Advertisement, aggressive, and possible seismic signals of the frog *Leptodactylus syphax* (Amphibia, Leptodactylidae)

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Advertisement calls from three geographically isolated populations of *Leptodactylus syphax* are remarkably similar. Aggressive calls of *L. syphax* sound to the human ear very different from the advertisement calls, although the basic structural components are similar. A male *L. syphax* responded with aggressive calls to a playback of his own advertisement call. The same male responded to playbacks of his aggressive calls with increased rate of aggressive calls and foot pounding behavior. The foot pounding produced audible clicks and, by its nature, seismic signals. This is the second known instance of *Leptodactylus* species producing seismic signals, each produced differently, however. It is not known whether *L. syphax* interprets the seismic signals. Seismic signalling in frogs may be much more common than currently believed.

Introduction

Leptodactylus syphax Bokermann, 1969 is restricted to rocky granitic outcroppings and is known from a few disjunct, widely separated, localities in Brazil (fig. 1). The first author recently recorded calls from three of these disjunct populations. We analyze the advertisement calls of the frogs from these three populations to determine whether there is any significant variation among them. At one locality, the first author was fortunate to observe and record *Leptodactylus syphax* aggressive calls and foot-pounding behavior. The foot-pounding may involve seismic communication, previously reported for the first time in frogs by Lewis & Narins (1985). We describe and comment on all of these calls and behaviors.

Fig. 1. – Known distribution of *Leptodactylus syphax* in South America. Triangles: sites from which recordings are analysed in this paper (westernmost triangle: Barra do Bugres, Mato Grosso State; northernmost triangle: São Raimundo Nonato, Piauí State; southernmost triangle: Alpinópolis, Minas Gerais State). Square: site from previously published recording by W. C. A. Bokermann (Chapada dos Guimarães, Mato Grosso State). Dots: other known localities (note that southernmost dot, the locality of Serra do Espinhaço, Minas Gerais State, was incorrectly placed in northeastern Brazil in Heyer, 1979, fig. 21).

METHODS AND MATERIALS

Recordings were made using a Uher Report 4000 reel-to-reel tape recorder. The recording information is:

(1) Tape ASN/AJC (Archivo Sonoro Neotropical/Adão J. CARDOSO) 13, cut 6, Brazil, Minas Gerais State, Alpinópolis, Fazenda Salto; no voucher specimen; recorded by A. J. CARDOSO; 11 October 1981; 21.00 hours; 22°C air temperature. Ten advertisement calls are analyzed from this individual.

(2) Tape ASN/AJC 84, cut 2, Brazil, Mato Grosso State, Barra do Bugres, Reserva Biológica Serra das Araras; no voucher specimen; recorded by A. J. CARDOSO; 19 November 1988; 20.30 hours; 26°C air temperature. Sixteen advertisement calls are analyzed from this individual.

(3) Tape ASN/AJC 101, cut 2, Brazil, Piauí State, São Raimundo Nonato, Parna, Serra da Capivara, localidade Caldeirão; voucher specimen ZUEC 8829 (Universidade Estadual de Campinas); recorded by A. J. CARDOSO; 4 March 1990; 20.00 hours; 27.5°C air temperature. Ten advertisement calls, 9 aggressive calls, and 1 foot pounding are analyzed from this individual.

The recordings were analyzed with "Canary" software from the Cornell Laboratory of Ornithology on a Macintosh IIci computer. The sampling rate used to convert the analogue signals to digital format was 22,254.5 Hz with 8-bit precision. Filter bandwidths of 353 Hz and frame lengths of 256 points were used for both audiospectrogram and spectrogram analyses.

Call terminology follows that defined in HEYER et al. (1990).

RESULTS

ALPINÓPOLIS DATA

Three individuals were calling at the recording site. The calling males were separated from each other by a distance greater than 100 m, far from water, in an area characterized by large rocks, among which crevices were abundant. The individual recorded was calling near one of these crevices, into which it fled after being approached to within about 10 m. Only the advertisement call was recorded; no playback was presented to the frog.

The advertisement call (fig. 2 A), is given at an average rate of 0.8 per second. Call duration ranges from 59 to 64 ms. The call is frequency modulated with a rapid rise time; the broadcast frequency range sweeps from 390 to 2110 Hz with maximum broadcast intensity between 1310 and 1330 Hz. The call is strongly partially pulsed, typically with 3 almost completely defined pulses. Harmonics are present (not particularly visible on fig. 2 A, but spectrogram analyses of calls [not shown] indicate their presence).

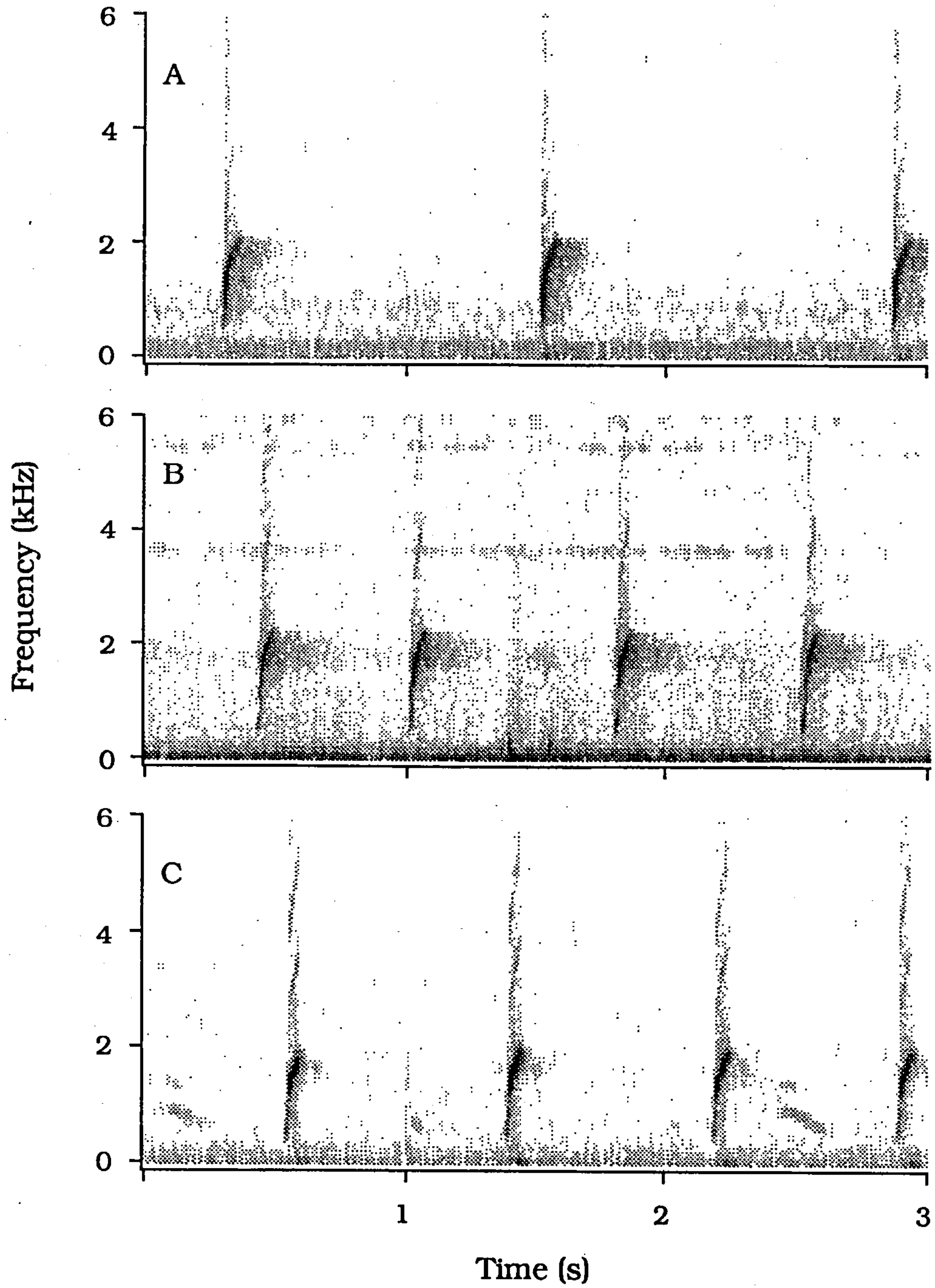


Fig. 2. – Audiospectrograms of advertisement calls of *Leptodactylus syphax*. Upper figure (A) recorded from Alpinópolis; middle figure (B) recorded from Barra do Bugres; lower figure (C) recorded from São Raimundo do Nonato.

BARRA DO BUGRES DATA

A single individual was calling from this locality, which was characterized by large sheets of rock and no water systems obvious in the area. Advertisement calls only were recorded. The individual stopped calling when approached within about 20 m and did not respond to playback of its call when broadcast from near the calling site.

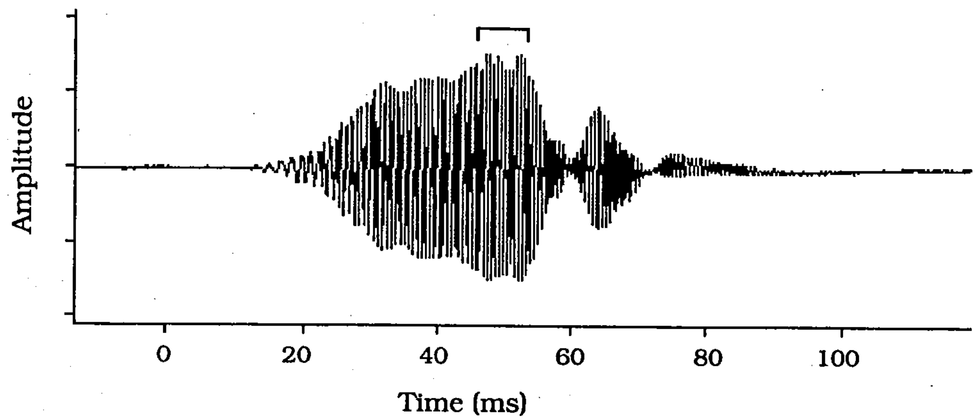
The advertisement call (fig. 2 B) is given at an average rate of 1.5 per second. Call duration ranges from 53 to 60 ms. The call is frequency modulated with a rapid rise time; the broadcast frequency range sweeps from 380 to 2300 Hz with maximum broadcast intensity between 1800 and 1850 Hz. The call is partially pulsed, with 3 to 5 weakly defined pulses (the recording has a low frequency component making precise determination of the number of pulses difficult). Harmonics are present (energy analyses of calls [not shown] indicate their presence).

SÃO RAIMUNDO NONATO DATA

Two individuals were calling at the site, about 200 m from each other. The individual recorded was calling from an extensive horizontal rock fissure. The opening of the crevice was about 30 cm high and 5 m long. The crevice extended about 4 m into the rock wall, on the face of a waterfall, which at the time had little running water.

Initially the advertisement call was recorded without the monitor on, such that the frog did not hear its own voice. At this time, the calling frog was about 4 m from the microphone. After the initial recording was made, the monitor button was engaged and the frog began to hear its own voice from the tape recorder speaker. Immediately after hearing its own voice, the individual started to emit aggressive calls intermixed with advertisement calls and jumped to within about 2 m of the tape recorder. The emissions were given at a very variable rate with considerable irregularity in the bursts of call types. After a while of recording under these conditions, a section of tape with a series of aggressive calls was played back to the frog. On hearing the playback of these aggressive calls, the frog increased its rate of aggressive calls and beat its forelimbs on the ground, thereby causing the foot pounding sound. The tape recorder was then stopped, recording was begun anew with the monitor engaged, such that the frog could hear its own sounds from the tape recorder speaker, including the foot pounding sounds. Soon thereafter, the frog jumped to the side of the tape recorder, emitted various sounds, and abruptly stopped calling. The frog was then collected to serve as a voucher for the recordings.

The advertisement call (figs. 2 C, 3), is given at an average rate of 1.2 per second. Call duration ranges from 56 to 64 ms. The call is frequency modulated with a rapid rise time; the broadcast frequency sweeps from 390 to 2060 Hz with maximum broadcast intensity between 1640 and 1680 Hz. The call is either composed of two extremely well-defined pulses (almost notes), the first with about 3 weakly defined partial pulses, or composed of about 4 weakly defined partial pulses. Harmonics are present.



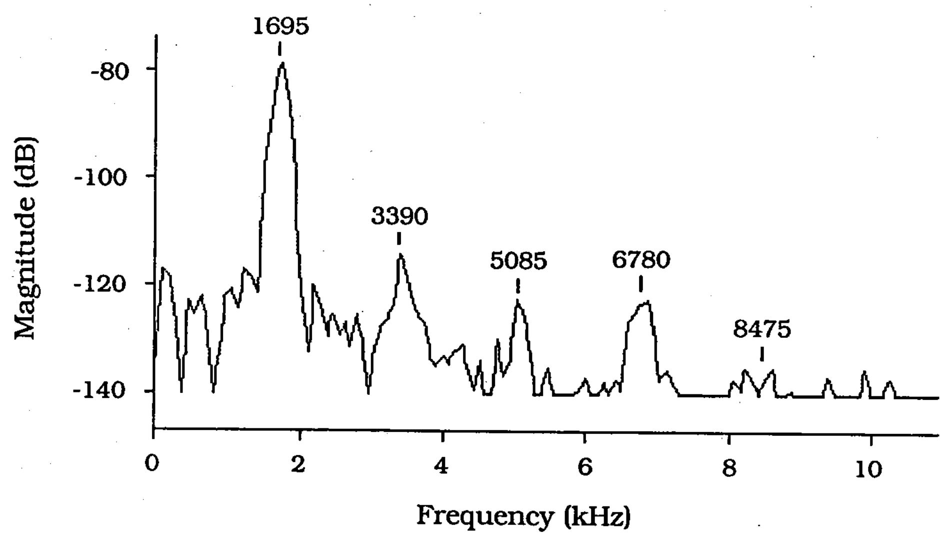


Fig. 3. – Wave form and energy analysis of advertisement call of *Leptodactylus syphax* recorded from São Raimundo do Nonato. Upper figure shows wave form (the pulse above the 80 milliseconds label is interpreted as microphone ringing, not a part of the call); bracket above wave form indicates portion of call used for spectrogram analysis of lower figure.

The aggressive call (figs. 4, 5) is given at an average rate of 0.7 per second. Call duration ranges from 162 to 206 ms. The call is frequency modulated in a complex fashion. There is an initial low intensity fast rise in frequency, the fundamental rising from 220-480 Hz to 920-1010 Hz, followed by a falling frequency, steeper initially, the fundamental from about 920-1010 Hz falling to 310-520 Hz. The call is partially pulsed with about 3 weakly defined pulses. There are at least 3 well-defined harmonics which have about as much broadcast energy as the fundamental.

There is no apparent transition in call when a male switches from advertisement to aggressive calls (and vice versa); the male utters either one kind or the other (fig. 5).

The pounding of the front foot results in a faint, but audible click (fig. 4), that has most energy at about 1800 Hz. Foot pounding, by its nature, produces seismic signals as well.

DISCUSSION

The calls from the three isolated populations of *Leptodactylus syphax* studied are remarkably similar, differing only in details that might be expected to occur among individuals from a single population (see GERHARDT, 1988, for a general discussion and RYAN, 1980, for a specific example analyzing fundamental frequency). The calls reported here are also similar to the call from Chapada dos Guimarães, Mato Grosso State, recorded by Werner C. A. BOKERMANN, previously reported (HEYER, 1979), with one exception. The previously analyzed recording from Chapada dos Guimarães gave very little indication of harmonic structure. However, harmonic structure is evident in the wave forms of the calls analyzed herein (e. g., fig. 3, above), and the spectrogram analysis indicates the presence of at least 3 harmonics in addition to the fundamental frequency (fig. 3, below). These differences in harmonic expression may be due to differences of recording and analytic equipment rather than actual call differences.

The modest differences in advertisement calls among the geographic samples analyzed are somewhat surprising. We do not know whether these similarities may be due to recent isolation of the presently disjunct populations of *L. syphax* or due to selection for stabilization of the advertisement call among all populations.

The advertisement and aggressive calls are very different sounding (and appearing when analyzed) calls. They sound as though they were calls of two different species of frogs. The advertisement and aggressive calls differ in duration and mode of frequency modulation. The calls do share the characteristics of being frequency modulated, having overlapping broadcast frequencies, and having harmonic structure. These similarities suggest that the same physical structural complex is involved in producing both calls and the differences are produced by a combination of behavioral controls regulating the duration of the call and manipulating tension of the laryngeal musculature which causes changes in the tension of the vocal cords resulting in differences of the physical structure of the emissions. These behavioral changes are not trivial, however. LEWIS & NARINS (1985) reported similar results for *Leptodactylus albilabris*. While the advertisement call of

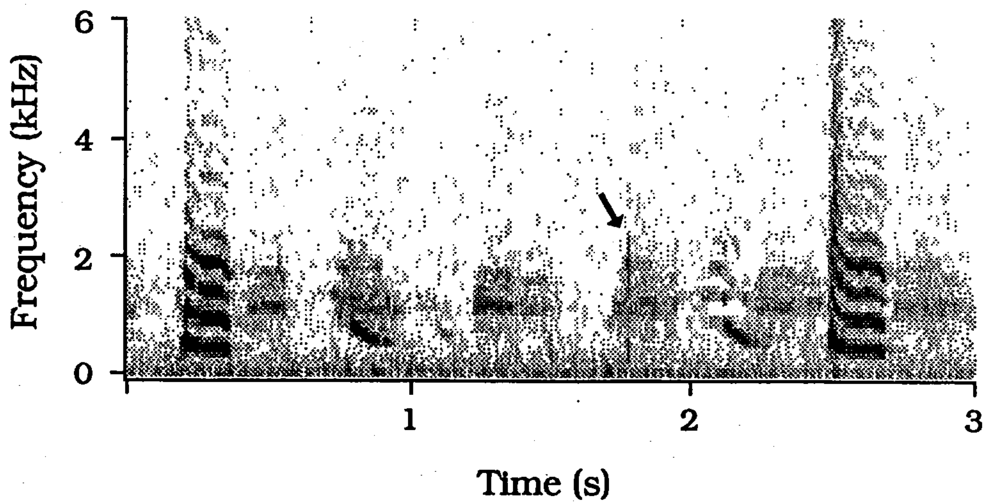


Fig. 4. – Audiospectrogram of two aggressive calls and foot-pounding of *Leptodactylus syphax* recorded from São Raimundo Nonato. The arrow indicates the foot-pounding sound.

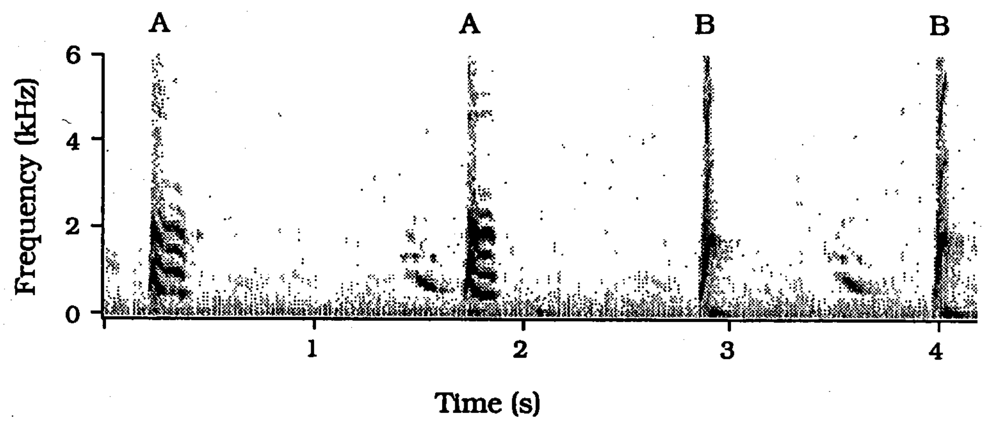


Fig. 5. – Audiospectrogram of continuous recording of a male *Leptodactylus syphax* from São Raimundo Nonato, uttering aggressive calls (A) followed immediately by advertisement calls (B) with no intermediate call structure between the two call types.

L. albilabris is short and rises from 1000 to 2300 Hz, the male-male interaction call is longer and descends from 2300 to 1000 Hz. Perhaps this pattern of frequency modulation reversal and time differences in advertisement and aggressive calls is common to all *Leptodactylus* species with rising whistle-like advertisement calls.

LEWIS & NARINS (1985) and NARINS (1990) reported that *Leptodactylus albilabris* produces and is capable of receiving and interpreting seismic signals. LEWIS & NARINS (1985) speculated that the different arrival times of the simultaneously produced seismic and airborne waves could provide a temporal clue to the distance from the source and could be used to help males establish and maintain territories. NARINS speculated that *L. albilabris* might be able to integrate the seismic and air-borne advertisement calls "to better communicate when high-level background noise obscures the acoustic channel" (NARINS, 1990: 273). This could also pertain to *L. syphax*, as the habitats they call from have noisy waterfalls during rainy periods.

The mechanism for producing seismic signals in *L. albilabris* was reported to be the rapidly expanding vocal sac contacting the ground. *Leptodactylus syphax* produce seismic signals by beating their forefeet on the ground. In contrast to the seismic signals of *L. albilabris*, which are not audible to the human ear, the foot pounding of *L. syphax* is weakly audible to the human ear, and is certainly within the frequency range of the advertisement call of *L. syphax*. We assume the audible nature of the foot pounding of *L. syphax* is possibly due to the presence of horny spines on the inner thumb of the male. In contrast to *L. albilabris*, the seismic signals made by *L. syphax* are not produced simultaneously with advertisement or aggressive calls. We do not know whether *L. syphax* is processing the air-borne click portion of the foot-pounding, the seismic signals, neither, or both. However, we report here the second known instance in frogs producing seismic signals, both within the genus *Leptodactylus*, but by very different methods. Obviously, this foot-pounding behavior of *L. syphax* merits further study as well as detailed study of other frogs to determine whether seismic signalling is much more common than currently believed.

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LITERATURE CITED

GERHARDT, H. C., 1988. — Acoustic properties used in call recognition by frogs and toads. *In*: B. FRITZSCH, M. J. RYAN, W. WILCZYNSKI, T. E. HETHERINGTON & W. WALKOWIAK (eds.), *The evolution of the amphibian auditory system*, New York, John Wiley & Sons: 455-483.
HEYER, W. R., 1979. — Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contrib. Zool.*, **301**: 1-43.
HEYER, W. R., RAND, A. S., CRUZ, C. A. G., PEIXOTO, O. L. & NELSON, C. E., 1990. — Frogs of Boracéia. *Arq. Zool.*, **31**: 231-410.
LEWIS, E. R. & NARINS, P. M., 1985. — Do frogs communicate with seismic signals? *Science*, **227**: 187-189.
NARINS, P. M., 1990. — Seismic communication in anuran amphibians. *BioScience*, **40**: 268-274.
RYAN, M. J., 1980. — Female mate choice in a Neotropical frog. *Science*, **209**: 523-525.

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