Calls and calling behavior of the frog *Leptodactylus natalensis* (Amphibia: Anura: Leptodactylidae)

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Abstract.—Leptodactylus natalensis has a prolonged calling season, typically from May to September. Individuals occur in and call from the most forested patch of habitat on the campus of the Universidade Federal de Sergipe. Two kinds of calls were recorded and analyzed—advertisement and chirp calls. The function of the chirp call is unknown. The advertisement call has two carrier frequency bands, known to date for only two other species of Leptodactylus. The two carrier bands may correspond to different frequency tuning sensitivities in males and females, as females have slightly larger tympani than males, corresponding with their larger overall size.

Published natural history information for the frog Leptodactylus natalensis Lutz, 1930, consists of comments on calling and microhabitat made by Lutz (1930) in his original description of the species and a recent study of some reproductive aspects, including the first description of the tadpole for the species (Oliveira & Lírio Júnior 1999). Calls of Leptodactylus natalensis have not been analyzed previously (Heyer 1994). One of us (CMC) had the opportunity to observe calling behavior and recorded the calls of L. natalensis. The purpose of this paper is to report these observations and describe the calls.

Methods and Materials

Observational data and recordings of *Leptodactylus natalensis* were made by CMC on the campus of the Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil. Incidental information on calls at Santo Amaro das Brotas, Sergipe, was also obtained by CMC.

Recordings were made from two individuals. Five recordings (USNM tape 323, cut 1) were made from specimen MZUSP 89945 (MZUSP = Museu de Zoologia, Universidade de São Paulo collection), SVL (snout-vent length) 33.9 mm, on 22 June 1998, at an air temperature of 25°C, water temperature 24°C, the last recording completed at 1955 h. One recording (USNM tape 323, cut 2) was made from specimen MZUSP 89947, SVL 32.4 mm, also on 22 June 1998, air 25°C, water 24°C, the recording completed at 2030 h. It was not raining when these recordings were made, but a brief heavy rain occurred at 2100 h.

Calls were recorded with a Sony TM-5000 cassette recorder with a M 44 N(C) Beyer Dynamic Soundstar II microphone.

Terminology follows that of Heyer et al. (1990), with the following clarifications. Carrier frequency is the frequency broadcast by the calling frog to the environment. Often, the carrier frequency embraces a range of frequencies loud enough to be heard by the intended receiver (male or female). The dominant frequency as used here is the single frequency value (or very narrow range of frequencies) that has the most sound energy in the call.

Recordings were analyzed using "Ca-

nary 2.1" software (Charif et al. 1995). Call rates and durations were measured from wave form displays, beginning and ending carrier frequencies from audiospectrogram displays, and dominant frequencies from spectral displays. Although the initiation of calls is clear on the wave form displays, the ends of the calls are not very distinct, perhaps due to the level of background noise and possible microphone ringing.

Advertisement call rates were based on six calling sequences ranging from 7.8 to 15.2 sec from each of six recordings. Frequency data were taken from 10 consecutive calls from each of the six recordings; call duration and pulse data were taken on the same 10 calls for recordings 2 and 5 of MZUSP 89945 and for MZUSP 89947.

Chirp call data are from the six chirps loud enough to analyze in the second recording of MZUSP 89945.

Behavior and Calling Site

Leptodactylus natalensis has a prolonged calling season coinciding with the rainy season, typically from May to September (also see Oliveira & Lírio Junior 1999). Calling starts around 1600 h. Calling activity is most intense around 1900 and continues until 2300 or 2400 h. However, on rainy days, especially at the beginning of the rainy season, males can be heard calling at 0800 h, and continuing throughout the day and night. Males do not call during hot and sunny days during the rainy season.

The general site the frogs occupy on the campus is a small patch (100 × 400 m) of second growth (capoeira) on the right bank of the Rio Poxim, a seasonally partially flooded area (varzea) with many ponds. The site has 5–6 m high trees, many young palm trees, a thick grass ground cover, shallow litter, and white sand. The *Leptodactylus natalensis* were only heard calling from the capoeira—never from the left bank of the Rio Poxim, which has more artificial open areas and patches of mangrove swamps.

MZUSP 89945 was calling very close to

the foot of a young palm tree surrounded by a pond with leaves in the water. The frog sat in the water, half submerged. A second male (MZUSP 89946) was about a half meter from the calling male. This second male was in a small burrow, with half the body exposed and uttered some "clicks" but no other calls. The "clicks" did not record adequately enough to analyze.

MZUSP 89947 was near the foot of a small tree, at the edge of a little channel of rain water, hidden in grass.

Leptodactylus natalensis infrequently jump when disturbed. Usually they take two or three steps backward and quietly hide under a leaf or other ground cover.

Advertisement Call

Calls (Fig. 1) consist of single notes given frequently when actively calling. Call rates vary from 3.4-4.1 per sec for MZUSP 89945 and at a rate of 3.0 per sec for MZUSP 89947. The call sequence with the least background noise is the fifth recording sequence for MZUSP 89945. In that sequence, each call (=a single note) has a duration of 0.06-0.07 (mode = 0.07) sec and consists of 5-7 pulses, modally 7. The call is partially pulsed (=incompletely amplitude modulated). In two other recordings with greater background noise, it appears that the terminal pulses are indistinguishable from the background noise in the wave forms. Three to five partial pulses (mode = 4) can be distinguished in calls from the second recording of MZUSP 89945, with an average duration of 0.04 sec. Two to three partial pulses (mode = 3) are distinguishable in the recording from MZUSP 89947, with an average duration of 0.02 sec. The calls are frequency modulated with extremely fast rise times (difficult to see because of time scale in Fig. 1, more visible in the two advertisement calls shown in Fig. 3). Beginning frequencies of the carrier (=fundamental) frequency range from averages of 550-600 Hz with the highest frequencies ranging from averages of 1370-



50 ms

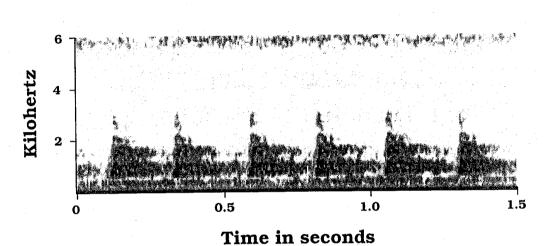


Fig. 1. Wave form (above) and audiospectrogram (below) of the advertisement call of *Leptodactylus natalensis*, USNM tape 323, cut 1, fifth recording. The wave form is of the first call shown in the audiospectrogram.

1830 Hz for MZUSP 89945. The average beginning dominant frequency for MZUSP 89947 is 650 Hz, with an average maximum of 1600 Hz. The dominant frequencies most often occur in two peaks in the calls of MZUSP 89945. For this frog, the first recording series usually has a dominant frequency of 760 Hz, with either a co-dominant or quieter frequency at 1050 Hz; the second recording has the dominant frequency at 770 Hz, with a secondary dominant at 1020 Hz; the third recording has the dominant frequency at 760 Hz, with a secondary dominant at 1040 Hz; the fourth recording has the most variation with either 780 and 1030 Hz being primary or secondary in loudness, 860 and 1030 Hz being primary or secondary in loudness, 1030 Hz loudest with a secondary dominant at 880 Hz, or a single dominant frequency at 1030 Hz; calls in the fifth recording have the dominant frequency at 1030–1040 Hz, with a secondary dominant at 760–770 Hz (Fig. 2). The calls of MZUSP 89947 have either a dominant frequency at 1030 Hz, or also with a secondary dominant at 875 Hz. The partial pulsing of the calls appears to be the cause of the sidebands weakly visible in the audiospectrograms (Fig. 1). Calls of MZUSP 89945 range from having no visible harmonics, a weak second harmonic, or intermediate strength second and third harmonics (Fig. 2). The calls of MZUSP 89947 have a weak second harmonic.

Chirp Call

Calls (Fig. 3) consist of either 1 or 2 notes. The loudest chirp calls are louder than the advertisement calls. In the two note

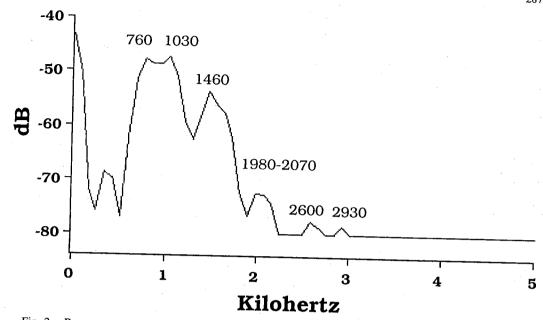


Fig. 2. Power spectrum of advertisement call of *Leptodactylus natalensis*, USNM recording 323, cut 1 (of second call in audiospectrogram of Fig. 1).

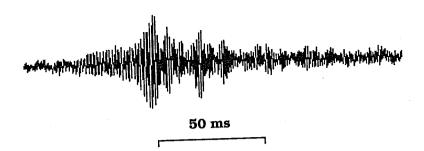
calls, the first note is shorter than the second (0.04 and 0.13 with an internote interval of 0.10 sec; 0.05 and 0.08 with an internote interval of 0.16 sec; 0.04 and 0.13 with an internote interval of 0.14 sec). The three single note chirp calls recorded range from 0.10-0.14 sec duration. From 3-10 partial pulses can be discerned in the wave forms. The calls are frequency modulated, at a noticeably slower rise time than the advertisement calls. The lowest carrier (=fundamental) frequency ranges from 530-650 Hz; the highest carrier frequency ranges from 990-1200 Hz. There is a suggestion of the carrier frequency briefly falling at the end of some calls, back to around 900-950 Hz. The dominant frequencies vary from 690-860 Hz. There are weak to strong second, second and third, or second, third, and fourth harmonics.

Discussion

The function of the chirp calls is unknown. Other members of the *L. melanonotus* group have these calls as well, which usually initiate calling bouts. In the case of

the *L. natalensis* recording, the chirp calls were uttered after there was a slowing down in the rate of advertisement calls. The chirp calls are much more variable than the advertisement calls.

Many species of Leptodactylus have frequency modulated calls that result in broadcasting their calls over a range of frequencies. Most of these calls have a single (or narrow range) dominant frequency, however. Leptodactylus natalensis is unusual in that there are two peaks of loudness. Only L. melanonotus and podicipinus within the L. melanonotus group share this condition (of those for which the calls are known, Table 1). We hypothesize that these separate dominant frequencies correspond to different tuning curves in males and females, as demonstrated in Eleutherodactylus coqui (Narins & Capranica, 1976), although no experimental data are available for L. natalensis. Morphological data do not contradict this hypothesis. Other things being equal, a larger tympanum will be more sensitive to lower frequencies than a smaller tympanum and vice versa. Morphological



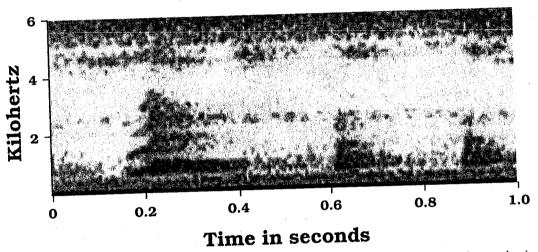


Fig. 3. Wave form (above) and audiospectrogram (below) of the chirp call of *Leptodactylus natalensis*, USNM tape 323, cut 1. In the audiospectrogram, a single-note chirp call is followed by two advertisement calls.

data are available from two localities represented by several males and females. The data indicate that the tympanum size does differ between males and females (Table 2). It would seem from the variability of calls in the fourth recording of MZUSP 89945 that an individual frog has control over whether more energy is broadcast in the lower or higher dominant frequency.

Sexual difference in tympanum size is the expected condition in most frogs, as most frog species are sexually dimorphic, with the females being larger. Broadcasting of higher and lower dominant frequencies, as seen in *L. natalensis*, is one solution to matching different receptor sensitivities to the advertisement call. The frequency modulation ob-

served in other *Leptodactylus* species, such as *L. fuscus*, is another solution.

Our observations apparently conflict with those of Adolfo Lutz regarding the call of *L. natalensis*. In the original description of the species, Lutz observed (1930:27, English version of text): "This frog has a call with the strength of a whistle but sounding more like the voice of a cricket. It seems to have also another sound, heard during copulation, like a soft clucking, sometimes repeated by other males, so as to form a general concert. The specimens were caught near to the water but generally well hidden." CMC has not heard cricket-like calls from *L. natalensis* at either the campus at São Cristóvão or Santo Amaro das Brotas,

Table 1.—Advertisement call characteristics of members of the *Leptodactylus melanonotus* species group. Data taken from Heyer (1994), Heyer et al. (1996), and for *L. melanonotus*, from USNM tape 83, cut 1. Note that *Leptodactylus diedrus* is no longer considered a member of the *L. melanonotus* species group (Heyer, 1998). The duration and pulse data for *L. natalensis* are from the recording with the least background noise.

Species	Call duration in sec	Number partial pulses per call	Carrier frequency range	Dominant frequency range		
L. griseigularis	0.01	1	1380–3060	2770		
L. leptodactyloides	0.02-0.04	1 or 3-5	650-1600	1100-1300		
L. melanonotus	0.07 - 0.08	46	820-2620	1320-1380 or 2330		
L. natalensis	0.06-0.07	57	550-1830	760-880 or 1020-1040		
L. nesiotus	0.03	4–5	1500-2000	1800–2000		
L. pallidirostris	0.03 - 0.05	1 or 2-5	15003500	3000–3500		
L. petersii A	0.04-0.05	3-4	700–1200	750–800		
L. petersii B	0.03 - 0.05	1 or 2-4	800-1600 or 1800-2800	N.A.		
L. podicipinus	0.02-0.04	37	1000-3500	1000–1200 or 3300–3500		
L. sabanensis	0.04-0.06	very weak	900-2300	1400–1800		
L. silvanimbus	0.15	about 20	420–1920	510		
L. validus	0.03-0.06	1 or 2-6	1300–3500	2300–3500		

but the call we describe as the advertisement call is a soft clucking call.

Advertisement calls in the L. melanonotus group are often not as species-specific as in other Leptodactylus, perhaps because the calls have a strong point-location orientation function overriding (or in addition to) a species-coding function (Table 1 and Heyer 1994:106-107). Leptodactylus natalensis has a disjunct geographic distribution relative to all other members of the L. melanonotus group. The species group member that most closely approaches the distribution of L. natalensis is L. podicipinus (compare Figs. 39 and 43 in Heyer 1994). Interestingly, as pointed out above, L. podicipinus is only one of two other known members of the L. melanonotus group beside L. natalensis to have two distinct loudest broadcast peaks in the dominant frequency band.

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Table 2.—Snout-vent length and tympanum diameter measurements for male and female *Leptodactylus natalensis* from two localities in the State of Sergipe, Brazil.

	n	Sex	Snout-vent length			Tympanum diameter		
Locality			Min.	Max.	Mean	Min.	Max.	Mean
Areia Branca	8	♂	28.7	36,5	33.1	2.2	3.2	2.8
Areia Branca	9	φ.	33.9	42.6	38.8	2.7	3.4	3.0
Santo Amaro das Brotas	7	♂	30.6	34.6	32.5	2.4	2.7	2.6
Santo Amaro das Brotas	14	9	33.1	37.0	35.1	2.5	2.9	2.7

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