spicuous. (Color slides of the pits are available, at cost, to those requesting them.)

JAMES THRALL, *Department of Biological Sciences, Illinois State University, Normal, Illinois 61761.*

THE FUNCTION OF THE EPIGLOTTIS IN SOUND PRODUCTION (HISSING) OF *PITUOPHIS MELANOLEUCUS*.—Since White (1884) first related the enlarged epiglottis of *Pituophis* to the quality and unusual loudness of the sound production (hissing) in these snakes, a number of workers have discussed this functional relationship. The enlarged epiglottis of *Pituophis*, a generic characteristic (Cope, 1891), forms a planar, keel-shaped structure lying in the median saggital plane immediately anterior to the rima-glotidis (Fig. 1). The posterior edge of the epiglottal keel bisects the air stream from the larynx during exhalant hissing. Klauber (1947, 1956), Perkins (1938), and Ditmars (1944) suggested that the epiglottis amplifies the sound of the hiss; while White (1884) and Bogert (1960) believed that the epiglottis also vibrates in the airstream, lending a pulsed quality to the sound. We present experimental evidence confirming sound amplification by the epiglottis in *Pituophis melanoleucus*.

The five male *P. melanoleucus* used in these experiments ranged in snout-vent length from 84 to 102 cm, while the single female measured 127 cm. This female and two of the males were purchased from a dealer who listed the locality for all three as 10 miles south of San Jose, California. The remaining three males came from Stunt Canyon, Los Angeles County, California; Sells, Arizona; and Lockhart, Texas. Preserved and freshly sacrificed specimens were used for anatomical observations.

In one experiment we gently probed a male (Stunt Canyon), housed inside a small terrarium with two wire-mesh sides, causing him to hiss repeatedly. We placed the microphone of a General Radio 1551C decibel meter less than 20 cm from the snake's mouth to monitor the amplitudes of the exhalant hisses. After surgically removing the epiglottal keel, we then recorded the sound amplitude measurements of the provoked hisses over the following two days.

In a second series of experiments, we sacrificed the five remaining snakes and placed air jets, connected to a compressed air source, in their tracheo-pulmonary cavities. A bleeder valve and aneroid pressure gauge in the tubing circuitry permitted the application of controlled pressures (see Martin, 1971). This artificial activation pressure[1] was changed in steps from 20 mmHg to 300 mmHg, or vice-versa. We placed the microphone of the decibel meter within 20 cm of the head of the preparation, but out of the trajectory of the air stream from the snake's glottis. The amplitude of the hiss was recorded three to five times at each pressure level, both before and after removing the epiglottis of each snake. In two experiments we applied a repetitive 1 v, 1 msec electrical stimulus to the laryngeal muscles during artificial activation to produce extreme opening of the rima-glotidis.

The sound amplitude measurements of the hisses produced by the Stunt Canyon male with epiglottis intact and later removed are shown in Fig. 2. The amplitude of the control hisses (epiglottis intact) had a mean

[1] For physical reasons these artificial activation pressures do not necessarily correspond to the pulmonary pressures developed during natural hissing.

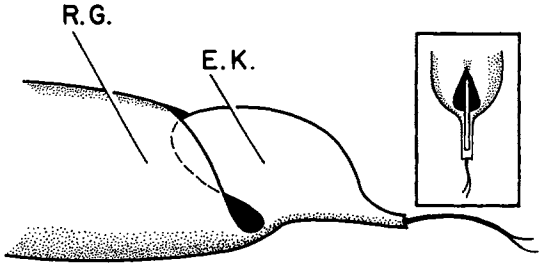

Fig. 1. Diagram of epiglottal keel (E.K.) showing its shape and orientation relative to rima-glotidis (R.G.).

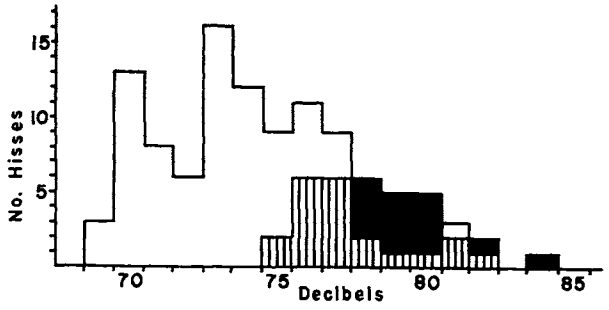

Fig. 2. Numbers of hisses at various amplitudes produced before (black) and after (white) removal of epiglottal keel of a single male *P. melanoleucus* from Stunt Canyon, California. Vertical lines: overlap between pre- and post-operative hisses.

value of 78.2 decibels (N = 35) compared with a mean of 73.7 decibels (N = 95) after removal of the epiglottal keel. These latter data are biased toward higher amplitudes because many post-operative hisses were below the ambient sound level of 65 decibels and could not be recorded.

Corroborative data were obtained in the artificial activation experiments. Except for the lowest activation pressures, control specimens produced higher sound amplitudes than did the experimentals, with the difference accentuated at higher activation pressures (Fig. 3).

We did not observe periodic vibration of the epiglottal keel in the above experiments, nor did we find evidence of vibration in sound spectrograms of recorded artificial and natural hisses. Manipulation of the size of the glottal opening by electrical stimulation failed to produce epiglottal vibration.

The results of these experiments confirm that the epiglottal keel of *P. melanoleucus* increases the sound amplitude (and hence, loudness) of the exhalant hiss. Furthermore, this is done without vibration of the keel. By analogy a playing card held parallel to and bisecting an air stream will produce a louder hiss, through an edge effect, than can the air stream itself. Slight twisting or lateral movement of the card in the air stream strongly attenuates the hiss: rapid movement from side to side produces a fluttering sound. If the epiglottal keel were to vibrate from side to side during exhalant hissing, it could lend a pulsed quality to the sound as observed by other authors and ourselves on previous occasions, but not dur-

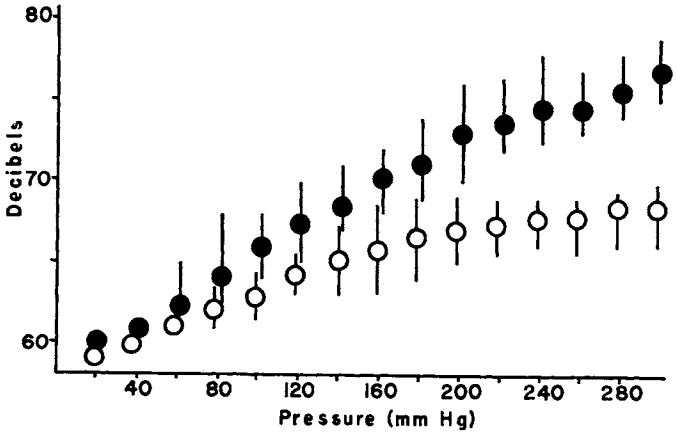

Fig. 3. Amplitudes of artificially activated hisses before (black) and after (white) removal of epiglottis of 109 cm snout-vent length male *P. melanoleucus* from Sells, Arizona. Vertical lines and circles represent sound amplitude ranges and means respectively at each pressure. N = 5 recordings at each pressure for control: N = 4 at each pressure after operation.

ing these experiments. Although our experimental data fail to confirm pulsations, it is possible that the proper experimental conditions or specimens were not obtained in these experiments.

Literature Cited

Bogert, C. M. 1960. The influence of sound on the behavior of amphibians and reptiles. *In*: Animal sounds and communication. Lanyon and Tavolga, eds., pp. 137–320. A.I.B.S., Pub. No. 7, Wash., D.C.

Cope, E. D. 1891. The epiglottis in colubrine snakes. Am. Nat. 25:156–157.

Ditmars, R. L. 1944. Snakes of the world. Macmillan, N.Y.

Klauber, L. M. 1947. Classification and ranges of the gopher snakes of the genus *Pituophis* in the western United States. Bull. Zool. Soc. San Diego 22:1–81.

———. 1956. Rattlesnakes, their habits, life histories, and influence on mankind. Univ. Calif. Press, Berkeley.

Martin, Wm. F. 1971. Mechanics of sound production in toads of the genus *Bufo*: passive elements. J. Exp. Zool. 176:273–294.

Perkins, C. B. 1938. The snakes of San Diego County with descriptions and key. Bull. Zool. Soc. San Diego 13:1–66.

White, C. A. 1884. On the character and function of the epiglottis in the bull snake (*Pityophis*). Am. Nat. 18:19–21.

Wm. F. Martin and R. B. Huey, *Department of Zoology, University of Texas, Austin, Texas 78712.*

WATER BALANCE IN A DESERT SNAKE.—Evaporative water loss in snakes has recently received special attention (Gans *et al.*, 1968; Prange and Schmidt-Nielsen, 1969). Some detailed reports on food consumption of snakes are also available (Brown, 1958; Dmi'el, 1967; Vinegar *et al.*, 1970). However, water balance under long term conditions has not been dealt with in these studies and, as far as is known, in any other work on the water economy of snakes.

Eight specimens of the desert colubrid *Spalerosophis cliffordi* (Schlegel) were studied during 3 months. Their mean body weight was 274 g. They were kept in individual cages at a constant 30°C (± 1°C) temperature, and were fed laboratory mice once a week. Those who showed special avidity were offered a second mouse after finishing the first. During the entire experimental period the snakes were deprived of drinking water. After swallowing the mouse, the snake was taken from its cage and placed in a weighted glass jar on a hard plastic net above paraffin oil. The jars were inspected daily for excretion. In many cases it was possible to separate the fresh semi-solid urine and the faeces. In addition, three samples of mice (n = 15 for each sample) of the same stock of those eaten by the snakes were analyzed for body composition. This analysis was made on shaved and nail-cut mice, since nails and hair were not digested by the snakes.

A small amount of excretion was sometimes found even on the fifth or the sixth day following eating. Therefore, metabolic rate was determined on the seventh day. Oxygen consumption and evaporative water loss were measured at a body temperature of 30 ± 0.1°C. The snakes were introduced into a large glass tube, its dimensions adjusted to the snake's size. Dried air was passed over the snake. The outcoming air (mean RH = 22%) was led to a series of

Table 1. Water Balance (mg/g/day) of Resting *S. cliffordi* at 30 C (N = 8; $\overline{W}$ = 274 g). Oxygen Consumption 3.17 ml O_2/g/day; Food Consumption: 22.0 mg/g/day. Values Are Mean ± S.E.

	Water Gain			Water Loss	
Food Component	% in Food	Wt. (mg)	Oxidative Water[1] (mg)	Source of Loss	Amount of Water (mg)
Protein	18.0 ± 1.10	3.96	0.773[2]	Urine	0.147 ± 0.02
Fat	7.2 ± 0.93	1.58	0.665	Feces	1.175 ± 0.09
Sugar	0.4 ± 0.03	0.09	0.020	Free fluid	0.806 ± 0.07
Ash	5.0 ± 0.71	1.11			
Free water	69.4 ± 2.42	15.27	15.270	Evaporation	12.350 ± 1.31
Total gain			16.728 ± 1.32	Total loss	14.478 ± 0.95

[1] Calculation based on the oxygen consumption. [2] 0.499 mg water per mg protein, as the main end product is uric acid.