The first experimental study of snake's behavioral responses to sounds was that of Manning (1923), who used a telephone receiver to play presumably pure tones to a group of rattlesnakes. The lowest trial frequency was 43 Hertz, and the frequency was consecutively doubled to reach the maximum trial frequency of 2752 Hz. Manning (1923) controlled neither the volume of the tone (which he described as "quite loud"), the stimuli duration, the distance of the stimulus from the snake, nor whether the sounds could be detected by either airborne and groundborne vibrations. Manning obtained positive results, particularly from one rattlesnake; as he remarked, "This snake responded by rattling energetically and regularly to both 43 and 86 vibrations per second. A momentary sounding of the telephone would instantly start the rattling . . . There could be no question as to cause and effect" (Manning 1923:243). Despite getting positive responses through two variations of his experiment, Manning (1923) concluded that rattlesnakes are deaf.

More recent experiments have provided positive evidence that snakes respond to groundborne vibrations. Burger (1998) reported that hatchling *Pituophis melanoleucus* retreated when exposed to vibrations produced by dropping a rock behind a screen; Randall and Matocq (1997) showed that *P. melanoleucus* was attracted to the sounds produced by a buried "artificial thumper," and Shivik et al. (2000) report *Boiga irregularis* being attracted to vibrational stimuli (though the snake's response to visually perceived motion could not be eliminated in that study). Young et al. (2000a) recorded the vibrations produced as potential predator and prey organisms locomoted over an array of geophones sensitive to the same frequencies as the snake ear. Their results indicated that while perception of groundborne vibrations could prove an effective detection system against potential predators, the maximum detection distances for most prey items (e.g., 128 cm for mice) were low enough that vibration detection may only be critical to predation under special circumstances (Young et al. 2000a).

One of those special circumstances, vibration detection by fossorial snakes, was explored in *Cerastes,* the Saharan sand vipers (Young and Morain 2002). These relatively small vipers lay partially, or completely, buried in the sand and then ambush their prey items, most commonly lizards and small rodents, with rapid strikes. The chemosensory system contributed little or no information to prey targeting; though snakes with their eyes obscured did show altered strike kinematics, they were still able to capture freely moving mice (Young and Morain 2002). A subsequent experiment using artificial targets eliminated thermal cues as the source of prey targeting and reinforced the conclusion that these snakes were hunting using vibration detection (Young and Morain 2002).

Young and Aguiar (2002) constructed a special acoustic chamber to eliminate groundborne vibrations and studied the behavioral response of rattlesnakes to airborne sounds. When specimens of *Crotalus atrox* were subjected to pulses of synthesized sounds presented at a level less than 10 dB over threshold (Wever 1978), defensive behaviors were observed in 85% of the trials (Young and Aguiar 2002).

QUESTIONS IN SNAKE HEARING

In addition to the questions raised above, there are other basic questions about audition in snakes which, to date, have received little attention. How do snakes locate the source of a groundborne or airborne vibration? As Saunders et al. (2000) noted, a small head size makes the use of interaural differences problematic, particularly at low frequencies. There is evidence that the tympanic membranes of some amphibians and birds can act as differential pressure detectors (e.g., Hill et al. 1980; Wang et al. 1996), but this solution is unavailable to snakes. In birds and mammals the neural pathway for sound localization is complex, with involvement of the cochlear nuclei (e.g., May 2000), superior olivary nucleus (e.g., Yang et al. 1999), the dorsal nucleus of the lateral lemniscus (e.g., Bajo et al. 1999), and the inferior colliculus (e.g., McAlpine et al. 2001; Euston and Takahashi 2002) which is equivalent to the torus semicircularis of snakes. As described above, there is little information about the nature of this neural pathway in snakes. Furthermore, the slow response times Hartline (1971b) described from the auditory neurons of the torus semicircularis are difficult to reconcile with spatial localization through temporal encoding. Nevertheless, there is evidence that at least some snakes are capable of auditory localization. Wever (1978) described differential signals recorded from the cochlea which were contralateral and ipsilateral to a sound source, Young and Morain (2002) reported that functionally blind snakes with dennervated chemosensory systems could still strike freely moving mice, and, though anecdotal, it is easy to get a snake to turn toward a loud sound.

Aspects of the auditory system in snakes show some ecological and phylogenetic patterns, but these patterns all have prominent exceptions (Baird 1970; Wever 1978; Miller 1980). In light of the impedance-matching problem of the snake auditory system (Wever 1978), fossorial, aquatic, and arboreal snakes should have qualitative, if not quantitative, differences in at least their middle and inner ear structure. The previous studies have all lacked a phylogenetic framework, thus ecological patterns could have been obscured by underlying phylogenetic trends (see Fay and Popper 2000). A more rigorous comparison—for example, between closely related arboreal and fossorial vipers—may provide more insight into the plasticity of the ophidian auditory system. Snakes have been shown to exhibit clear behavioral reactions to both airborne (Young and Aguiar 2002) and groundborne (Young and Morain 2002) vibrations, but to date no study has explored behavioral responses to aquatic pressure waves. Given the numerous aquatic and semiaquatic taxa among snakes, including the specialized sea snakes (Hydrophiidae) and the unique file snakes (Acrochordidae), it seems plausible that some species use vibration (pressure) detection for at least predator/prey interactions.

The recent behavioral studies of snake audition (Young and Aguiar 2002; Young and Morain 2002) suggest that snakes may be able to contextualize sounds. Rattlesnakes and sand vipers were used as experimental subjects, in part, because they have suites of very different defensive and predatory behaviors (e.g., Young et al. 1999a, 2002). *Cerastes* responded to groundborne vibrations (real and artificial) with predatory behaviors, while *Crotalus* responded to every airborne stimulus with defensive behaviors. This contextualization is particularly significant in that both groups of test subjects were sensory deprived: the *Cerastes* through surgical manipulation and the *Crotalus* by an isolation chamber. Wharton's (1969) hypothesis that *Agkistrodon piscivorus* foraged using groundborne vibrations assumes some level of contextualization. This contextualization is suggestive of something like the mammalian auditory association center, though the presence (in the dorsal ventricular ridge?), prevalence, and limitations of such a "higher center" remain to be conclusively demonstrated.

SOUND PRODUCTION

Even before Pliny the Elder described the serpent Basilisk, whose exhaled breath was alleged to cause death (Bostock and Riley 1855), there were numerous accounts of snakes speaking or making other dramatic sounds. The natural history accounts of more recent times still present an interesting array of reported snake sounds, including snakes vocally mimicking their prey (Fawcett 1953), producing sounds like human infants (e.g., Corkill 1959; Behura 1962), or in the case of the "crowing crested cobra" crowing like a rooster (Shircore 1944; Shuker 1991)! Most recent accounts have, if anything, erred on the other extreme by only discussing the hissing and rattling sounds produced by snakes, and treating both of these rather stereotypically. The sounds produced by snakes have been previously reviewed (Mertens 1946; Bogert 1960; Gans and Maderson 1973; Young 1997); Carpenter and Ferguson (1977) and Greene (1988) provide taxonomic surveys of sound production in snakes and discussions of the behavioral significance of these sounds.

TAIL VIBRATION

The distinctive rattle of the rattlesnake (genera *Crotalus* and *Sistrurus*) is arguably the most recognized sound produced by any snake, and has a long and colorful representation in the natural history literature (for a review see Klauber 1956). The rattle consists of a series of keratinized cones bearing (typically) two constrictions around their circumference which interlock the cone with the adjacent segments of the rattle (Klauber 1940; Zimmerman and Pope 1948). When the tail is vibrated the adjacent keratinized surfaces collide with one another to produce the distinctive rattling sound (Williams 1920; Klauber 1956). Young and Brown (1995) argued that the rattle could best be understood as a two-dimensional oscillator in which the size of the basal segment was the best predictor of the acoustic properties of the sounds produced, although this relationship could be influenced by environmental factors. Comparative studies of the acoustics of the rattle have shown no interspecific specializations; snake and rattle size are the main influences on the sound produced (Young and Brown 1993; Cook et al. 1994). The rattling sound is very broadband, spanning from roughly 2,000–20,000 Hz with a dominant frequency near 10,000 Hz (Fenton and Licht 1990; Young and Brown 1993, 1995). Pylka et al. (1971) described ultrasonic components (up to 50 kHz) within the rattling sound, but these observations have not been confirmed by any subsequent study.

Sound production by the rattle is driven by the specialized shaker muscles in the tail. These muscles are unusual among vertebrate striated muscle in that they combine fast contraction times (around 90 Hz) with extreme fatigue resistance (Chadwick and Rahn 1954; Martin and Bagby 1972). Morphologically these muscles are characterized by almost exclusively fast twitch fibers (Clark and Schultz 1980; Schultz et al. 1980), an unusually high density of mitochondria and glycogen, and low density of contractile elements (Schaeffer et al. 1996). Physiologically, the shaker muscles exhibit rapid H^+ and lactate efflux associated with very high blood flow rates (Kemper et al. 2001), rapid calcium cycling (Rome et al. 1996), as well as high glycolytic flux and inhibition of oxidative phosphorylation (Conley et al. 2001). These properties of the shaker muscles result in a very low metabolic cost per twitch contraction (Conley and Lindstedt 1996), a feature shared with other vertebrate sound-producing muscles (e.g., Rome et al. 1996). The morphological and physiological specializations of the shaker muscles may hold the key to understanding the phylogeny of rattlesnakes (Moon 2001).

Numerous functions have been proposed for the rattle, including the discharge of poison dust (Spaulding 1944), use in predation—either as a lure or to charm the prey—(e.g., Fitch 1903; Gillam 1916; Curran and Kauffeld 1937), and as an electrostatic organ (Vonstille and Stille 1994, but see Schwenk and Greene 1995). Though some rattlesnakes do caudal lure (e.g., Jackson and Martin 1980; Rabatsky and Farrell 1996), the rattle is not vibrated during this behavior. The only proposed function to be supported by observations and experiments is that the rattle serves as a warning device (see Klauber 1956 for a detailed treatment of this idea). The behavioral ecology of rattling is still poorly understood; experimental studies have shown that the snake's propensity to rattle is influenced by temperature and biological conditions such as reproductive status and size (e.g., Goode and Duvall 1989; Graves

1989; Rowe and Owings 1990; Kissner et al. 1997). California ground squirrels, which are both potential prey and harassers of rattlesnakes, use the rattling sound to gauge the relative danger posed by the snake (e.g., Rowe and Owings 1996; Swaisgood et al. 1999). Burrowing owls produce a defensive sound similar to that of the rattle as an apparent form of Batesian mimicry (Rowe et al. 1986; see Vane-Wright 1986 for a similar claim). Of particular interest in understanding the behavioral ecology of rattling is the defensive behavior of the small pigmy rattlesnakes (*Sistrurus*). These snakes routinely vibrate their rattles when disturbed but the small physical size of the rattle results in unusual acoustics (e.g., Cook et al. 1994) and amplitudes that are very low, and sometimes inaudible (Young, personal observation).

Rattlesnakes may have evolved on the plains of North America where the rattling sound served as a deterrent against large ungulates (e.g., Barbour 1926; Klauber 1956). Support for this scenario is found in the presence of rattleless rattlesnakes on the coastal islands off North America which are devoid of large ungulates (Radcliffe and Maslin 1975; Rubio 1998). A more recent hypothesis (Schuett et al. 1984) argued that the rattle evolved to enhance caudal luring, though as Greene (1988) and Tiebout (1997) have argued, this hypothesis is difficult to support. The best approach to understanding the evolution of the rattle, in addition to a robust phylogeny of crotalids, is an understanding of the possible precursors (see Greene 1992). A number of snakes, including vipers, support a variety of keratinized spikes or nobs on the tip of their tail which may be used for sound production (Garman 1892, 1889; Greene 1988, 1992). Tail displays in which a portion of the tail is elevated have been explored by Greene (1973, 1979), but no similar treatment exists for tail vibration, though general discussions can be found (Mertens 1946; Alfred 1960; Carpenter and Ferguson 1977; Greene 1988). Defensive tail vibration is particularly common among the Viperidae and occurs widely among the Colubridae; it is more restricted among the Elapidae and Boidae, and among the basal (non-Macrostomata) taxa is only well known from *Xenopeltis* (Tweedie 1953, but see Lazell 1988).

Among snakes there is considerable variation in tail length and associated number of postcloacal or caudal vertebrae (e.g., Klauber 1943; Hoffstetter and Gasc 1969). Snakes such as *Pituophis* with relatively short, thick tails tend to vibrate the tail rapidly, with the tail seeming to move as a rigid unit, whereas snakes with elongate thin tails, such as *Spilotes,* tend to vibrate the tail slowly with prominent sinusoidal waves evident along the length of the tail (Young, personal observation). These differences in tail kinematics result in acoustic differences; *Pituophis* produces a higher pitched, more vibratory sound (which has been likened to the sound of a rattlesnake's rattle: Kardong 1980), while *Spilotes* produces lower frequency, "rustling" sounds (Young, personal observation). Unfortunately, to date, quantitative studies of the kinematics of tail vibration and sound production have only been conducted on rattlesnakes. The sound produced by tail vibration in snakes without rattles is determined not only by the kinematics of the tail but also by microhabitat. Cottonmouths (*Agkistrodon piscivorus*) regularly tail-vibrate as part of their defensive displays (e.g., Burkett 1966; Werler and Dixon 2000); the sound produced by this vibration differs significantly when the snake is in shallow water, on fresh grass, or on dry leaves (Young, personal observation). Without a better understanding of the relationships among tail kinematics, microhabitat, and sound production, the behavioral significance of tail vibrations, and potentially the evolutionary precursor of the rattle, remains poorly understood (see also Sisk and Jackson 1997).

CLOACAL POPPING

Cloacal popping is essentially controlled flatulence. This defensive behavior is regularly observed in only two species, the Sonoran coral snake, *Micruroides euryxanthus,* and the western hook-nosed snake, *Gyalopion canum* (e.g., Woodin 1953; Duellman 1955; Tanner and Robinson 1960). The cloacal pops of *M. euryxanthus* are fairly consistent, low amplitude (50–53 dB) sounds characterized by prominent harmonics and a moderate frequency range (440–5500 Hz) (Bogert 1960; Young et al. 1999b); those of *G. canum* are higher in amplitude (70–73 dB), have a broader frequency range (350–15,200 Hz), lack distinct harmonics, and tend to diminish over time (Young et al. 1999b). Cloacal pops appear to be produced by synchronized contraction of extrinsic cloacal musculature which alternately expand then rapidly compress the cloacal volume; upon compression the air passes out the cloacal vent and over the free edge of the anal scale. In *G. canum* these "expulsions" are accompanied by cloacal evagination (Young et al. 1999b).

Roze (1996) reported cloacal popping in some *Micrurus fulvius*—Young et al. (1999b) examined eight specimens of *M. fulvius* but observed no cloacal popping—and there are unpublished accounts of episodic cloacal popping from individuals of other species. Cloacal popping only occurs during defensive interactions; in fact, it required direct tactile stimulation to initiate the behavior in both species (Young et al. 1999b). Given that the venomous *M. euryxanthus* and nonvenomous *G. canum* are sympatric fossorial species (Wright and Wright 1957), their common form of sound production may have evolved in response to a common (fossorial?) predator, or may represent a form of acoustic Batesian mimicry.

SCALE ABRASION

A common defensive behavior, particularly among small to moderate sized vipers, is to arrange the body into overlapping c-shaped coils, or simply tightly packed horizontal coils, and to then slide one segment of the body along an adjacent segment (e.g., Carpenter and Ferguson 1977; Greene 1988). In three groups of vipers (*Bitis caudalis, Cerastes,* and *Echis*), this behavior produces a clearly audible "rasping" sound (Gans and Baic 1974; Spawls and Branch 1995; Young et al. 1999a). This form of sound production also occurs in the harmless colubrid egg-eating snake (*Dasypeltis*), which has been interpreted as a Batesian mimic of this viper complex (Sternfeld 1913; Gans and Richmond 1957; Gans 1961; Young et al. 1999a). In those species that produce sound through scale abrasion, the lateral body scales incorporate species-specific patterns of ridges and similar surface projections (Gans and Baic 1974; Joger and Courage 1999).

Analyses of the acoustic properties of scale abrasion revealed fairly consistent minimum frequencies (225–750 Hz), but highly variable maximum frequencies (4.0–11.0 kHz), with a considerable range of sound intensities (49.5–64.5 dB, SPL); overall the sound produced by the colubrid *Dasypeltis* was most similar to those of the *Cerastes* examined (Young et al. 1999a). During scale abrasion the lungs may function as resonating chambers (Gans and Richmond 1957); Young et al. (1999a) could find no support for this hypothesis, but it merits closer scrutiny. The common distribution of these species in arid habitats suggests that sound production via scale abrasion, as opposed to hissing, may be a strategy for water conservation, but the absence of scale abrasion among other desert-dwelling snakes suggests that physical factors may not be the primary selective force. A further understanding of the evolution of the specialized scales, and the behavior of those vipers (i.e., *Atheris*) which scale-rub without specialized scales, would shed light on the evolution of this defensive behavior.

HISSING

Sound production using an exhalent airstream is the most common form of sound production in snakes. Hissing has been reported from within every major group of snakes (for surveys see Carpenter and Ferguson 1977; Greene 1988). The respiratory system of snakes is essentially an elongate hollow cylinder, and thus is well suited for sound production. The ophidian larynx is reduced compared to that of most vertebrates and is located near the front of the oral cavity (Young 2000); the trachea, though elongate, generally resembles the "typical" vertebrate pattern of incomplete c-shaped blocks of hyaline cartilage linked by a connective tissue membrane (e.g., Göppert 1937; Wallach 1998). Most snakes possess only one functional lung, which is a hollow cylinder (for a detailed review see Wallach 1998); at its caudal end the lung is continued by the avascular lung or airsac, which may fill the remainder of the body cavity and functions as an air reservoir (Brattstrom 1959; McDonald 1959).

In *Thamnophis elegans* ventilatory airflow was driven by localized movements of the ribs (the costal pump) and the larynx remained patent during inhalation and exhalation (Rosenberg 1973). Additional studies have described the same basic pattern of ventilatory airflow in other ophidian species (e.g., Clark et al. 1978; Stinner 1982; Milsom 1991). A study on mechanics of airflow during hissing in puff adders (*Bitis arietans*) revealed the same results—the airflow was driven by localized movements of the ribs and the glottal opening remained patent throughout the hiss (Young et al. 1999c). This study suggests that hissing in snakes may be nothing more than loud, forced ventilation. This would represent a distinct departure from most terrestrial vertebrates where ventilation and "vocalization" involve different pathways.

Young (1991) surveyed the acoustic properties of the hisses produced by 21 species of snakes; these hisses all had a broad frequency span (approximately 3–13 kHz) with evidence of neither temporal patterning, nor amplitude or frequency modulation, nor even harmonics. The typical snake hiss is very similar to white noise. There are, however, some distinct variations on the basic snake hiss. *Pituophis melanoleucus* appears to be unique among snakes in having a vibratory laryngeal septum or "vocal cord" (Young et al. 1995). These snakes produce two different defensive sounds depending on the relative tension on the laryngeal septum; both sounds are characterized by a wide frequency range (around 2–10 kHz), prominent harmonics, and high amplitudes (up to 90 dB, SPL). Surgical removal of the laryngeal septum eliminates one of the two sounds, dramatically reduces the harmonics, and significantly decreases the amplitude of the sounds (Young et al. 1995). Previous analyses of *Pituophis* had proposed that the cartilaginous epiglottal keel located immediately in front of the glottis produced the high amplitude hisses of this species (Saiff 1975). Removal of this keel produced no significant effect in the recent study (Young et al. 1995), and in an earlier study some higher amplitude hisses were recorded following keel removal (Martin and Huey 1971).

The terminal course of the exhalent airstream also varies; some snakes hiss while holding the mouth open, others hiss through a closed mouth, and others hiss through the nasal passageway. Among the nasal hissers that have been examined, all appear to be obligate nasal hissers in that occlusion of the external nares terminates all hissing; though there are no known morphological or functional barriers, the snakes will not simply hiss through their oral cavity (Wall 1921; Young and Lalor 1998; Young et al. 1999c). In one of these obligate nasal hissers, Russell's viper (*Daboia russelii*), the external nares are flared and result in high amplitude (mean 82 dB, SPL) hisses (Young 1998a). Temporal variation in the displacements of the ribs, perhaps combined with differential resistance to airflow, results in a considerable range in the duration of hisses. Stebbins (1954) describes long, steady hisses from *Boa constrictors* with durations of 11–16 seconds; shield-nosed cobras (*Aspidelaps scutatus*) produce short, explosive hisses with durations of less than 0.5 seconds (Young, personal observation). As a generality, vipers produce long hisses while elapids produce brief hisses. The relative durations appear to be "fixed," despite the absence of any morphological or physiological limitations (i.e., there is no obvious reason why *Aspidelaps* could not produce a long hiss). Viperids generally have greater body size than elapids, which would translate into greater respiratory volume (Sparing 1976, cited in Wallach 1998). Respiratory volume alone is not adequate to explain the differences in hiss duration, since there are thin colubrids that produce long hisses (e.g., *Spalerosophis*) and even some very small blindsnakes are capable of hissing (Annable 1993). Presumably the different durations of hisses combine with other aspects of the defensive displays, such as gaping or strikes, to maximize the deterrent value for given predators, though this has yet to be tested experimentally.

Adduction of the ribs compresses the underlying segment of the respiratory system, creating an increase in internal air pressure (Young et al. 2000b); if the glottis is patent this would result in an exhalent airstream, possibly audible as a hiss (see Young et al. 2001 for an unusual manifestation of this respiratory pressure). As Pope (1937) and Bellairs (1970) described, some snakes are capable of hissing during inhalation. This occurs when the velocity and magnitude of rib abduction is approximately equal to that of rib adduction. The resulting pattern has been called a quadraphasic hiss in that it consists of four distinct segments: 1) the exhalatory hiss; 2) a short silent phase (when the ribs are slowing down and changing direction); 3) the inhalatory hiss; and 4) the breathholding pause or apnea (Young and Lalor 1998; Young et al. 1999c). This quadraphasic pattern is not evident in all hissing snakes—suggesting an imbalance between rib adduction and abduction in some—and among those that exhibit the pattern the inhalatory hiss varies in duration and amplitude relative to the exhalatory hiss. A startled rattlesnake uses rapid body expansion, generated by rib abduction, to increase in size, but this rapid intake of air results in a brief low amplitude hiss (Klauber 1956; Kinney et al. 1998). Given the prevalence of body inflation as a defensive behavior in snakes (Carpenter and Ferguson 1977), it is likely that other species produce similar epiphenomenal inflationary hisses.

The functional morphology of hissing in snakes has been studied more than the associated behavioral ecology, thus there remain questions concerning the ecological and phylogenetic distribution of hissing. Though hissing is a common component of the defensive behavior of snakes, it occurs predominantly in terrestrial species; there are few or perhaps no examples of arboreal species which routinely hiss. Lillywhite and Henderson (1993) described the emphasis on crypsis in many arboreal snakes, and reviewed the other defensive behaviors common to arboreal serpents, though they did not mention hissing. Three possible explanations for the relative scarcity of hissing among arboreal snakes include: 1) the common body posture of coiling around a tree limb may interfere or limit the dilation and contraction of the body needed for hissing; 2) arboreal snakes tend to have thinner bodies than terrestrial snakes (Johnson 1955; Guyer and Donnelly 1990; Lillywhite and Henderson 1993), which would reduce the volume of the respiratory system; and 3) arboreal snakes often perform visual displays as part of their defensive behaviors, some of which are incompatible with hissing (Noble 1921; Lillywhite and Henderson 1993; Young et al. 2000b). None of these explanations, in and of themselves, seem adequate to explain the skewed ecological distribution of hissing in snakes.

An example of the interesting phylogenetic distribution of hissing can be found in the large vipers of the genus *Bitis* in central and southern Africa. Three species, the puff adder (*B. arietans*), the gaboon viper (*B. gabonica*), and the rhinoceros viper (*B. nasicornis*) are all large, heavy-bodied snakes, with generally similar body patterning and coloration which provide crypsis within the surrounding vegetation; there is limited sympatry and hybridization among the three species (e.g., Broadley and Parker 1976). Despite these similarities there is a marked gradient in their proclivity to hiss: *B. gabonica* will generally only hiss after strong provocation (such as being stepped on), *B. nasicornis* will frequently hiss if approached closely, while *B. arietans* is noted (and named) for its exaggerated sound production (e.g., Isemonger 1968; Spawls and Branch 1995). My own experience with captive specimens leads me to suspect that there is not much difference in the tendency to hiss between *B. nasicornis* and *B. gabonica,* but that *B. arietans* is much more "vocal" than the other two species. *Bitis arietans* has the largest geographic distribution of the three and thus presumably the least specialized crypsis; could this explain the greater tendency toward overt defensive behavior? No experimental studies, either in the laboratory or field, have explored intra- or interspecific differences in the proclivity to hiss.

GROWLING

The growl is a specialized form of hissing, best known in the king cobra, *Ophiophagus hannah* (Mertens 1946; Harrison 1950; Whitaker 1978; Young 1991). In this species the trachea supports a series of connective tissue diverticula which are open to the tracheal lumen but extend into most of the body cavity in the neck region (e.g., Beddard 1903; Young 1991). These tracheal diverticula appear to function as resonating chambers, filtering out the higher frequencies of the hiss; the growl of the king cobra typically spans from around 75–1200 Hz and appears to emanate from the throat rather than the mouth or nares (Young 1991). Tracheal diverticula also occur in some colubrid snakes (Thompson 1914; Brongersma 1957; Young 1992; Wallach 1998), but only one of these, *Gonyosoma oxycephalum,* has also been shown to "growl" (Young 1991). The Dhaman or Indian ratsnake (*Ptyas mucosus*) produces a very similar sound (e.g., De Rooij 1917; Wall 1921; Minton 1966), but lacks tracheal diverticula. The tracheal membrane of this species is expanded, and when the snake laterally compresses its neck during defensive displays the expanded tracheal membrane folds over in such a way that it functions as a resonating chamber (Young et al. 1999d). Though the growl produced by *P. mucosus* has a higher frequency range (400–6400 Hz) than that of the king cobra, the frequency overlap between the growls of the two species, and their mutual divergence from a "typical" snake hiss, suggest that *P. mucosus* may be a Batesian mimic of *O. hannah* (Young et al. 1999d).

Intraspecific Acoustic Communication in Snakes

Despite some early claims to the contrary, particularly in rattlesnakes (e.g., Koenig 1906; Gillam 1916; Babcock 1929; for a full discussion see Klauber 1956), there is no evidence for intraspecific acoustic communication in snakes. Neither territorial nor mating calls have ever been documented in snakes. Though male snakes may produce their typical defensive sounds during combat encounters with other males (e.g., Bogert and Roth 1966; Carpenter and Ferguson 1977), there is no evidence that this sound influences the behavior or physiology of the other snake. One key reason for the apparent absence of intraspecific acoustic communication in snakes is the fundamental acoustic imbalance between sounds produced by snakes and their acoustic sensitivity. As detailed above, the frequency range of snake hearing rarely exceeds 500 Hz, while few of the sounds produced by snakes have much acoustic energy below 1500 Hz. As has been noted several times (Pylka et al. 1971; Gans and Maderson 1973; Frankenberg and Werner 1992; Young 1997, 1998b), this basic imbalance means that snakes cannot hear most of the sounds produced by other snakes, thus minimizing the chance of acoustic communication.

An additional complication arises from the acoustic properties of the sounds produced by snakes. The relative lack of temporal patterning, absence of frequency or amplitude modulation, and the scarcity of harmonics significantly reduce the possible information content of the sounds produced by snakes (Young et al. 1999c). Blumstein and Armitage (1997) have argued that a minimum threshold of information content is necessary for intraspecific acoustic communication to evolve; the evidence from snakes suggests that this threshold has not been met. The simple acoustic qualities of the sounds produced by snakes may reflect their relatively static and simple respiratory system. Another, not mutually exclusive, possibility is that the neural control of sound production in snakes is not well developed compared to that of other vertebrates. Little work has been done on the neural control of vocalization in reptiles (see Butler and Hodos 1996), though Kennedy (1975) was able to generate species-specific sound production in *Gecko gecko* by electrical stimulation of the laminar nucleus of the mesencephalon.

Ladich (1999) has argued that vocalization and auditory sensitivity evolved independently in otophysan fishes. Our current understanding of snake bioacoustics suggests that the varied forms of sound production have evolved independently (and presumably later) than the auditory system. The independent evolution of these two systems would offer an additional explanation for the apparent absence of intraspecific acoustic communication in snakes.

This is not to say that intraspecific acoustic communication in snakes is impossible. Low frequency wave propagation in water may offer a form of acoustic communication in snakes; the aquatic *Acrochordus* has a large basilar papilla and more hair cells than any other snake (Wever 1978). A wave communication system complex enough to demarcate breeding territories was recently described in the anuran genus *Bombina* (Seidel 1999; Seidel et al. 2001). Similarly, many snakes, including fossorial forms, vibrate or thrash their bodies during defensive displays (Carpenter and Ferguson 1977). Depending on the frequency and magnitude of these body vibrations, and the physical properties of the surrounding soil, these vibrations could form a type of simple seismic warning call. Seismic communication of this type, though with greater information content, has been documented from a number of semifossorial rodents (e.g., Randall and Lewis 1997; Rado et al. 1998) and in anurans (Narins 1990).

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