

Tests of Two Hypotheses for the Origin of the Crotaline Rattle

NORMAN R. SISK AND JAMES F. JACKSON

We suggest that the capability to retain terminal scale (here renamed sclerophymal) exuviae that were mobile, i.e., origin of the prorattle, was contingent on prior evolution of longitudinal bilobing of the sclerophyma. Two hypotheses for initial functional advantage of such bilobing are tested: the luring effectiveness hypothesis based on putatively greater visual attractiveness during caudal luring, and one version of the dual contact hypothesis based on putatively greater sound intensity and/or greater audiospectral equitability during tail vibration. Simulated caudal luring that included a bilobed sclerophyma was not more attractive to fence lizards than luring with a conical sclerophyma. Sound intensity produced from mechanically vibrated models of bilobed sclerophymae was lower than sound intensity from other types of sclerophymae, whereas broad-bandedness of the sound was similar to that of other types. In the absence of support for either hypothesis, we discuss possibilities for future research, particularly the need to determine the form of the relationship between sound intensity and the force exerted by the sclerophyma.

THE evolutionary origins of complex adaptations have fascinated biologists since Darwin (1859) discussed the evolution of eyes, the interest stemming in large part from the challenge of understanding the functional advantage of an incipient stage (Salvini-Plawen and Mayr, 1977). Mivart (1871) questioned the evolutionary effectiveness of natural selection by suggesting that rudimentary stages of complex structures could not have been advantageous if functional advantage depends on component coadaptation. In response to such criticism, Darwinians have tested hypotheses of function in rudimentary stages (Ostrom, 1976; Kingsolver and Koehl, 1985; Ruben, 1991). The crotaline rattle is a complex structure believed to have arisen once (Knight et al., 1993), adapted for aposematic sound production (Klauber, 1972) and produced by intricately coordinated patterns of integumentary growth and resorption (Zimmermann and Pope, 1948). Yet the challenge of understanding the function of its incipient stages has certainly not been met, and arguably the problem has not been stated in a fully cogent format of alternative hypotheses applicable to incipient stages. We discuss alternative hypotheses for incipient stage function and test predictions from two of these.

Three ideas have been advanced for the selective advantage of the incipient rattle. The

earliest Darwinian hypothesis, that the incipient rattle's function was aposematic sound production directed at potentially trampling ungulates (Hay, 1887), has been modified recently. Schuett et al. (1984) doubted whether an incipient rattle could produce sound intensity sufficient to alert a large ungulate, and Greene (1992) argued convincingly that small vertebrate predators were the target of aposematic sound from the incipient rattle. Another hypothesis suggested that the incipient rattle served to enhance a tail display that diverted a predator's attack away from the head (Garman, 1890; Williams, 1966). Last, Schuett et al. (1984) hypothesized that the functional advantage of the incipient rattle was enhancement of caudal luring. Less thought has been focused on the morphology necessary to initiate the evolution of the rattle. Garman (1892) suggested that a constriction at the base of the terminal caudal scale (tail cap) was necessary and sufficient to retain successive exuviae of the tail cap; however, in the iguanid dorsal spines he used as analogs of the incipient rattle, he noted that the exuviae were too tightly appressed to rattle. In this paper, we present a different hypothetical morphology of the incipient rattle, introducing a neologism and associated terms that facilitate description and discussion.

Terms.—Garman (1888, 1890, 1892) hypothesized that the incipient stage of the rattle

evolved through modification of the large terminal caudal scale of an ancestral taxon similar to *Agkistrodon* or *Lachesis*. He usually referred to this ancestral integumentary unit as a "tail cap" although he sometimes employed "button" as a synonym; both he and Klauber (1972) also used "tail cone." Campbell and Lamar (1989) used the term "tail spine." Because in crotalines (except *Bothriechis* and arboreal *Trimeresurus*) and in certain colubrids this structure differs markedly from the small terminal caudal scale of viperines, elapids, and most colubrids (Greene, 1992), and because the terms tail cap and tail cone do not make this distinction clear, we propose the term sclerophyma (Gr *scleros* hard + *phyma* swelling) for a caudal terminus that is enlarged and hardened. Since not all such caudal termini are spinelike, sclerophyma is preferable to tail spine. Based on a survey of caudal termini (JFJ, unpubl. data), we define a sclerophyma as the structures enclosed by, and including, a terminal scale whose ventral side is more than twice as long as the subcaudal scale bordering it anteriorly and whose surface is less easily indented, when pressed with a dissecting needle, than is the subcaudal scale bordering it anteriorly. Sclerophymae differ considerably in shape among species. In taxa other than rattlesnakes, we recognize three sclerophymal morphotypes: symmetric conical (Fig. 1A), asymmetric conical (Fig. 1B), and dorsally curved (Fig. 1D). Because we follow Garman (1890) in considering the prebutton and button of rattlesnakes homologues of sclerophymae of other crotalines, we refer to the prebutton as a unilobed sclerophyma (Fig. 1E) and to the button as a longitudinally bilobed sclerophyma (Fig. 1F). A segment of the crotaline rattle is considered the exuvia of a multilobed sclerophyma.

Hypotheses.—The hypotheses that we tested are for a functional advantage of the bilobed sclerophyma over sclerophymae of other shapes, one of which must have been ancestral to the bilobed sclerophyma if the rattlesnake clade arose from a crotaline taxon that lacked the rattle. We believe there are several reasons for considering the origin of the bilobed sclerophyma as the crucial event to be explained.

First, dynamic lobation is the characteristic feature of the crotaline rattle. Each new segment is shifted relative to its predecessor by adding a lobe to the sclerophyma (= end-body) proximally and eliminating a lobe distally (Zimmermann and Pope, 1948). (The assumption that sclerophymal accretion-resorption is autapomorphic in rattlesnakes should be tested by histological studies of sclerophymal molt cycles

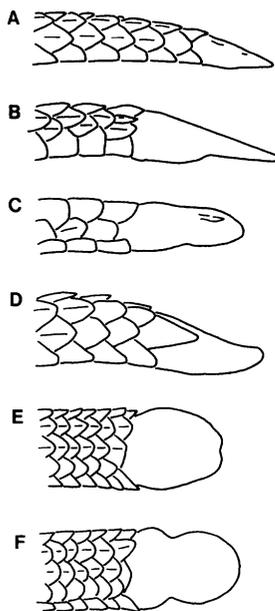


Fig. 1. Sclerophymal morphotypes. (A) Symmetric conical, *Porthidium godmani* (CM 41788); (B) asymmetric conical, *Bothrops asper* (ANSP 32832); (C) asymmetric conical with partial bilobing, *Porthidium nummifer* (ANSP 24676); (D) dorsally curved, *B. newwiedi* (CM 34805); (E) unilobed, *Sistrurus miliarius barbouri* (USL uncataloged); (F) bilobed, *S. m. barbouri* (USL uncataloged).

in other crotaline taxa.) This dynamism of the lobes is the principal aspect that creates the mobile articulation between adjacent rattle segments necessary for sound production by shaking. Lacking evidence for an origin of dynamic lobation by macromutation, we believe the reasonable assumption is that static lobation preceded the dynamic condition.

Second, it is doubtful that a sclerophyma retaining an exuvia could produce sound by being shaken (as opposed to being scraped on a substratum), unless the exuvia were mobile on the sclerophyma. The mobility of adjacent segments allows the rattle to produce sound as a multidimensional oscillator (Young and Brown, 1995). A basal constriction without lobation, as hypothesized by Garman (1892), could not lead to a mobile retained exuvia, but a bilobed sclerophyma could if the exuvia of the sclerophyma, instead of everting, was pulled posteriorly during ecdysis until stopped at the sulcus, and subsequently became detached from the rest of the caudal exuvia.

Finally, structural features that are transitory within early ontogeny have often been interpreted as evidence of ancestral condition (Jenkins, 1969; Brylski and Hall, 1988; Hall, 1992).

The universal precedence of the button to the rattle during ontogeny suggests the hypothesis that a bilobed sclerophyma was antecedent to the rattle phylogenetically. Incomplete bilobing of conical sclerophymae (Fig. 1C) occurs as an infrequent variant in several nonrattlesnake crotaline species (JFJ, unpubl. data).

We tested two hypotheses for a functional advantage of a bilobed sclerophyma. The first is a modified form of the luring effectiveness hypothesis (LEH) of Schuett et al. (1984), which they framed in terms of the functional advantage of a segmented rattle. For the reasons outlined above, we believe what requires explanation is the adaptive origin of the trait that subsequently allowed incipient retention of sclerophymal exuviae. Applying the LEH to a segmented rattle (Schuett et al., 1984) begs the question by requiring saltational evolution between a nonlobed sclerophyma and the rattle. Consequently, we have modified the LEH to apply to a bilobed sclerophyma: in the protorattlesnake the functional advantage of the bilobed sclerophyma was improvement of caudal luring. The prediction from the LEH is that potential prey will respond more readily to luring by a tail ending in a bilobed sclerophyma than to luring by a tail ending in an asymmetric conical sclerophyma.

The second hypothesis tested is the dual contact hypothesis (DCH). This hypothesis proposes that bilobing of the sclerophyma was functionally advantageous because the bilobed sclerophyma enhanced aposematic sound production. Several predictions are possible from this hypothesis (see Discussion). The one we have tested is that a bilobed sclerophyma, when scraped on a substratum, produces greater sound intensity or sound that is more broad-banded than do symmetric conical, dorsally curved, or unilobed sclerophymae when scraped with equal force. Accepting an aposematic function for tail vibration, the potential advantage of greater sound intensity is clear. Rattlesnake rattling produces broad-banded sound that is in this respect similar to warning sounds of other taxa produced in other ways (Rowe et al., 1986; Fenton and Licht, 1990). The hypothesis then assumes greater aposematic effectiveness from greater equitability of sound energy across the frequency spectrum.

MATERIALS AND METHODS

Caudal luring experiment.—The purpose of this experiment was to determine whether there exists differential attraction of potential prey to a model snake simulating caudal luring when the

model snake is fitted with model sclerophymae of different types. More specifically, the following statistical hypotheses were tested: H_0 —potential prey show no difference in response to caudal luring by a model snake equipped with a bilobed model sclerophyma or with an asymmetric conical model sclerophyma; H_a —potential prey respond more frequently to caudal luring by a model snake equipped with a bilobed model sclerophyma than to caudal luring by a model snake equipped with an asymmetric conical model sclerophyma; and H_b —potential prey respond more frequently to caudal luring by a model snake equipped with an asymmetric conical model sclerophyma than to caudal luring by a model snake equipped with a bilobed model sclerophyma.

The statistical test employed was a two-tailed restricted sequential binary plan with $2\alpha = 0.05$, power = $1 - \beta = 0.95$ and $\theta_1 = 0.75$ (Armitage, 1975; McWilliams, 1989). A sequential procedure does not set sample size a priori but, rather, on a graph representing the sequential change in net “preferences” during the experiment, specifies boundaries that allow, upon one of them being reached, the rejection of the other two hypotheses. Significance level and power are chosen a priori and, together with θ_1 , determine the placement of the boundaries. Sample size depends on the number of preferences required to reach a boundary. We chose a sequential procedure to assure a high power in the contingency that H_0 were not rejected.

The third factor involved in setting rejection boundaries is θ_1 , the hypothesized probability that the preference will be for bilobed in any binary comparison where a preference exists. This probability is a function of π_1 and π_2 , the hypothesized probabilities of positive responses to bilobed and asymmetric conical sclerophymae, respectively $\{\theta_1 = [\pi_1 \times \pi_2] / [\pi_1 \times \pi_2 + (1 - \pi_1)(1 - \pi_2)]\}$. In a preliminary experiment, we found the actual probability of a positive response to luring without a sclerophyma attached to the model was near 0.5. For defining θ_1 , we set π_1 as 0.75 and π_2 as 0.50. This amounts to testing the hypothesis that bilobed shape increases the probability of the prey's positive response by 50% over that of an asymmetric conical shape, raising the probability from 0.50 to 0.75.

Model snakes for the luring experiment were cast of latex rubber in a plaster mold made using a preserved specimen of *Sistrurus miliarius streckeri*. The models were 20.8 cm SVL, 24.7 cm TL, and approximately in the configuration of the snake illustrated in figure 1D of Jackson and Martin (1980). The distal 4 mm was cut from

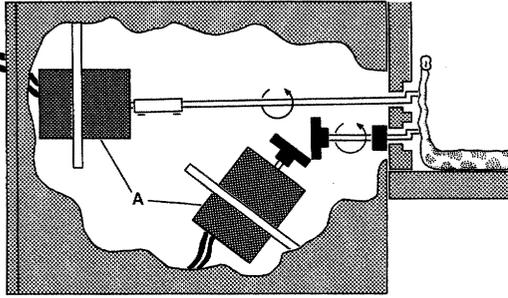


Fig. 2. The apparatus for simulating caudal luring. Motors indicated by A. Cams at the distal ends of the shafts imparted sinuous movement to the model's tail.

the models' tails to provide a blunt surface for attachment of the model sclerophymae via a pin inserted into the cut surface. The models were painted with acrylic paints to resemble typical coloration of *S. m. streckeri*. Model sclerophymae were cast of epoxy in latex rubber molds created by brushing latex over sclerophymae of preserved specimens. Molds for the bilobed model sclerophymae were made on buttons of two preserved specimens of *Crotalus c. cerastes*, whereas those of the asymmetric conical model sclerophymae were made on sclerophymae of two preserved *Agkistrodon piscivorus leucostoma*. The bilobed and asymmetric conical models were of equal length and, relative to tail diameter, were slightly larger than the button of *Sistrurus*. Slightly larger models were selected to enhance visibility of the model sclerophymae to the experimental subjects.

Experimental trials were conducted in a semi-circular arena with a radius of 50 cm and wall height of 91.4 cm. A thin layer of chipped pine bark covered the floor to 10 cm from the walls. The uncovered central portion of the floor was marked with concentric semicircular lines 5 cm apart centered on the model sclerophyma at the midpoint of the straight wall. The model snake was fixed to the floor with its tail positioned vertically and attached to two 1-mm diameter steel rods that served as cams due to double right angles (Fig. 2). The cams penetrated the straight wall and attached to the tail at 5 and 15 mm above the floor. The distal end of the sclerophyma was 30 mm above the floor. Each cam was rotated at approximately 8.25 rpm by a small, high-torque DC motor. This apparatus provided the means to move the posterior part of the tail continuously in a wavelike pattern very similar to actual crotaline caudal luring.

The experimental subjects were *Sceloporus undulatus hyacinthinus* collected in west-central Louisiana and toe-clipped for individual identi-

fication. The lizards were maintained at approximately 23 C on a 14L:10D photoperiod, fed mealworms, and acclimated to captivity for at least one week prior to testing. Because the motors produced noise that could have decreased the probability of a response to simulated luring, the lizards were habituated by continuous exposure to a repeating audio recording of the motors during the acclimation period.

A preference was determined by making pairwise comparison of the responses of two lizards when each was separately exposed to luring involving one or the other type of model sclerophyma. In a control trial, the model snake was fitted with an asymmetric conical model sclerophyma, and in an experimental trial, the model snake was fitted with a bilobed model. The subjects of paired trials were of the same sex and approximate size (± 3 mm SVL). Different subjects were used in each trial to avoid possible habituation of the subjects to luring. Pairings were determined a priori, and subjects were not fed for two days prior to testing. The order of pairings (E-C) or (C-E) was randomized. Once the type of trial had been determined, the particular model used (of the appropriate type) was selected randomly to ensure that the experiment tested for the effect of sclerophymal shape. Although only 90 lizards (45 pairs) provided data points for the sequential test, due to the strict testing criteria of the experiment, 202 lizards were collected, maintained and processed.

Each trial lasted 30 min and was videotaped from above the arena. All trials were conducted during the light portion of the photoperiod. The audio recording of the motor noise was played during trials to mask the noise produced near the model snake. The protocol for each trial was as follows: (1) the appropriate model sclerophyma was attached to the model snake; (2) the appropriate lizard was placed into the arena and allowed to acclimate for 1.5 h; (3) after acclimation, a small mealworm was offered to the lizard in a petri dish at the apex of the arena (if the lizard ate the mealworm, we proceeded to step 4; if the lizard did not eat the mealworm within 5 min, the trial was halted); (4) the camcorder was started; (5) simultaneously, a stopwatch and the motors were started; and (6) the trial was terminated after 30 min. An acclimation period of 1.5 h was chosen because a pilot study showed that shorter periods resulted in fewer positive responses to luring, whereas longer periods did not increase the probability of a response. The mealworm was offered immediately prior to the test to demonstrate that the lizard had sufficient appetite

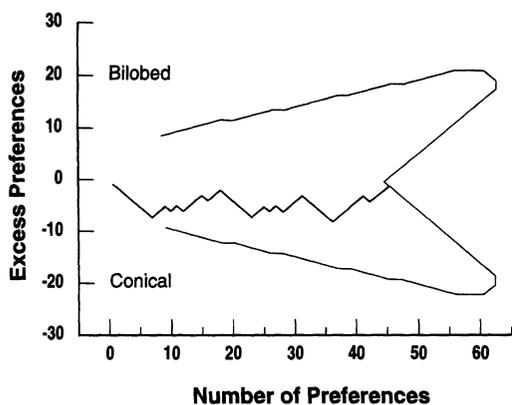


Fig. 3. Sequential plot of paired trial outcomes in the caudal luring experiment with the rejection boundaries of the restricted sequential binary test design. Intersection of the plot and the middle boundary terminated the experiment with the conclusion that neither type of sclerophyma was significantly more attractive in caudal luring (power = 0.95).

and health to respond if deceived by the luring and to position the lizard at the arena apex without handling it.

A positive response to luring was defined as the lizard approaching the luring tail such that any portion of the lizard crossed a reference line 13 cm from the lure while the lizard was orienting its head toward the simulated luring. This brought the lizard close enough to the model's head that an actual luring crotaline would typically have captured it. For a pair of trials to provide a datum for the test, a preference must be scored for one of the sclerophymal types. If neither trial of a pair showed a positive response, no datum was plotted on Figure 3. If one trial in a pair showed a positive response and the other trial did not, the preference was simply assigned to the sclerophymal type with the positive response, and the preference was added to the plot on Figure 3. If a positive response occurred in both trials of a pair, then subsidiary criteria were used to score a preference. If in one such trial, the lizard bit the tail of the model snake, and in the other trial there was no biting, the trial including biting was awarded the preference. If multiple bites occurred in both trials, the preference was scored for the trial having the most bites. If both trials showed a positive response without biting, the trial in which the lizard approached the tail more closely (measured in mm on video monitor) was awarded the preference.

Tail vibration simulation experiment.—The purpose of this experiment was to test whether

sclerophyma type influenced the sound intensity and audiospectral characteristics produced by simulated tail vibration of model sclerophymae. Before designing a device to simulate tail vibration, we videotaped tail vibration in 12 colubrid species and three subspecies (*Bogertophis subocularis*, *Coluber constrictor flaviventris*, *Elaphe bairdi*, *E. bimaculata*, *E. obsoleta lindheimeri*, *E. taeniurus*, *Lampropeltis c. calligaster*, *L. getula californica*, *L. g. holbrooki*, *L. triangulum amaura*, *Masticophis flagellum testaceus*, *Pituophis melanoleucus affinis*, *P. m. lodingi*, *Rhinocheilus l. lecontei*, *R. l. tessellatus*) and five crotaline species (*Agkistrodon bilineatus*, *A. c. contortrix*, *A. piscivorus leucostoma*, *Bothrops atrox*, *Sistrurus miliarius barbouri* neonates) to learn the nature of contact between sclerophyma and substratum to be simulated. A tail vibration simulation device (hereafter termed "the device") was then constructed to scrape a model sclerophyma across a substratum without creating other sources of sound. Digital audio recordings were made of scraping sclerophymae and were subsequently analyzed to obtain data that could be treated statistically.

The device housing was a plywood box (15 cm square \times 18 cm high) with one side open and with the inner surfaces covered by foam. A 9.5 mm threaded rod mounted perpendicularly to the floor served as the fulcrum for a miniature ball joint and 3 \times 12.7 mm steel rod that constituted the vibrating arm. The height of the fulcrum was adjustable by being threaded through a coupling nut mounted in a rubber stopper that dampened transmission of vibration from the arm/ball joint/fulcrum assembly to the device housing. At the distal end of the vibrating arm was a 0.79 mm diameter threaded rod onto which model sclerophymae could be screwed. A slot below the distal end of the vibrating arm allowed insertion of substrata on which the model sclerophyma scraped.

The vibrating arm driver was a "200 lb" electromagnet (further specifications unavailable) used in conjunction with a rubber band. The face of the electromagnet was mounted flush with the inside surface of one side wall. Outside this wall, a small plywood compartment enclosed the external portion of the electromagnet and was filled with dry ice to prevent overheating of the electromagnet. One end of a number 18 rubber band was attached to the vibrating arm, and the other end was attached to the side wall opposite the electromagnet. An amplified sine wave signal to the electromagnet set the vibrating arm in motion. As the voltage on the sine wave cycle increased, the electromagnet's force of attraction increased proportionally and pulled the vibrating arm toward the

magnet. As the voltage decreased, the electromagnetic force decreased sufficiently that the rubber band pulled the vibrating arm away from the magnet, and one cycle was completed. The sine wave signal was generated by a BK Precision model 3011B 2 mHz digital function generator. Output from the signal generator was connected to an input jack of a Pioneer model VSX-3000 stereo audio receiver for signal amplification. Amplified output was then sent to the electromagnet.

Model sclerophymae were cast of epoxy resin in latex rubber molds made on prototypes sculpted in clay to represent symmetric conical, dorsally curved, unilobed, and bilobed shapes (Fig. 1). When the resin in the molds was partly solid, a 0.79 mm screw was tapped into the proximal end of each cast and unscrewed the following day to leave threads in the resin for attachment of the model sclerophyma to the vibrating arm. Ten sets of prototypes, each with the four shapes, were sculpted. For realism, the smallest scale at which the shapes of the prototypes could be practically manipulated was chosen; the result was a scaling only slightly larger than actual sclerophyma sizes. The mass of each prototype was determined. The three sets that differed least in mass were selected to be used in the study, and the others were discarded. From numerous casts made, we selected three of each type in each set and adjusted them to similar masses (61.9 ± 0.92 mg) by sanding the proximal facets.

Our recording apparatus utilized a Peavey model PVM 480 condenser microphone (frequency response 20–20,000 Hz) connected to a Peavey MD III 12×2 mixer. The mixer was in turn connected to a TEAC DA-P20 DAT recorder set to a sampling rate of 48,000 samples/sec (frequency response of the recorder is 20–20,000 Hz at this sampling rate). The mixer was used to preamplify the signal because the built-in level controls of the DAT recorder did not provide sufficient gain to record the signal properly. Recordings were made on Ampex 467 digital audio tape in a quiet room in a building free of other human activity. The receiving end of the microphone was positioned at the open side of the device 10 cm from the sclerophyma model and aimed to the center of the model's arc at an angle of 30° from the horizontal. Vibrating arm frequency and arc amplitude were held constant at 15 Hz and 5 mm, respectively, and were verified on each trial using a General Radio model 631-BL Strobotac strobe light. The downward force of the model to the substratum was held constant at 7845.3 dynes (8.0 g) by adjusting the number and height of a set of per-

manent magnets mounted below the vibrating arm. The substratum scraped by the vibrating arm was a piece of art paper taped to a block of pine wood.

Testing order of the model sclerophymae was randomized across all 36 models. Preliminary runs of 30 sec determined the arm position at which each model produced maximum sound intensity as measured by a digital voltmeter receiving the audio signal. The vibrating arm was then reconfigured to the position of maximum sound intensity, and with a fresh substratum of art paper a 30-sec audio recording was made at that position. For the bilobed models, an additional recording was made with both lobes contacting the substratum, irrespective of sound intensity at that arm position. Between recordings of model sclerophymae, we also recorded the device in operation without the sclerophyma contacting the substratum to demonstrate that sound was not produced by the mechanical linkages.

Three-dimensional FFT sound spectra from the audio recordings were obtained using a modified version of AMESH, a real time 3-D FFT viewing program for UNIX operating systems. The program was modified to provide "snapshot" FFT images, as well as the output of numerical FFT data to disk files. The FFT data for each recording consisted of 10 temporally consecutive 0.0853333-sec intervals. A 4096-point FFT with no overlapping of data defined each interval.

The FFT data were then represented graphically and subjected to statistical analyses using Statistical Analysis Systems (Cary, NC). A nested ANOVA was performed to analyze relative sound intensity levels using the following hierarchy: type, set, cast, and time interval. Sound intensity levels were determined as the integral of each FFT time interval (Fahy, 1989) through summation of the intensity values across the frequency domain from 234–24,000 Hz using a program in QuickBASIC. Frequencies below 234 Hz were not included because of low signal-to-noise ratios inherent to this region of the spectra. To analyze the relative broad-bandedness of the recordings, a nested ANOVA with the same hierarchical and frequency parameters was performed on an index of equitability (E) that was calculated for sound intensity across frequencies by applying the Shannon-Wiener index of diversity (H) (Smith, 1980) to the FFT data. Tukey's multiple range tests were also performed on the sound intensity and equitability data.

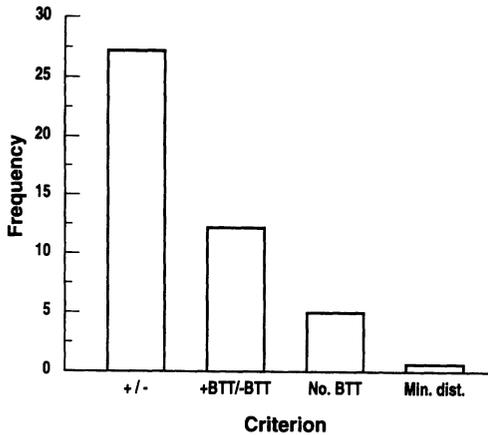


Fig. 4. Frequencies of criteria used to determine preferences in paired trials. (1) Pair composed of a positive and a negative response (+/-); (2) pair composed of two positive responses, one of which involved bites to the lure (+BTT/-BTT); (3) pair composed of two positive responses; both involved bites to the lure; preference to trial with most bites (no. BTT); (4) pair composed of two positive responses with no bites to the lure; preference to trial with closest approach to lure (min. dist.).

RESULTS

Caudal luring experiment.—Of the 56 pairs of trials, both lizards gave negative responses in 11, and a preference was established in 45. The lizard crossed the 13 cm reference line in 63 of 112 trials. During the trials lizards usually moved their heads in ways suggesting observation of the simulated caudal luring. Often, and always in positive trials, the lizard would orient its head toward the caudal lure and then run rapidly toward the lure. Biting of the lure occurred in 35% (39/112) of trials. These behaviors were indistinguishable from behaviors seen when *S. undulatus* preys on insects. In most pairings in which a preference was expressed, the preference was decided on positive versus negative responses. When both trials had positive responses, subsidiary criteria were required to award a preference. The usage frequency of each subsidiary criterion is shown in Figure 4. The results of the restricted sequential binary test showed no significant difference in preference by the test subjects for bilobed and asymmetric conical model sclerophymae (Fig. 3). There was no indication that the bilobed model was more attractive to the lizards; although the plot outlining the course of the experiment seemed random in character, there were never excess preferences in favor of the bilobed sclerophyma.

TABLE 1. HIERARCHICAL ANOVA OF TOTAL SOUND INTENSITY ACROSS THE SPECTRUM (234–20,000 Hz) PRODUCED BY MODEL SCLEROPHYMAE. SS and MS are presented as actual values/ 10^6 .

Source	DF	SS	MS	F	P
Total	449	6495.8			
Type	4	876.1	219.0	2.82	<0.10
Set	10	775.4	77.5	0.56	ns
Cast	30	4160.4	138.7	82.14	<0.0001
Error	405	683.9	1.7		

Tail vibration survey.—The following generalizations from videotaping tail vibration in the 17 species are relevant to evaluating the realism of the tail vibration simulation experiment. First, typically only the distal 1–4 cm of the tail actually vibrated. Second, there was always vibratory motion in the horizontal plane. Third, in some cases, there was an additional component of motion vertically. Fourth, in all species observed, except for two colubrids, the sclerophyma was pressed against the substratum during lateral vibration, either continuously or periodically. This was sometimes accomplished by simple inflection of the tail just anterior to the sclerophyma and other times by dorsally arcing a more anterior portion of the tail and then inflecting the posterior portion ventrally from the raised portion. Finally, frequency of tail vibration ranged from 5 to > 30 Hz.

Tail vibration simulation experiment.—Statistical analysis of FFT data from the tail vibration simulation involved symmetric conical, dorsally curved, unilobed, and bilobed models; the bilobed models provided data in two configurations: in the position providing maximum sound production; and in the position with both lobes contacting the substratum. Graphical representations of the FFT spectra did not reveal any clear distinctions among the spectra of the five model types, although spectra of the same type across different sets did show subtle similarities. Overall the spectra resembled those of rattlesnake rattling by being broad-banded and by lacking temporal structure of frequency pattern (Fenton and Licht, 1990; Cook et al., 1994).

Analysis of variance showed significant differences among casts (separate casts from the same mold) for both sound intensity and equitability, but differences among sets (sculpted independently) were not significant for either variable (Tables 1–2). Differences among types were nonsignificant ($0.05 < P < 0.10$) for in-

TABLE 2. HIERARCHICAL ANOVA OF EQUITABILITY OF SOUND INTENSITY ACROSS THE SPECTRUM (234–20,000 Hz) PRODUCED BY MODEL SCLEROPHYMAE.

Source	DF	SS	MS	F	P
Total	449	0.369			
Type	4	0.060	0.01488	3.68	<0.05
Set	10	0.040	0.00404	0.47	ns
Cast	30	0.261	0.00868	425.73	<0.0001
Error	405	0.008	0.00002		

tensity (Table 1). Significant differences ($P < 0.05$) among types were found for equitability across the audio spectrum (Table 2). Because the type level in the nested ANOVA for intensity approached significance, Tukey's test ($\alpha = 0.05$) was performed on the intensity data for sclerophymal type and revealed three significantly different groups (Table 3). Tukey's test ($\alpha = 0.05$) on the equitability data for sclerophymal type showed each type significantly different (Table 3). The most important result from this experiment was that the bilobed sclerophyma with both lobes contacting the substratum produced significantly less intense sound than the other types.

DISCUSSION

The caudal luring experiment falsified the prediction from the luring effectiveness hypothesis (LEH) that *S. undulatus* would respond more readily to caudal luring that included a bilobed sclerophyma. A defender of LEH might argue that a test using a single prey species is not sufficiently broad to reject LEH conclusively. We agree but believe that *Sceloporus* is probably the most ecologically realistic taxon for testing LEH if the prorattlesnake originated in arid montane southwestern North America. The scaling of the model components and the model/test subject size ratios are other factors that could play a role in the outcome of the experiment and could become variables in more comprehensive tests. Cook et al. (1994) have suggested that a slender tail may make a more effective lure. Because *S. miliaris* possesses one of the most slender tails among rattlesnakes and the bilobed model we used was slightly larger than typical for that species, we expected that this combination would be particularly attractive. Nevertheless, model sclerophymae of other sizes could be tested. Likewise, luring could be simulated in a horizontally positioned tail rather than in the vertical position we used.

TABLE 3. MEANS FOR SOUND INTENSITY AND EQUITABILITY OF SOUND INTENSITY PRODUCED BY EACH TYPE OF MODEL SCLEROPHYMA. Intensity data represent units of relative power summed between 200 and 20,000 Hz. Bilobed (M) is bilobed sclerophyma positioned for maximal sound production. Bilobed (BL) is bilobed sclerophyma positioned with both lobes contacting the substratum. For intensity, results of Tukey's test ($\alpha = 0.05$): [symmetric conical and dorsally curved] [unilobed and bilobed (M)] [bilobed (BL)]. For equitability, results of Tukey's test ($\alpha = 0.05$): [unilobed] [dorsally curved] [bilobed (BL)] [symmetric conical] [bilobed (M)].

Type	Intensity	Equitability	N
Symmetric conical	12646.6	0.905	90
Dorsally curved	12323.7	0.915	90
Unilobed	11325.3	0.921	90
Bilobed (M)	11233.4	0.887	90
Bilobed (BL)	8676.1	0.910	90

Another attempt to save LEH could be made by suggesting that the true θ_1 is much closer to 0.5 than the θ_1 we tested, so that the power of our test would be lower than 0.95. Detection of a small luring advantage by the bilobed model would require a much larger sample size. To test for a 10% advantage of bilobing ($\theta_1 = 0.55$, based on $\pi_1 = 0.55$ and $\pi_2 = 0.5$) at $2\alpha = 0.05$ and $1 - \beta = 0.95$ could require as many as 1778 binary preferences (Armitage, 1976:54) and, if so, would involve processing several thousand experimental subjects. In evaluating the merit of a massively larger experiment, we note that, if only a slightly greater attraction by the bilobed sclerophyma could be shown, support for the LEH would not be strong because such a result would suggest that the putative selection differential for the bilobed condition was small, especially given that crotaline snakes with nonbilobed sclerophymae lure effectively in experimental situations (Neill, 1960; Szazima, 1991).

The tail vibration experiment falsified the version of the dual contact hypothesis (DCH) that was tested. Although significant differences were found among sclerophyma types in both sound intensity and equitability, the mean values for the bilobed type were not in the predicted directions. The equitability of sound energy across the frequency spectrum was intermediate for the bilobed model with both lobes contacting the substratum and was lowest for the bilobed model in the position of maximum loudness. Although the hypothesis of enhanced broad-bandedness was falsified, the narrow range of mean equitability indices observed suggests that an origin of a bilobed sclerophyma

due to other selective pressures probably would not have resulted in substantially reduced broad-bandedness during tail vibration. The bilobed model with both lobes contacting the substratum produced the lowest sound intensity in contradiction to the prediction from the stated version of DCH.

Despite the lack of support for the version of DCH discussed above, there are reasons why it, as well as other versions of DCH, merit further consideration. Vertically acting force on the sclerophymae was held constant in our experiment; therefore when the bilobed model had both lobes touching the substratum, the force per contact point must have been reduced. This would have been a physical necessity in a protorattlesnake as well, but whether it would have led to reduced or increased sound intensity would have depended on the shape of the relationship between the force on a sclerophyma contact point and the sound intensity produced. If the functional relationship were concave upward, sound production would have decreased (Fig. 5A). However, if the relationship were concave downward, sound production would have been increased by the origin of a bilobed sclerophyma (Fig. 5B). Complete evaluation of the sound intensity enhancement version of DCH will require an estimate of the relationship between force and sound production for sclerophymae, but it would be better to approach such a task through methods other than the tail vibration simulation device. Studies that have used mechanical models to evaluate function have usually dealt with structures much larger than sclerophymae (Fisher, 1977; Weishampel, 1981). One reflection of using realistically small scale in our experiment is the significant variation found among casts (Tables 1–2) due to the impossibility of controlling surface features of submillimeter scale and the consequent variation in the exact nature of model-substratum contact. Any attempt to estimate the force-sound intensity curve probably should utilize computer-generated sound based on acoustic mathematical models involving finite-element analysis of vibrating structures (Jensen et al., 1994) to control sclerophymal shapes and how they contact the substratum. Even if the protorattlesnake's force-sound intensity curve was concave upward, the force exerted on the sclerophyma would not necessarily have remained constant during the evolution of the incipient rattle. Given a mutational origin of a bilobed shape that moderately reduced sound intensity, selection could have proceeded against the new shape, but it also could have favored individuals that applied greater force. The latter course

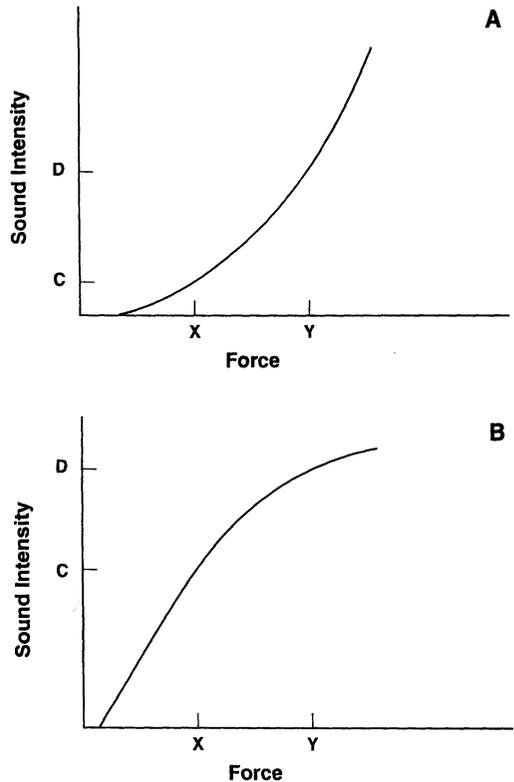


Fig. 5. Two hypothetical relationships are shown between vertical sclerophymal force and sound intensity. (A) Force Y is that exerted by a conical, dorsally curved, or unilobed sclerophyma, and sound of intensity D is produced. Force X is half of Y and is that exerted by each of the lobes of a bilobed sclerophyma, and the total sound intensity produced is $2C$, where $2C < D$. (B) The variables are the same as above. However, because of the asymptotic relationship between force and sound intensity, $2C > D$.

could have preserved the bilobation and potentially increased total sound intensity. Hence, another desideratum is data on the extent of intra- and interindividual variation in the vertical force applied during tail vibration.

A second version of DCH can be enunciated: bilobation of the sclerophyma could have been advantageous in raising the probability of contact during tail vibration on an irregular substratum. As a sclerophyma is scraped across an irregular substratum, loss of contact may occur when the extreme ventral point of the sclerophymal convexity passes over local depressions in the substratum. Assuming random dispersion of depressions, doubling the number of convexities on the ventral side of the sclerophyma should increase the probability that at least one convex extremity contacts the substratum at any given point along the vibrational arc. The spe-

cialized posterior subcaudals of *Lachesis muta* suggest the possibility of such a function. These scales are more numerous in a transverse plane than the paired subcaudals anteriorly, are spinelike, and have their apices directed posteriorly rather than posteriorly (Campbell and Lamar, 1989; Garman, 1888); thus they may serve, as auxiliary to the sclerophyma, to increase the probability of substratum contact. If the specialized subcaudals are implicated in enhanced sound production (Greene, 1988), then experimentally manipulating them, as analogs to a multilobed sclerophyma, could offer a means to test both versions of the DCH in living *Lachesis*.

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- DEPARTMENT OF BIOLOGY, UNIVERSITY OF SOUTHWESTERN LOUISIANA, LAFAYETTE, LOUISIANA 70504-2451. E-mail: (JFJ) jfj7964@usc.usl.edu. Send reprint requests to JFJ. Submitted: 25 Jan. 1996. Accepted: 5 Dec. 1996. Section editors: D. Cundall and F. Irish.