STRUCTURE AND SOCIAL SIGNIFICANCE OF VOCALIZATION BY *Anolis grahami grahami* (SAURIA:IGUANIDAE)

by

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INTRODUCTION

Aside from several reports of lizards hissing, most saurians are mute. Vocalizing species are, however, scattered throughout the suborder. The ability of geckos (Gekkonidae) to produce loud vocalizations is well-known (Wever et al. 1963, Campbell 1966, Goin and Goin 1971). Five other families, as well, have vocalizing species, although none have been studied in depth; these other families are Lacertidae, Varanidae, Chamaeleonidae, Teiidae, and Iguanidae.

Three lacertid species vocalize. Falck (1953) described "shrew-like" squeals produced by Lacerta agilis, and Simms (1970) reported squeaks made by L. vivipara. Both species apparently vocalize when alarmed by movements of objects or shadows. Vogel, as reported by Gans and Maderson (1972), stated that L. galloti produces a loud squeal in territorial defense. Of the varanids, Pianka, as reported by Gans and Maderson (1972), described the vocalization of Varanus gouldii flavirufus, and Cowles (1930) was told by Zulus that a monitor (Varanus albigularis) makes a "loud roaring". B. von Rosen (1950) found that Chamaeleon affinis and C. bitaeniatus (family Chamaeleonidae) produce at least two types of vocalizations. He stated that males "bark", particularly when competing, and that females "croak" most often in the presence of males. The teiid lizard, Cnemidophorus tigris, utters 'squeaks' when handled

(Campbell 1966). There are three genera of Iguanidae known to vocalize. Gambelia w. wislizenii produces sounds of a wailing or moaning character when alarmed (Wever et al. 1966). Dipsosaurus dorsalis has been heard to squeak when injured (Campbell 1966), and 13 species of Anolis are known to produce vocalizations. These 13 are: A. biporcatus, A. chocorum, A. cybotes, A. garmani, A. grahami, A. isolepis, A. lucius, A. occultus, A. opalinus, A. roquet, A. valencienni, A. vermiculatus, and A. vociferans.

The vocalizing Anolis species appear throughout the phylogenetic scheme of the genus (Fig. 1 and 2). However, most references to Anolis vocalizations are very brief and anecdotal. Myers (1971) lists the following four species as vocalizing: A. biporcatus (petersi Series), A. chocorum (Alpha Section, Series undetermined), A. roquet (latifrons Series), and A. vociferans (petersi Series). Ruibal (1964) lists A. isolepis (carolinensis Series), and Williams et al. (1965) and Webster (1969) noted vocalizing by A. occultus (Alpha Section, Series undetermined). Jenssen (pers. comm.) adds A. cybotes (cristatellus Series), A. garmani (grahami Series) and A. valencienni (Beta Section, Series undetermined). There are three references to vocalization by A. grahami and A. opalinus (both grahami Series) (Underwood and Williams 1959, Myers 1971, Jenssen pers. comm.) These authors state that the lizards squeak in

response to capture or handling, but do not mention vocalizations by free-ranging animals. Jenssen (pers. comm.), however, states that he has occasionally heard in the field A. grahami males producing loud squeaks, and once witnessed one protesting loudly while being chased down a hallway by a Jamaican maid with a broom.

Though scanty, more descriptive information exists for only two Anolis species. A. lucius (carolinensis Series) are said to squeak when active around the mouths of their cave habitat, as well as when being captured; it is "the most vocal of Cuban anoles" (Ruibal 1964). However, from the descriptions of Neill and Allen (1957), the Cuban A. vermiculatus (carolinensis Series) seems even more vocal. This species is described as able to "squeak like a mouse, mew like a kitten." A specimen trapped by the authors leaped open-mouthed at its captors, producing a loud squeak. Some individuals when held in the hand squeaked loudly, others mewed plaintively, and still others did not vocalize. Although iguanids, and lizards generally, do not possess acute hearing (Peterson 1966, Wever and Peterson 1963, Wever et al. 1966, Werner 1972), A. vermiculatus respond readily to sounds. The snapping of a twig would send them diving into the water from their usual perches on overhanging branches, whether day or night. Neill and Allen state that this species has no dewlap, which would indicate a shift in reliance from visual to auditory communicative displays.

They did note, however, the presence of a nuchal crest and headbobbing, which are parts of the usual Anolis territorial display.

Despite the fact that a number of iguanid lizards are known to vocalize, including anoles, no study has focused on this phenomenon. The present investigation of A. g. grahami is the first serious study of vocalizations by iguanid lizards, and its goals are to: (1) accurately describe the lizards' sounds, (2) determine the contexts in which vocalizing occurs, (3) evaluate the sounds for their communication potential, and (4) isolate the sound-producing structure of the species.

METHODS AND MATERIALS

The 16 adult male and five adult female Anolis g. grahami used in this study were collected during two trips to Jamaica. Lizards were caught during July, 1972 near Negril, Westmoreland County, and on the campus of the University of the West Indies in Mona, near Kingston, in November, 1973. Capture was accomplished with a slip noose of monofilament fishing line attached to a thin stick or fishing rod; this technique insured injury-free specimens. After capture, the animals were placed in plastic sandwich bags with some crumpled paper. These in turn were placed in a styrofoam ice chest and transported to the behavior laboratory at the Virginia Polytechnic Institute and State University. The lizards spent as many as four days in the bags without food or water during transit and showed no ill effects.

The housing of A. grahami subjects and the recording of their vocalizations were made in three types of cages. The first kind measured 1.8m x 0.6m x 0.8m high and was constructed of an angle iron frame fitted with masonite and wood panels. The top was screening and the front was glass. The second type of enclosure was of similar construction to the first, but measured 1.2m x 0.6m x 0.6m high. The third type of cage was identical to the second, except its front glass was angled so that the top projected about 10 cm beyond the bottom. Cage temperatures were maintained at

27 ± 2 C.

The cages initially were furnished with branches and leaves to serve as perches and cover for the lizards. However, the sound produced by these dried materials when the animals moved during recording sessions made it necessary to use something less noisy. Large limbs laid across tree stumps and supplied with plastic leaves stapled to the wood were substituted. In the largest cages, the leaves were clustered around two stumps situated at opposite ends of each cage; this tended to divide the cage into two regions, and leaves were placed along horizontal limbs to reduce straight-line visibility between the ends of the enclosure.

Fluorescent and incandescent lamps supplied the light. The lamps were turned on and off by an automatic timing device set on a 12 h light-12 h dark cycle.

Individuals were identified by toe-clipping and individually unique features such as pre-existing missing toes, regenerated tail lengths and pattern peculiarities. When toe-clipping, only the claw was removed, leaving the pad intact. Each animal was also given an individualized paint mark on its dorsum. The painted code was renewed approximately once a month because of ecdysis.

During the warmer months, lizards were fed sweepings from grassy fields. In the winter and spring the lizards were fed mealworms (Tenebrio larvae), brown crickets (Gryllus domesticus) from a commercial supplier, and

occasionally lab-reared houseflies. Food was usually supplied six days per week.

Distilled water was available in water dishes; their primary purpose was to increase the relative humidity inside the cages, but the lizards were also seen to drink from them. Once or twice a day the habitat was sprinkled heavily with water which was lapped from the plastic leaves by the lizards.

Observing A. g. grahami was difficult because the animals are extremely wary; even subtle movements (e.g. observer's eye movements) outside a cage would usually inhibit the caged subjects. To overcome this problem, three methods were used. It was usually sufficient to sit quietly about 4 m away with the room lights out. A second method was to use a black-and-white Sony (Model 3600) television camera, tape deck and monitor. This equipment allowed observation from another room, and appeared to be least disruptive to the lizards' activity. It also allowed recording the lizards' behavior and provided immediate replay for closer analysis. The inherent graininess of black and white television images, however, made some details (e.g. exact distance separating lizards) difficult to distinguish. The final observation method was the use of a blind. The blind was 1.8 m high, and 0.9 m wide and deep. Its top, sides, and lower half of the front were plywood painted flat black. The top half of the front was glass, and the back was a

curtain of black cloth. When placed before a lizard cage, it permitted close observation of activities inside the cage, and the animals showed no indications of being able to see into the blind. This method was most successful in diminishing any effects of the observer upon the subjects and at the same time allowing close observation of such minute activity as the lizards' eye movements.

All sounds emitted by the lizards were recorded with a Uher 4000 Report-L tape recorder. Recordings were made at either 19.05 cm.p.s. or 9.53 cm.p.s. The Uher M514 microphone supplied with the tape recorder was used for all recording. In most situations, the microphone was grounded. This achieved a great reduction in the level of background noise emanating from the 60 Hz AC electricity that existed in the laboratory. When sounds were transferred from the original tape to a summary tape, another Uher 4000 Report-L served as the second tape recorder.

Spectrum analysis of the recordings was performed on a Kay Elemetrics Model 7029-A sound spectrograph. Two types of sound spectrographs were made. In one, duration (x-axis), frequency (y-axis), and loudness were displayed. In the second type, called sectioning, amplitude (loudness) and frequency were displayed for a given point in time, with frequency depicted on the vertical axis and amplitude on the horizontal. Three of the spectrograph's recording-time/

frequency-display settings were used: 40-4,000, 80-8,000, and 160-16,000 Hz.

Sonagrams were analyzed by means of a clear plastic overlay with a grid marking increments of kHz (y-axis) and 1/10 sec (x-axis). Sonagrams were measured with the overlay for: (1) maximum frequencies produced, (2) midpoint frequencies, (3) duration of the sound, and (4) rate of occurrence if the sound was rhythmic. Harmonics were identifiable by a vertical pattern of dark areas on the sonagram, and other variations in loudness were also noted. The mean, variance, standard deviation, and standard error were calculated for the vocalization characteristics. These calculations were performed for the entire group of animals, and for individuals and sex when there were adequate sample sizes.

Recordings were made in two situations: while the animal was held in the experimenter's hand within a few cm of the microphone, and while the animal was free in a cage. In the hand-held situation, the recordings were made in a special soundproof room. This room (2.9m x 1.6m x 1.6m) was sufficiently insulated to exclude all background noise except that which was produced by the tape recorder itself. The lizards, while held, would often vocalize without further stimulation, whether they were still or struggling. Occasionally a lizard would jerk its head to one side in an attempt to bite the experimenter, and simultaneously produce

a loud squeak. Lizards were also stimulated to vocalize by pinching the tail or a leg, or by gently squeezing the head or pectoral region. Infrequently used stimuli to elicit vocalizations were: mildly shaking the whole animal or an appendage, and tapping near the head, which would usually produce a bite attempt. Rarely the lizard was squeezed in the abdominal or thoracic region.

Unrestrained animals would vocalize during agonistic encounters. To produce fights, an intruder was placed in a glass jar or a clear plastic box, and then the container was situated in a conspicuous spot in the resident's enclosure. Because the intruder could not leave the resident's territory, this technique produced extended interactions and extensive displaying by the resident. The resident lizards appeared to be unaware of the container's presence, and in an attack would run into it and try to push it to one side. In these experiments, the microphone was hung within 30 cm of the intruder's container. In order to establish which lizard was vocalizing, early experiments included a microphone inside the intruder's container in addition to the one outside in the resident's enclosure. When it became apparent that the lizard being attacked remained silent, the intruder's container was no longer monitored. The visual and auditory responses of many of these extended encounters were videotaped.

A second method used to stimulate attacks was to release a lizard into an occupied cage. This would often result in fights with the resident, although less often than did the above method. Using an unrestrained intruder more closely resembled natural conditions, but quality of the recordings was poorer than those obtained by the first method because there was more noise generated by the lizards' footsteps, and the fights often occurred farther from the microphone.

A series of experiments was performed to determine if the lizards would respond to 'attack' vocalizations. A loudspeaker was placed toward one end of an animal's cage. The speaker was activated when the subject was laterally oriented to the speaker, so that a cause-and-effect relationship would be more clearly demonstrated if the lizard moved to face the sound source. Two taped vocalizations were used. One consisted of two squeaks and the other had five; all were of the type produced during an attack. Six adult males were tested by repeatedly playing one or the other of the two taped vocalizations between 10 min intervals. Each lizard was given six to 10 trials, and any body, head, or eye movements were noted. In five other trials, attack squeaks were broadcast while a resident was actively displaying at an intruder, with a record made of any unusual or defensive reactions by either lizard.

In another series of playback experiments, a recording

of snapping twigs was broadcast to the lizards. This stimulus sound was created by walking over a number of dry sticks, ranging in size from 0.5 to 2.0 cm in diameter. This stimulus was selected to test if A. g. grahami would respond to a sound having some possible ecological relevance (i.e. approach of a possible predator). Five lizards were tested in a manner similar to that of the attack stimuli.

Dissections were performed upon five preserved A. g. grahami to isolate the sound-making mechanism. In two, the entire respiratory system was studied to determine its attachments, relations to other organs, and possible sites of sound production. The larynx and a portion of the trachea were removed for study from three other specimens. The larynx was also removed from specimens of two other vocalizing species, A. cybotes and A. garmani, and from a non-vocalizing species, A. lineatopus.

An attempt was made to produce sounds artificially from ethanol-preserved specimens by placing a thin glass tube into the trachea and forcing air through the larynx with a rubber bulb. The entire lower jaw with the larynx and approximately 0.5 cm of the trachea were removed from the animal, and the posterior 0.25 cm of the trachea was cut free from surrounding tissues. The tube was inserted into this portion, and a fine thread was tied around the trachea and tube to prevent leakage of air.

RESULTS

Sound Types

Anolis g. grahami produces seven types of vocalization. Two types are produced by animals in fights; all others were recorded when hand-held, and are presumably produced while held by a predator.

The two fight sounds are similar (Fig. 3 and 4), but one has a longer duration (Tables 1 and 2), and they are heard in different types of fights. The 'attack squeak' is produced by an aggressor at the instant that it jumps open-mouthed at its adversary to deliver a bite, and the other, the 'fight squeak', is heard when one lizard holds a bite on another.

The experiments with an intruder in a jar revealed two things about attack squeaks: (1) the attacked lizard remained silent, and (2) the aggressor vocalized before actually biting. Sonagrams of 89 attack squeaks showed that it is a short sound (0.11 $\pm$ SE 0.01 sec) covering a wide frequency range (1900 $\pm$ SE 110 Hz). The mean dominant frequency is 1700 Hz ($\pm$ SE 55 Hz). Its sonagram pattern is diffuse without many distinct characters, and appears largely as a few dark spots with a large amount of gray area (Fig. 3). There is sometimes a distinct inverted-V in a small frequency range within an attack squeak sonagram.

The attack squeak seemed restricted to the agonistic context described above, although on one occasion a lizard was heard to produce the same sound when jumping at a large cricket. This lizard lunged four times at the cricket which was on the other side of a sheet of hardware cloth; with each lunge a squeak was produced. Unfortunately the sounds were not recorded on this unplanned occasion and later attempts to duplicate the situation were not successful.

Only four males produced attack squeaks; two others would attack silently, and a third group of ten could not be induced to attack. Two females were heard to produce sounds similar to the attack squeak while attacking other females, but the tape recordings were not clear enough to produce usable sonagrams.

The 'fight squeak' is produced when a lizard bites another and holds its grip, usually near the head. In fights, the lizards may move several steps and one may even attempt to jump to another perch, while the attacker holds its bite and squeaks. Like the attack squeak, the fight squeak covers a wide frequency range (mean 1900 $\pm$ SE 165 Hz) and has its dominant frequency near 1700 (mean 1650 $\pm$ SE 130 Hz), but its duration is longer (3-4 sec), and the sound is produced after the attack. This sound is not rhythmic, but it is produced in bursts, with pauses separating the segments

(Fig. 4 and Table 2); even the segments are somewhat longer than attack squeaks. The mean duration of a fight squeak segment was 0.111 ± SE 0.0204 sec as compared with the mean duration of 0.081 ± SE 0.0090 sec for an attack squeak. The fights in which this sound is heard are serious, often resulting in bloody wounds, but never in death.

The most frequently-heard vocalization from hand-held lizards was the 'growl'. It occurs when the lizard is held with slight or no squeezing. Often a silent lizard will growl with no apparent stimulation beyond being held; at the moment of vocalization, the mouth can be either open or closed. Only males were heard to growl; females struggled more than males when restrained, and growls were heard only from motionless animals. To the ear, the sound resembles a low growl as a dog would produce. Sonagrams show this sound as a series of separate, very short energy bursts, each less than 0.01 sec long (Fig. 5). A growl may have from 3 to over 1000 such bursts at a highly variable rate which ranged from 11 to 316 per sec (Table 3). The duration is also highly variable, ranging from 0.10 to 14.51 sec (mean 2.26 ± SE 1.05 sec).

Three other sounds were heard in association with the growl. They were: (1) a vocalization that sounded like a rapid growl ('hurried growl'), (2) a chirp-like sound, and (3) a loud squeal. These other sounds were always associated

with growls and may grade into or out from the growl. Structurally, however, only one of these auxiliary sound types resembles the growl.

The 'hurried growl' has a sonagram pattern similar to the growl type, and to the ear they are indistinguishable from each other. In the former sound type, however, the sonagrams show that the pulses of sound occur so rapidly they almost form a continuous mark on the sheet, and there is a distinctive horizontal layering (Fig. 6). The layering usually divides the sonagram into four or five frequency bands separated by thin, slightly darker, lines. The dominant, top, and bottom frequencies are close to those of the growl (Table 4). Hurried growls occur only within growls; they are produced if the growling lizard is squeezed slightly harder, so that the rate increases until it becomes a hurried growl. When the stimulation is removed, the sound becomes a growl again.

A sound associated with growls but having a different structure, is the 'chirp' (Fig. 7). This is a brief (mean duration 0.06 $\pm$ SE 0.01 sec), bird-like sound that comes at the end of growls. They are produced by motionless lizards, and have no apparent special stimulus; although a growl could be elicited by squeezing the animal, chirps seemed to occur randomly. They consist of two energy bands, at 1.2 $\pm$ SE 0.05kHz and at 2.0 $\pm$ SE 0.14kHz. Both lower bands were of approximately equal loudness, with the lowest

slightly stronger. Chirps were infrequently heard.

The 'squeal-growl' is structurally similar to the 'squeal' which is discussed below, but has a more restricted frequency range (<5 kHz), and is usually more prolonged. The squeal-growl begins at or near its highest frequency and drops off (Fig. 8); this spectral structure is in contrast to the squeal sound type which has an arch-like sonagram pattern. Both sounds, however, have several harmonics and are much louder than growls. The squeal-growl usually precedes a growl, and is produced by a struggling lizard that then becomes still and begins to growl; the sound is also produced occasionally within growls if the lizard struggles briefly. These squeal-growls within growls are short and have a much more restricted frequency range than the usual form (Fig. 9).

The seventh sound type is the 'squeal'. It is produced in two situations involving violent movements: (1) when startled, as when noosed, and (2) when attempting to bite the holder's hand. Sonagrams show the squeal has a different structure than attack squeaks or squeal-growls, despite a similarity to the ear (Fig. 10 and 11); squeal sonagrams show an arch pattern, indicating that the frequency increases rapidly to a peak and then drops off rapidly. Squeals cover a wide frequency range, often beginning below 0.5 kHz. and reaching above 8 kHz (Table 7). This was the only vocaliza-

tion type that females produced very often.

Response to Sounds

Experiments with broadcast recordings of squeaks produced ambiguous results, but seem to indicate that A. g. grahami sometimes respond to sounds. Of the five adult males tested, one made eye movements in four of 15 trials and another made eye movements in one of 11 trials. One other lizard may have responded once in five trials (its eyes opened) and the other two showed no reaction in five and three trials, respectively. Playback of attack squeaks while one lizard was about to attack another produced no visible reaction in either, even though this was the social context in which attack squeaks are produced.

Broadcast of snapping-twig sounds produced more clear-cut results: one of five lizards made body movements (eye movements, raised head) in all five trials, and another moved in four of six trials. Two more lizards may have made small movements in five trials each, and the fifth remained motionless in all four trials. Those that reacted did so on hearing the sound the first time and reacted less to later broadcasts; those that made small movements did so after all broadcasts (five each), but it is not possible to be sure that these were responses rather than random movements.

Vocal Structures

The sound-producing structure is in the larynx. Dissections showed that no other part of the respiratory system is directly connected to any muscles, and cleared and stained specimens revealed no bony or cartilaginous structures of other organs that could be used to pinch parts of the trachea. The contextual predictability and complexity of the vocal repertoire is too great for the sounds to be accidental or produced by a simple massive exhalation; thus, a distinct sound-producing mechanism is involved. Although vocal cords are found in two lizard families, Gekkonidae and Chamaeleonidae (Weichert 1970, Kelemen 1963), none were found in A. g. grahami larynges, which were quite smooth inside. The larynx of A. g. grahami has, however, well-developed arytenoid and cricoid cartilages with muscles that open and close the glottis, and a mucous membrane around the margin of the glottis. Comparative dissections of three other anole species showed that A. lineatopus, the examined silent species, had thinner, softer laryngeal walls than the vocalizing species (A. cybotes, A. garmani, plus A. g. grahami) and the smallest mucous membrane as well.

From the dissections and from Kelemen's (1963) statement that some reptiles have membranous folds that serve as vocal cords, it is concluded that the mucous membrane of the glottis is probably the vibrating structure responsible for sound production. Although Kelemen appeared to be speaking

of special folds within the larynx, he did seem to be referring to soft structures lacking the ligamentous vocal cords of mammals.

In function, the mucous membrane could operate in a way similar to mammalian vocal structures. The usually accepted myoelastic-aerodynamic theory of sound production states that the vocal folds are pressed together at the beginning of speech, and are opened by the force of air behind them. They rapidly close again because of the elasticity of attached muscles and cartilages, and because of the rapidly-flowing air creating a negative pressure upon them (Bernoulli's theorum). The vibrations of the folds' margins during these movements produce the actual sound (Kaplan 1971, Broad 1973).

Artificial Sound Production

Blowing air through larynges of lizards preserved in 70% ethanol produced no sound with the larynx either open or pinched partially closed. However, several times when the rubber bulb used to blow air was released and air was sucked back through the larynx, a high-pitched tone of low volume was produced. Lizards exhale during vocalization, and so this sound is not comparable to theirs, but it does show that the larynx has a structure that can vibrate as air passes over it. In the living animal, with more control over the larynx shape, this membrane could be the organ

responsible for the species' vocalizations.

DISCUSSION

The loudest vocalizations produced by Anolis g. grahami are those associated with struggling, fighting, or being seized; these are the same situations in which many reptiles make loud hissing noises. The hisses produced by rapid air flow past the larynx's arytenoid cartilages would become true vocalizations if a vibratory membrane were present. Therefore, if an ancestral form of A. grahami produced arytenoid hisses, as some anoles do, the appearance of the glottal membrane found in extant A. grahami would allow it to generate louder noises. Refinement of control of exhalation and of the glottis size would then allow the species to expand its vocal repertoire.

Animals of many taxa, including A. grahami, threaten antagonists before beginning a wounding fight; in many, the threats include vocalizations. Although A. grahami's attack squeak occurs too late to serve as a true warning, it does come after a prolonged visual display; a pause of one or two seconds between the squeak and the attack would augment the agonistic displaying with vocalization. If vocalizing is a recently acquired ability, the species may very likely be in the evolutionary process of extending its threat display.

Fight squeaks may already serve the purpose of reducing

the likelihood of wounds. If the vocalizations increase the fright of the victim, fights could be shortened and counter-attacks discouraged. The selection responsible for the evolution of this suggested behavioral interaction and its concomitant vocalizations could be explained by the decreasing number of animals seriously bitten and killed through subsequent infections. Bites by A. grahami males can be serious wounds because this is a stout species with powerful jaws.

Vocalization may be selected for even more strongly in the context of interspecific conflicts, as when a lizard is attacked by a predator. The sudden loud squeal a startled lizard produces might well cause a cautious predator to release its prey; because a common predator of A. grahami is birds, which respond to sound, a vocalizing ability could have distict survival value. Further, the growl made by a steadily-held lizard might intimidate a predator enough that it would loosen its grip, and a prolonged growl mixed with A. grahami's characteristic intermittent struggling and squeal-growls may be enough to cause an already uncertain predator to loose its prey.

The hurried growl is produced in a similar, but more threatening situation (i.e. a tighter grip); its spectral differences are probably a result of the increased rate of air flow over the membrane, and this may simply be caused

by the tighter squeeze of the hand. The squeal-growl also occurs with growls, and would seem to have a general function similar to growls, but being louder and having a wider frequency range, the protest is more intense. Finally, the chirp is a brief sound with little volume and can be correlated with no particular situation, other than usually being heard at the end of a growl. This sound type may have no real function, but could merely be an incidental sound created by suddenly closing the glottis during a growl to allow swallowing.

At present, vocalization appears to have little intraspecific function. Attack and fight squeaks do not occur until after a fight begins, and there is no sign of vocalization during courtship or territorial assertion displays. Vocalizations of the hand-held type were never heard in intraspecific conflicts. The present status of sound production in A. g. grahami, therefore, appears to be primarily an anti-predation phenomenon, while also being a preadaptation for intraspecific communication

Phylogenetically, the vocalizing ability of anoles is scattered with no apparent pattern throughout the genus. Of the 13 vocalizing species, seven are in the Alpha Section and six in the Beta Section. Within sections, vocalizing is also scattered: at least two species series in each section contain sound-producing species. Attempts at correlating

vocalization with other factors are equally unsuccessful: (1) small species, such as A. opalinus, and large, as A. vermiculatus and A. garmani, both vocalize; (2) there is no evidence of nocturnal habits being prevalent in vocalizing species; and (3) there is no correlation with habitat, since A. vociferans lives in mist-shrouded mountains, A. grahami in dry lowlands, and A. vermiculatus is partly aquatic.

This scattered distribution of vocalization suggests that the vocal membrane is a simple structure evolved from the mucous membrane of the glottis which is probably common to all members of the genus. It is very likely that many more species vocalize than have been reported. When more comparative data are available for the genus, it may be possible to correlate an ecological factor with the trend for anoles to vocalize.

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Table 1. Descriptive statistics of the auditory characteristics of the 'attack squeak' by four male *Anolis g. grahami*.

Highest frequency reached (Hz)	
Number of measurements	102
Mean	2700
Standard error	110
Lowest frequency reached (Hz)	
Number of measurements	101
Mean	700
Standard error	25
Size of frequency range (Hz)	
Number of measurements	99
Mean	1900
Standard error	110
Dominant frequency (Hz)	
Number of measurements	93
Mean	1700
Standard error	55
Duration of squeak	
Number of measurements	89
Mean	0.11
Standard error	0.01

Table 2. Descriptive statistics of the auditory characteristics of the 'fight squeak' by three male *Anolis g. grahami*.

Highest frequency reached (Hz)	
Number of measurements	22
Mean	2900
Standard error	170
Lowest frequency reached (Hz)	
Number of measurements	22
Mean	945
Standard error	70
Size of frequency range (Hz)	
Number of measurements	22
Mean	1900
Standard error	165
Dominant frequency (Hz)	
Number of measurements	18
Mean	1650
Standard error	130
Duration of segments (sec)	
Number of measurements	22
Mean	0.11
Standard error	0.02

Table 3. Descriptive statistics of the auditory characteristics of the 'growl' by nine male *Anolis g. grahami*.

Highest frequency reached (Hz)	
Number of measuremnts	379
Mean	2000
Standard error	55
Lowest frequency reached (Hz)	
Number of measurements	379
Mean	680
Standard error	20
Size of frequency range (Hz)	
Number of measurements	379
Mean	1300
Standard error	65
Dominant frequency (Hz)	
Number of measurements	378
Mean	1350
Standard error	40
Rate (number of pulses per sec)	
Number of measurements	375
Mean	112
Standard error	10.8
Duration of entire growl (sec)	
Number of measurements	188
Mean	2.26
Standard error	1.05

Table 4. Descriptive statistics of the auditory characteristics of the 'hurried growl' by six male *Anolis g. grahami*

Highest frequency reached (Hz)	
Number of measurements	52
Mean	1950
Standard error	40
Lowest frequency reached (Hz)	
Number of measurements	52
Mean	570
Standard error	15
Size of frequency range (Hz)	
Number of measurements	52
Mean	1350
Standard error	40
Dominant frequency (Hz)	
Number of measurements	52
Mean	1250
Standard error	20
Duration of sound (sec)	
Number of measurements	54
Mean	0.38
Standard error	0.05
Number of energy bands in vocalization	
Number of measurements	52
Mean	5.18
Standard error	0.16

Table 5. Descriptive statistics of the auditory characteristics of the 'chirp' by six male *Anolis g. grahami*.

Highest frequency reached (Hz)	
Number of measurements	11
Mean	2000
Standard arror	140
Lowest frequency reached (Hz)	
Number of measurements	13
Mean	1200
Standard error	53
Size of frequency range (Hz)	
Number of measurements	8
Mean	955
Standard error	55
Distance between energy bands (Hz)	
Number of measurements	13
Mean	725
Standard error	40
Duration of sound (sec)	
Number of measurements	16
Mean	0.06
Standard error	0.01

Table 6. Descriptive statistics of the auditory characteristics of the 'squeal-growl' by seven male *Anolis g. grahami*.

Highest frequency reached (Hz)	
Number of measurements	78
Mean	3200
Standard error	145
Lowest frequency reached (Hz)	
Number of measurements	78
Mean	570
Standard error	20
Size of frequency range (Hz)	
Number of measurements	78
Mean	2650
Standard error	137
Dominant frequency (Hz)	
Number of measurements	77
Mean	1230
Standard error	25
Duration of sound (sec)	
Number of measurements	78
Mean	0.57
Standard error	0.06
Number of harmonics in vocalization	
Number of measurements	78
Mean	4.6
Standard error	0.13

Table 7. Descriptive statistics of the auditory characteristics of the 'squeal' by four male and four female *Anolis g. grahami*.

	Males	Females
Highest frequency reached (Hz)		
Number of measurements	68	23
Mean	5330	6030
Standard error	200	595
Lowest frequency at same time highest frequency reached (Hz)		
Number of measurements	68	23
Mean	1300	1760
Standard error	45	170
Size of frequency range (Hz)		
Number of measurements	68	23
Mean	4050	4300
Standard error	190	510
Dominant frequency (Hz)		
Number of measurements	67	22
Mean	1530	2300
Standard error	40	160
Duration of sound (sec)		
Number of measurements	68	23
Mean	0.15	0.08
Standard error	0.02	0.01
Number of harmonics in vocalization		
Number of measurements	68	23
Mean	4.30	3.52
Standard error	0.18	0.33

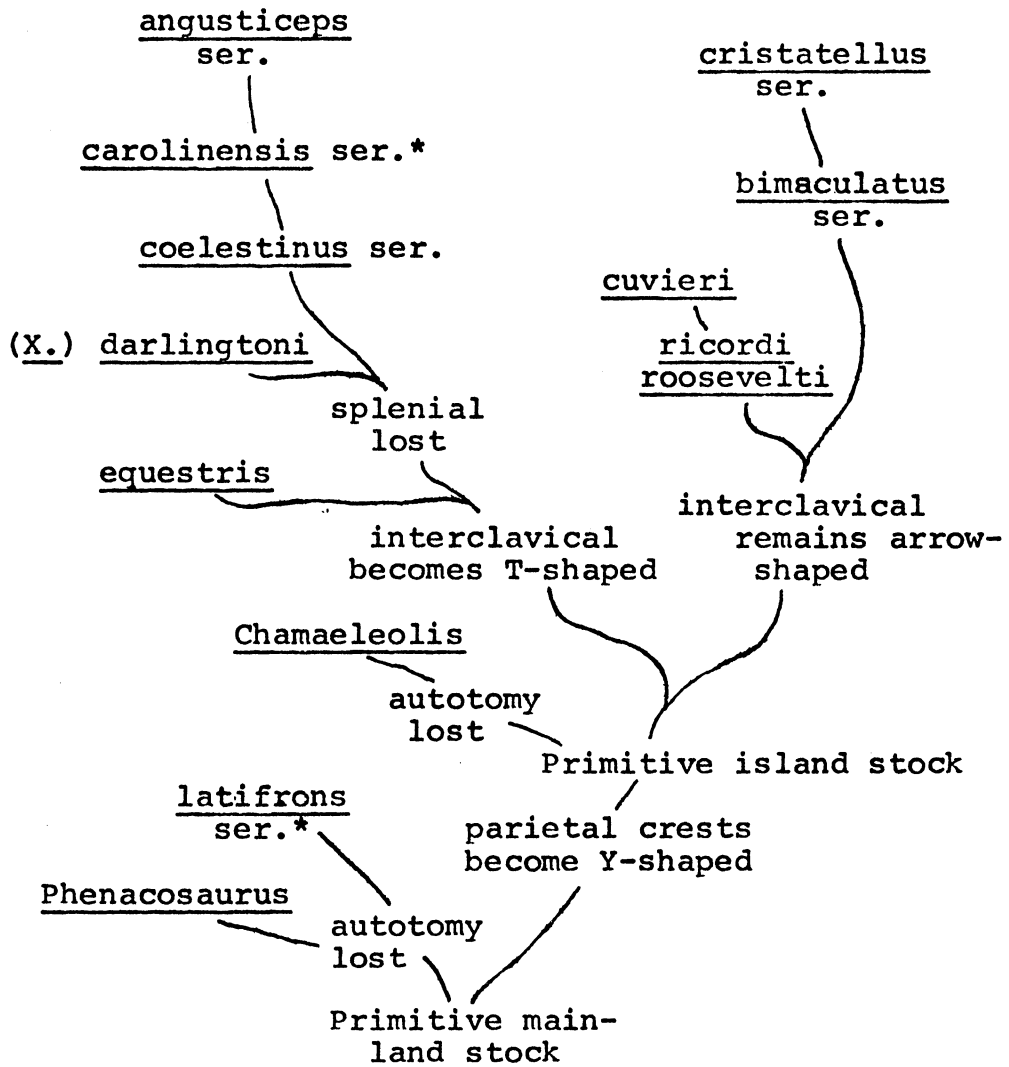


Fig. 1. Proposed relationships of the Alpha Section of Anolis and related genera (from Etheridge 1959). Asterisk indicates series with at least one vocalizing species.

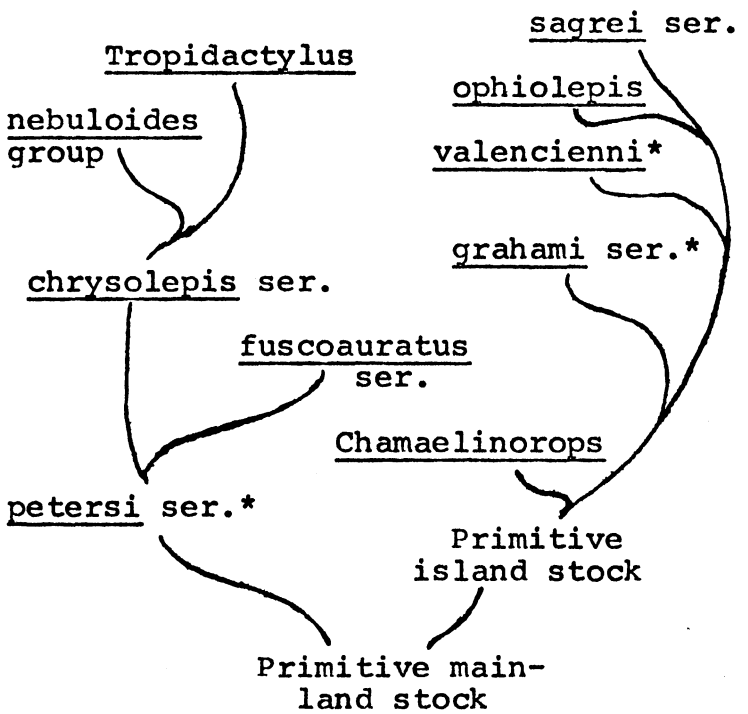


Fig. 2. Proposed relationships of the Beta Section of Anolis and related genera (from Etheridge 1959). Asterisk indicates Series with at least one vocalizing species.

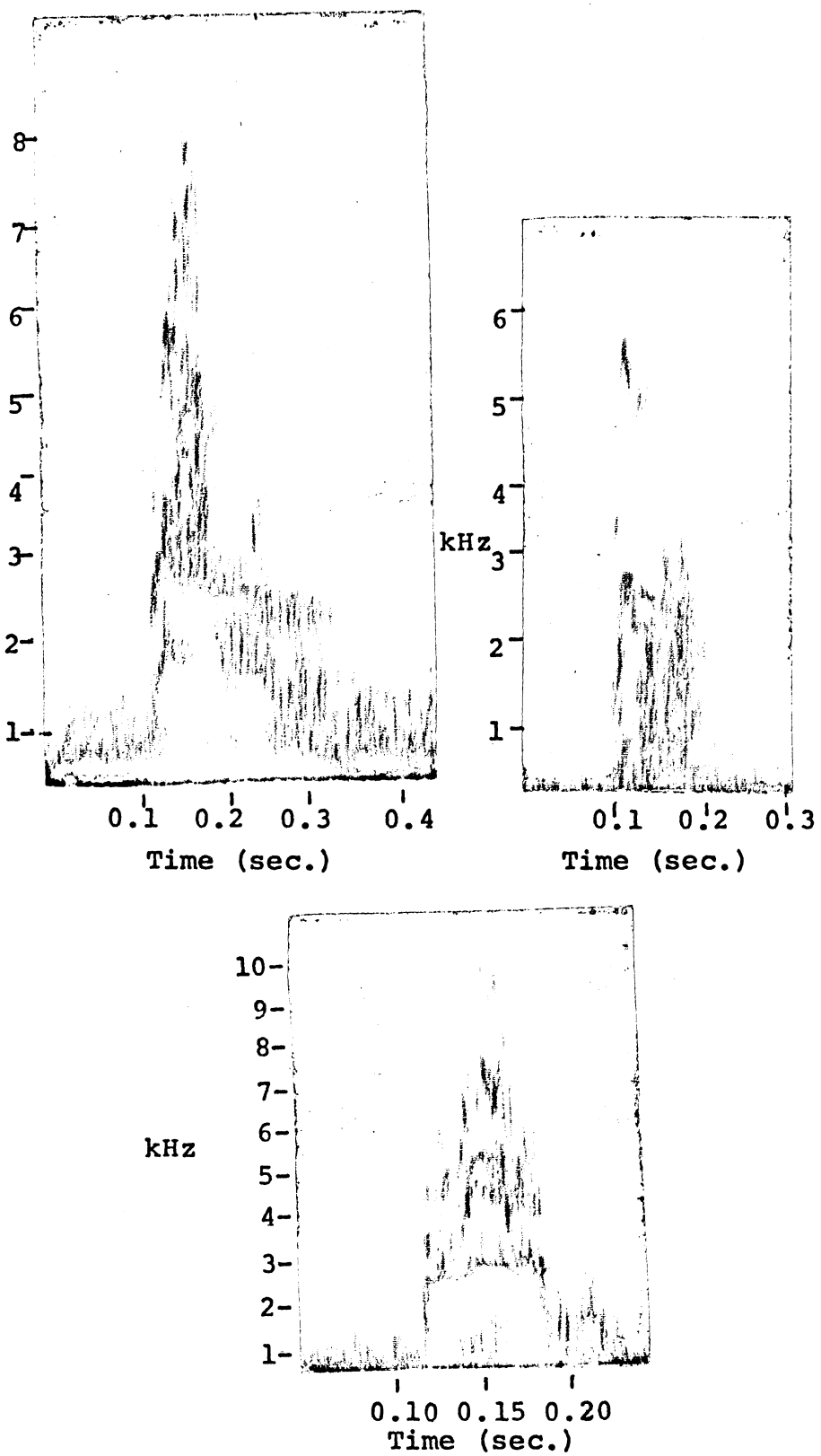


Fig. 3. Sonagrams of three separate fight squeaks.

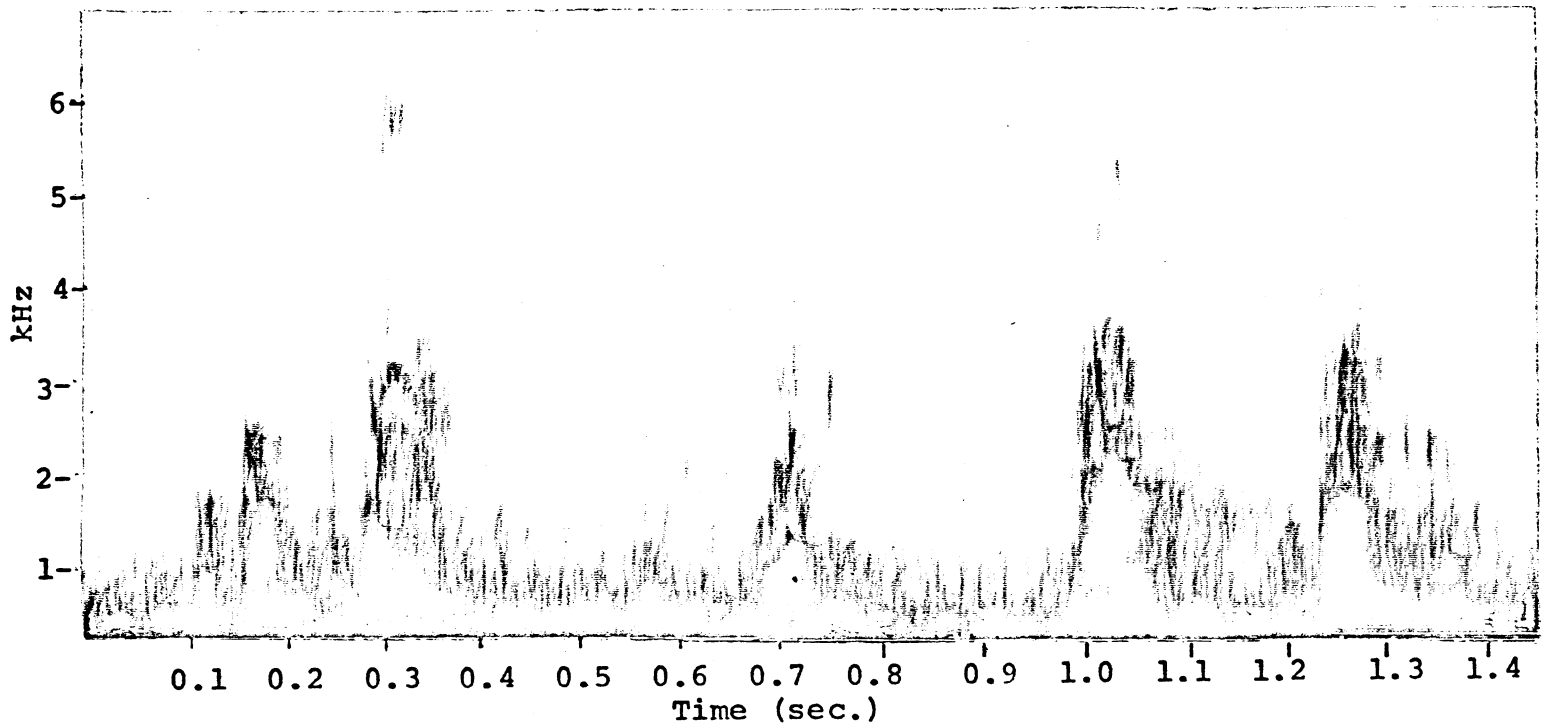


Fig. 4. Sonagram of a single fight squeak.

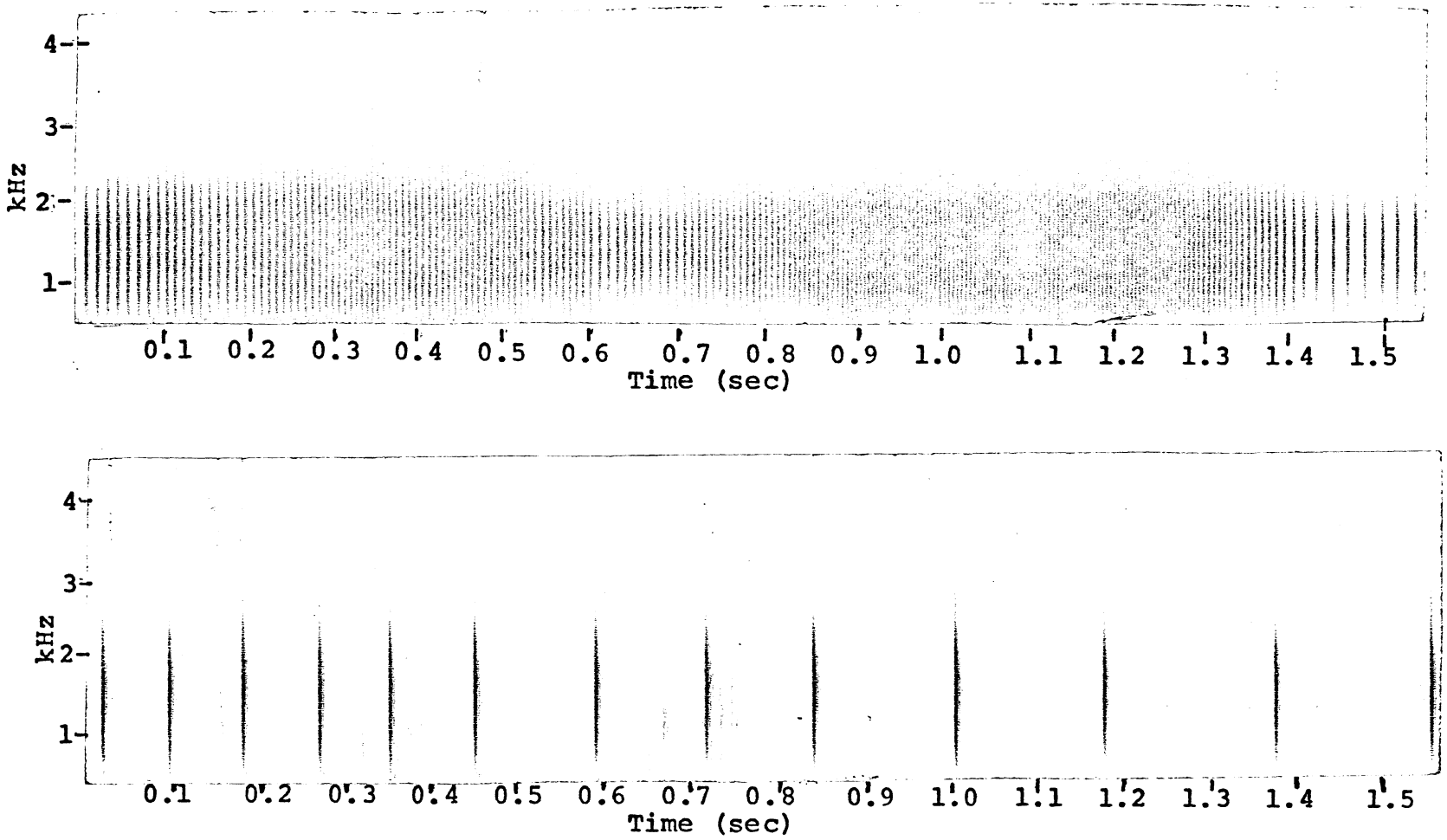


Fig. 5. Sonagrams of two growls. Top growl's rate is 140 pulses/sec; bottom is 8.4/sec.

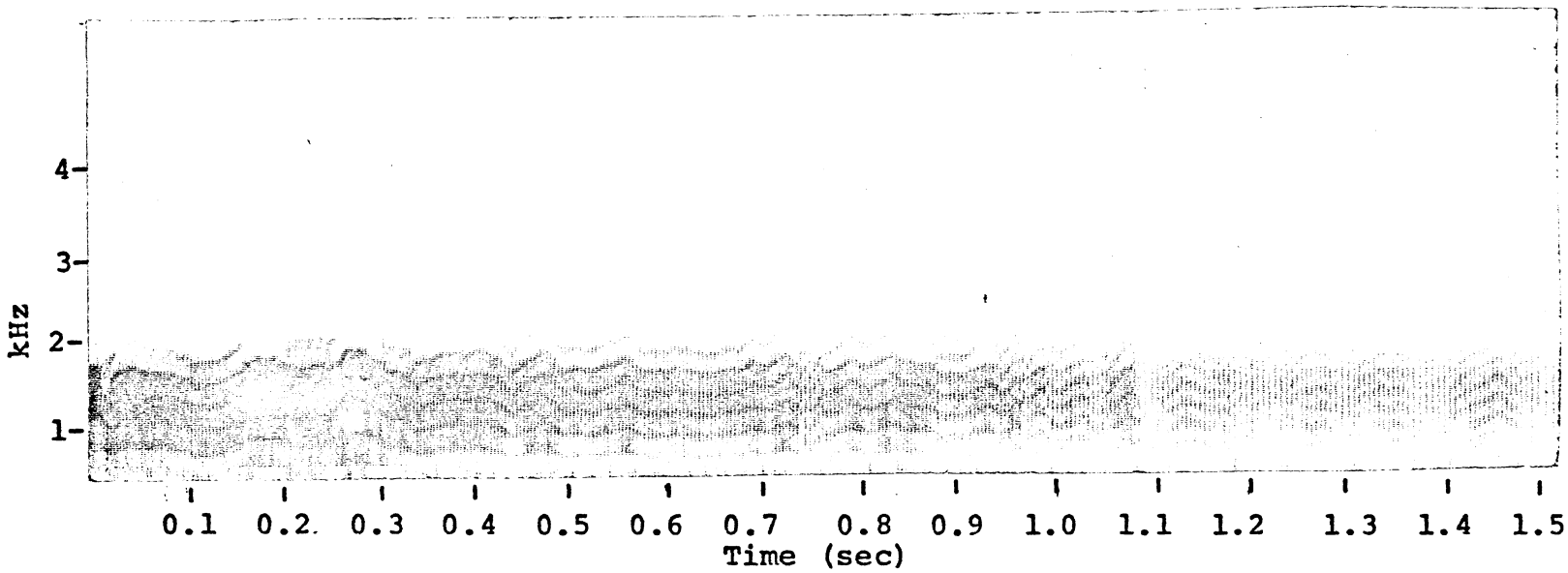
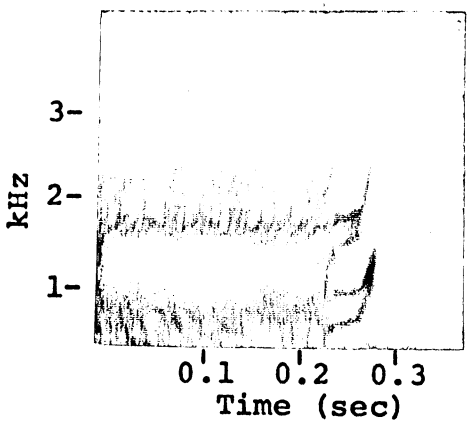


Fig. 6. Sonagram of hurried growl. At 0.87 sec it begins to fade into a simple growl.



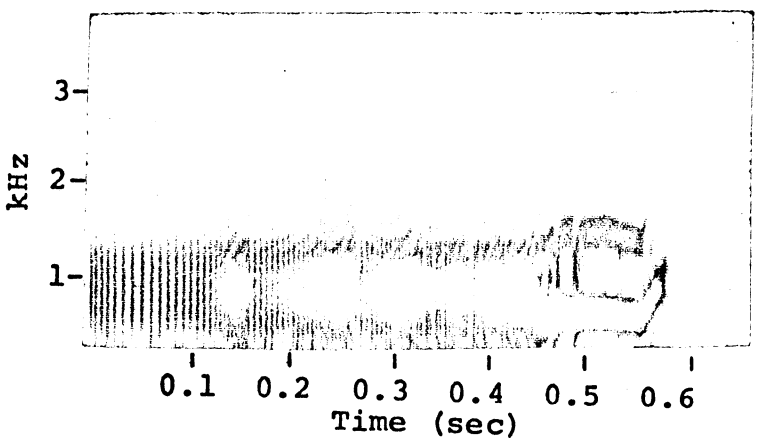


Fig. 7. Sonagrams of two chirps.

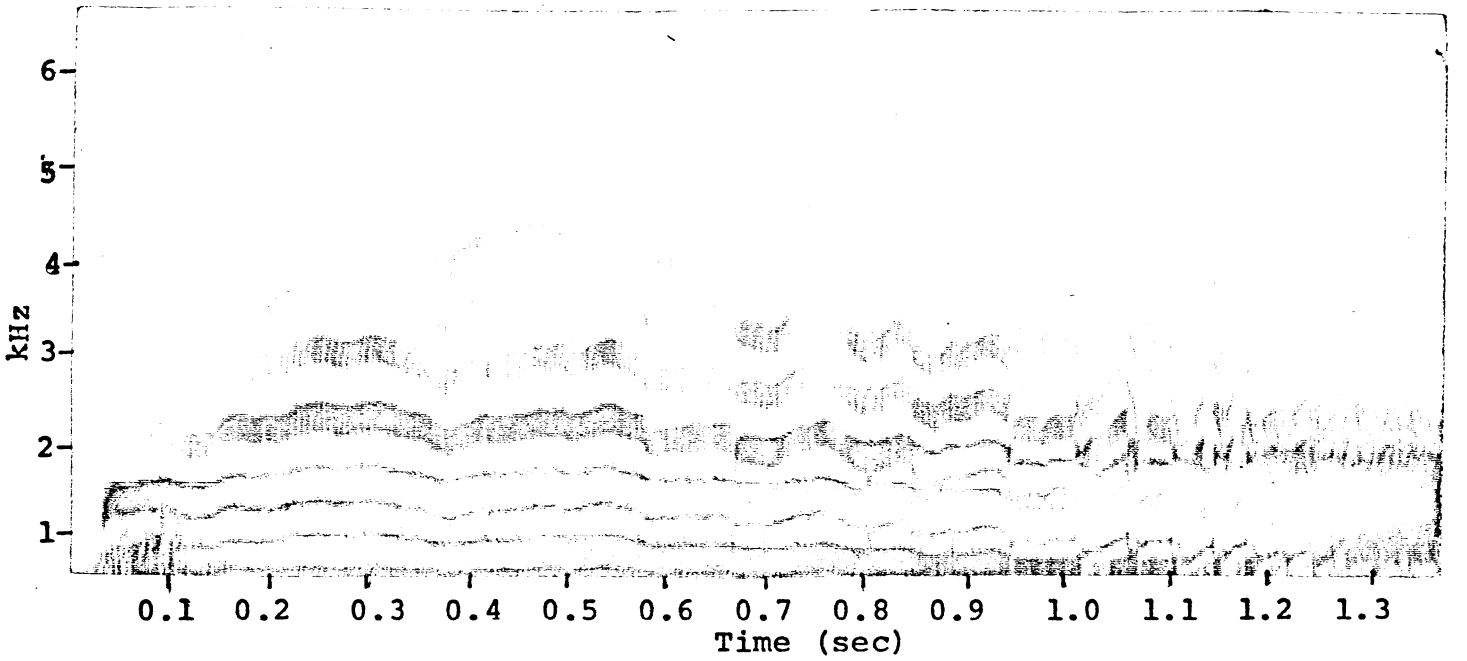


Fig. 8. Sonagram of long squeal-growl that fades into simple growl around 1.3 sec.

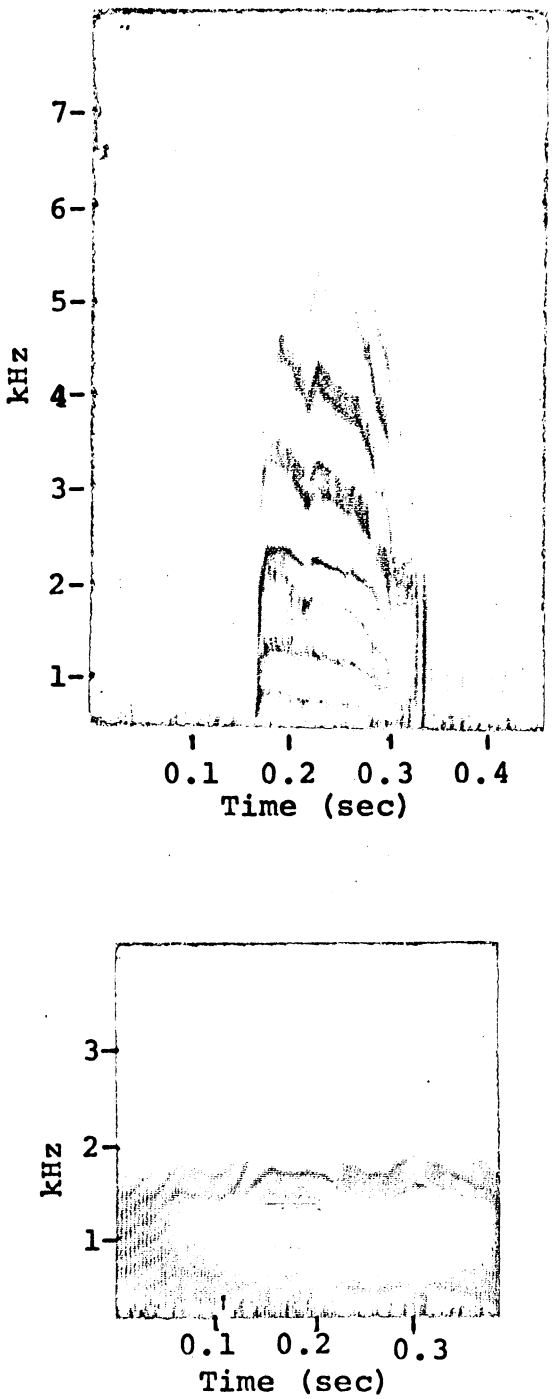


Fig. 9. Sonagrams of two squeal-growls. Top is short sound; bottom is squeal-growl within growl.

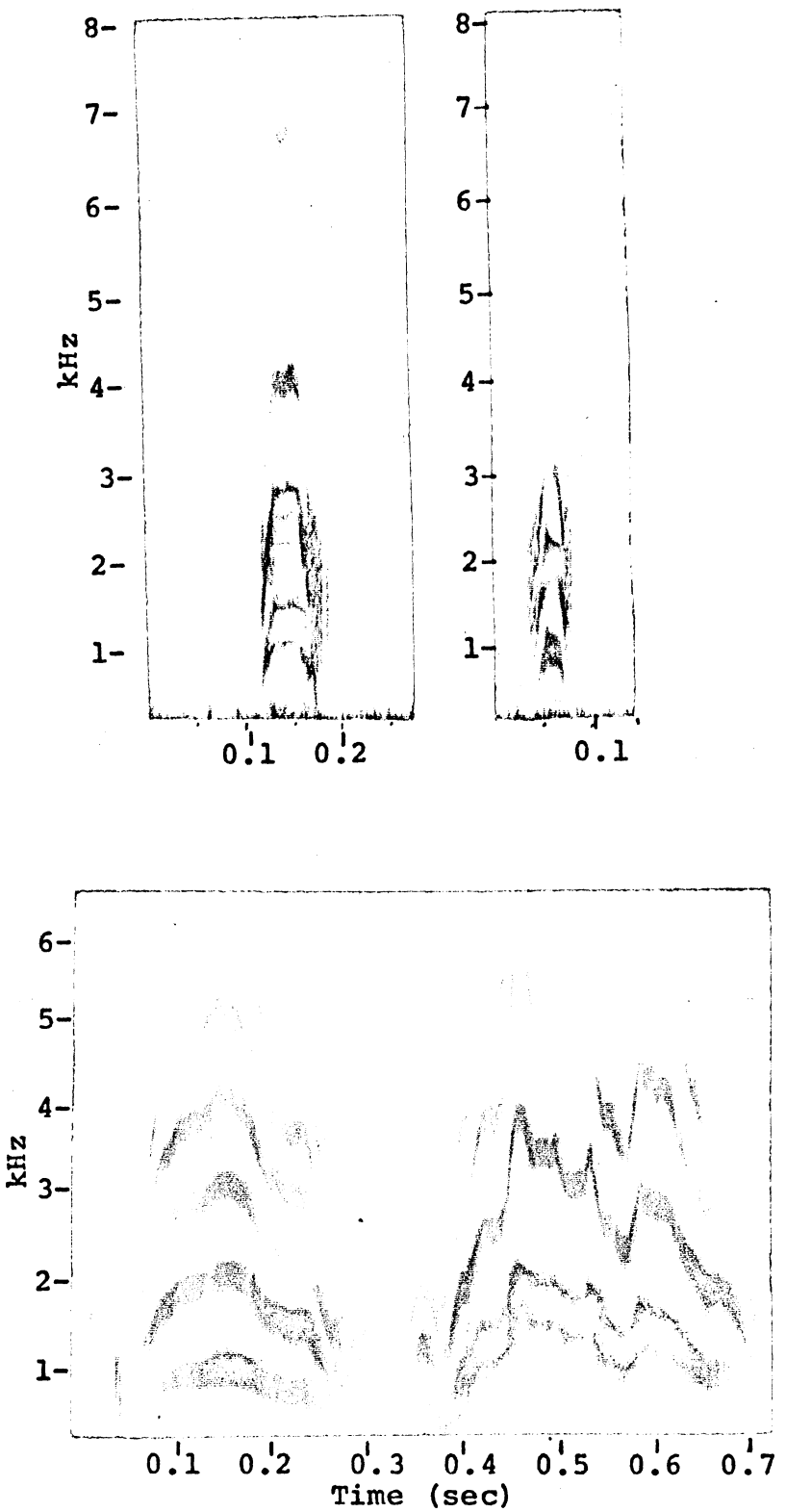


Fig. 10. Sonagrams of squeals. Two at top are by females. Bottom is longer than most, by male.

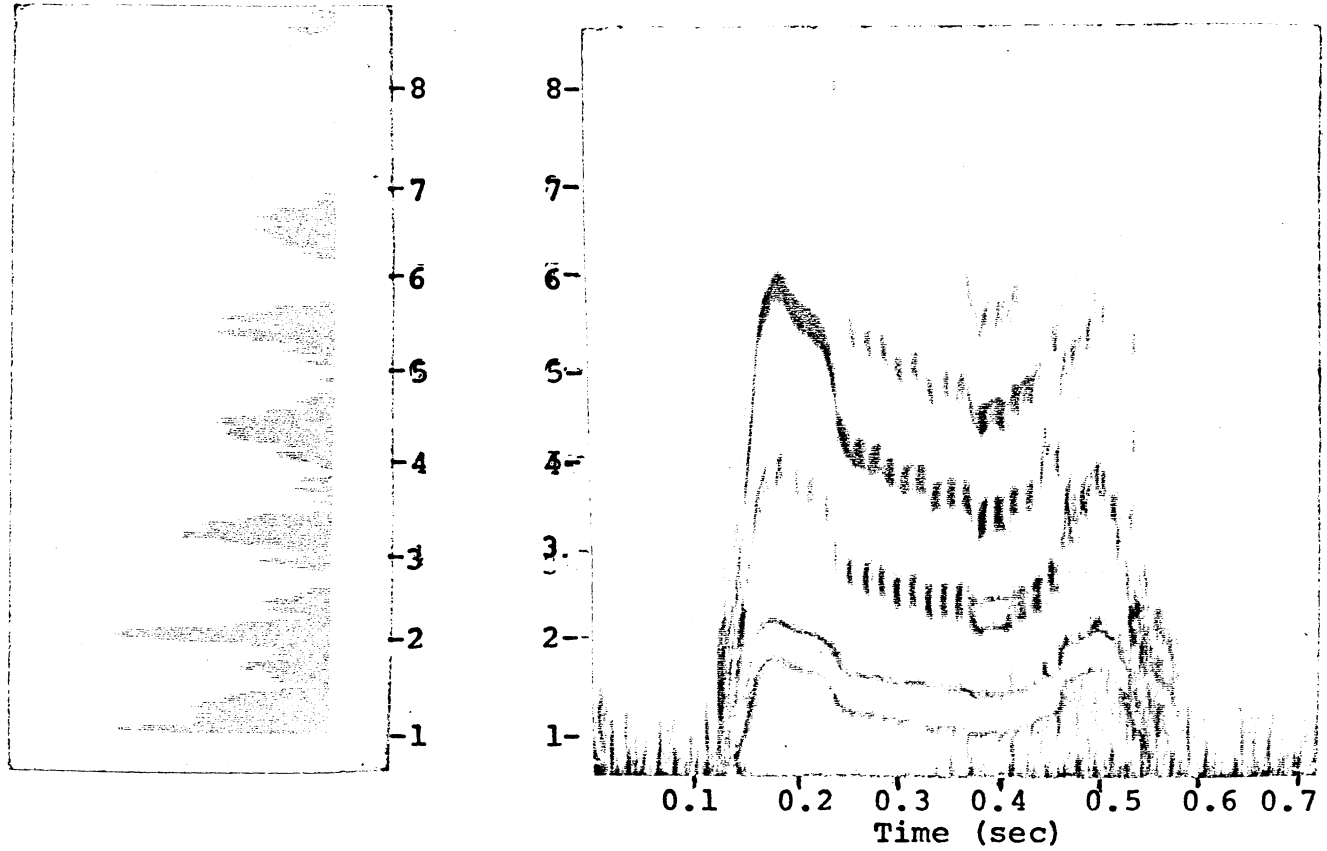


Fig. 11. Squeal by male. On left is section of sonagram (right) at 0.04 sec.

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STRUCTURE AND SOCIAL SIGNIFICANCE OF VOCALIZATION BY *Anolis grahami grahami* (SAURIA:IGUANIDAE)

by

Thomas Hamilton Milton

(ABSTRACT)

Even though the ability to produce vocalizations by the vibration of a membrane is widespread throughout the lizard suborder, only the sounds of geckos (Gekkonidae) have been closely studied. The purposes of this study were to describe the physical structure, social significance, and means of sound production by *Anolis g. grahami*, one of the 13 anoline species known to vocalize.

Recordings were made of 16 adult males and five adult females within two general situations: (1) while held in an experimenter's hand, and (2) while unrestrained within a cage. Hand-held lizards produced five types of vocalizations: (1) two kinds of growls, (2) two kinds of squeals, and (3) a chirp. Unrestrained lizards vocalized during fights only, producing one type of sound in attacks and another during prolonged fights.

Lizards responded only slightly to recorded vocalizations and little more to environmental sounds. This suggests that they do not respond to sounds generally and that vocalizations therefore have little intraspecific use. The most important use of vocalizations is probably in defense

against predators, and it is a preadaptation for social communication.

Vocalization is scattered throughout the genus and therefore seems to be produced by a structure present in most species which is more highly elaborated in vocal species. Dissections revealed that vocal cords are absent, but that the larynx is nevertheless the site of sound production. A thin membrane within the glottis is proposed as the vibrating structure.