

THE ADVERTISEMENT CALL OF *LEPTODACTYLUS LATICEPS* (AMPHIBIA, ANURA, LEPTODACTYLIDAE): PREDATORY AURAL LURING?

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Aggressive mimicry, where a predator deceives its victim by imitating something desirable, is a fascinating phenomenon that has been well documented in arthropods (e.g., fireflies—Lloyd 1981; jumping spiders—Jackson and Wilcox 1998). We do not know of any case of aggressive mimicry in frogs, but may have found such a system operating in the Gran Chaco of South America. Some frog predators use advertisement calls of the prey species to locate their prey (e.g., bats—Ryan 1985: Chapter 8), including frogs (*Bufo marinus* and *Leptodactylus pentadactylus* feeding on *Physalaemus pustulosus*—Rand 1983:414). We know of no instance where a frog uses its advertisement call as a lure to attract prey. We present data that are consistent with the hypothesis that male *L. laticeps* not only use their advertisement calls to attract conspecific females, but also as an aural lure to attract *L. bufonius*, upon which they have been shown to prey.

Leptodactylus laticeps (Fig. 1A) is a species characteristic of the Gran Chaco of South America. The species produces toxic skin secretions and has bright coloration and aggressive behavior, presumably aposematic in function (Ceï 1980; Scott and Aquino, in press). *Leptodactylus laticeps* often co-occurs with viscachas (*Lagostomus maximus*: Rodentia), and uses their burrow systems, including

calling from the burrow entrances (Lavilla et al. 1995). To date, neither advertisement call nor larvae of *L. laticeps* have been described. Although Eterovick and Sazima (2000: Table 1) reported the call of *L. laticeps* as unpulsed, this is a mistake and refers to *L. labyrinthicus* instead (P. Eterovick, pers. comm.). Herein, we describe the advertisement call of *L. laticeps*.

Leptodactylus laticeps is a member of the *L. pentadactylus* species group (Heyer 1979), but its call has features similar in many respects to those of *L. bufonius* (Fig. 1B), a *L. fuscus* group member. We suggest that the advertisement call of *L. laticeps* acts as an aural lure to attract female *L. bufonius* as prey, in addition to attracting female *L. laticeps*. We further propose that the call of *L. laticeps* underwent selective pressure to be similar enough to the advertisement call of *L. bufonius* as to serve as an aural lure for female *L. bufonius*.

MATERIALS AND METHODS

The junior author recorded the calls of several sympatric species of *Leptodactylus*, including *L. laticeps*, at Filadelfia, Departamento Boquerón, Paraguay. For comparative purposes, we also analyze the advertisement calls of *L. labyrinthicus* and *L. stenodema*. The recording data are presented in the Appendix. Each recording represents a single individual. Recordings were made with an Uher

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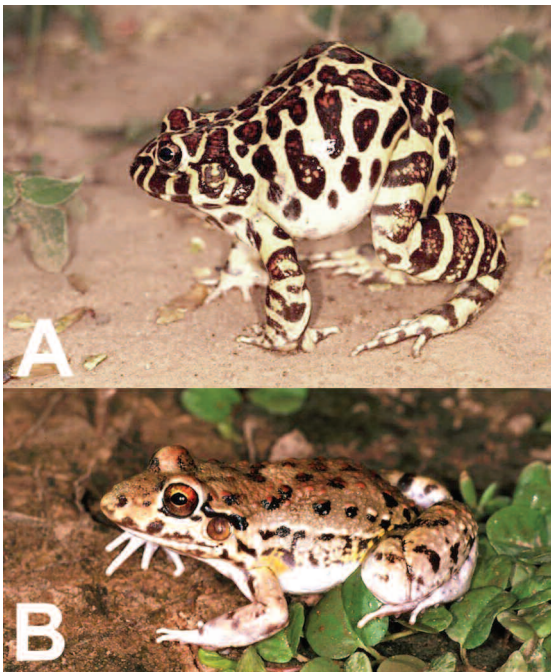


Figure 1. (A) *Leptodactylus laticeps*, showing posture in response to disturbing it, presumably making itself as large as possible to warn the disturber that it has noxious skin secretions. (B) *Leptodactylus bufonius*. Both images by Joe Furman, taken in the Paraguayan Chaco.

model 800 reel-to-reel tape recorder at a recording speed of 15/16 ips. Because of the low recording speed, the upper frequencies are truncated at about 3 kHz. As the call of *L. latinasus*, which occurs syntopically with *L. laticeps*, has fundamental frequencies above 3 kHz, we use a recording from a different locality that was made at a faster speed (Appendix).

Canary 1.2 software (Charif et al. 1995) was used to analyze the recordings. Calls were digitized at a sample rate of 22050 Hz, a sample size of 16 bits, and at an input speed of 1x. Call component terminology follows Duellman and Trueb (1986) and Heyer et al. (1990), unless specified otherwise. Call duration was measured from the wave form. Dominant frequency was determined using the spectrum analysis of Canary with settings of analysis resolution filter bandwidth 349.70 Hz, FFT size 256 points; window function hamming; amplitude logarithmic; clipping level -79.79 dB; number of frame 1. The beginning and ending frequencies were measured from the audiospectrogram display ("spectrogram" in Canary terminology) using settings of analysis resolution filter bandwidth 349.70

Hz and frame length 256 points; grid resolution of time 5.805 ms, overlap 50%, frequency 86.13 Hz, FFT size 256 points; window function hamming; amplitude logarithmic; clipping level -80 dB; display style smooth. Particularly for the calls of *L. bufonius* and *L. laticeps* the frequency display on the audiospectrogram is rather wide, making it difficult to measure any given maximum frequency throughout the call precisely. For these two species, a selection of 10 ms (or just greater) was made at the beginning and end of the calls. These 10 ms selections were analyzed with the power spectrum feature in Canary. Frequency sweep is the difference of the ending frequency and beginning frequency. Call amplitude modulation was evaluated from visual inspection of expanded wave form displays. Harmonics were determined using both expanded wave form displays and power spectrum displays.

The multidimensional scaling analysis was done with SYSTAT 10 using Kruskal's loss function with the log option (Wilkinson 2000:119–127). The distance matrix used was standardized Euclidean distances based on mean parameter values for each species. The Euclidean distance matrix was produced using SYSTAT10 (Wilkinson et al. 2000). As we have six quantitative parameters in our study, we examined our data using two dimensions.

THE ADVERTISEMENT CALL OF *LEPTODACTYLUS LATICEPS*

The call (Fig. 2) consists of single notes given at a rate of 45–48 calls/min. Call duration is 0.18–0.21 s. The dominant frequency (= fundamental) range is 1015–1033 Hz. The beginning frequency range is 844–861 Hz; the ending frequency range is 1015–1033 Hz. The frequency sweep range is 159–184 Hz. The call is pulsatile and contains at least a second harmonic.

PREDATORY AURAL LURING?

WRH was struck by how similar the calls of *L. laticeps* were to those of *L. bufonius* in the field (Campo Grande, Salta, Argentina, December 1999; calls not recorded) and how different the call of *L. laticeps* was from its closest relative among the large species of the *L. pentadactylus* species group (Heyer 1979). However, when the calls of *L. bufonius* and *L. laticeps* are heard immediately after each other, they can be consistently distinguished by the human ear.

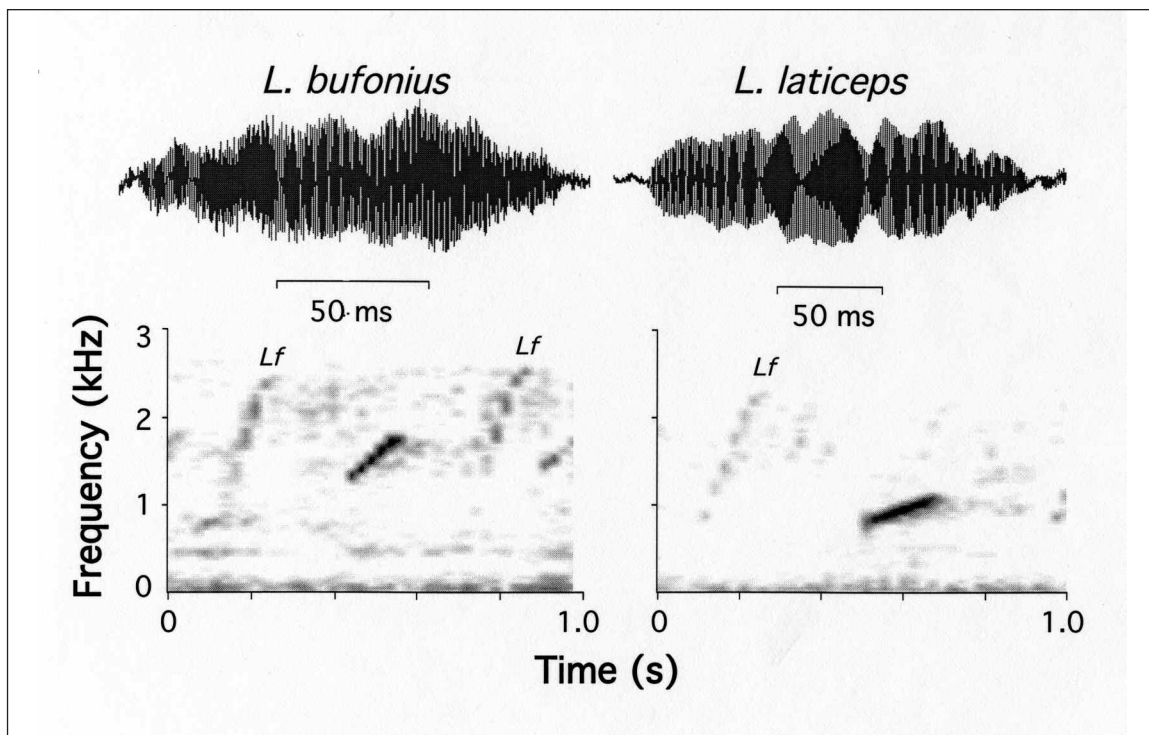


Figure 2. Wave form and audiospectrogram displays of advertisement calls of *Leptodactylus bufonius* and *L. laticeps* from Filadelfia, Paraguay. The background call of *L. fuscus* (Lf) is visible as two calls in the *L. bufonius* audiospectrogram and one call in the *L. laticeps* audiospectrogram. Audiospectrograms were made with narrow band frequency settings (43.07 Hz).

It was this initial field impression that led us to explore the possibility of predatory aural luring in *L. laticeps*. Two elements are required if *L. laticeps* is indeed an aural lurer of *L. bufonius*: (1) *L. laticeps* must feed on the presumed prey (*L. bufonius*) it would attract; and (2) the call of *L. laticeps* must be attractive to *L. bufonius*. If these two requirements are met, or at least not falsified, a corroborating piece of evidence would be that the calls of *L. bufonius* and *L. laticeps* are more similar to each other than *L. laticeps* is to other members of the *L. pentadactylus* species group. Each of these is discussed in turn.

Does *Leptodactylus laticeps* Feed on *L. bufonius*?

Adult *L. laticeps* (mean male SVL 98 mm) are much larger than adult *L. bufonius* (mean female SVL 54 mm). In addition to size differences, *L. laticeps* would have no difficulty visually distinguishing potential mates (mean female SVL 90 mm) from prey *L. bufonius*. *Leptodactylus laticeps* has the most visually distinctive color pattern in life of any *Leptodactylus* species (Fig. 1A), presumably an

aposematic warning of its toxic skin secretions (Norman 1994:23, 157). *Leptodactylus bufonius* lacks any bright colors and is a gray or brown/tan frog in life (Fig. 1B). Based on visual acuity studies under low light conditions in other species of frogs (Straughan 1966), *L. laticeps* would be expected to easily distinguish *L. bufonius* from *L. laticeps* individuals at all size classes under nocturnal conditions. *Leptodactylus bufonius* and *L. laticeps* occur syntopically and both species can be heard calling at the same time. *Leptodactylus bufonius* was reported to be the most abundant item in the stomach contents of *L. laticeps* (Ceï 1956:46), although Scott and Aquino (in press) found only two *Bufo major* and one unidentified frog in 19 stomachs. There are no data on whether female *L. bufonius* are over-represented in the stomach contents of male *L. laticeps*, however, which would corroborate the aural luring hypothesis.

Is the Call of *Leptodactylus laticeps* Attractive to *L. bufonius*?

We do not know whether the call of *L. laticeps* is attractive to female *L. bufonius*. It should be,

based on what is known about the features of calls that are attractive to female frogs. The only real difference between the calls of *L. bufonius* and *L. laticeps* is in the frequency range: they are very similar in terms of call duration, amplitude modulation, and harmonic structure (Table 1, Fig. 1). Experimental work has shown that female frogs actually prefer lower frequencies of calls than are produced by most conspecific males (see Sun et al. 2000, and the summary in Ryan and Keddy-Hector 1992).

In order to evaluate frequency data, calls should be standardized for temperature. The recorded calls of *L. bufonius* and *L. laticeps* were made on different nights. The *L. laticeps* call was recorded at 28°C. The temperature for the *L. bufonius* recording was not noted, but the call of *L. fuscus*, which was recorded after the call of *L. bufonius* on the same night was recorded at 30°C. It is safe to presume that the call of *L. bufonius* was recorded at 30°C or higher. Given the well established relationship between frequency and temperature (Duellman and Trueb 1986:104), the data for our recordings would be more similar in frequencies to each other if the data were temperature standardized (we lack sufficient data to standardize for temperature).

There does appear to be a gap between the frequencies of the two calls that exceeds the window of neural frequency tuning for the basilar papilla based on other studies (e.g., the range of best frequencies in the basilar papilla of *L. albilabris* spans 300 Hz [Christensen-Dalsgaard and Narins 1993:656]). *Leptodactylus bufonius* should be able to process *L. laticeps* calls through the amphibian papilla (which is sensitive to frequencies lower than 1500 Hz), but we do not know if female *L. bufonius* would respond to signals processed by the amphibian papilla in terms of mate selection. However, loud intensities can stimulate anuran sound receptors and the basilar papilla of female *L. bufonius* could be activated if the calls of *L. laticeps* were loud enough. The call of *L. laticeps* is much louder than the call of *L. bufonius* (NJS, pers. obs.). Female *L. bufonius* may perceive the calls of *L. laticeps* to be super attractive male *L. bufonius*. The available data neither robustly support nor falsify this particular element.

The most appropriate species of the *L. pentadactylus* group to compare call features with *L. laticeps* is *L. labyrinthicus*. The two species occur in open habitats with parapatric distributions. *Leptodactylus labyrinthicus* is considerably larger

than *L. laticeps*, so a second member of the *L. pentadactylus* group is included that matches the size of *L. laticeps*—*L. stenodema* (maximum SVL for male *L. laticeps* 110 mm, for *L. stenodema* 100 mm; see Appendix, Table 1). One feature of the call of *L. laticeps* that is different from calls of *L. labyrinthicus* and *L. stenodema* and supports our hypothesis is the higher frequency of the call of *L. laticeps* (Table 1).

Leptodactylus laticeps has a restricted geographic range (Fig. 7 of Heyer [1979] is modestly expanded by new locality records). The following are the only other species of *Leptodactylus* that occur throughout all of the range of *L. laticeps* (they also have more extensive distributions): *L. bufonius*, *L. chaquensis*, *L. fuscus*, *L. latinasus*, and *L. mystacinus*. *Leptodactylus chaquensis* is a member of the *L. ocellatus* species group with a call very distinct from all others considered in this paper (Barrio 1966). There are no other frogs in the areas where *L. bufonius* and *L. laticeps* co-occur that have a call that is even remotely similar to the rising whistle calls found in *Leptodactylus*. *Leptodactylus bufonius*, *L. fuscus*, *L. latinasus*, and *L. mystacinus* are all members of the *L. fuscus* species group (Heyer 1978). As can be seen from the data (Table 1) and a multidimensional scaling analysis of the quantitative data (Fig. 3), the call of *L. laticeps* is more similar to the call of *L. bufonius* than it is to any other syntopic *fuscus* group species.

Alternative Explanations and Suggestions for Future Work

The call of *L. laticeps* may be under conflicting selective pressures: for lower frequencies by female *L. laticeps* and for higher frequencies for aural predation on female *L. bufonius*. This evolutionary conflict might prevent a really good match between predator and prey ever developing, analogous to the short- and long-distance call conflicts described by Sun et al. (2000).

There are two other aspects of the system that could argue against aggressive mimicry occurring between *L. laticeps* and *L. bufonius*. The similarity of the calls of *L. bufonius* and *L. laticeps* could be accounted for on the basis of selection for call transmission through the same habitat. Also, the call rate of *L. laticeps* is lower than that of *L. bufonius*; if females discriminate on the basis of call rate, male *L. laticeps* would not represent super-attractive stimuli for female *L. bufonius*. We have no data at this time to address these issues.

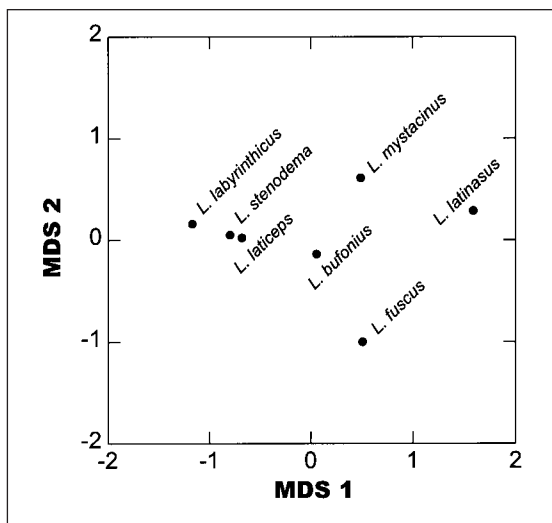


Figure 3. Multidimensional scaling results for quantitative variables of advertisement calls of *Leptodactylus* species. Values of MDS1 > 0 are characteristic of species in the *L. fuscus* species group, whereas values of MDS1 < 0 characterize frogs of the *L. pentadactylus* species group in this analysis.

Although the present data are not as robust as desired to be absolutely confident in our assertion of predatory aural luring, the hypothesis is certainly falsifiable in ways that would be convincing. For predatory aural luring to work, one would predict that the lurer would have to be less abundant than the males of the lured species. This requirement is met based on personal observations by both authors, but actual abundance data should be gathered to confirm this point. Additional natural history observations would be informative, such as whether male *L. laticeps* feed most frequently underground or aboveground and whether most of their food is taken during the time they are actively calling. The most convincing test we can think of would be to determine whether gravid female *L. bufonius* respond positively to the advertisement calls of *L. laticeps* and whether, in fact, they actually prefer the calls of *L. laticeps* to the calls of *L. bufonius*. Performing this test is realistic, as the critical factor of obtaining gravid female *L. bufonius* for playback experiments is very possible.

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- Leptodactylus fuscus* (n = 10).— PARAGUAY: Boquerón, Filadelfia, USNM recording 327, cut 2, unvouchered. Air temperature 30°C, no time recorded. 28 November 1982. Recorded by N.J. Scott, Jr.
- Leptodactylus labyrinthicus* (n = 10).— BRAZIL: Paraíba, São José de Bonfim, USNM recording 233, cut 3, photo voucher by A.J. Cardoso. Air temperature 22°C, time 2130 h. 24 February 1990. Recorded by A.J. Cardoso.
- Leptodactylus laticeps* (n = 4).— PARAGUAY: Boquerón, Filadelfia, USNM recording 327, cut 5, unvouchered. Air temperature 28°C, time 0003 h. 30 November 1982. Recorded by N.J. Scott, Jr.
- Leptodactylus latinasus* (n = 10).— ARGENTINA: Salta, Embarcación, USNM recording 19, cut 5, unvouchered. Air temperature 21.3°C, time 2230 h. 23 December 1971. Recorded by W.R. Heyer.
- Leptodactylus mystacinus* (n = 10).— PARAGUAY: Boquerón, Filadelfia, USNM recording 327, cut 6, unvouchered. Air temperature 24°C, time 2206 h. 7 December 1982. Recorded by N.J. Scott, Jr.
- Leptodactylus stenodema* (n = 8).— COLOMBIA: Vaupés, Wacará, USNM recording 129, cut 1, unvouchered. Air temperature 26.8°C, time 1720 h. 6 June 1973. Recorded by W.F. Pyburn.

APPENDIX

Recording data

Leptodactylus bufonius (n = 6 calls).— PARAGUAY: Boquerón, Filadelfia, USNM recording 327, cut 3, unvouchered. No temperature, no time recorded. 28 November 1982. Recorded by N.J. Scott, Jr.