

THE MECHANICS OF SOUND PRODUCTION IN THE PUFF ADDER *BITIS ARIETANS* (SERPENTES: VIPERIDAE) AND THE INFORMATION CONTENT OF THE SNAKE HISS

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Accepted 3 June; published on WWW 9 August 1999

Summary

Puff adders (*Bitis arietans*), like many other snakes, hiss as part of their defensive repertoire. In *B. arietans*, the hisses have a clear quadraphasic pattern consisting of an initial exhalatory hiss, a brief transitional pause, an inhalatory hiss and a rest or breath-holding phase. Simultaneous recordings of body diameter, electrical activity in the intrinsic laryngeal musculature, airflow through the nasal passageway and sound production revealed that the anterior respiratory tract plays a passive role in hissing and that the costal pump is responsible for generating the quadraphasic pattern. During hissing, *B. arietans* uses the same mechanics previously described for normal respiratory ventilation in snakes. Analyses of artificial hisses reveal that the anterior respiratory tract of *B. arietans* has little ability to modify an exhalant airstream

acoustically. The combination of the simple ventilatory mechanics used during hissing and the lack of acoustic modification of the exhalant airstream results in the production of an acoustically simple hiss. Cross-correlation matrix analyses of a variety of snake hisses showed a high degree of acoustic similarity between the sounds, almost approaching the levels determined for white noise. This high level of acoustic similarity reflects the low level of acoustic specialization within the sounds produced by snakes and the low potential for encoded information content.

Key words: respiration, acoustics, snake, ventilation, functional morphology, information content, *Bitis arietans*.

Introduction

Snakes exhibit a wide range of interactive behaviours with both predators and conspecifics (Carpenter and Ferguson, 1977; Greene, 1988). While sound production is frequently used as a defensive behaviour, there is no evidence of intraspecific acoustic communication in snakes. The auditory system of snakes can respond to both ground-borne and air-borne vibrations (Hartline, 1971; Wever, 1978). While some snakes have specialized mechanisms for sound production (Mertens, 1946; Gans and Maderson, 1973; Frankenberg and Werner, 1992; Young, 1997; Young et al., 1999), most species use airflow through the anterior respiratory tract to produce sound. These sounds may be produced by either exhalatory or inhalatory airflow, and in a few species anatomical specializations of the respiratory system may influence the airstream acoustically (Kinney et al., 1998; Young, 1991, 1999; Young and Lalor, 1998). With the possible exception of the 'vocal cords' in *Pituophis melanoleucus* (Young et al., 1995), these anatomical specializations appear to play a passive role in shaping the acoustic profile of the sound. As a result, the defensive sounds produced by snakes are devoid of acoustic specialization and approach broad-band

white noise. It has been hypothesized (Young, 1997, 1998) that the sounds produced by snakes have too low an information content to transmit information beyond a simple general warning.

Ventilatory airflow in snakes appears to be produced solely by localized movements of the ribs, a system referred to as the costal pump (Rosenberg, 1973). While there is some inconsistency in the literature (Wang et al., 1998), ventilation in snakes appears to be biphasic, with an initial active exhalatory phase followed by an active inhalatory phase (Gans and Clark, 1978; Clark et al., 1978). Although the exact pattern of ventilation varies, it is normally arrhythmic, with apnoeic phases of varying duration following each inhalatory phase (Milsom, 1991). Constriction of the glottal opening may enable snakes to maintain pressure within the respiratory tract during this apnoeic phase.

In some snakes, the defensive hisses exhibit a simple temporal pattern termed a quadraphasic hiss (Young and Lalor, 1998; Young, 1999). These hisses are characterized by an initial exhalatory hiss, a brief pause, an inhalatory hiss, then a second pause or rest period. There is a significant correlation between the duration and amplitude of the

exhalatory and inhalatory hisses, and the duration of the pause between exhalation and inhalation is rather consistent (Young and Lalor, 1998; B. A. Young, personal observation). The present study was undertaken with two main goals. The first was to apply cross-correlation matrix analysis, a technique for comparing the acoustic profile of two sounds (Clark et al., 1987; Hopp et al., 1998), in an attempt to assay the relative information content of the defensive sounds produced by snakes. This cross-correlation analysis is an initial test of the hypothesis that snake sounds are characterized by low information content (Young, 1997, 1998). The second goal was to test the hypothesis that the quadruphasic pattern of sound production is simply an audible manifestation of the biphasic pattern of ventilatory airflow in snakes. Analyses of the mechanics of hissing may also identify the limitations, if any, of the anterior respiratory system that are responsible for the simple acoustic features that characterize snake sounds.

Materials and methods

Live animals

Eight adult (snout–vent length range 74.5–128 cm) puff adders (*Bitis arietans* Merrem) were obtained commercially. Snakes were maintained for at least 4 months at a temperature of 29–32 °C on a 12 h:12 h L:D photoperiod and on a diet of dead mice. All animal maintenance and experimental procedures comply with the existing guidelines for both live reptiles and venomous snakes.

Acoustics of the hiss

Individual snakes were placed on a table within a large quiet room, and defensive hisses were evoked by the presence of the investigators. The sounds were recorded using an ND 757B (Electro-voice) microphone (frequency response 50 Hz to 22 kHz) positioned approximately 15 cm from the snake's head. Audio recording and acoustic analyses were performed using a P511 amplifier (Grass Instruments), an Instrunet analog/digital converter (GW Instruments), a Power Macintosh 8500 (Apple Computer), SoundScope software (GW Instruments) and a WLFDAF 1.0 digital filter (Zola Technologies). The amplitudes of the hisses were confirmed using a 840029 digital sound meter (SPER Scientific) positioned 50 cm away from the snake's head. Sonograms were generated using a fast-Fourier transformation (FFT) of 2048 points and a filter bandwidth of 59 Hz (29 ms). The SoundScope software was used to quantify the duration of each component of the hiss.

Mechanics of hissing

Three specimens were anaesthetized with Isoflurane, then intubated and maintained on 0.5–1.5 % Isoflurane in oxygen at a flow rate of 1.5–2.0 l min⁻¹ using a Vapor Stick Plus (J. A. Webster, Inc.) anaesthesia machine. A hypodermic needle was used to pass 50 µm diameter wire (California Fine Wire) through the lower jaw, and the free ends of the wire were used

to construct bipolar electromyogram (EMG) leads, which were implanted into the dilator laryngis and constrictor laryngis muscles. A 4 mm×3.5 mm strain gauge (EA-13-062AK-120, Measurements Group, Inc.) was attached non-occlusively over an external naris using cyanoacrylate gel. Exhalatory airflow through the nares stretched the strain gauge, producing a decrease in voltage output. A Hall effect sensor was constructed using a 3503 SPREG chip from Allegro Industries and a 1.0 mm diameter neodymium/boron/iron ceramic magnet from Indigo Industries. The sensor was mounted on the dorsolateral surface of the body (near the midpoint of the snout–vent length, SVL) using cyanoacrylate gel and supplied with a constant voltage from a 6 V lantern battery. The sensor was constructed such that any reduction in distance between the magnet and the SPREG chip, as would happen during body deflation, would produce an increased voltage output.

With the surgery complete, the animal was ventilated with pure oxygen until recovery and then transferred to a 57 l terrarium lined with moistened newspaper. An ND 757B (Electro-voice) microphone was mounted in one corner of the terrarium. The two EMG leads and the microphone were connected to P511 preamplifiers (Grass Instruments), and the strain gauge was connected to a P122 preamplifier (Grass Instruments). These preamplifiers, as well as the Hall effect sensor, were connected to an Instrunet analog/digital converter (G.W. Instruments). Simultaneous real-time recordings were taken from all five data sources at a sampling rate of 22 kHz. Multiple hisses were recorded from each individual, and the data were analyzed (using SoundScope) for patterns of temporal congruence. Following data collection, the animals were lightly anaesthetized, the experimental equipment was removed and the snakes were allowed to recover fully.

Analysis of artificial hisses

Three specimens were individually anaesthetized with Isoflurane, and their bodies were suspended in a sling of fabric. A midventral incision was made at the level of the caudal end of the trachea, and two endotracheal tubes were implanted. The first endotracheal tube was directed caudally into the lung and was used to maintain anaesthesia (1.5 % Isoflurane in oxygen with a flow rate of 1.5 l min⁻¹). The second endotracheal tube was implanted with its free end directed cranially up the trachea. This second endotracheal tube was used to pass compressed air (flow rate 200–250 ml s⁻¹) through the trachea and larynx and out through the open mouth. The acoustics of the resulting sound were captured using an ND 757B (Electro-voice) microphone mounted 20 cm away from the oral cavity and a TCD-D8 DAT recorder (Sony). The recorded sounds were subsequently analyzed using the SoundScope (G.W. Instruments) data analysis package.

Using the compressed airstream, three types of artificial hiss were produced: short-duration pulsatile hisses, hisses in which the glottal opening was manually constricted, and hisses in which the glottal opening was constricted through

electrical stimulation of the constrictor laryngis. To produce short-duration pulses of air, a solenoid was placed between the compressed airline and the endotracheal tube. An S88 stimulator (Grass Instruments) triggered the solenoid in 30 ms pulses at a rate of 6 pulses s^{-1} . A constant flow of compressed air was maintained through the trachea and larynx following removal of the solenoid. Using equal pressure on either side of the arytenoid cartilages, the glottal opening of the larynx was manually constricted and then allowed to dilate in response to the airflow. Several repetitions were performed at differing rates of glottal closure. Lastly, the oral epithelium over the larynx was removed to expose the constrictor laryngis muscle. Using the S88 stimulator, the contralateral muscles were repeatedly stimulated (10 V, 150 ms duration) to induce glottal constriction. The specimens used to analyze the artificial hisses were killed while still fully anaesthetized.

To explore further the functional role of the glottis, a series of defensive sounds was recorded from a single specimen (SVL 113 cm), which was then lightly anaesthetized with ice, and a shortened tracheal tube was inserted into the larynx. The outer diameter of the tracheal tube was similar to the inner diameter of the larynx, and a flange on one end of the tube held it in place within the larynx. With the tube in place, there was unrestricted airflow through the larynx, but no possibility of constriction of the glottal opening. Once the tube had been fitted in place, the snake was warmed up and a second series of defensive hisses was recorded. The tracheal tube was removed immediately after the sounds had been recorded, and the snake was allowed to recover fully. The pre- and post-manipulation sounds from this specimen were recorded and analyzed as described above.

Cross-correlation analysis of snake hisses

This analysis was performed using existing audio recordings of the defensive hisses of seven snake species (puff adder *Bitis arietans* Merrem; eastern diamondback rattlesnake *Crotalus adamanteus* Palisot de Beauvois; Russell's viper *Daboia russelii* Shaw; eastern hognose snake *Heterodon platyrhinos* Latreille; cape cobra *Naja nivea* L.; Indian ratsnake *Ptyas mucosus* L.; and long-nosed viper *Vipera ammodytes* Linnaeus). None of the hisses was acoustically filtered, but they were digitally amplified such that each hiss had the same mean amplitude. A 0.75 s segment of each hiss was analyzed in 0.05 s intervals. A power spectral analysis was performed on each interval, and the amplitude was determined for 16 frequencies starting at 2.0 kHz and extending to 9.5 kHz in 0.5 kHz increments. This frequency range was selected because it contained the dominant frequency of each species, and each species produced sound throughout this range. The data matrices generated were exported to Systat, and cross-correlation matrix analyses were performed among all the species.

For comparison, similar cross-correlation analyses were performed on three other data sets. The first consisted of synthesized white noise, which was analyzed using the same

parameters used for the snake hisses. The second data set consisted of calls from six birds (eastern whip-poor-will *Antrostomus v. vociferus* Wilson; upland plover *Bartramia longicauda* Bechstein; common loon *Gavia i. immer* Brunnich; eastern screech owl *Otis asio naevius* Gmelin; eastern bluebird *Sialia s. sialis* L.; and blue-winged warbler *Vermivora pinus* L.) taken from a commercial digital recording. The bird calls were analyzed in 0.05 s intervals using 16 frequencies ranging from 0.3 to 9.3 kHz in 0.6 kHz increments. The third data set were recordings of four adults speaking the same sentence, with analysis performed on the same three words from each adult. For this analysis, the same frequency range was sampled (312.5–5000 Hz, in 16 increments of 312.5 Hz), but the temporal duration varied to encompass the same three words in 16 equal increments.

Results are presented as means \pm S.D.

Results

Cross-correlation analyses

The minimum correlation determined from the analyzed segments of synthesized white noise was 0.98, and all the comparisons were significant (using Bonferroni probabilities of $P < 0.05$). Most of the correlation coefficients calculated for the snake hisses ranged from 0.6 to 0.8 with fairly low levels of variation (Fig. 1A). The percentage of significant values for these correlation coefficients ranged from 0 to 1.00. In five of the 21 comparisons, over 60% of the compared matrices had significant correlations. Cross-correlation analysis of adult humans uttering the same three words produced lower correlation coefficients (0.38–0.55) with higher variation (Fig. 1B). Most of these correlation coefficients were not significant. Analyses of bird calls produced lower correlation coefficients (mostly between 0.3 and 0.4), with levels of variation similar to those for human speech. In only one of the comparisons was there any significant correlation between the matrices (Fig. 1C).

Quadruphasic hiss

With little provocation, puff adders (*Bitis arietans*) will inflate their body and produce a lengthy series of loud hisses (Fig. 2). Analysis of these hisses reveals a distinct quadruphasic pattern characterized by an initial exhalatory hiss, a brief transitional pause, an inhalatory hiss and a second pause or rest phase (Fig. 3). In 30 hisses produced by a 92 cm SVL specimen of *B. arietans*, the exhalatory hiss had a mean duration of 1.54 ± 0.2 s (range 1.2–2.2 s) and a mean amplitude of 67.2 ± 2.8 dB RMS (range 61.9–75 dB RMS), the transitional pause had a mean duration of 0.05 ± 0.01 s (range 0.04–0.08 s), the inhalatory hiss had a mean duration of 1.87 ± 0.23 s (range 1.55–2.5 s) and a mean amplitude of 55.9 ± 1.67 dB (range 53.2–58.9 dB) and the second pause or rest phase had a mean duration of 0.75 ± 0.52 s (range 0.11–1.94 s). Similar values were obtained from the other specimens examined, although there was a non-significant trend towards louder and longer hisses with increasing body size.

A						
<i>Crotalus adamenteus</i>	0.06					
	0.65±0.07					
<i>Daboia russelii</i>	0.75	1.00				
	0.59±0.14	0.62±0.11				
<i>Heterodon platyrhinos</i>	0	0.25	0.13			
	0.51±0.17	0.68±0.10	0.58±0.16			
<i>Naja nivea</i>	0.13	0	0.13	0.44		
	0.67±0.09	0.66±0.08	0.66±0.08	0.75±0.10		
<i>Ptyas mucosus</i>	0	0	0.38	0.19	0.63	
	0.40±0.11	0.56±0.10	0.43±0.13	0.68±0.10	0.75±0.11	
<i>Vipera ammodytes</i>	0.38	0.31	0.06	0.69	0.94	0.13
	0.74±0.06	0.72±0.07	0.65±0.07	0.79±0.07	0.85±0.05	0.65±0.10
	<i>Bitis arietans</i>	<i>Crotalus adamenteus</i>	<i>Daboia russelii</i>	<i>Heterodon platyrhinos</i>	<i>Naja nivea</i>	<i>Ptyas mucosus</i>
B						
2	0.13					
	0.51±0.21					
3	0	0.06				
	0.38±0.20	0.40±0.24				
4	0.06	0.06	0.13			
	0.46±0.18	0.40±0.20	0.55±0.22			
	1	2	3			
C						
Common loon	0					
	0.38±0.15					
Whip-poor-will	0	0				
	0.37±0.20	0.32±0.23				
Upland sandpiper	0	0	0			
	0.27±0.16	0.19±0.21	0.36±0.23			
Eastern screech owl	0	0.19	0	0		
	0.32±0.13	0.52±0.27	0.37±0.24	0.16±0.11		
Eastern bluebird	0	0	0	0	0	
	0.34±0.11	0.17±0.10	0.23±0.15	0.32±0.22	0.25±0.13	
	Blue-winged warbler	Common loon	Whip-poor-will	Upland sandpiper	Eastern screech owl	

Fig. 1. Results of cross-correlation analysis of acoustic matrices. The top number is the percentage of correlation coefficients (out of 16) that are significant using a Bonferroni probability of $P < 0.05$, the bottom number is the correlation coefficient (presented as mean \pm S.D.). (A) An analysis of the defensive hisses of seven snake species, (B) an analysis of the same three words spoken by four human adults, (C) an analysis of calls from six bird species.

Mechanics of the hiss

The three specimens examined all produced distinctive quadraphasic hisses shortly after recovery from the anaesthesia. Neither the amplitude nor the duration of these hisses differed significantly from the pre-operative values. The data were consistent between hisses and among individuals. *Bitis arietans* is an obligate nasal breather; thus, the strain gauge mounted over the external naris was deflected during both exhalation and inhalation (Fig. 4). The transitional pause, the second phase of the quadraphasic hiss, was marked by a plateau in the output from the strain gauge. The Hall effect sensor mounted at midbody showed an increase in voltage associated with adduction of the ribs at the onset of the

exhalatory hiss (Fig. 4). The slope of the voltage output from the Hall effect sensor increased with increased amplitude of sound production. The transitional pause was marked by a very short plateau in voltage output from the Hall effect sensor prior to a steep reduction in voltage caused by rib abduction at the onset of the inhalatory hiss.

The dilator laryngis was active immediately before the exhalatory hiss and showed continuous activity throughout that portion of sound production (Fig. 4). At the onset of the transitional pause, the amplitude of the signal from the dilator laryngis decreased substantially. Low-amplitude activity was recorded from this muscle for most of the inhalatory hiss; generally, the electrical activity in the muscle terminated as the

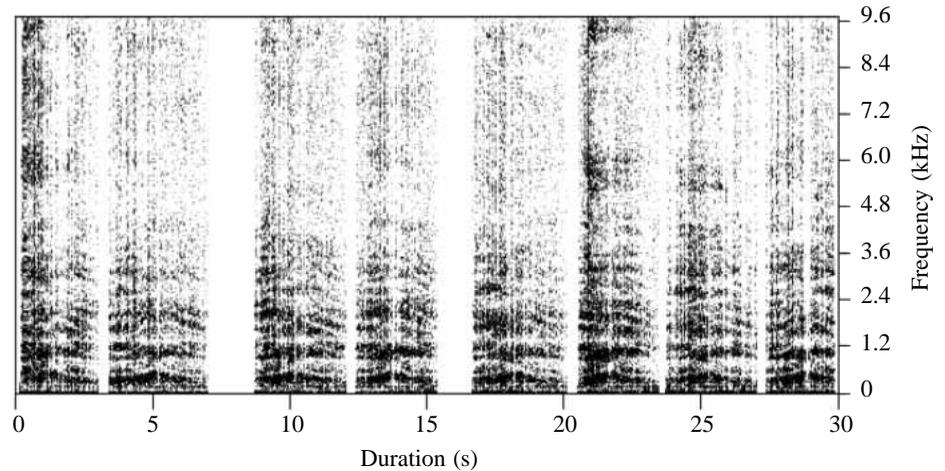


Fig. 2. A series of defensive hisses from a 89 cm snout-vent length specimen of *Bitis arietans*. Note the variable pause between the hisses.

inhalatory hiss began to drop in amplitude. The constrictor laryngis was inactive throughout the exhalatory hiss, the transitional pause and much of the inhalatory hiss. Electrical activity was recorded from this muscle only near the termination of the inhalatory hiss (Fig. 4). Although activity was not continuous, the constrictor laryngis was frequently active during the apnoeic phase.

Artificial hisses

Pulses of air lasting 30 ms passed through the trachea and larynx of anaesthetized specimens of *Bitis arietans* underwent only minor acoustic modifications. There was no evident temporal expansion of the pulses, a slight decrease in amplitude and some of the lower-frequency sound was lost (Fig. 5). Artificial constriction of the glottis, whether produced manually or by electrical stimulation of the constrictor laryngis muscle, produced consistent results. As the glottis constricted, there was a distinct decrease in the amplitude of the sound (Fig. 6), without a concurrent shift in frequency. Frequency modulation of the artificial hiss was never observed. When the glottal opening was closed, sporadic higher-frequency sounds were produced by air

passing through small gaps between the opposing glottal rims. These higher-frequency sounds were of very low amplitude (approximately 18 dB) compared with the artificial hiss, which had an amplitude of 56 dB.

The defensive sounds recorded prior to the insertion of the tracheal tube had a duration similar to those observed in the other specimens: exhalatory hiss (1.48 ± 0.20 s, mean \pm s.d.), transitional pause (0.07 ± 0.01 s), inhalatory hiss (1.86 ± 0.15 s; $N=10$). The insertion of the tracheal tube changed the behaviour of the animal. Although the specimen would still hiss, it appeared more lethargic. Insertion of the tracheal tube resulted in exaggerated changes in body diameter (both inflation and deflation) during sound production. The quadruphase nature of the hiss was retained (Fig. 7), but the first three phases of the hiss were temporally expanded. The durations recorded with the tracheal tube in place were as follows: exhalatory hiss (2.96 ± 0.16 s); transitional pause (0.35 ± 0.07 s); inhalatory hiss (4.78 ± 0.73 s; $N=10$). The durations of these three phases were all significantly longer (two-tailed t -test, $P < 0.05$) than the respective initial values. This temporal expansion is evident when comparing Figs 2 and 7.

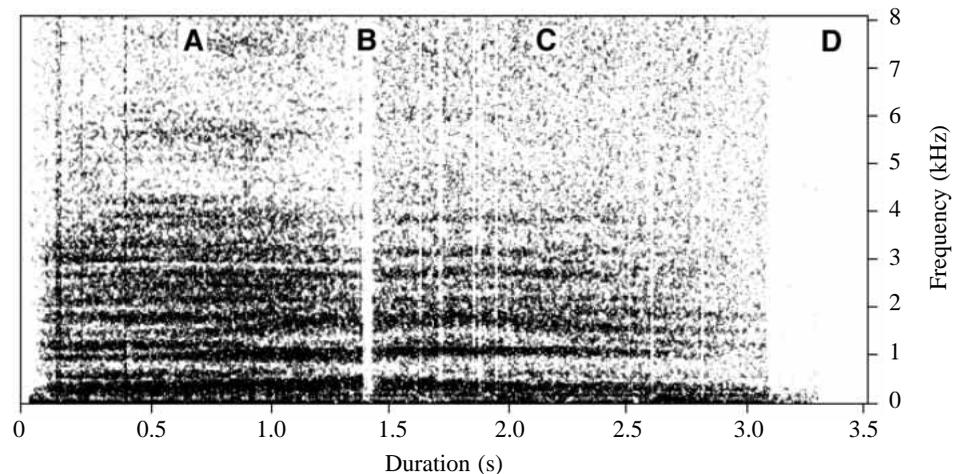


Fig. 3. A quadruphase hiss recorded from a 96 cm snout-vent length specimen of *Bitis arietans*. (A) Exhalatory hiss; (B) transitional pause; (C) inhalatory hiss; (D) rest or apnoeic phase (shown incomplete). Note the abrupt termination of the exhalatory hiss.

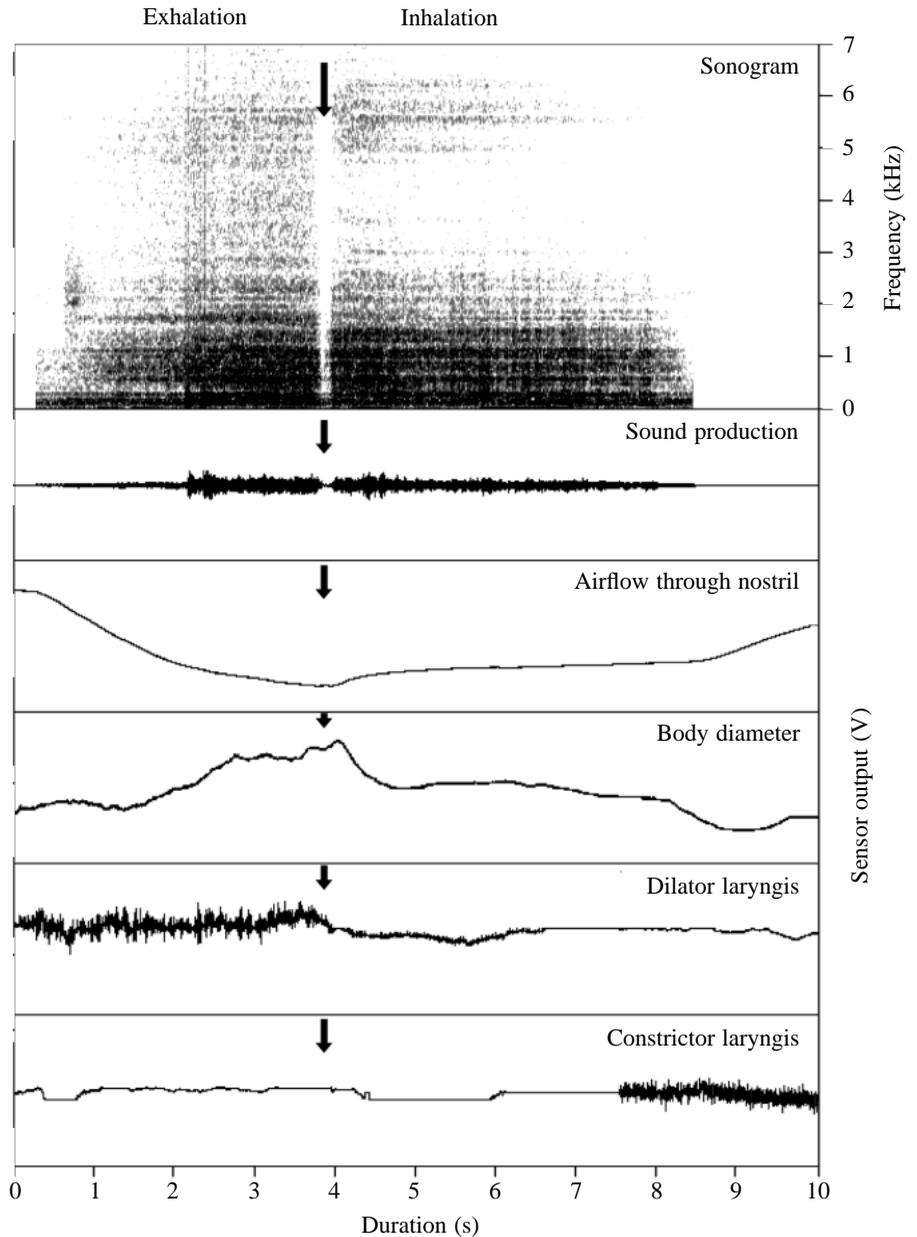


Fig. 4. Data recordings for a single hiss recorded from a 128 cm snout-vent length specimen of *Bitis arietans*. All five data channels were recorded simultaneously, with the arrow serving as a time marker. The sonogram was produced from the audio tracing using a fast-Fourier transformation (FFT) of 2048 points and a filter bandwidth of 59 Hz (29 ms). Note that the body diameter (as measured by the Hall effect sensor) tracks sound production, and note the absence of electrical activity in the constrictor laryngis during the exhalatory hiss, transitional pause and most of the inhalatory hiss.

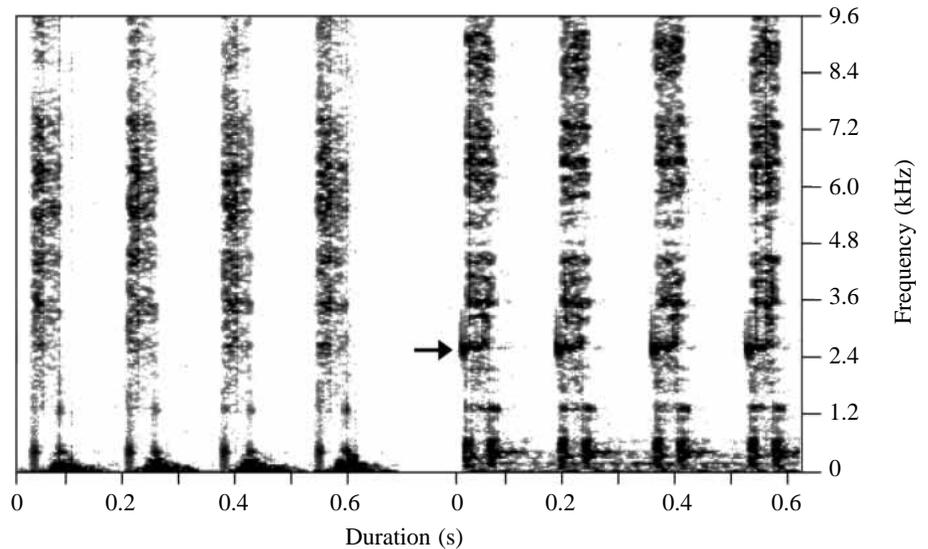
Discussion

The quadruphasic hiss produced by the puff adder (*Bitis arietans*) is similar to that described previously for other snakes (Young, 1999; Young and Lalor, 1998). The abrupt termination of the exhalatory hiss, the fairly consistent duration of the transitional pause and the rapid onset of the inhalatory hiss (Fig. 3) all reflect a physiological or mechanical control of the quadruphasic pattern. Although the airflow associated with sound production is passed through the nasal passageways (Fig. 4), in *B. arietans*, as in many snakes (Parsons, 1970), the nasal passageways are essentially static and could not modulate the airflow to produce the quadruphasic pattern.

Alternating patterns of glottal dilation and constriction could produce the quadruphasic pattern observed in the defensive hisses of *Bitis arietans*. However, the electrical activity recorded from these muscles during hissing

demonstrates that the glottal opening and the larynx are essentially passive conduits during defensive sound production. The dilator laryngis opens the glottal aperture prior to the exhalatory hiss (Fig. 4), and the glottis remains patent until near the end of the inhalatory hiss. No electrical activity was recorded from the constrictor laryngis during the transitional pause, indicating that the glottal aperture was not occluded during this transition. Our experimental results indicate that the glottis is closed only during the final apnoeic period of the quadruphasic hiss and that, as suggested by Clark et al. (1978), contraction of the constrictor laryngis may not be necessary to keep the glottis closed. When the glottal opening was held patent with a shortened tracheal tube, the quadruphasic pattern was retained, albeit in a temporally expanded form (Fig. 7). This temporal expansion, coupled with the marked changes in body diameter, suggest that

Fig. 5. Artificial hisses produced by 30 ms pulses of compressed air flowing at 250 ml s^{-1} . The first four pulses were recorded prior to implanting the endotracheal tube, the last four pulses were recorded from the oral cavity of an anaesthetized 85 cm snout–vent length specimen of *Bitis arietans* following implantation. Note that the trachea and larynx of the snake had little acoustic influence on the airstream. The long dark pulse in the last four recordings (arrow) is a marker.



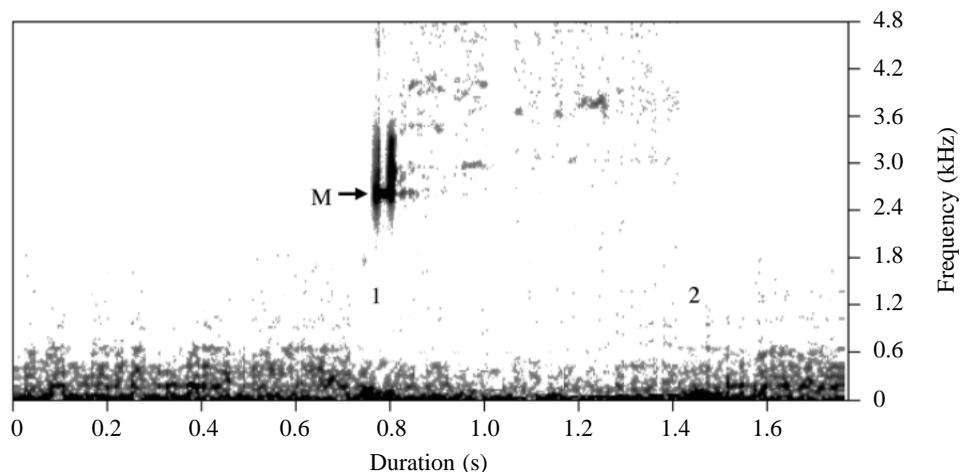
forcing the glottis to remain patent interfered with a reflex or physiological feedback control on the costal pump.

The output of the Hall effect sensor (Fig. 4) strongly suggests that the quadraphasic pattern evident in defensive sounds produced by *Bitis arietans* is generated by the costal pump. Rib adduction increases pressure within the lung and avascular air sac, resulting in the exhalatory hiss. At some point, the rotary motion of the ribs is reduced and then reversed to begin abduction; this results in a brief period of low pressure, and then no pressure, in the respiratory system that is manifested by the short transitional pause. Abduction of the ribs produces negative pressure in the lungs and air sac, which results in the inhalatory hiss. As the negative pressure decreases, so does the volume of air being taken in and, as a result, the inhalatory hiss gradually decreases in amplitude (Fig. 3). It is not clear why the exhalatory hiss is terminated abruptly; it may reflect a mechanical limitation of the rib–lung coupling or could be a behavioural specialization to maximize the amplitude of the hiss or to maintain body inflation for intimidation and/or biomechanical advantage during striking. The *B. arietans* we

examined appeared to use its entire body trunk as a costal pump during defensive sound production, rather than more localized groups of ribs.

Our results suggest that the quadraphasic hiss is driven by the same basic mechanics responsible for pulmonary ventilation. The biphasic arrhythmic pattern of pulmonary ventilation is easily reconciled with the quadraphasic pattern of hissing described for *Bitis arietans* and other snakes. Studies of ventilatory airflow have shown a very sharp transition between the initial exhalation and the subsequent inhalation (Karlstrom, 1952; Gans and Clark, 1978; Gratz, 1978; Stinner, 1982), as was seen during the transitional pause of the quadraphasic hiss. Additional studies have shown a clear temporal pattern between changes in body wall diameter and ventilatory airflow (Donnelly and Woolcock, 1977; Clark et al., 1978; Bartlett et al., 1986); a similar linkage between rib movement and sound production was found in *B. arietans* (Fig. 4). Rosenberg (1973) detailed the functional morphology of the costal pump in garter snakes (*Thamnophis sirtalis*) and recorded the electrical activity of the intrinsic laryngeal muscles during ventilation. The temporal pattern

Fig. 6. Artificial hisses produced by electrical stimulation of the constrictor laryngis to force occlusion of the glottis against an exhalant airstream of 250 ml s^{-1} compressed air. M, marker for the onset of stimulation; 1, initiation of glottal occlusion; 2, glottal dilation. Note the decrease in amplitude of the airflow, the lack of frequency modulation and the presence of intermittent low-amplitude sounds in the range 3–4 kHz. This recording was filtered to emphasize the upper frequency sounds produced during glottal occlusion.



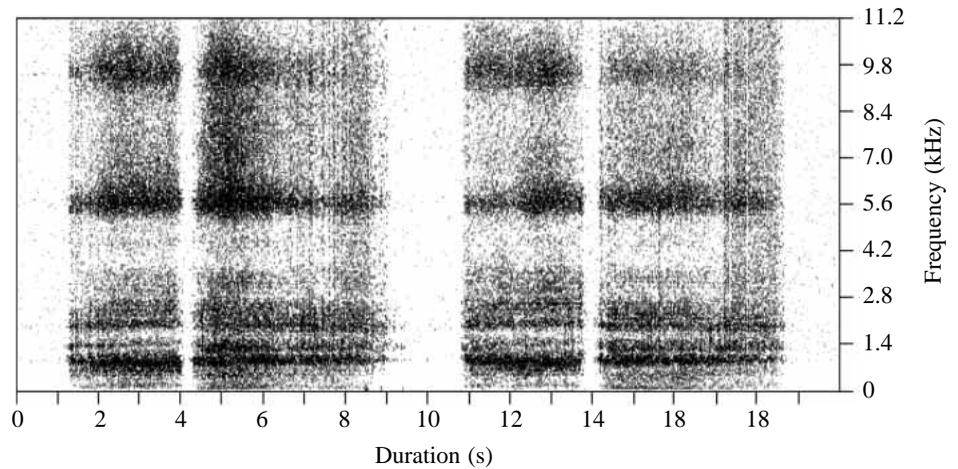


Fig. 7. Impact of continued glottal patency (through insertion of a plastic tube) on the quadraphasic pattern. Note the presence of marked temporal expansion in the exhalatory, transitional pause and inhalatory phases of the hiss (evident when compared with Fig. 2).

between ventilatory airflow and muscular activity in the larynx described by Rosenberg (1973) is nearly identical to the pattern observed during hissing in *B. arietans*. In both cases, there was a distinct reduction in amplitude in the electrical activity in the dilator laryngis at the onset of inhalatory airflow, although the significance of this decrease in amplitude is unknown.

The results of the present study indicate that the defensive hiss produced by *Bitis arietans* is really nothing more than high-intensity, unmodulated ventilatory airflow. This is unusual for terrestrial vertebrates, which generally produce sounds incorporating temporal patterns and acoustic modulation that are independent of ventilatory airflow. Our analyses of artificial hisses suggest that, at least for *B. arietans*, it would be almost impossible to produce an acoustically complex hiss. The trachea of *B. arietans* imparts no distinct acoustic signature to the exhalatory airstream (Fig. 5), and even with forced occlusion the larynx was unable to produce frequency modulation in the exhalatory airstream (Fig. 6). The combination of low compliance in the body wall and high compliance in the snake lung (Perry, 1998) makes it unlikely that a snake could produce sounds with complex temporal patterns simply by rapid movements of the ribs.

The low temporal variation in the acoustic properties of the quadraphasic hiss is evident in Fig. 2. Temporally constant yet acoustically complex sounds are possible (for instance, through multiple harmonics) but have never been described in snakes (Young, 1997). The temporal and acoustic simplicity of snake sounds is evident in the high correlations determined by the cross-correlation analysis. The bird calls examined, which presumably conveyed varying biological messages, had the lowest correlations, indicating the highest degree of individuality to each call. For human speech, we kept the biological message constant (by using the same three words from within the same sentence) but compared four different speakers. This resulted in slightly higher correlation values. The snake hisses examined had even higher correlations and lower levels of variation (Fig. 1). These high correlations indicate little temporal variation within the calls, in either frequency or amplitude. The high correlation among the snake

hisses, coupled with their simple acoustic properties, suggests that none of these snake sounds is capable of conveying a complex message. These results support the hypothesis (Young, 1997, 1998) that the defensive sounds of snakes are well-suited as general warning calls, but lack the higher information content required for intraspecific acoustic communication (e.g. Blumstein and Armitage, 1997).

The authors wish to thank the Academic Research Committee of Lafayette College for its financial support, and H. I. Rosenberg and C. Holliday for their comments on this manuscript.

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