

Sound Production in *Pituophis melanoleucus* (Serpentes: Colubridae) With the First Description of a Vocal Cord in Snakes

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ABSTRACT The pine, gopher, or bull snake (*Pituophis melanoleucus*) makes two different defensive sounds. Hisses are characterized by lack of frequency and amplitude modulation; bellows have a brief initial period of high-amplitude, broad-frequency sound followed by a longer period of lower-amplitude, constant-frequency sound. Both defensive sounds contain distinct harmonic elements. The modulation and harmonic nature of these sounds seems to be unique among snakes. The larynx of *Pituophis* is unusual in having an epiglottal keel, a dorsal expansion of the cricoid cartilage, previously proposed to contribute to sound production; however, this study shows that it plays only a small role in increasing the amplitude of bellows. Within the larynx of *Pituophis* is a "vocal cord," the laryngeal septum, which is a flexible, horizontal shelf of tissue that divides the anterior portion of the larynx. Removal of the laryngeal septum alters the defensive sounds and eliminates their harmonic elements. The laryngeal septum is unique among previously described vertebrate vocal cords or folds because it is supported by the cricoid (as opposed to arytenoid) cartilage and is a single (as opposed to bilaterally paired) structure. © 1995 Wiley-Liss, Inc.

Pituophis melanoleucus (the pine, bull, or gopher snake) is an abundant North American snake (Stull, '40; Sweet and Parker, '90). When disturbed, individuals coil up and vibrate the tail tip, and produce a distinctive defensive sound. This sound has been described as "a terrible loud hissing noise, sounding very hollow and like distant thunder" (Bartram, 1791, p. 272). Other descriptions note the "raspy" texture of this sound and its resemblance to the bellowing of a bull (e.g., Lockwood, 1875; Garman, 1892; Loennberg, 1894).

Pituophis is unique among snakes in the possession of a pronounced vertical ridge of tissue located immediately anterior to the glottal rim. Cope (1891), building on the description of White (1884), interpreted this structure as the ophidian epiglottis, and the distinguishing characteristic of his proposed genus *Epiglottophis*. Later workers referred to it as the epiglottal keel (e.g., Martin and Huey, '71) or the preglottal keel (e.g., Saiff, '75). Because of the spatial relationship between the epiglottal keel and the glottal rim, several workers have proposed that the epiglottal keel figured in the production of the defensive sounds of *Pituophis* (e.g., White, 1884; Garman, 1892; Herrera, 1889; Perkins, '38; Ditmars, '44; Klauber, '47; Bogert, '60). Martin and Huey ('71) claimed that the epiglottal keel altered the exhalent air-

stream and in doing so increased the amplitude of the sounds produced by *Pituophis*.

Sound production is a common defensive behavior in snakes—reviewed by Carpenter and Ferguson ('77) and Greene ('88)—yet little is known about the mechanisms by which snakes generate sound. As part of an ongoing study of the morphological basis of sound production in snakes (Young, '91, '92; Young and Brown, '93, '95), the current study examines the mechanics of sound production in *Pituophis*. Accordingly, the morphology of the epiglottal keel and adjacent larynx is described, and an acoustic profile of the defensive sounds of *Pituophis* is compared to that of a "typical" snake hiss (sensu Young, '91).

MATERIALS AND METHODS

Anatomy

The larynx and epiglottal keel of 14 adult specimens of *Pituophis melanoleucus* were examined. Nine were dissected, and three (including Field Museum Natural History FMNH, 4163) were examined by light microscopy. One specimen was ex-

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amed using scanning electron microscopy, and the last was cleared and stained. Tissues examined by light microscopy were removed and fixed in 10% neutral-buffered formalin, and then dehydrated, cleared, and embedded in paraffin. Sections were cut at 10 μm ; one specimen each in the parasagittal, frontal, and transverse planes. Slides were stained using Milligan's trichrome, Mallory-Heidenhain (Humason, '72), Verhoeff's elastin (Luna, '68), or Fast Green-Ponceau S (Clark, '81).

For scanning electron microscopy, the larynx and epiglottal keel were removed and fixed in Karnovsky's fixative. The tissue was washed with a sodium cacodylate buffer, pretreated with 2% osmium tetroxide, dehydrated through an acetone series, treated with Peldri II, and coated with 400 \AA of gold/palladium. For clearing and staining, after fixing in 10% neutral-buffered formalin and washing, the tissue was stained with a 0.12% solution of Toluidine blue for 3 days (Burdi, '65; Hildebrand, '68). The tissue was then dehydrated in alcohol, cleared using potassium hydroxide, and stored in glycerol.

Acoustic analysis

Recordings were made of snakes unrestrained in a chamber 43 cm \times 43 cm \times 66 cm tall, which was lined with 7.6 cm of acoustic insulation. This recording chamber was placed within a 353-cm \times 269-cm room, all interior surfaces of which were covered in acoustic insulation. The acoustic properties of the recording chamber were determined by placing a speaker in the bottom of the chamber and playing a click of known acoustic profile. The click was recorded with an Electrovoice 635A microphone (frequency response 80–13,000 Hz; 60–15,000 Hz with a loss of 5 dB), which also was used to record the snakes. The microphone fed into the Tucker Davis Technology System II hardware for the analog/digital conversion. The output was analyzed using the Computerized Speech Research Environment analysis package with a sampling frequency of 32 KHz, a window width of 1,024, and a window overlap of 15%.

Multiple ($n > 10$) defensive sounds were recorded from each of seven adult (all between 85–170 cm SVL) specimens of *Pituophis melanoleucus*, representing three different subspecies (northern pine snake, *P. m. melanoleucus*, $n = 4$), (bull snake, *P. m. sayi*, $n = 2$), (Great Basin gopher snake, *P. m. deserticola*, $n = 1$). The snakes were maintained at 27°C; all recordings were taken with the snake at this temperature. Because

the snakes produced a series of defensive sounds, recordings were taken from different portions of this series (i.e., both the initial and fourth exhalent sound would be recorded). We used a custom program within the MATLAB analysis package to eliminate the acoustic profile of the recording chamber from the recorded sounds. The resulting signals were analyzed for harmonic structures, amplitude/duration relationships, temporal patterning, and overall acoustic profile.

Quantifying amplitude is difficult because of variations in the snake's behavior, distance of the microphone from the snake, the angle of the microphone to the exhalent airstream, and the amplification of the signal prior to recording (although this could be corrected). In view of these potential difficulties, amplitudes are expressed herein as maximum relative amplitude; this is the single maximum amplitude present in any portion of the particular defensive sound without any correction for amplification (which was a constant) or the other factors listed above.

Alteration of the system

Once a series of recordings was obtained from four of the seven specimens, hypothermia was induced, and the epiglottal keel was excised at the level of the floor of the oral cavity. Following a 24-hr recovery period, another series of recordings was taken. Then these four snakes were again anesthetized by hypothermia, and the laryngeal septum or "vocal cord" was disrupted with fine forceps or a scalpel; the extent and exact location of the damage to the laryngeal septum was inconsistent. The inner lining of the larynx was not damaged, and excessive bleeding was not induced. The remaining three snakes were subjected to the same procedures, only in the reverse order—the laryngeal septum was disrupted with the epiglottal keel intact, and after recordings, the epiglottal keel was then removed.

RESULTS

Anatomy

Anatomy of the epiglottal keel

The epiglottal keel is a thin, elongate plate of tissue located immediately anterior to the larynx (Fig. 1). In a fresh specimen the dorsal portion of the epiglottal keel, particularly the margins, will appear almost translucent. From the cranial margin of the glottal opening the epiglottal keel extends both dorsally and anteroposteriorly (Fig.

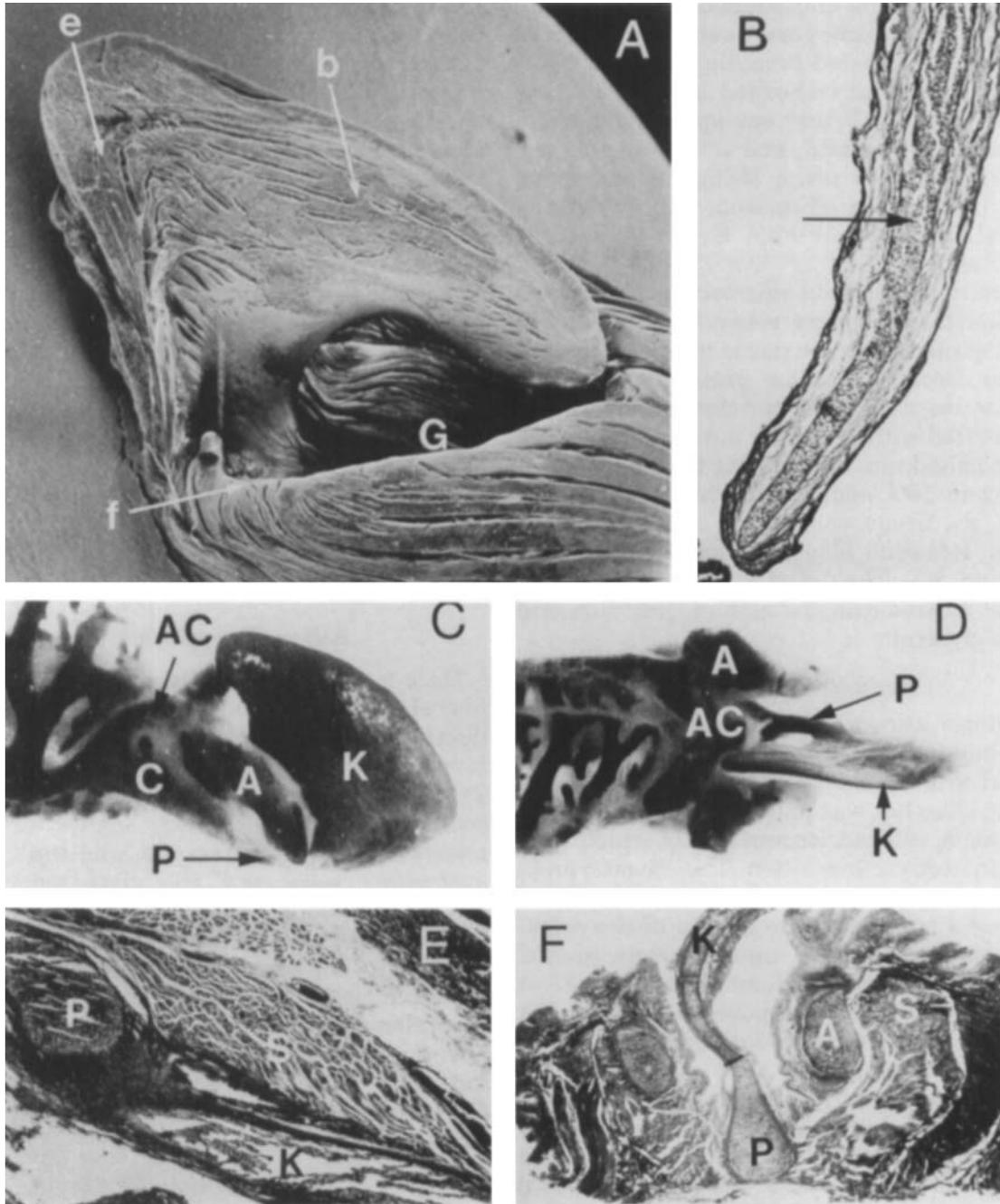


Fig. 1. The epiglottal keel of *Pituophis melanoleucus*. **A**: dorsolateral view of the epiglottal keel in relation to the glottal rim ($\times 12$). b, e, and f indicate the plane and approximate position of the other sections represented in this figure. **B**: Frontal section through the dorsal portion of the epiglottal keel showing the elastic supporting cartilage (arrow) ($\times 24$). **C**: Lateral view ($\times 3$) of the cleared and stained larynx. **D**: Frontal view ($\times 3$) of the cleared and stained larynx. **E**: Fron-

tal section at the base of the epiglottal keel near its junction with the main body of the cricoid ($\times 13$). **F**: Transverse section through the epiglottal keel showing its connection to the epiglottal process ($\times 18$). Abbreviations: A, arytenoid cartilage; AC, arytenoid cornua; C, cricoid cartilage; D, M. dilator laryngis; K, epiglottal keel; P, epiglottal process; G, glottal rim; S, M. sphincter laryngis.

1A,C,D). This anteroposterior elongation of the epiglottal keel results in the posterior portion of the keel extending through the glottal rim into the larynx. The posterior and anterior surfaces of the epiglottal keel are concave, with the greatest anteroposterior length occurring roughly one-quarter from the top of the keel (Fig. 1A).

The shape and rigidity of the epiglottal keel is maintained by a thin vertically oriented plate of elastic cartilage. This plate of cartilage is a dorsal extension of the epiglottal process, an anterior extension of the cricoid cartilage (Fig. 1C,D,F). The contours of the epiglottal keel are shaped by the connective tissue surrounding this cartilage plate (Fig. 1B). On its posterior surface the connective tissue extends as a thin septum which passes through the glottal rim into the vestibule of the larynx; this connective tissue septum is more pronounced in the ventral portions of the epiglottal keel. The anterior surface of the epiglottal keel has a thicker layer of connective tissue than does the posterior surface, a difference that becomes more pronounced near the base of the epiglottal keel.

With the exception of the free apical margins, there are vascular elements along the surface of the epiglottal keel. These vascular elements appear to support only the connective tissue: No vascular sinuses or specialized vascular chambers normally associated with erectile tissues were observed. At the level of the epiglottal process, the ventral surface of the epiglottal keel is the site of insertion of the *M. sphincter laryngis* (Fig. 1E,F). At this same level there are several isolated muscle fibers within the oral mucosa that contact the epiglottal process. Muscle fibers are only found at this ventral portion of the epiglottal keel; for the remainder of its length the epiglottal keel is composed almost exclusively of elastic cartilage and connective tissue.

Anatomy of the "Vocal Cord" of *Pituophis*

A horizontal septum, the laryngeal septum, projects into and subdivides the anterior portion of the laryngeal lumen (Fig. 2A). The laryngeal septum is attached to the inner surfaces of the arytenoidal cornua, the paired vertically directed processes of the cricoid which form the dorsal rim of the glottis (Fig. 1C,D). The free caudal surface of the laryngeal septum extends across the lumen of the larynx partitioning the larynx into a small dorsal chamber (located dorsal to the septum, following the inner contours of the arytenoidal cornua) and the larger laryngeal vestibule, which is

continuous with the tracheal lumen and glottal rim (Fig. 2A–C).

The laryngeal septum is predominantly dense connective tissue (but see below), with no distinctive elastic component. Cartilaginous supports are located along the lateral margin of the laryngeal septum (Fig. 2C): The relative size of these cartilage bodies increases cranially to form a solid band of cartilage near the anterior border of the laryngeal septum. On the caudolateral margin of the laryngeal septum is a small band of smooth muscle, the *M. tensor laryngis*. This muscle originates from the medial side of the supporting cartilage and courses medially toward the midline of the septum (Fig. 2D).

Laterally the laryngeal septum is covered by the same pseudostratified ciliated epithelium that lines the larynx and trachea. Near the midline of the septum this changes to a low cuboidal epithelium which also supports cilia (Fig. 2C,D). The distinct tapered shape of the laryngeal septum (see Fig. 2B) coupled with the absence of cartilaginous support in the caudal midline, and possibly the epithelial transition in this region, makes the free caudal surface of the laryngeal septum quite pliable. In an anesthetized or preserved specimen the caudal free surface of the septum can be freely displaced.

Acoustics

Acoustics of the defensive sounds

Pituophis exhibits a biphasic ventilatory chain in which a brief pause separates inhalation and exhalation (Stinner, '82); each exhalation produces a defensive sound. Once alarmed the animals normally produce defensive sounds for several subsequent exhalations, resulting in a temporal series of defensive sounds. Two different acoustic profiles, hereafter termed hiss and bellow, are observed within these temporal series of defensive sounds: The duration of each exhalation can be characterized as either a hiss or a bellow. The hiss was characterized by no frequency variation or temporal modulation, and a frequency range of approximately 2,000–9,500 Hz, with lower-amplitude sounds extending down to 500 Hz (Fig. 3). Distinct harmonics are found in the hiss, with a fundamental frequency of about 500 Hz (Fig. 3B). The hiss was found in exhalent bursts later in a series of defensive sounds (i.e., as the third or fourth defensive sound in a series).

The bellow, the second type of acoustic profile found in *Pituophis*, was characterized by distinct

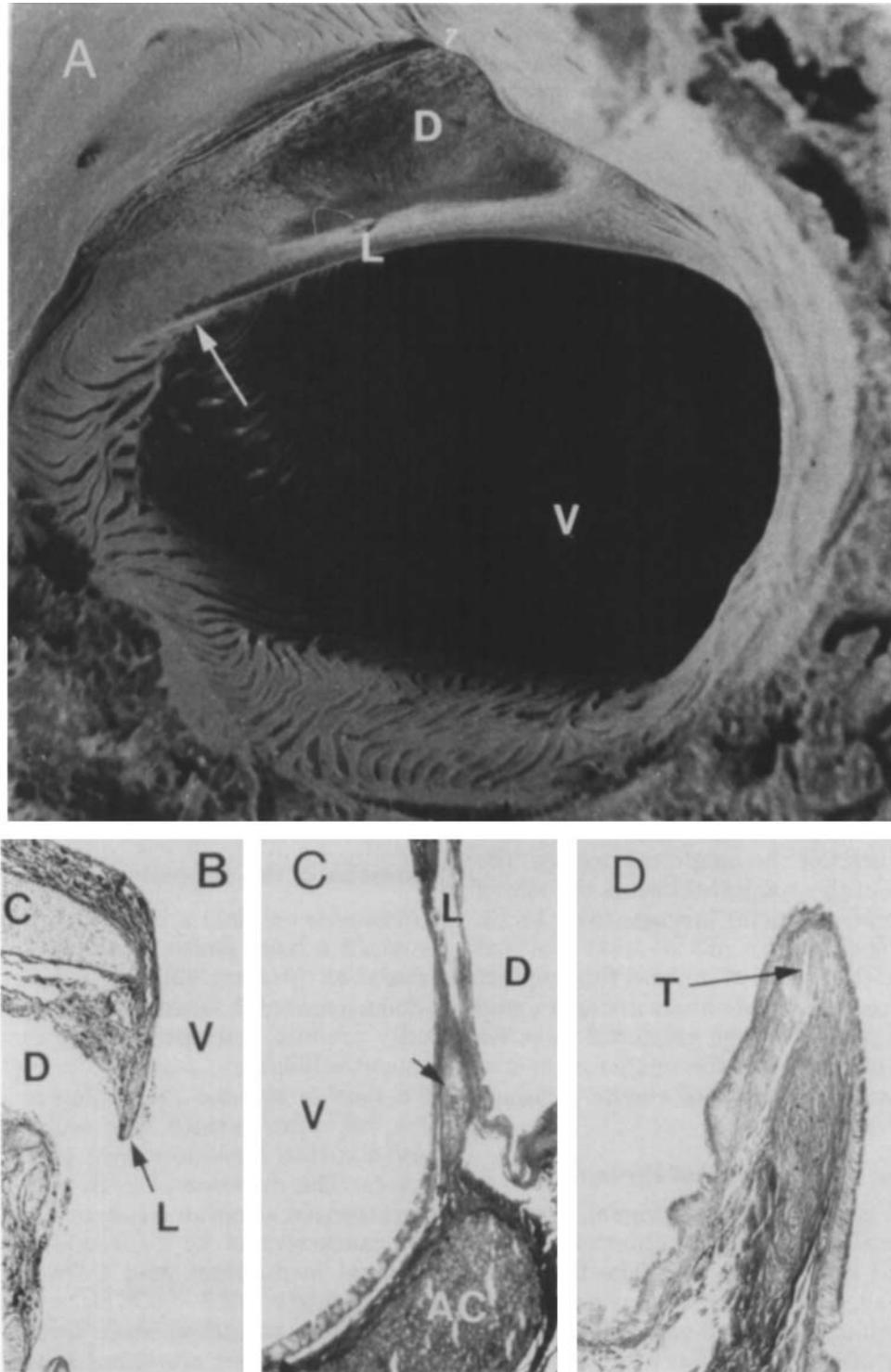


Fig. 2. The laryngeal septum of *Pituophis melanoleucus*. **A:** Caudal view of the larynx ($\times 50$); note transition in epithelium on the laryngeal septum (arrow). **B:** Parasagittal section (rotated vertically) through the septum ($\times 55$). **C:** Transverse section (rotated vertically) showing the lateral attachment of the laryngeal septum to the wall of the larynx ($\times 60$); note the

isolated supporting cartilage (arrow) and the transition in epithelium between the vestibule and the laryngeal septum. **D:** Transverse section (rotated vertically) through the caudal edge of the septum ($\times 80$). Abbreviations: AC, arytenoidal cornua of cricoid; D, dorsal chamber; L, laryngeal septum; T, M. tensor laryngeum; V, vestibule of larynx.

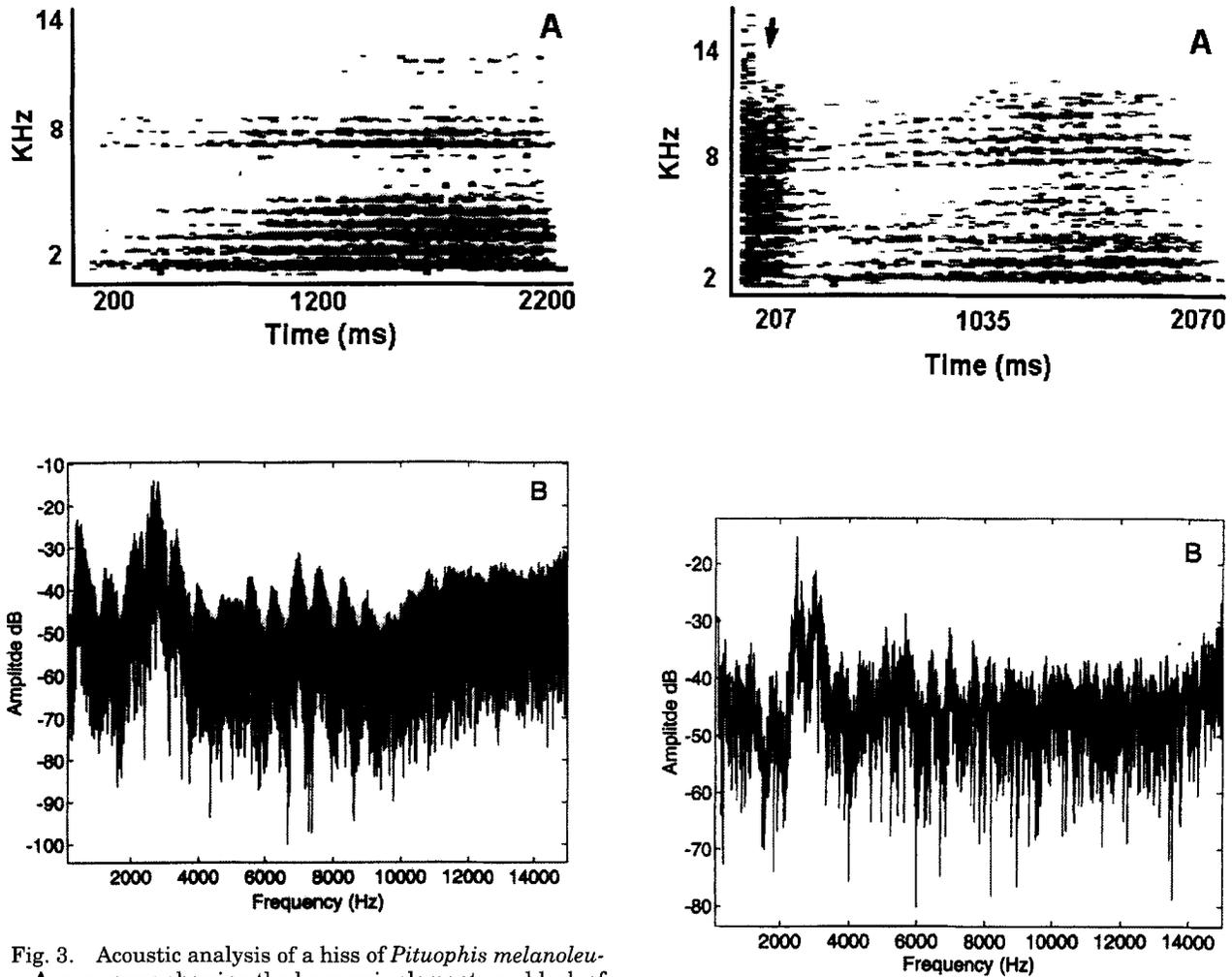
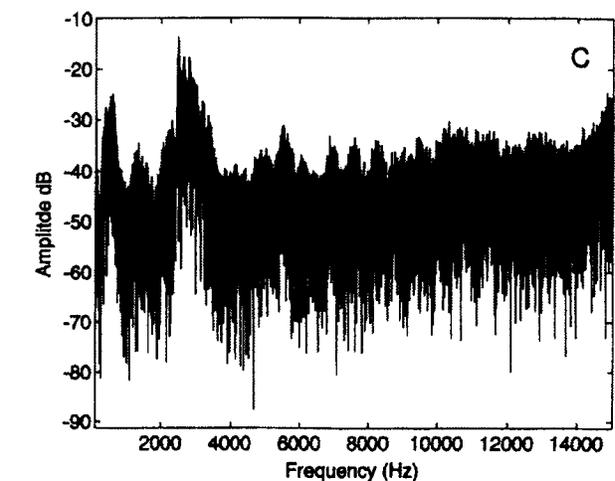


Fig. 3. Acoustic analysis of a hiss of *Pituophis melanoleucus*. **A**: sonogram showing the harmonic elements and lack of modulation; to enhance clarity some of the lowest-amplitude sounds have been filtered out. **B**: FFT analysis of the same hiss (without filtering); note the distinct harmonics. Y axis is relative amplitude.

amplitude and temporal modulation (Fig. 4A). The bellow includes a brief (< 0.2-sec) pulse of broad-spectrum, high-amplitude sound with a frequency range of 2,000–9,500 Hz, with lower-frequency sound extending down to 500 Hz, and a dominant frequency of approximately 2,600 Hz (Fig. 4B). This initial pulse leads into a longer-duration, lower-amplitude, constant sound characterized by an acoustic range of roughly 500 to 10,000 Hz.

Fig. 4. Acoustic analysis of a bellow of *Pituophis melanoleucus*. **A**: sonogram showing the initial high-amplitude pulse (arrow) and the later lower-amplitude constant portions of the bellow; to enhance clarity some of the lowest-amplitude sounds have been filtered out. **B**: FFT analysis of the initial pulse shown in A (without filtering); note the rather "noisy" nature of this sound. Y axis is relative amplitude. **C**: FFT



analysis of the later lower-amplitude portion of the sound depicted in A (without filtering); note the presence of distinct harmonic elements. Y axis is relative amplitude.

Distinct harmonics are present in this later portion of the bellow (Fig. 4C). The later portion of the bellow is similar to the hiss, although it normally has a lower amplitude: It is the short initial burst that distinguishes the bellow. The bellow is typically the first defensive sound made in a series and is the sound that most typifies *Pituophis*.

These two defensive sounds are produced with amplitudes ranging from approximately 65 to 90 dB (Fig. 5). The 10–20 dB difference between bellows and hisses is statistically significant ($t = 6.35$, $\alpha = 0.05$). Although there is substantial variation, an inverse relationship exists between the duration and amplitude of the defensive sounds. Amplitudes are also dependent on gap; *Pituophis* is capable of producing louder hisses when the mouth is only partly opened.

Visual observations during the defensive behavior reveal glottal kinematics associated with these two different acoustic profiles. If the glottal opening is constricted at the end of inspiration then dilated at the onset of exhalation (as during the initial defensive sound), a bellow is recorded. Subsequent defensive sounds within the series are generated with little or no alteration of the glottal opening. If the glottal opening remains fully patent prior to and during exhalation a hiss is produced.

Acoustic effects of altering the system

Removal of the epiglottal keel has limited impact on the acoustic profile of the sounds (Fig. 6A).

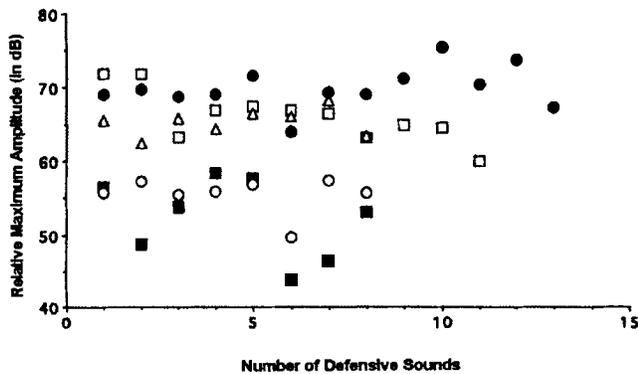


Fig. 5. Summary of the relative maximum amplitudes of the two defensive sounds made by a single adult *Pituophis melanoleucus* over 5 days, and the affects of alterations of the sound production mechanism. Symbols: solid circle—hisses; open triangle—sounds produced after disruption of the laryngeal septum; open square—hisses following removal of the epiglottal keel; open circle—bellows following removal of the epiglottal keel; solid squares—bellows.

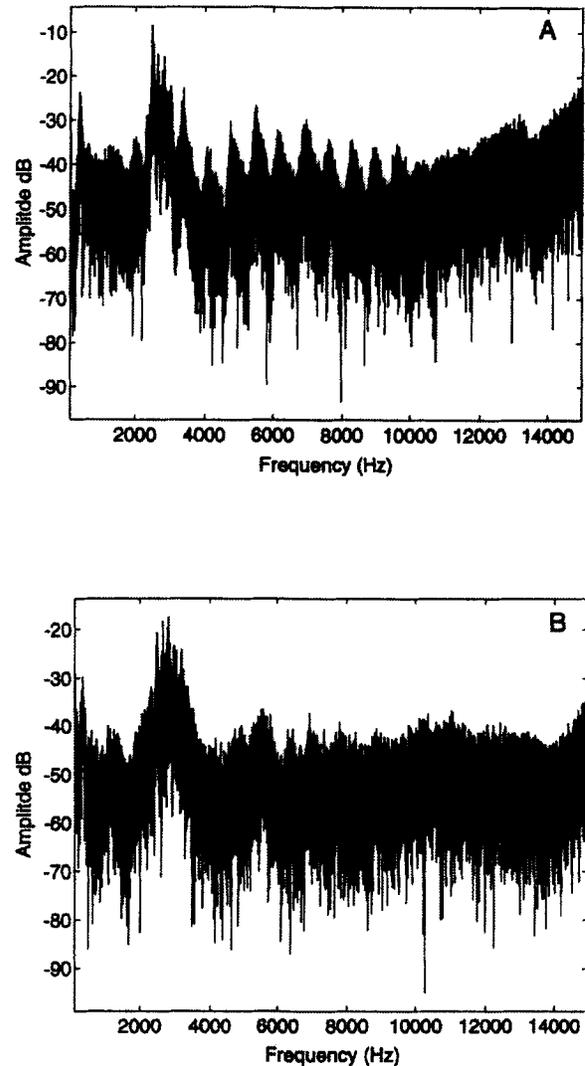


Fig. 6. FFT analyses of defensive sounds produced by the same specimen of *Pituophis melanoleucus* as Figure 4, Y axis is relative amplitude. **A:** Hiss produced following removal of the epiglottal keel. **B:** defensive sound produced following disruption of the laryngeal septum; note the strong reduction/elimination of harmonic elements.

Both hisses and bellows are still recorded, both still with distinct harmonics. Although the mean maximum relative amplitude of bellowing increased after removal of the epiglottal keel, its removal had no statistically significant influence on the amplitude of the sounds (Fig. 5).

Following disruption of the laryngeal septum the snakes were no longer capable of producing a bellow, and the harmonic nature of the defensive sounds was greatly reduced (Fig. 6B). This result was independent of the presence or absence of the

epiglottal keel. The amplitudes of the defensive sounds generated after removal of the laryngeal septum are significantly lower than a bellow (with or without the keel), but do not differ from those of a hiss (Fig. 5). Because the disruption of the laryngeal septum was not consistent, the degree of its impact on the acoustic profile showed some variation.

DISCUSSION

Anatomy

The epiglottal keel and the laryngeal septum represent distinct morphological specializations of the ophidian larynx (for previous descriptions of the larynx, see Dubois, 1886; Gopert, 1889, '37; Hoffman, 1890; Guibe, '70; Kardong, '72a,b). While the epiglottal keel is one of the distinguishing characteristics of *Pituophis*, it has been misdescribed in the literature. The epiglottal keel is a dorsal expansion of the epiglottal process (or processus medianus, e.g., Ludicke, '62). Gans and Maderson ('73) follow Ditmars ('44) in describing the epiglottal keel as "erectile"; the epiglottal keel lacks vascular specializations associated with vasodilatory erection, nor are there muscles that could elevate the epiglottal keel relative to the glottal rim. Saiff ('75) states that the keel is not attached to any other structure—as Figure 1 clearly shows, it is in fact an extension of the cricoid cartilage. The anterior extension of the cricoid cartilage is well known (e.g., Henle, 1839; List, '66; Kardong, '72a,b), and differing degrees of development of this epiglottal process could account for the variations in preglottal structures summarized by Saiff ('75).

The laryngeal septum appears to be unique to *Pituophis*. In the ophidian larynges previously described, there has been no record of internal partitions. Nor have we found a similar structure in the many larynges we have examined, including closely related Lampropeltine snakes. The structural features of the laryngeal septum—the epithelial transition, the presence of the M. tensor laryngis, the tapered free caudal surface, and the horizontal orientation—suggest that the laryngeal septum is capable of vibrating during exhalation. A variety of vocal cords and folds have been described from vertebrates (see Kelemen, '63 and Kirchner, '88 for reviews). Even among reptiles and amphibians significant anatomical diversity in vocal cords and folds exists (e.g., Schneider, '70; Steinwarz, '90; Moore et al., '91). Despite this diversity, two anatomical features separate the laryngeal septum of *Pituophis* from all previously

described vocal cords or folds: The laryngeal septum is a single (rather than bilaterally paired) structure and is supported by the cricoid (rather than the arytenoid) cartilage.

Morphology of sound production

The bellows of *Pituophis* include temporal variation and harmonics, two features that have not been previously documented in ophidians (Young, '91; Young and Brown, '93, '95). As such, there is clear support for the anecdotal descriptions of the unusual sounds made by *Pituophis* (e.g., Bartram, 1791; Lockwood, 1875; Garman, 1892; Loennberg, 1894).

The current study indicates that the harmonic elements in the defensive sounds of *Pituophis* are produced by vibrations of the laryngeal septum. Harmonics are present in all defensive sounds produced by intact *Pituophis*, although they are swamped out during the early high-amplitude portion of the bellow. The epiglottal keel cannot be responsible for these harmonics, because they are not eliminated by its removal.

The slight shifts in the acoustic profile following removal of the epiglottal keel appear to reflect changes in the configuration of the cricoid cartilage. Removal of the anterior portion of the cricoid cartilage, the epiglottal process and its large epiglottal keel, changes the cricoid relative to the remainder of the larynx. Because the dorsal portion of the cricoid supports the laryngeal septum, alteration of the cricoid produces corresponding alterations in the acoustic profile of the defensive sounds. The absence (or substantial reduction) of harmonics following removal of the laryngeal septum strengthens this functional interpretation. Thus, two of the apparently unique attributes of *Pituophis*, the harmonic sounds and the laryngeal septum, are seen as having a causal relationship.

The bellow of *Pituophis*, with its early brief period of high-amplitude, broad-frequency sound, differs from the hisses of "typical" snakes, which include no temporal variation (Young, '91). The later portion of the bellow resembles the hiss of *Pituophis* in having no modulation but clear harmonics. Removal of the epiglottal keel does lower the amplitude of the bellow (Fig. 5), although this difference was not statistically significant.

We propose that the M. tensor laryngis (Fig. 2D) plays a key role in producing a bellow. Bellows are only recorded immediately following glottal dilation. If changes in the glottal opening (via the M. sphincter laryngis or M. dilator laryngis) are

associated with contractile changes in the M. tensor laryngis, then the tension in the laryngeal septum could be incompatible with harmonic generating vibrations. In this hypothesis the brief temporal duration of the bellow (< 0.2 sec) is the time lag associated with tensile changes in the laryngeal septum. In subsequent defensive sounds produced in a series the glottal opening is not constricted and dilated (i.e., the glottal rim remains patent during inhalation and exhalation), and only hissing, not bellowing, is recorded. We hypothesize that bellowing results from an imbalance between the exhalent air pressure and the tension of the vocal cord, a situation that has been previously explored in other systems. Ohala ('83) attributed "universal" phonological patterns, especially stops, to underlying physical patterns between tracheal airflow and vocal cord tension. Similarly, Muta and Fukuda ('88) studied the relationship between airflow, subglottal pressure, and vocal cord tension and noted that relative vocal cord tension is a key determinant of phonation.

Martin and Huey ('71) argued that the epiglottal keel of *Pituophis* increases the amplitude of the sounds. A reduction in the amplitude of bellowing was observed in the current study following removal of the epiglottal keel (Fig. 5), as Martin and Huey ('71) would have predicted. While this difference was not significant, this may be a reflection of the sample size. Martin and Huey ('71) only presented data from a single specimen, and following removal of the epiglottal keel their specimen was capable of producing amplitudes greater than the majority of those recorded from the intact animal. Furthermore, Martin and Huey ('71) quantified defensive sounds over a long period of time: Our own experience suggests that *Pituophis* can quickly adapt to laboratory conditions, producing a distinct reduction in the defensive response.

Martin and Huey ('71) proposed that the epiglottal keel produced an edge effect: The current study suggests that the epiglottal keel functions instead as a flow divider (i.e., a symmetrical body located normal to the flow which effectively splits the flow—Ehrfeld, '83). The position, shape, and orientation of the epiglottal keel (Fig. 1A) is such that the exhalent airstream can be accelerated by the epiglottal keel, resulting in an increase in the amplitude of the produced sound.

That the epiglottal keel functions as a flow divider is supported by three findings. First, the amplitude produced by *Pituophis* tends to go up when the mouth is closed slightly; closing the mouth

would enhance the influence of a flow divider, but would have no impact on an edge tone. Second, the current study showed that any increase in amplitude associated with the epiglottal keel was restricted to short periods of high flow rates (i.e., the initial periods of a bellow); in the longer-duration lower-amplitude hisses the epiglottal keel had no apparent influence on the amplitude (Fig. 5). This pattern is consistent with a flow divider which would have an increased influence with increased flow rates. Last, Martin and Huey ('71) reported the results of experiments in which they altered airflow rates through isolated respiratory tracts of euthanized *Pituophis*. Their results showed that amplitude would increase with increasing airflow, which is consistent with the epiglottal keel functioning as a flow divider. Martin and Huey ('71) were quite correct in stating that vibrations of the epiglottal keel would produce a pulsatile quality to the sound; they found no trace of this in their study, nor was any found in the sounds analyzed in the current study.

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