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A FUNCTIONAL ANALYSIS OF THE MATING CALLS OF THE NEOTROPICAL FROG GENERA OF THE *LEPTODACTYLUS* COMPLEX (AMPHIBIA, LEPTODACTYLIDAE)

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ABSTRACT

Functional characteristics or design features of mating calls for 19 species in the complex are given and analysed for patterns of relationship and convergences due to functional constraints. Two basic mating call patterns can be defined. The first, a quiet, incessant popping produced by exploding a burst of air through the glottis usually with little amplification by secondary structures, is characteristic of riparian species that call resident females over short distances. The second call consists of a single tone burst (note) produced by passing a pulsed stream of air through the glottis. Often a change in tension of laryngeal musculature produces frequency modulation through the note. In the latter call, resonance in the vocal sacs provides finer frequency tuning and better radiation of the call for attracting females over much longer distances. Patterns of structural similarities in calls are consistent with relationships based on morphology in some instances and apparently contradict morphological evidence in others, indicating that convergence in mating call characters may occur.

INTRODUCTION

Straughan (1973) suggested that since the Neotropical genus *Leptodactylus* and the Australian genus *Limnodynastes* showed marked similarities in form and habits, these two genera would provide a good basis for studying relationships and convergences based on functional mating call characteristics. This paper summarizes the present data on species of *Leptodactylus* and closely related genera and attempts to

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delineate patterns of mating call structure in relation to function to provide hypotheses for future testing. Mating calls are now known from nineteen species recently referred to as *Leptodactylus,* sixteen of which have been described from audiospectrograms previously in the literature. The calls of two species are described here for the first time and more elaborate analyses of the functional components are reported for many of the calls. Observations on reproductive behavior, especially calling habits are integrated with data on call structure to elucidate functional aspects of calls and examine possible convergences.

MATERIALS AND METHODS

Field recordings were made at 19 cm/sec on Uher series 4000 portable tape recorders through Senheisser microphones. Audiospectrograms were made with Kay Electronics Sonograph models 6061 or 6061B employing the 80-8000 Hz frequency scale and narrow band filter (45 Hz) using the Uher tape recorder for playback. To examine internal call structure with greater resolution the tape recorded signal was fed into a Tektronics 502 dual beam oscilloscope along with a 1 KHz time base and photographed continuously with a Nihon Kodin camera at film speeds of 100 mm/sec. Pulse lengths, pulse repetition rates and carrier frequency were measured in reference to the time base. Effective (defined by Littlejohn, 1965) temperature, location and behavior of all individuals used in analysis were taken at the time of recording. Call repetition rates were measured in the field by counting consecutive calls over one minute. Specimens and tapes will be deposited in the Natural History Museum of Los Angeles County.

Functional components of the calls described herein relate to patterns in frequency spectra and temporal patterns of frequency and amplitude within each call. Nomenclature for temporal components of a call is not consistent in previous descriptions, so clarification of terms used in this paper is presented: *"Call"* refers to the complete behavioral fixed (or modal) action pattern; i.e., the temporal sequence is repeated with a fixed pattern and time relationships are not influenced by environmental conditions (*e.g.,* temperature). Some calls will be very short (a single "pop"); neither the repetition rate nor number of these sounds given is fixed, for a single bout of calling. Other calls may be much longer and complex in temporal pattern, but provided this pattern is rigid, we define this sound as a single call which itself may be repeated at a fairly regular rate with this latter rate being subjected to irregularity and change due to environmental disturbance. Long calls may be a single continuous note unbroken in time by amplitude modulations. This we refer to as a single note call. A call may consist of more than one such note and the notes within a call may differ in their internal characteristics (*e.g.,* frequency spectra or modulations). The notes themselves may not be continuous but broken into pulses by amplitude modulations. The shortest cycles of amplitude modulation of a carrier frequency in a call are referred to as pulses. The next level is that of discrete notes and then calls. When calls are short and without internal temporal structure the difference between a pulse and a note is purely an arbitrary one based on the length of the call.

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SPECIES ACCOUNTS

Previous descriptions are summarized and analysis of functional characteristics presented for each species which we were able to analyze. Information is presented by species listed alphabetically.

Adenomera hylaedactyla

Heyer (1973) figured the calls of three individuals as *Leptodactylus hylaedactylus* recorded by Werner C. A. Bokermann. Call characters were based on three notes from a single individual recorded from Jataí, Goiás, Brasil at 26°C: mean duration = 0.13 sec; repetition rate 82/min; dominant range 3700-4833 Hz; frequency spectrum is not well defined, an apparent fundamental below 500 Hz, an harmonic of 1860-2600 Hz, and two higher harmonics at 5966-6600 Hz and 8000 Hz were reported in the description by Heyer (1973). The dominant range is the frequency bandwidth of greatest intensity which acts as the carrier frequency for the signal. A true harmonic structure is not common in frog calls, and the harmonics referred to here are frequency bandwidths of high intensity which are more or less multiples of a fundamental frequency. The notes seem to lack frequency modulation but apparently are intensity modulated. Recordings of three calls of a single individual from Sto. Antonio de Leverger, Mato Grosso, Brasil, provided the following characteristics at 29°C; mean duration = 0.11 sec; repetition rate = 82/min; dominant range 3833-5133 Hz; frequency spectrum again ill defined, an apparent fundamental below 500 Hz, a well defined harmonic at 5925-7300 Hz, an ill defined harmonic around 8000 Hz; the notes apparently lack frequency and intensity modulation. Seven calls of a single individual of the same morphological form recorded at Chapada dos Guimarães, Mato Grosso, Brasil, at 19°C show considerable divergence: mean duration = 0.08 sec; repetition = 190/min; dominant range 4240-5830 Hz; frequency spectrum with an apparent fundamental below 500 Hz, well defined harmonics at 2000-3270 Hz, 4240-5830 Hz, and 6375-7725 Hz. The notes seem to lack frequency modulation but appear to be intensity modulated. Differences between the two call types from Mato Grosso, which are geographically close, are of a magnitude indicative of species differentiation in other genera. The differences could be due to the recorded temperature differences, but are inversely correlated from what one would expect. Further field work in the state of Mato Grosso is necessary to determine the meaning of the observed variation in calls.

Tapes of the calls were not available for oscilloscope analysis but visual inspection of the audiospectrograms allows the following speculation. A call consists of a two part note produced by a single puff of air from the lungs (*cf. L. melanonotus*). The initial untuned part of the call (explosive crack at beginning) is followed by a tuned portion probably consisting of a partially pulsed complex as described for *V. discodactylus* (melodious end).

Adenomera marmorata

Barrio (1965) described and figured the call of a specimen from Paranapiacaba, São Paulo, Brasil, recorded at 20°C. Heyer (1973) figured the call of a specimen from Tijuca, Rio de Janeiro, Brasil, at 22°C. The calls are distinctive and may represent distinct species. [Unfortunately, the specimens were not captured for positive identification. Two closely related species are found in Southeast Brasil, and could be associated each with one of these call types]. Barrio (1965) described the calls of the specimen from São Paulo: call duration = 0.1 sec; repetition = 75/min; frequency spectrum with two apparently equal energy envelopes at 2200-3200 Hz and 5200-6000 Hz; intensity modulation through calls. Calls of the specimen from Rio de Janeiro have: duration = 0.1 sec; repetition rate = 94/min; dominant range 4500-5600 Hz, with an apparent broad fundamental frequency below 1000 Hz; intensity modulation through call apparent.

No tapes were available for oscilloscope analysis, but the audiospectrogram tracings appear similar to those of *A. hylaedactyla* with respect to possible mechanism of production of the call.

Leptodactylus bolivianus

Fouquette (1960) described and figured audiospectrograms (as *L. insularum*). The Panamanian specimen had: call duration = 0.1 sec; repetition rate = 114/min; dominant range 200-900 Hz; frequency modulation present. Analysis of 16 calls from three specimens from Guanacaste Province, Costa Rica indicate: mean call duration = 0.07 sec; repetition rate = 142/min. The frequency component consists of a well tuned single carrier frequency (close to sine wave) that begins at ca. 400 Hz and rises smoothly to ca. 1300 Hz at the end of the note. Differences between Costa Rican and Panamanian calls are apparent: 1) A harmonic was present in the Panamanian audiospectrogram but direct examination of the Costa Rican tracings show a lack of harmonics; 2) Fouquette (1960) described the frequency modulation rising from 200-900 Hz, then dropping back to 750 Hz; whereas the Costa Rican calls frequency rises smoothly throughout. The harmonic may be due to recording and/or analyzing artifact, but the differences in frequency modulation pattern cannot be so explained. Superficially it appears that the upward sweep is the same in both calls but the

Panamanian call has the additional down sweep in the extra three milliseconds at the end. The differences in absolute frequency range could be due to larger body size of the Panamanian specimens.

Leptodactylus bufonius

Barrio (1965) described and figured the call (at 21°C) as a single note: duration = 0.2 sec; repetition rate = 75/min; dominant frequency rising from 1000 to 2000 Hz through the note with three harmonics present. His recording was of a specimen from Salinas Grandes between the Provinces of Cordoba and La Rioja, Argentina. Our recordings were made at Embarcacion, Salta, Argentina, at 21.3°C. The audiospectrograms are similar; however, direct inspection indicates that the Embarcacion call has a simpler frequency structure with a single pure tone (sine wave) which is swept upward through the call. The temporal pattern is more complex than is apparent from audiospectrograms in that there is distinct amplitude modulation resulting in basically two notes: the first is a single pulse of 26-28 msec duration followed by complete amplitude modulation and a pause of up to 9 msec. The second note is longer (102-110 msec) and has a partial amplitude modulation giving two indistinct pulses. The first note has a frequency of 1400 Hz and the second sweeps from 1500 Hz-1800 Hz (Fig. 1).

Leptodactylus chaquensis

Barrio (1966) described and figured the mating call. The vocalizations consist of two distinct types. A typical sequence of calling apparently consists of several calls (Type 1) repeated at 8 to 10 per minute, followed by a single second type (Type 2). Type 1 calls consist of a trilled or pulsed note of 80-100 msec duration consisting of 7-9 pulses with a mean pulse repetition rate of approximately 90/sec. The frequency is in the range of 250 Hz-500 Hz but is noise rather than sinusoidal. The Type 2 call produces an audiospectrogram with: duration = 0.6 sec; a fundamental frequency below 250 Hz, a dominant frequency of 250-1000 Hz; fundamental and dominant frequencies have periodic (ca. 0.05 sec) rising and falling frequency modulation. This is an unusual type of vocalization for *Leptodactylus* and may be only peripherally related to breeding behavior.

Leptodactylus fuscus

Barrio (1965) described and figured the call (as *L. sibilator*) based on specimens from northern Argentina (Provincia de Chaco) and Mato Grosso, Brasil. At 23°C, call duration = 0.2 sec; repetition rate = 60/min; dominant frequency of 800-2800 Hz with frequency modulation and well defined harmonics. Our audiospectrograms at 21.3°C, from Embarcacion, Salta, Argentina, are nearly identical to those described by Barrio (1965). The harmonic structure apparent in both sonograms is artifactual. The call is a single partially pulsed note with amplitude modulations at 25% of sustained amplitude producing 4-5 pulses of almost equal duration. Duration of the entire note is 160-170 msec. There is a smooth frequency sweep from 100 Hz-2400 Hz through the note (Fig. 2).

Leptodactylus gracilis

Barrio (1965) described and figured the call from eastern Argentina. At 21°C it consists of a single note: duration = 0.1 sec; repetition rate = 240/min; frequency sweeps rapidly from 500-2400 Hz through the call.

Leptodactylus labialis

The call is based on analyses of ten consecutive calls of 17 individuals recorded at 25±1°C from nine separate localities within the province of Guanascaste, Costa Rica: duration = 0.2 sec; repetition rate = 104/min.

The internal structure of the call can best be defined as two notes separated by an extremely short time gap of approximately 3 msec and a broken sound production phase of another 3 msec. The first note is the longest (170 msec versus 23 msec) and is pulsatile, consisting of 24-29 pulses. Pulse repetition rate averages 153 p.p.s. (range 141-167) at 25°C. Pulse length is usually 7 msec and amplitude modulation is complete. The first three to five pulses and the last two or three are shorter (4-6 msec) and at lower amplitude with less complete modulation. This note has almost perfect tone beginning at ca. 1000 Hz and rising slowly to 1100 Hz at the end.

The second note follows after a 6 msec delay of silence and garbled noise. It is not pulsed, and is 23 msec long. The frequency of this note is about 1700 Hz giving the call a distinct terminal ping (Fig. 3).

Fouquette (1960) and Heyer (1971) described and figured the call of specimens from Texas and Panama. Average note duration for both populations was 0.2 seconds; repetition rate varied from 72 (Panama) to 114 (Texas)/min; dominant frequency varied from 600-1200 Hz (Texas) to 1000-2200 Hz (Panama); notes were frequency modulated and had two apparently well defined harmonics. Frog calls recorded from near Cuatro Caminos, Michoacan, Mexico are intermediate in dominant frequency between the Texas and Panama samples, ranging from 730-1600 Hz.

Leptodactylus latinasus

Barrio (1965) described and figured the call (as *L. prognathus*) based on specimens from the provinces of Buenos Aires and Chaco in Argentina. Calls from both localities were similar: duration = 80 msec; single note frequency modulated; dominant frequency range 3000-3500 Hz (Provincia de Buenos Aires, 26°C), 3500-4000 Hz (Provincia de Chaco, 20°C); repetition rate 180/min (Chaco), 300/min (Buenos Aires). Ten calls of each of two specimens from Embarcacion, Salta, Argentina at 22°C have very similar calls; duration = 64 msec; repetition rate = 140/min; frequency is swept smoothly through the note from 3100 Hz-3700 Hz. Their single note call is almost pulsatile with low amplitude modulation — the overall amplitude envelope is fusiform (Fig. 4).

Leptodactylus melanonotus

The following call characteristics are based on the consecutive calls of 25 individuals all recorded at 25±1°C at five locations within the province of Guanacaste, Costa Rica:

The call is a single explosive short yet compound note repeated rapidly but irregularly at an average of 150-160 calls/min. The minimum time between calls in a sustained period of calling averages 0.2 sec.

The internal structure resembles somewhat the second part of the call of *L. labialis* (i.e., the initial three msec of untuned white noise and a pulse of 23 msec of well tuned frequency). The note may be regarded as having two parts which are produced by one explosive stream of air over the vocal cords (i.e., a single pulse). The change in frequency tuning may be due to a jump in tension of the vocal cords part way through the pulse. This call pattern of a single pulse is consistent over the Pacific coast lowlands. The first part is almost white noise with a lower limit of 1100 and upper limit of 2600 Hz, and a slight peak in power at 2200 Hz. It occupies the first one fourth of the pulse (7-8 msec). The well-tuned second part (23-26 msec) starts at 2400 Hz and drops smoothly to 2000 Hz. Duration ranges from .03 sec to .04 sec at 25°C and has an explosive popping quality (Fig. 5).

Fouquette (1960) described and figured the call based on specimens from western Mexico and Panama; Heyer (1970) described and figured the call, and commented on variation in western Mexico. In the Mexican and Panamanian samples, duration varied from .04 to .09 sec, repetition rate was constant at 166/min; dominant frequency (2000-3000 Hz) and full spectral range (50-8000 Hz) were also consistent.

Leptodactylus mystaceus

Barrio (1965) described and figured the call of a specimen from Província de Chaco, Argentina (24.5°C): duration = 0.3 sec; repetition rate = 120/min; dominant frequency 700-1500 Hz; well defined harmonics; and frequency modulated. Sonograms of recent recordings from Finca los Alicangaros, Caquetá, Colombia and Limoncocha, Napo, Ecuador, are similar among themselves and differ from the Argentine sonogram. Calls recorded between 23 and 25°C have: mean duration = 0.14 sec; repetition rate = 128/min; dominant frequency 920-1718 Hz; and weakly differentiated harmonics. The notes are frequency modulated, but the rise in frequency occurs continuously through each note rather than rapidly in the middle of the note as depicted in Argentine calls. Differences between the audiospectrograms from northern and southern South American frogs are striking. In northern calls, the single note is pulsatile with 13-15 pulses which are similar except for the last. The amplitude envelope of each pulse is elliptical, 7-11 msec in duration, pulse repetition rate is 80-90 p.p.s. The last pulse lasts 23-32 msec with a partial modulation at 10-15 msec. The frequency of each pulse is well tuned without harmonic structure. Frequency increases from pulse to pulse through the call from 925 Hz at the beginning to 1460 Hz at the end (Fig. 6).

Leptodactylus mystacinus

Barrio (1965) described and figured the call of a specimen from the Província de Cordoba, Argentina, recorded at a temperature of 20.5°C. The calls were a single note with a duration of 0.1 sec; repetition rate of 300-400/min, and dominant frequency of 2200-2500 Hz.

Leptodactylus ocellatus

Barrio (1966) described and figured the call of specimens from the province of Santa Fé, Argentina (19.5-20°C): duration = 0.4 sec; dominant frequency = ca. 100 Hz; 8 to 10 moderately to poorly differentiated harmonics; and weak frequency modulation. Specimens from Utinga, Pará, Brasil, display similar calls but with shorter duration. The call consists of a single prolonged note with a mean duration of 0.27 sec which is partially pulsatile. The envelope is fusiform with maximum amplitude at 100 msec and slight modulations at 80, 120, and 200 msec. Frequency falls off through the call in discrete steps rather than in a steady sweep. The carrier frequency is virtually sinusoidal, starts at 1000 Hz and drops to 930 Hz at 80 msec, 860 Hz at 120 msec, 710 Hz at 200 msec and 630 Hz at the end. The apparent harmonic or overtone structure in sonograms is due to partial pulsing.

Leptodactylus pentadactylus

The call is based on 14 individuals (10 consecutive calls each) from a single population at Rincon de Osa, Província de Puntarenas, Costa Rica: duration = 0.26 to 0.28 sec. Repetition rate is irregular and reaches a maximum of 35/min. The single note has 9-11 well defined pulses and additional weak pulses at beginning and/or end. Amplitude modulation is rarely complete but always greater than 50%. The pulses vary in length from 21-30 msec tending to increase through the call. Pulse repetition averages 40 p.p.s. (5 individuals at 25±1°C) but slows slightly through the note. Frequency changes upward with each pulse from 200 Hz at the beginning to 600 Hz at the end of the note.

Fouquette (1960) described and figured the call from a specimen from Panama recorded at approximately 23°C: duration = 0.27 sec; repetition rate = 31/min; dominant frequency 200-450 Hz; weakly defined harmonics; and frequency modulation. Two notes of a frog from Santa Cecília, Napo, Ecuador, at a temperature of 23.5°C differ only in having dominant frequency of 425-800 Hz (Fig. 7).

Leptodactylus podicipinus

Barrio (1965) described and figured the call of a specimen from the Província de Santa Fé, Argentina (21.5°C). The single note had an approximate duration of 0.1 sec, repetition rate of 210 notes/min, a broad dominant frequency component of 500-3000 Hz, and no frequency or intensity modulation.

Leptodactylus poecilochilus

Fouquette (1960) described and figured the call (as *L. quadrivittatus*) of a specimen from Panama (27°C). The call is a single note of mean duration 55 msec, repetition rate of 102/min, fundamental frequency of 350-550 Hz, several well-defined harmonics, and frequency modulation. Frogs from Guanacaste Province, Costa Rica, produce similar sonograms with slightly longer notes (mean = 80 msec). The note is non-pulsatile and sweeps smoothly from a beginning frequency of 700 Hz to 1300 Hz at the end without harmonic structure.

Leptodactylus syphax

Bokermann (1969) described and figured the call of a specimen from Chapada dos Guimarães, Mato Grosso, Brasil (28°C). The call is a single note with a duration of approximately 0.1 sec, a repetition rate of 55-70/min, dominant frequency of from 1500-3200 Hz, well-defined harmonics, and frequency modulation.

Leptodactylus wagneri

Calls from four different origins are distinctive, so are described separately. The call of a specimen from Belém, Pará, Brazil (29°C), is a single note of duration 0.09 sec, dominant frequency of 1000-3400 Hz with most energy between 2900-3200 Hz. There are two weakly differentiated harmonics, one of 5300-5900 Hz, and the second at 7700-8300 Hz. Four calls of a specimen from Rancho Grande Research Station, Aragua, Venezuela (23°C), have a mean duration of 0.13 sec, repetition rate of 54/min, a broad frequency response of 1175-3450 Hz with most energy between 2800 and 3100 Hz. Two calls display weakly defined harmonics, one between 4900-5500 Hz, the second at 7000-7750 Hz. Four calls of a specimen from Santa Cecilia, Napo, Ecuador (23°C), have an average duration of 0.09 sec, repetition rate of 54/min, a broad frequency bandwidth of 925-3175 Hz with the greatest energy between 1900-2600 Hz and two weakly defined harmonics one at 3700-4700 Hz and a second at 5200-6500 Hz. Twenty-one calls from three specimens from Limoncocha, Napo, Ecuador (24-25°C), have a mean duration of 0.03 sec, a repetition rate of 96/min, a restricted frequency bandwidth of 1097-1676 Hz; some notes have a faint harmonic from 1900-2100 Hz, to 2600-3000 Hz. No calls are intensity modulated. The note is a single pulse of 17 msec duration with an elliptical amplitude envelope. Frequency is swept very rapidly from below 1000 Hz to 1200 Hz within the pulse (Fig. 8).

Vanzolinius discodactylus

A call consists of a series of notes repeated frequently. Analysis of 14 notes from a single individual indicates that each note has a mean duration of 0.07 sec, a mean repetition rate of 60/min; dominant frequency range from 2580±131 to 3407±142 Hz. No harmonic structure is present and the note lacks frequency modulation (air temperature = 23.4°C, water temperature = 23.6°C). The fine structure of each note is unlike that of any other species of the *Leptodactylus* complex examined. The note is initiated by a slow rising pulse of 11-15 msec which is poorly tuned and ill-defined in frequency. This is followed by a better tuned portion (ca. 3000 Hz) broken by 13 to 15 amplitude modulations varying within each note between 20% and 100% (Fig. 9).

Heyer & Bellin (1973) discussed the correlation of calling frequency with heavy rains in this species.

Mating call patterns

Four factors must be taken into account in analyzing mating call patterns: 1. the sound production mechanism; 2. the sound reception mechanism; 3. the environment the sound is being produced in exclusive of other animal sounds; and 4. the other animal sounds in the environment, particularly from closely related species. Each of these aspects will be examined and generalizations drawn for the species discussed here.

Frogs produce calls by passing air over the vocal cords located in the larynx. The resultant sound will have a fundamental frequency component dependent on the mass and tension of the cords. This is often the same as the dominant frequency (Martin, 1972). The sound is amplified to a degree by resonance in the buccal cavity and radiated through the floor of the mouth or the vocal sacs. All adult male *Leptodactylus* have vocal sacs, but they range from a internal condition with virtually no modification of the floor of the mouth, to paired vocal sacs which are thin walled ballon-like extensions of the floor of the mouth. In frogs with internal vocal sacs, the frequencies that originate from the vocal cords will be least modified when radiated, and will not be greatly amplified. In those with well developed external vocal sacs resonance in these air chambers further amplifies the sound. Also, the frequency spectrum can be modified because the vocal sac is itself a resonance chamber which vibrates at its own natural frequency that may differ from vibrations of the vocal cords. The fundamental frequency then becomes merely the originating sound for the resonance chamber and may be lost in the final call. When well developed vocal sacs are involved the resultant sounds have well-tuned frequencies and high intensity. Further modification of calls can come from passage of air over the vocal cords in two ways. First, a burst of air can be explosively forced through the vocal cords which results in poor tuning and a pulse of broad frequency noise. Secondly, a steady stream of air can be passed over the vocal cords causing vibrations of the elastic cords which give the fundamental frequency. Martin (1972) has experimentally shown that in *Leptodactylus* with frequency modulated calls, such as *L. fuscus*, the rise in fundamental frequency is due to contraction of laryngeal muscles changing the tension of the vocal cords. In the production of specific notes in some species such as *L. labialis* the glottis is closed until pressure due to body wall muscle tension reaches a critical level and it then opens. This produces an initial explosive pop of noise followed by a steady flow of the basic note.

The female sound reception mechanism must be able to distinguish male calls from other environmental sounds. Straughan (1973) indicates that in species that have been experimentally tested the female auditory apparatus is most sensitive to very low frequencies and frequencies corresponding to the dominant frequency emitted by males of the same species. Lombard & Straughan (1974) have shown that this is also true for *L. melanonotus*. Straughan (1973, 1975) suggested the frequency component of the call is directed toward channelization of species specific sounds to avoid interference.

According to Straughan (1973) the optimum type of sound with respect to locating the sound source by frogs is a pulse of "white" noise repeated at frequent intervals. In contrast, a sound source of narrow band intermediate frequency, which fades in and out, and is sporadically produced, would be very difficult to locate. The mating calls of *Leptodactylus melanonotus, podicipinus,* and *wagneri* come very close to the optimum sound for maximum localibility. These species have internal vocal sacs and thus are not able to amplify the call to any great extent. In order for frog calls to be amplified, the frequency response must be narrowed. Low frequencies travel much further than higher frequencies, but high frequencies are easier to locate than low frequencies (Konishi, 1970). One compromise to the problem of maximizing both amplification and a broad dominant frequency response is to modulate frequency over a very short time span. Several species of *Leptodactylus* use this compromise.

The final consideration in female sound reception is distinguishing the proper male sound source which must be distinctive, including a critical difference from any mating calls of a closely related species. Five or six species of *Leptodactylus* occur sympatrically over broad geographic areas. Not all species call at the same time, however. The female auditory apparatus is able to distinguish two components of the calls: 1. the dominant frequency, as discussed previously, and 2. the time component, which in the case of *Leptodactylus*, is the duration of an individual note or the pulse repetition rate of pulsatile calls.

Comparison of the mating calls of different *Leptodactylus* species that are calling at the same time in the same place should indicate how the sound environment is partitioned. Data are available for only a few localities.

At Embarcación, Salta, Argentina, *Leptodactylus bufonius, L. fuscus* and *L. latinasus* were actively calling on the same nights in similar microhabitats. All three species have well tuned frequency modulated calls. The call of *L. latinasus* does not overlap the other two species in dominant frequency and can be regarded as being in a separate sound channel. The dominant frequency of *L. fuscus* (1100-2600 Hz) completely includes the dominant frequency of *L. bufonius* (1350-2025 Hz). The calls of *L. bufonius* and *L. fuscus* are quite similar, however, in having a mean note duration of 0.15 sec (*bufonius*) and 0.17 sec (*fuscus*) note repetition rate of 54/min (*bufonius*) and 75/min (*fuscus*). The *L. bufonius* call is composed of two notes, each non-pulsed, the *L. fuscus* call is partially pulsed. Male *L. fuscus* modulate the frequency from 1350 to 2025 Hz (the range of the *L. bufonius* call) in 0.05 sec, which contrasts with the 0.15 sec that male *L. bufonius* modulate the same frequency range. The combination of different pulse structures and effective call duration allows discrimination by females.

At Limoncocha, Napo, Ecuador, *V. discodactylus*, *L. mystaceus* and *L. wagneri* call at the same time, but (male) interaction is avoided since each species calls from distinctive microhabitats (Heyer & Bellin, 1973). Individual females still need to discriminate because they pass by calling males of other species on the way to conspecific breeding assemblages. Calls of all three species are distinctive in dominant frequency. Depending on the sharpness at frequency filtering in the ear, these species operate in different acoustic channels. However, channelization is not complete, and differences of pulsation, note duration, and frequency modulation provide species specific information suitable for discrimination.

In Costa Rica and Panama, several species occur sympatrically. At some localities six species form complex assemblages. *L. poecilochilus* is spatially separated from the others, but the other five species call at the same time from the same general habitat. The calls are to some extent frequency stratified as follows: *L. pentadactylus*, 200-600 Hz; *L. bolivianus*, 400-1300 Hz; *L. labialis*, 1000-1300 Hz; *L. melanonotus*, 2400-2000 Hz. Overlap in frequency between *L. bolivianus* and *L. labialis* above and *L. pentadactylus* below can be tolerated because both the latter have pulsed notes whereas *L. bolivianus* has a single continuous note. However, at Rincón, Osa Peninsula, Costa Rica, spatial separation between *L. labialis* and *L. bolivianus* within the same habitat is apparent.

Knowledge of call mechanisms and environmental constraints is sufficient to recognize two mating call patterns in *Leptodactylus*. The first pattern may be described as a quiet-popping call. A short burst of air is forced through the vocal cords producing a call of not well defined frequency. It is altered little by buccal and vocal sac chambers and is therefore not strongly amplified. Field observations on such species as *V. discodactylus* and *L. wagneri* (Heyer & Bellin, 1973) indicate that frogs with this pattern call during or immediately after heavy rains from shallow water. Species with this type of call are riparian, so males and females are already present in the microhabitat when breeding conditions are favorable. Females need only be attracted over short distances. There are two subpatterns. In the first, the calls are not pulsed. Included in this subpattern are *L. melanonotus*, *L. podicipinus*, and *L. wagneri*. A second subpattern consists of a complex pulsation of the call with frequency or intensity modulation. Tentatively included in this latter subpattern are *V. discodactylus*, *A. hylaedactyla* and *A. marmorata*.

The second pattern may be described as a rising (or falling) type of call. The sound production mechanism is a stream of air passing between the vocal cords, setting up vibrations of the cords, with greater (or lesser) tension being applied to the cords by contraction or relaxation of the laryngeal muscles. Often the fundamental frequency is amplified and modified by expanded vocal sacs. There are several subpatterns of this basic call type.

Several species have a loud rising call. The call of *L. mystaceus* in an example, in which the male calls away from standing water attracting females from considerable distances, and calling is more independent of specific climatic conditions than in *L. wagneri* (Heyer & Bellin, 1973). The call is either non-pulsed (*L. bufonius*), partially pulsed (*L. fuscus*, *L. latinasus*) or completely pulsed (*L. labialis*, *L. mystaceus*, *L. pentadactylus*). The pulsatile condition is not known for *L. gracilis*, *L. mystacinus*, or *L. syphax*, which have loud calls.

Some species have a quiet-rising or falling call. The call is either rising and non-pulsed (*L. bolivianus*, *L. poecilochilus*), or partially pulsed and rising and falling (*L. ocellatus*). The pulsatile condition of the call of *L. chaquensis* is not known. The ecological significance of this type of call is not known. *L. bolivianus*, *L. chaquensis*, and *L. ocellatus* call from grassy pond edges or marshes, but *L. poecilochilus* calls from the banks of small ponds.

Mating calls and species relationships

All species reported upon were recently included in the genus *Leptodactylus*. Generic and species group partitioning were based primarily on morphological evidence (Heyer, 1974a, 1974b). Therefore it is of interest to compare the interrelations based on morphology with the results of functional call analysis. The composition of the groupings with the species for which the calls are known are: *Adenomera* — *hylaedactyla*, *marmorata*; *Leptodactylus* — *melanonotus* group, *melanonotus*, *podicipinus*, *wagneri*; *ocellatus* group, *bolivianus*, *chaquensis*, *ocellatus*; *pentadactylus* group, *pentadactylus*, *syphax*; *fuscus* group, *bufonius*, *fuscus*, *gracilis*, *labialis*, *latinasus*, *mystaceus*, *mystacinus*, *poecilochilus*; *Vanzolinius* — *discodactylus*.

Certain of these morphological groupings demonstrate a concordance with mating call patterns. The *melanonotus* group members all have non-pulsed quiet-popping calls. *Vanzolinius* has a partially pulsed quiet-popping call; further analysis will have to be done to determine whether *Adenomera* calls are functionally the same as the *Vanzolinius* call.

All species of the *fuscus*, *ocellatus*, and *pentadactylus* groups have a rising or falling type of call; however, call types within this general pattern with species groupings are inconsistent. Most members of the *fuscus* group have loud rising calls, but *L. poecilochilus* is an exception. Members of the *ocellatus* group are all quiet callers, but the call may be non-pulsed or partially pulsed. It appears that convergences in call have occurred among the members of the *fuscus*, *ocellatus*, and *pentadactylus* groups.

Several members of the *fuscus* group have developed pulsatile calls — most noticeably in the widespread species *L. labialis* and *L. mystaceus* which are sympatric with different congeners in different parts of their range. This temporal pattern provides species specific information for recognition in situations where separation into distinct frequency channels in lacking. In the sense of Straughan (1973), the *melanonotus* group has the most primitive call type in which no two species can call at the same time and place because the calls are basically only location calls and there would be no discrimination. *Fuscus* group calls are channelized so that several species can call together without interference. Advanced calls in this group and in *pentadactylus* are pulsatile.

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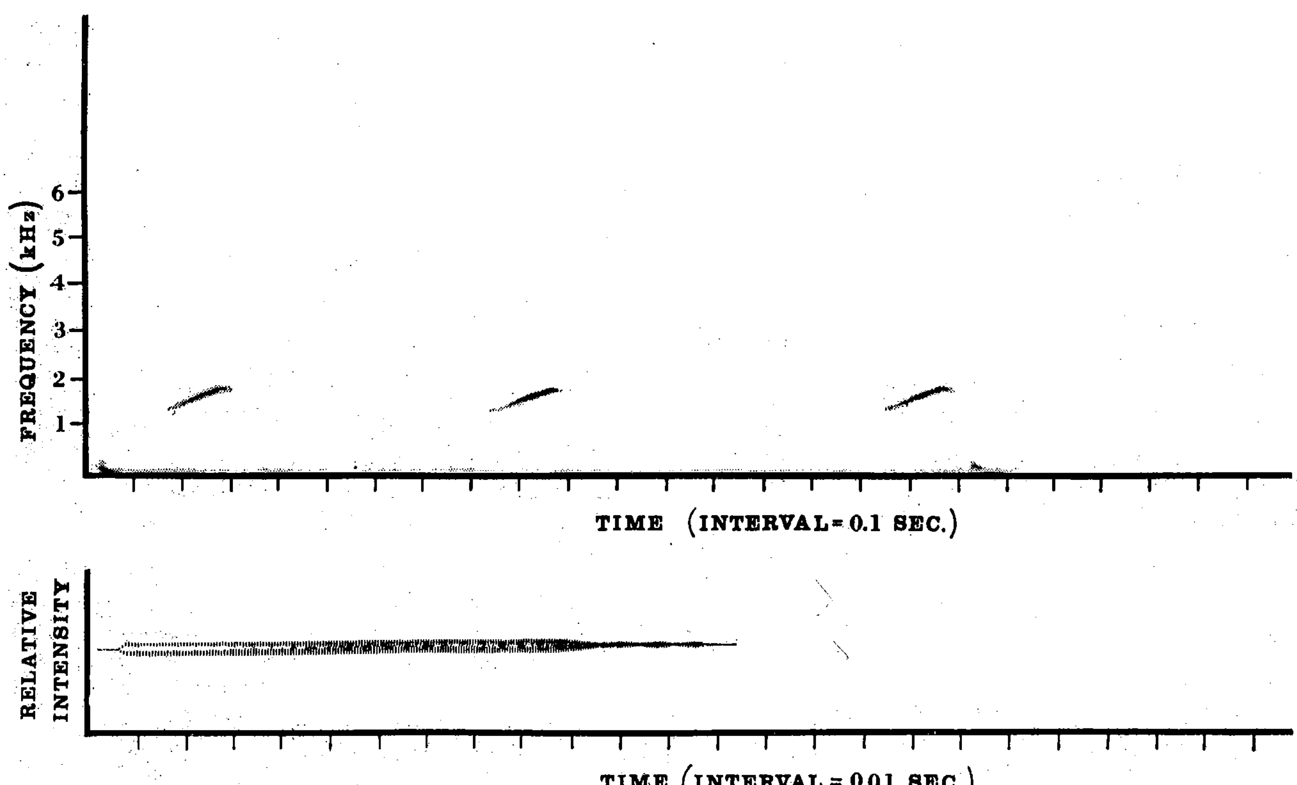

Fig. 1. Sonogram of calls of *L. bufonius* (above) and oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

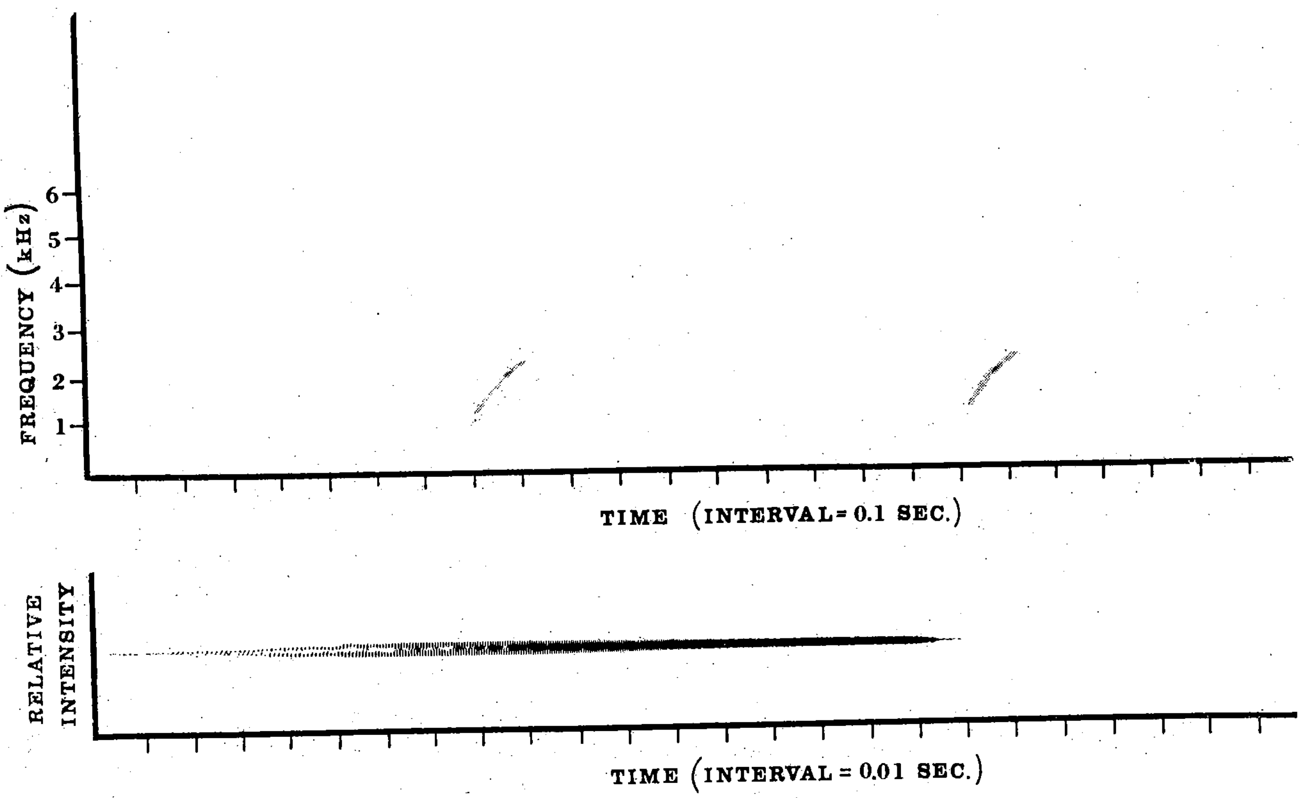

Fig. 2. Sonogram of a series of calls of *L. fuscus* (above) and oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

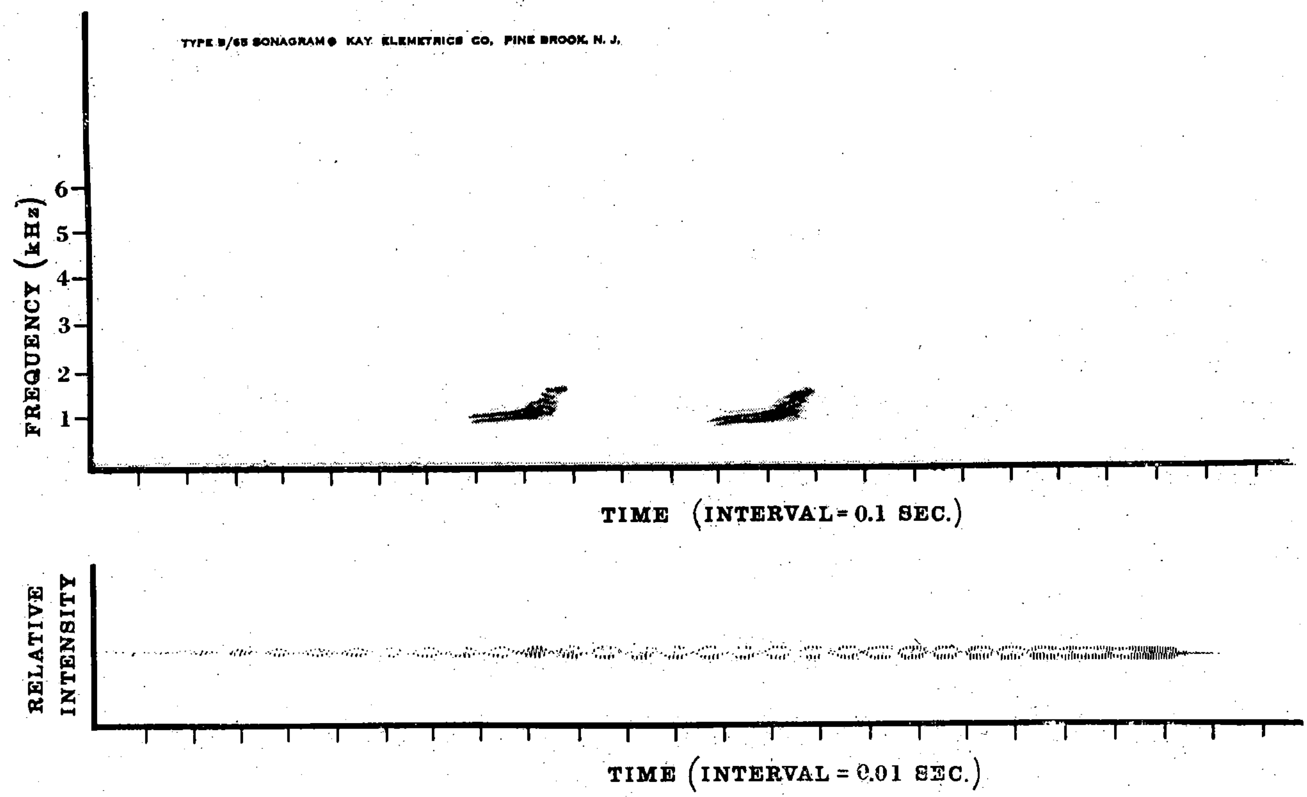

Fig. 3. Sonogram of a series of calls of *L. labialis* (above) and an oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

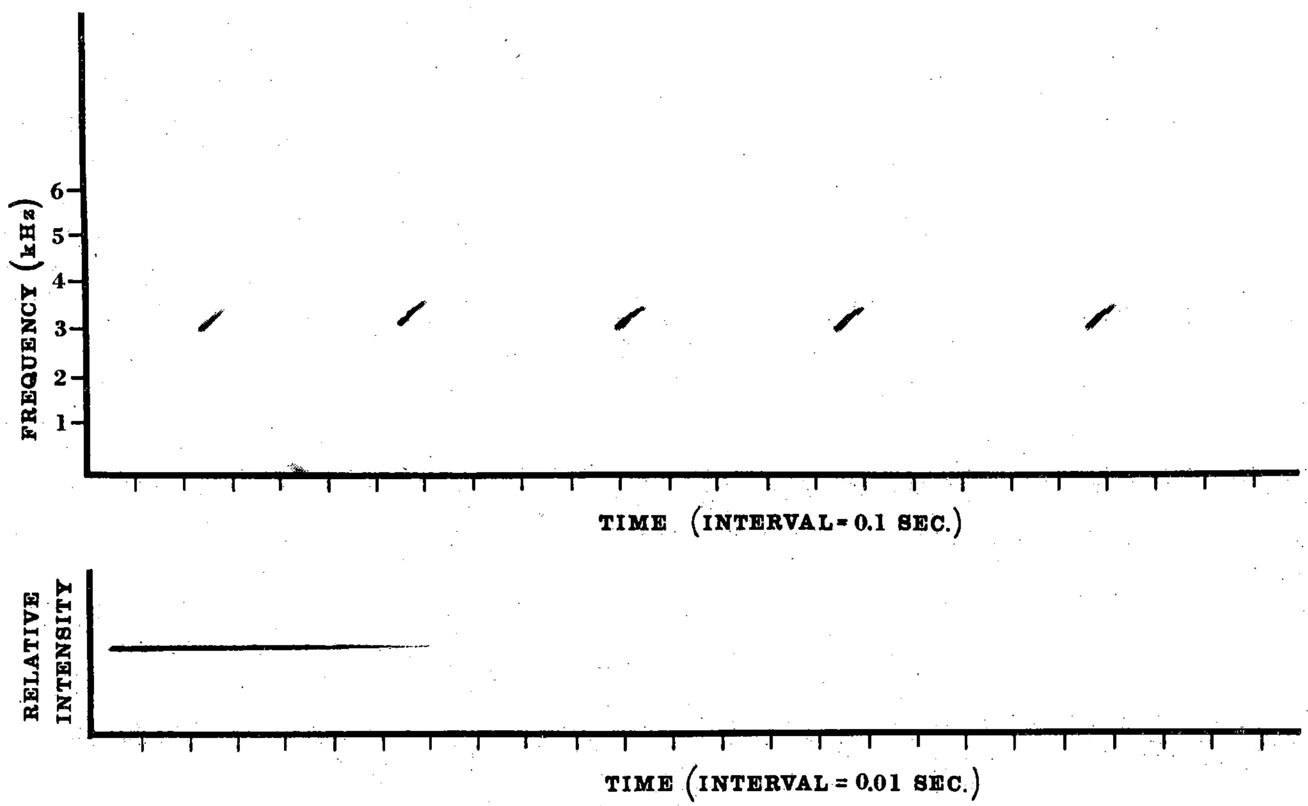

Fig. 4. Sonogram of a series of calls of *L. latinasus* (above) and an oscilloscope trace a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

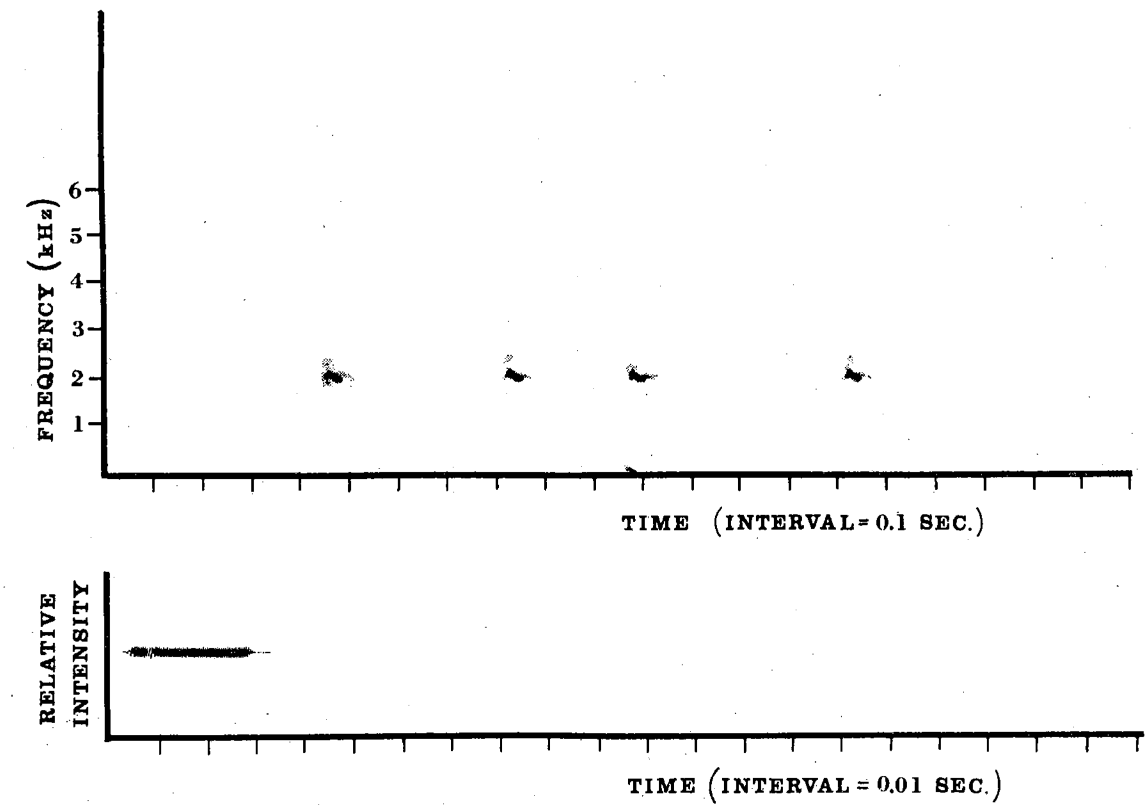

Fig. 5. Sonogram of a series of calls of *L. melanonotus* (above) and an oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

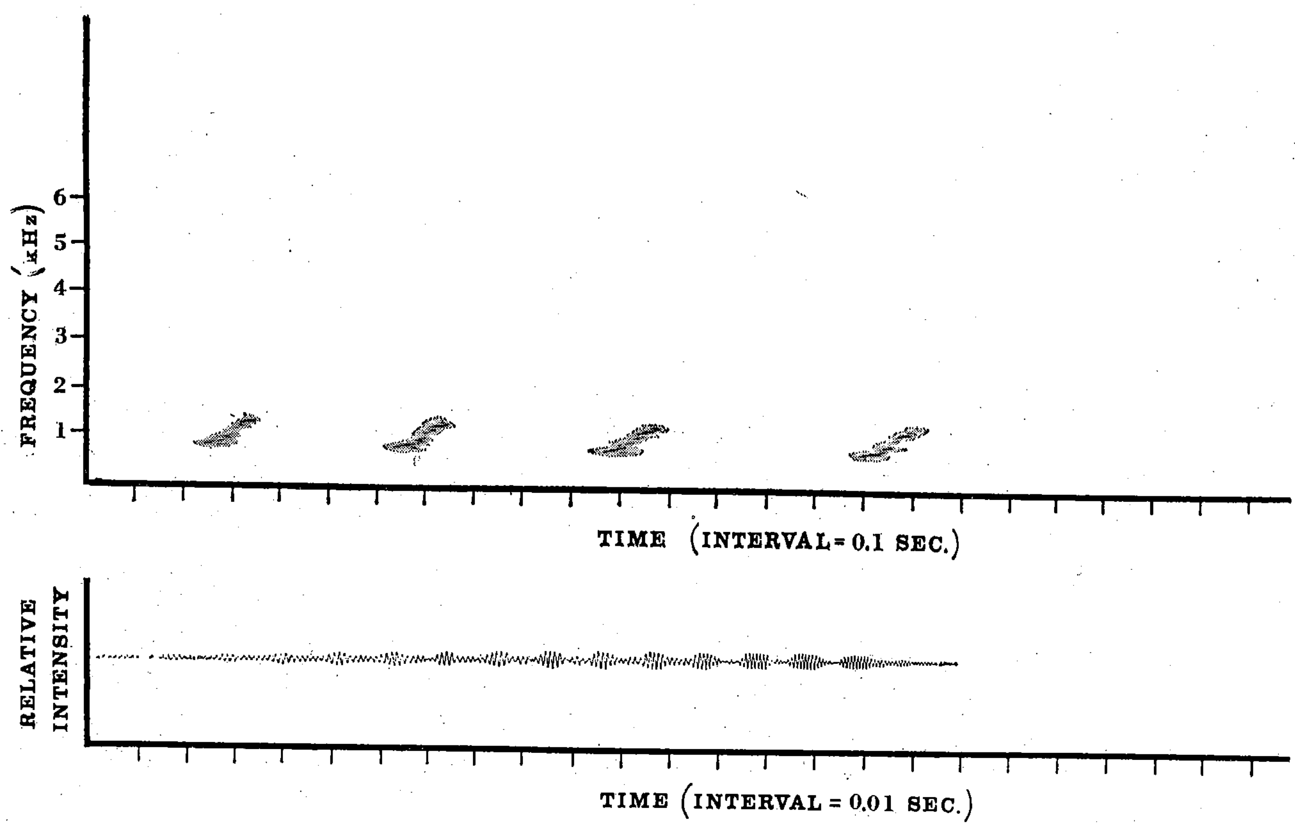

Fig. 6. Sonogram of a series of calls of *L. mystaceus* (above) and an oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

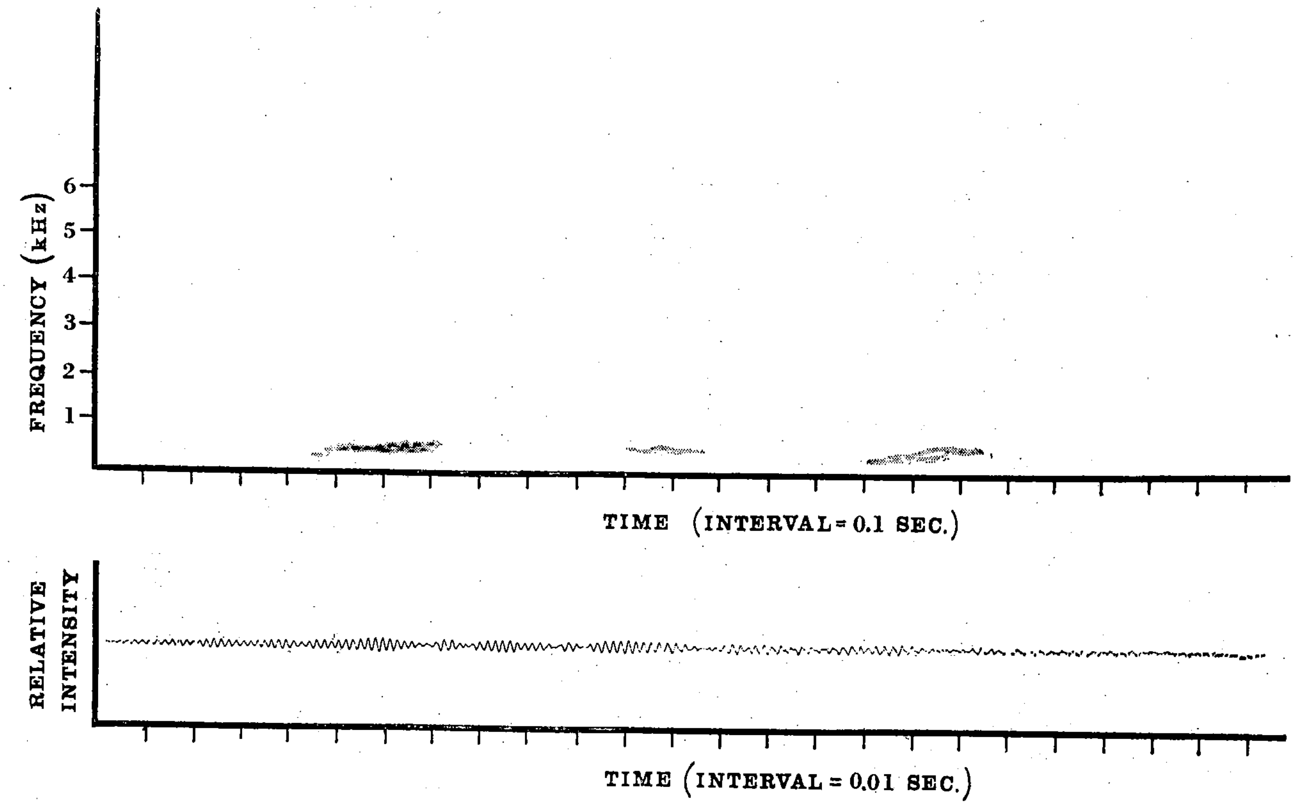

Fig. 7. Sonogram of a series of calls of *L. pentadactylus* (above) and an oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

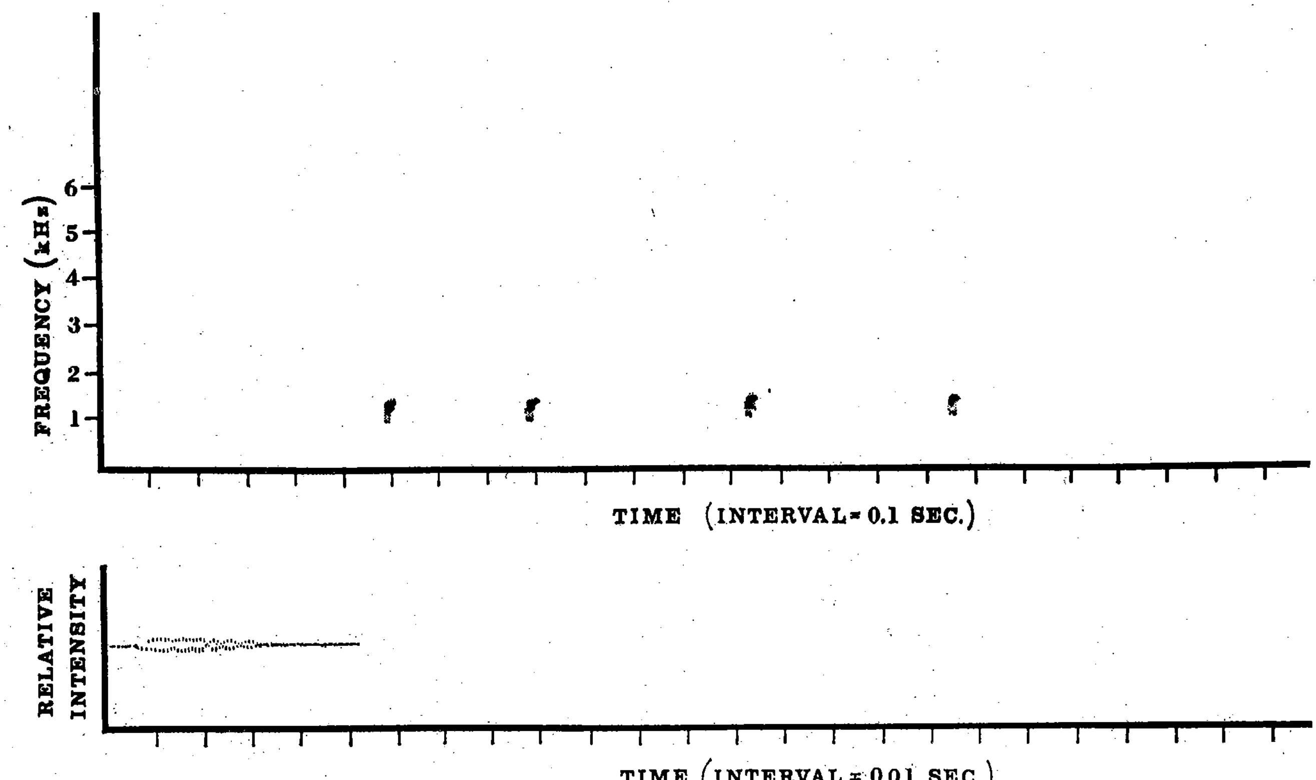

Fig. 8. Sonogram of a series of calls of *L. wagneri* (above) and an oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.

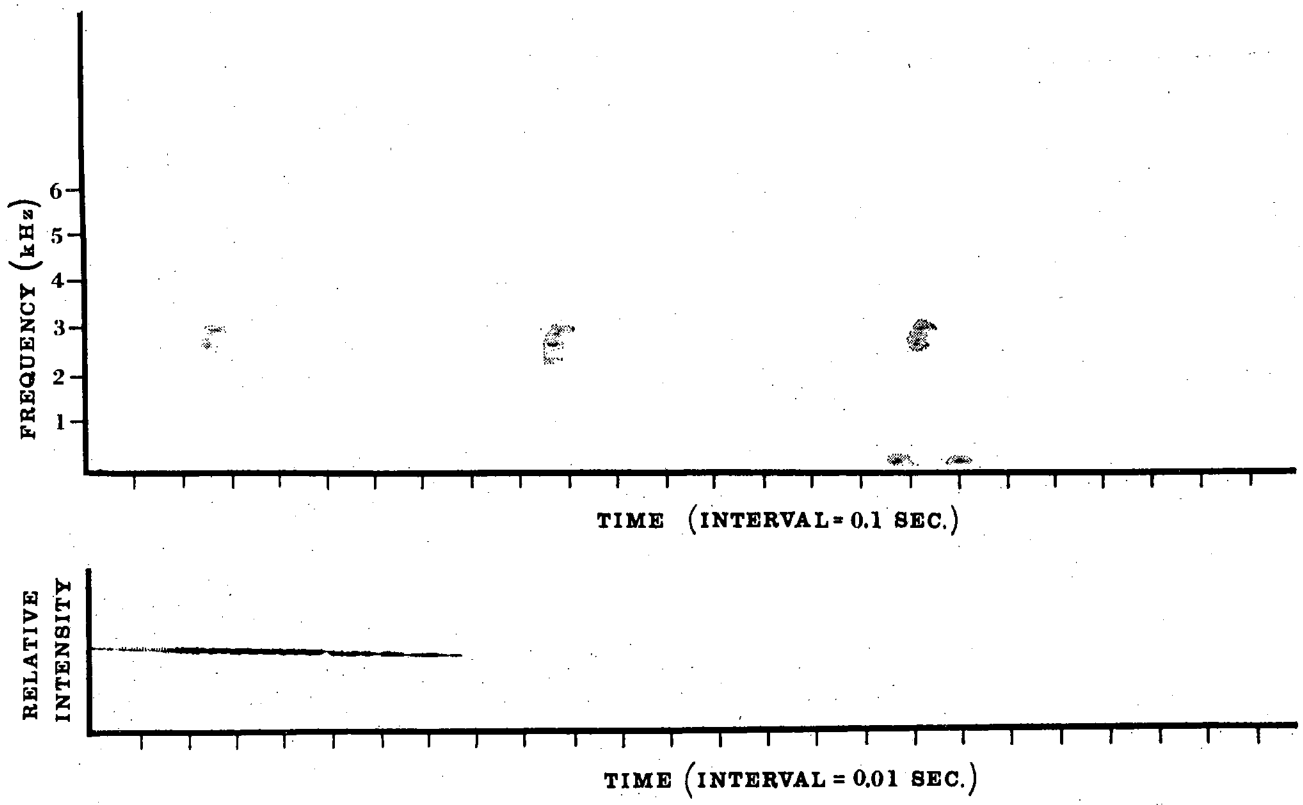

Fig. 9. Sonogram of a series of calls of *Vanzolinius discodactylus* (above) and an oscilloscope trace of a single call at 10x speed to show the amplitude (relative intensity) pattern with time.