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VOCAL REPERTORY OF TWO SPECIES OF THE *LEPTODACTYLUS PENTADACTYLUS* GROUP (ANURA, LEPTODACTYLIDAE)

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ABSTRACT: Among frogs, vocalizations play important roles in their social interactions. Herein we describe five new types of vocalizations for two foam-nesting species of the *Leptodactylus pentadactylus* group, *L. syphax* and *L. labyrinthicus*. Behavioral observations and recordings were done in four localities within the Cerrado biome, at southeast and central Brazil. Before emitting advertisement calls, males of *L. syphax* often started producing a sequence of notes, which gradually turned into the advertisement call. These different notes may be an introductory call, which would serve to prepare the vocal structures for the emission of the high-frequency/amplitude advertisement calls. A male of *L. syphax* was emitting advertisement calls when a female approached and started to emit brief and low-amplitude calls; these vocalizations probably are reciprocation calls. Males of *L. labyrinthicus* involved in agonistic interactions can emit vocal cracks (encounter call) and deep rough sounds (territorial calls). Five courting males of *L. labyrinthicus* released screams with their mouth slightly opened in response to the approach of human observers. We conclude that these screams do not represent distress or territorial calls.

Key Words: Leptodactylus labyrinthicus, L. syphax, *male vocalizations, female vocalization.*

INTRODUCTION

Among frogs, acoustic signals are related to female attraction, territorial demarcation, and predator avoidance (Gerhardt and Huber 2002). The advertisement, courtship, territorial, encounter, reciprocation, release and distress calls are main kinds of anuran vocalizations (Duellman and Trueb 1994; Gerhardt and Huber 2002). Besides advertisement call, some species of *Leptodactylus* of the *L. pentadactylus* group (sensu Heyer 1979, 2005) present reciprocation, release and distress calls (Heyer 1979; Hödl and Gollmann 1986; Hero and Galatti 1990; Kaiser 1994; Davis et al. 2000; Heyer and Thompson 2000; Heyer 2005; Toledo et al. 2005). The vocal repertory of *L. labyrinthicus* includes advertisement, courtship, distress, and territorial calls (Márquez et al. 1995; Toledo et al. 2005; Zina and Haddad 2005). Males of *L. syphax* produce advertisement and aggressive calls and non-vocal clicks (Cardoso and Heyer 1995).

Herein we report and describe for the first time a reciprocation call in *L. syphax* and show that its advertisement calls can be preceded by introductory notes. For *L. labyrinthicus*, we describe an encounter call and a new kind of vocalization produced by courting males in response to observer presence; we also present new types of territorial calls.

MATERIAL AND METHODS

Behavioral observations and recordings were done between September and late December (2002 – 2006) in the Brazilian municipalities of Uberlândia (18°55'S, 48°17'W), Araguari (18°29'S, 48°30'W), Santana do Riacho (Serra do Cipó National Park; 19°12'S, 43°30'W) (all in the state of Minas Gerais), and Caldas Novas (17°43'S, 48°40'W) (state of Goiás). All localities are in the Cerrado Biome (Central South America savanna) and present a wet/hot season from September to April, a dry/mild season from May to August, and with an annual mean

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precipitation of around 1,500 mm (Oliveira and Marquis 2002).

Most vocalizations were recorded with a Boss 864 digital recorder (44,100 Hz; 16-bit) coupled to a Sennheiser ME67 microphone; a Nagra E tape recorder (19 cm/s) and a Sennheiser MKH816T microphone were also used. All recordings were made from distances less than two meters from the calling individual. Audiospectrograms were produced using Sound Ruler software (Gridi-Papp 2004); sample rate was set at 44,100 Hz, with 16-bit resolution, and FFT (Fast Fourier Transformation) length at 1024 was used. The analog recording was digitized at a 22,050 Hz sampling rate. The sound files presented in the results do not correspond exactly to the call sections pictured in the figures (sonograms). The terminology used for the description of the vocalizations essentially follows Heyer et al. (1990).

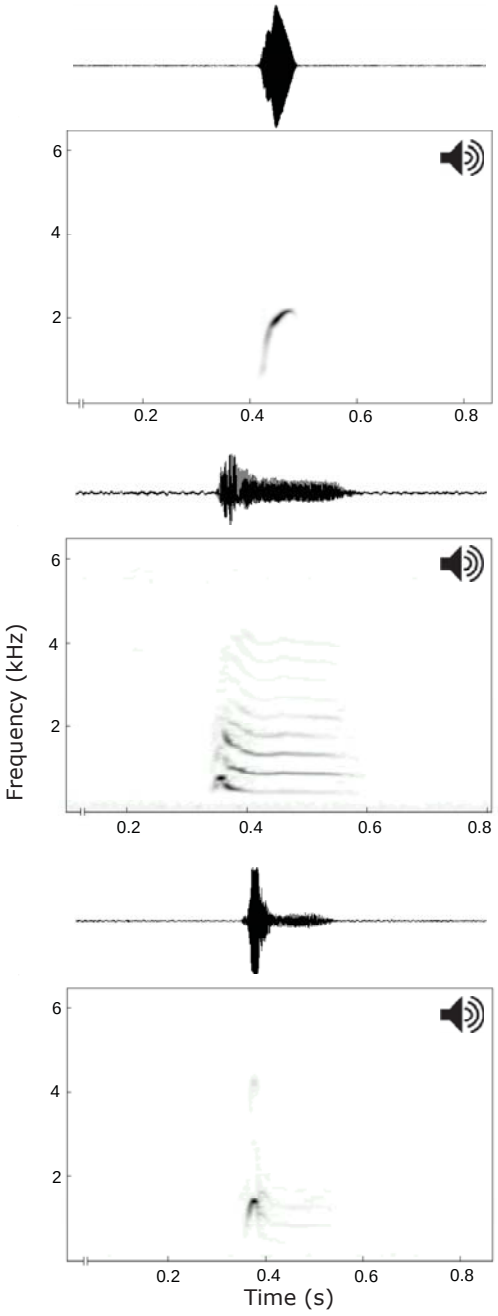

Figure 1. Oscillogram (above) and audiospectrogram (below) of vocalizations emitted by males of *Leptodactylus syphax*: Upper figure - One note of the advertisement call (recording file: Leptodsyphaxmg5AAGd, 20 November 2005, 20:00h, air 27.3°C, Araguari); Middle figure - Introductory call: note as those in the beginning and middle of the introductory sequence (Leptodsyphaxmg4aAAGd, 20 November 2005, 18:50h, air 26°C, Araguari); Lower figure - Introductory call: intermediate sound between those from the beginning/middle of the sequence and typical advertisement call (Leptodsyphaxgo1AAGd, 22 November 2004, 18:30h, air 23.5°C, Caldas Novas). Click on the speaker icons to hear the recordings.

RESULTS AND DISCUSSION

Leptodactylus syphax vocalizations

Advertisement and introductory calls

We analyzed 25 advertisement calls and 23 introductory calls of five males from three populations (Caldas Novas, Araguari and Serra do Cipó Park). The fundamental frequencies of the advertisement call (Figure 1, upper) are equal to the dominant frequencies (1806.3 ± 159.6; 1633 – 2089.9 Hz) (mean ± SD; range). This call lasts 72 ms (± 7.3; 56 – 92.3) and inter-call intervals average 0.92 s (± 0.45; 0.37 – 1.92; n = 16 measurements).

Before emitting advertisement calls (Figure 1, upper), males (n = 11) often started emitting a sequence of notes (11 ± 5.6; 3 – 20) (Figure 1, middle) with increasing sound intensity; these notes gradually turned into the typical advertisement call. Notes in the beginning and middle of the introductory sequence (Figure 1, middle) have 4 – 9 harmonic bands, with a fundamental frequency of 400.4 Hz (± 20.5; 384 – 441) and a dominant frequency of 979.6 Hz (± 269.8; 618 – 1513), lasting 219.4 ms (± 25.6; 184 – 267). Intervals between the calls average 1.78 s (± 0.39; 1.16 – 2.53; n = 14 measurements). Between these introductory sequence and typical advertisement calls, 3 – 5 intermediate notes (between those from the beginning/middle of the sequence and typical advertisement call) (n = 9 calls analyzed, 4 males from 3 populations) could be identified (Figure 1, lower). Each intermediate note lasts 168.7 ms (± 18; 140 – 190), has 2 – 4 harmonic bands, a fundamental frequency of 472 Hz (± 55.4; 423 – 579) and a dominant frequency of 1533.2 Hz (± 262.4; 1204 – 1965). The mean time interval between these notes is 1.91 s (± 0.9; 1.84 – 2.06; n = 5 measurements).

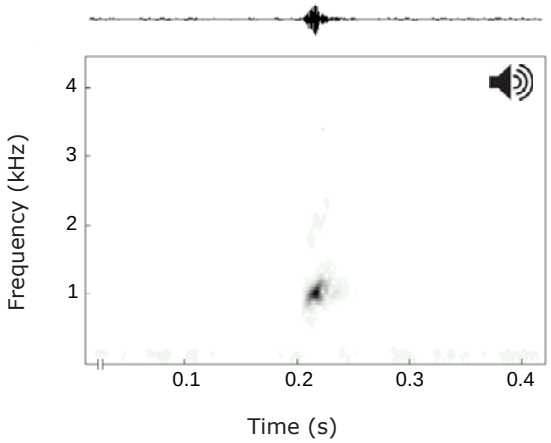

Figure 2. Oscillogram (above) and audiospectrogram (below) of the reciprocation call emitted by a female of *Leptodactylus syphax*. Recording file: Leptodsyphaxgo3bAAGd (air 23.3°C; 22 November 2004, 23:30h, Caldas Novas).

The advertisement calls we describe are in agreement with those presented by Cardoso and Heyer (1995). The calls we interpreted as introductory (Figure 1, middle) were obtained by Cardoso and Heyer (1995) by playbacking advertisement calls to a male. These authors recognized these calls as aggressive (territorial), because they failed to find intermediate notes in their sample (such as that we present in figure 1, lower). In our records, the increasing intensity of the calls emitted prior to the advertisement calls and the existence of transitional sounds indicate that they may be introductory vocalization, which would serve to prepare the vocal structures for the emission of the high-frequency/amplitude advertisement calls. Considering the contradictory interpretation of the function of these calls, further studies are necessary to determine precisely their function.

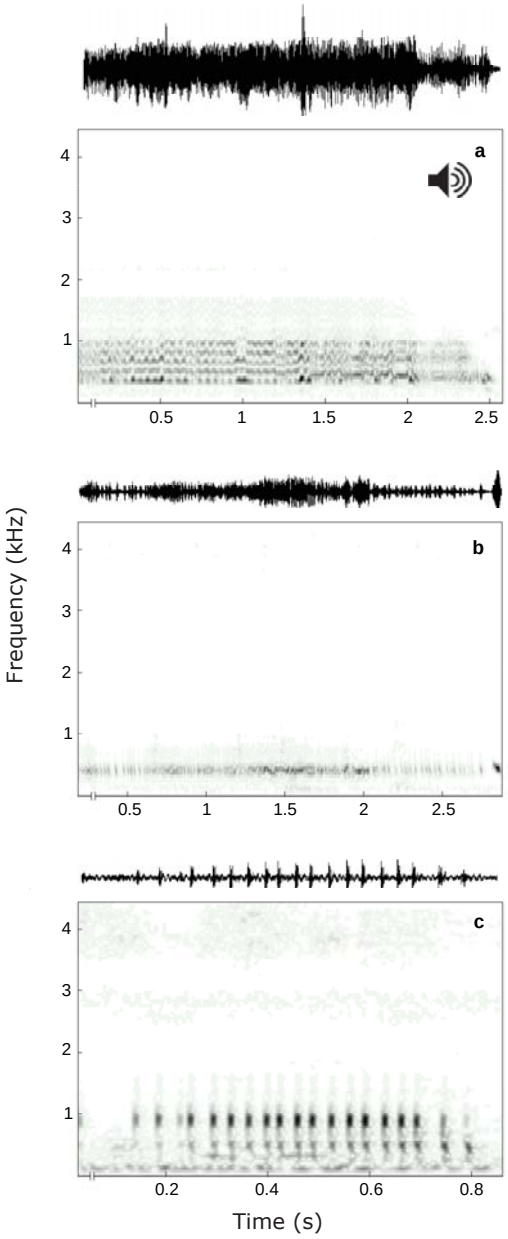

Figure 3. Oscillogram (above) and audiospectrogram (below) of different sounds (a – c) of the territorial call of *Leptodactylus labyrinthicus*. Recording file: Leptodlabyringo5AAGd (air 24.2°C; 01 November 2005, 20:50h, Caldas Novas).

Reciprocation call

A male was observed emitting advertisement calls when a conspecific female approached (< 5 cm) and started to release brief and low-amplitude calls (n = 32) (Figure 2). The male kept emitting advertisement calls while the female was vocalizing (3 min.). We kept observing the pair by five hours, but amplexus did not occur. We captured and examined the female and found that she was bearing mature eggs. Her calls (n = 11 analyzed) have a fundamental frequency of 1012.4 Hz (± 21.2; 969 – 1048) and last 19.1 ms (± 4.1; 11.6 – 25.1). The inter-call intervals average 3.9 s (± 2.4; 1.9 – 8.9; n = 9 measurements).

These vocalizations are reciprocation calls (sensu Duellman and Trueb 1994; Gerhardt and Huber 2002), because a receptive female emits them in response to advertisement calls of a conspecific male in a close-range interaction. As *L. syphax* males are territorial and have sharp-horny spines in their chest and thumbs (Heyer 1979; Cardoso and Heyer 1995; personal observation), we suggest that females could emit reciprocation calls to signalize their sex and receptivity to prevent male attacks (review in Schlaepfer and Figeroa-Sandí 1998). The reciprocation call was reported for few anuran species (Schlaepfer and Figeroa-Sandí 1998; Bernal and Ron 2004). As for *L. syphax*, the reciprocation call of *L. fallax* (*L. pentadactylus* group) consists of brief and low-amplitude sounds (Davis et al. 2000).

Leptodactylus labyrinthicus vocalizations

Territorial call

Two males were heard advertisement calling under rock stones (out of our sight) about one meter apart of one another when one of them started to emit very deep rough calls (Figure 3). These vocalizations have very low frequencies, amplitude modulation and different types of sounds. These calls (n = 10 analyzed) have a dominant frequency of 462 Hz (± 153; 384 – 891) and last 0.6 s (± 0.3; 0.3 – 1.2). The mean time interval between the calls is 8.1 s (± 10; 1.9 – 37; n = 9 measurements).

We regard these aggressive vocalizations as territorial calls (sensu Duellman and Trueb 1994; Gerhardt and Huber 2002), because a male produced them in the presence of other conspecific male that are also emitting

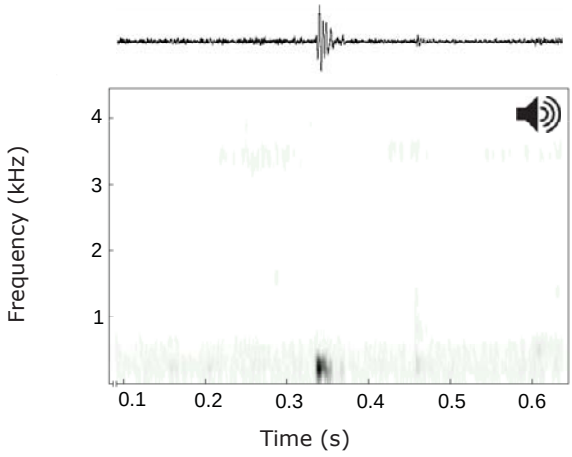

Figure 4. Oscillogram (above) and audiospectrogram (below) of an encounter call (vocal cracks) produced by a male of *Leptodactylus labyrinthicus* during a close-range agonistic interaction. Recording file: Leptodlabyringo1AAGd (air 24.7°C; 22 November 2004, 20:10h, Caldas Novas).

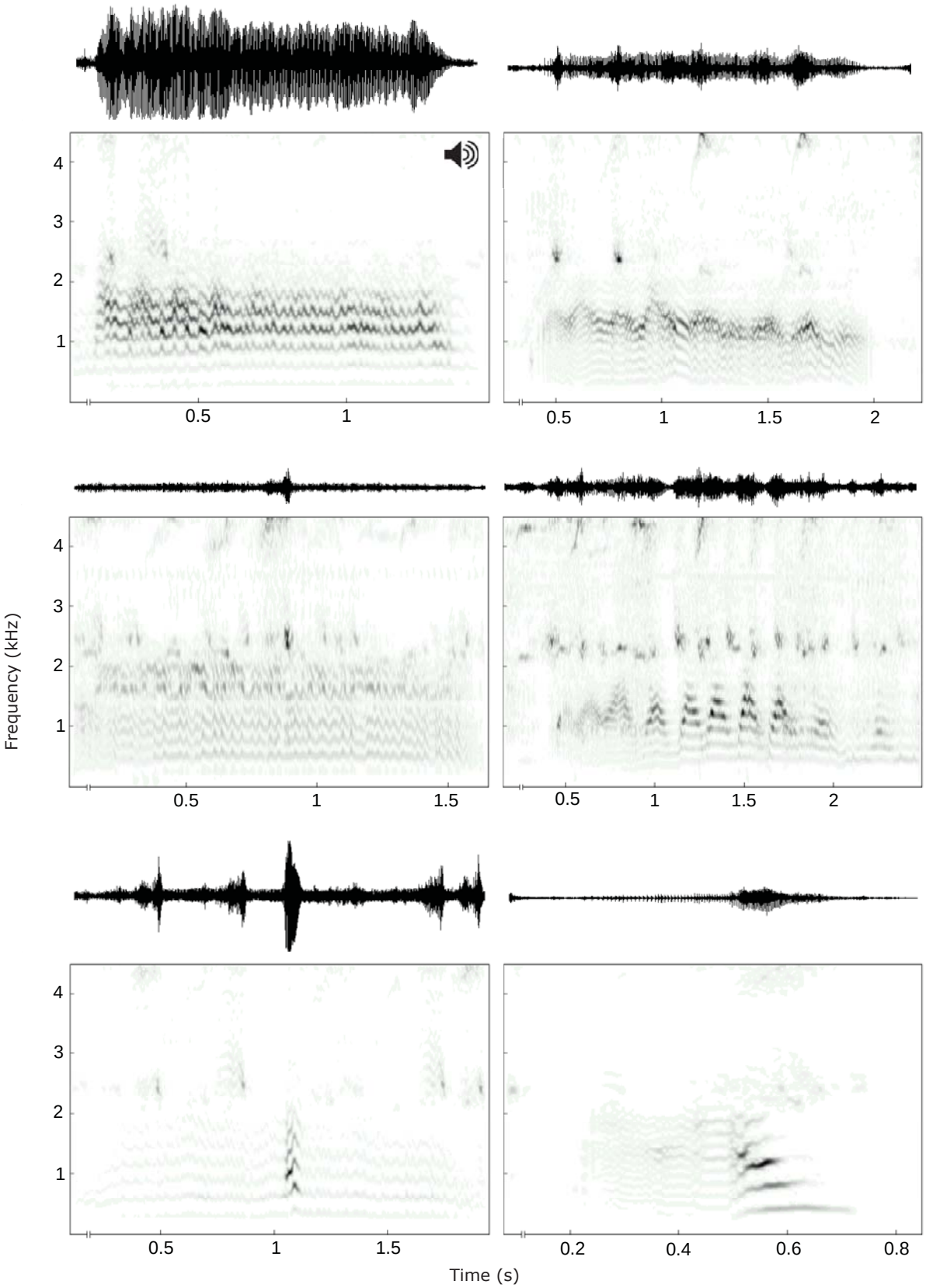

Figure 5. Oscillogram (above) and audiospectrogram (below) of different screams emitted by a courting male of *Leptodactylus labyrinthicus* in response to approach of human observers. The calls appearing above 2.5 kHz are of *Dendropsophus minutus* (Hylinae) and *Elachistocleis ovalis* (Microhylidae). Recording file: LeptodlabyrinAAG26 (air 21.6°C; 15 January 2002, 20:40h, Uberlândia).

advertisement calls. A different territorial call has being described to this species (Zina and Haddad 2005). In our records, the sound pictured in the figure 3b is that which most closely resemble the territorial call previously published. The different kinds of sounds of the territorial call of this species may represent differences in the level of male irritation. Probably, the male was very irritated during the emission of calls with greater amplitude (see Figure 3a).

Encounter call

Once we found two males that were close (< 1.5 m), but out of sight of one another. The larger male (hereafter dominant) was emitting advertisement calls and the smaller was silent. Close (< 30 cm) the silent male, we imitated the advertisement calls (an easily reproducible "uuup") what caused the approximation (10 cm) of the larger male, which started to emit vocal cracks (Figure 4). These sounds were produced with the mouth closed and the emission was coincident with a slight dilation of the vocal sac. The cracks were intercalated with advertisement calls. The silent male remained motionless during the emission of the cracks, but the larger male stopped calling and jumped on him; after this attack, the smaller male run out of sight of his aggressor (> 1 m). Each crack is a single note of very low sound amplitude; it lasts 40 ms (± 10) and has fundamental frequency of 194 Hz (± 12; 170 – 205; n = 9 calls analyzed). The time interval between the calls is 4.2 s (± 3.2; n = 6 measurements). These vocal cracks fit well the definition of an encounter call (Duellman and Trueb 1994), because they were emitted by a male just preceding an agonistic interaction. Encounter calls probably are emitted to avoid fights (Wells 1977).

Intimidatory (?) screams

Courting males (n = 5) often release screams in the presence of human observers. Once we observed (20:40 h) a male excavating a basin at the edge of a temporary pool (≈ 200 m², 60 cm deep) and there was a receptive female nearby (< 2 m). When we approached to record this male (< 4 m), he started releasing a sequence of screams (Figure 5) with his mouth slightly opened. As the screams apparently were directed to the observers, we moved away (10 m) and remained hidden for about 10 minutes. The male stopped screaming and restarted to emit advertisement calls. During a second approach (< 2 m), he restarted screaming. We moved away once more and he stopped screaming again. The screams often were intercalated with advertisement calls. The following day, we returned to that site and encountered an egg clutch in the basin he was building. On four other occasions and localities, courting males released screams as a result of the presence of receptive females and human observers. All these five cases were of males not accustomed to human presence; seven other courting males from areas with intense human visitation (garden around swimming pools; see Silva et al. 2005) did not respond aggressively.

The screams are quite variable in duration and six types of sounds can be recognized (Figure 5). In general, the screams are low, rough, short and are frequency and amplitude modulated. These screams differ mainly in the amount of sound intensity (amplitude). Each scream (n = 14 analyzed; two males recorded) lasts about 1.6 s (± 0.6; 0.8 – 3.1), and has a fundamental frequency of 308 Hz (± 42; 240 – 373) and a dominant frequency of 1425 Hz (± 236; 969 – 1751). The time intervals between the screams average 2.7 s (± 2.9; 0.4 – 11.2; n = 13 measurements).

The distress call of frogs (sensu Hödl and Gollmann 1986) is a loud scream emitted with mouth wide open, generally when an individual is grasped by a predator. This call has clear harmonic bands and often reaches high frequencies above 6 kHz (Hödl and Gollmann 1986). We conclude that the screams we witnessed do not represent distress calls. First, they were emitted with the mouth just slightly open. Second, the males were not grasped or handled. Third, males emitted advertisement calls alternately, which reflect sexual excitement and could attract predators instead of scaring them away (Gerhardt and Huber 2002). The distress call of *L. labyrinthicus* is known (Toledo et al. 2005; personal observation) and it is different from the screams presented here. The distress call of this species is emitted by handled individuals, has clear harmonic bands and the frequencies can reach 9 kHz (Toledo et al. 2005). The screams cannot be regarded as a territorial call either, because they are different (e.g. higher frequencies) from the territorial call of the species (Zina and Haddad 2005; present study) and we have observed close range non-courting males in several occasions and they had never reacted in this way.

Courting males seemed to be disturbed with our presence, because they started screaming only when we approached them, stop screaming and resuming advertisement call when we moved away. Future studies could test the hypothesis that these vocalizations are "intimidatory screams" with the function of repelling heterospecific disturbers (not necessarily a predator), which could promote the evasion of receptive females from the reproductive site. Probably, males rely on their large size (up to 195 mm SVL, ≈ 750 g) and irritating skin secretions (Heyer 1979; Cei 1980; personal observation) to react this way. Besides, large free-ranging *L. labyrinthicus* males can confront humans by jumping on or grasping approached hands, feet or long sticks (n = 3 unpublished personal observation).

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