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Advertisement calls, notes on natural history, and distribution of *Leptodactylus chaquensis* (Amphibia: Anura: Leptodactylidae) in Brasil

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Abstract.—Three types of advertisement calls of *Leptodactylus chaquensis* from the Cerrado of Minas Gerais, Brasil are described – growls, grunts, and trills. Additional variation includes calls that start with growls and end with trills. The growl call has not been reported previously. Tadpoles are described and agree with previous descriptions. A female was found associated with tadpoles for at least 20 d. The female communicated with the tadpoles by pumping behavior and also exhibited aggressive behavior toward potential predators. The data reported herein are the first conclusive evidence that *L. chaquensis* occurs in the Cerrado of Minas Gerais. Other reported Brasilian records for *L. chaquensis* come from the southern portion of the Cerrado. Additional field work is necessary to determine whether *L. chaquensis* occurs in the northern Cerrado (in the states of Bahia, Distrito Federal, Maranhão, Pará, and Tocantins).

The systematics of the phenetically defined *Leptodactylus ocellatus* species group is chaotic and confusing. This group of species has never undergone a taxonomic revision covering its entire distributional range. There are two phenetically distinct species complexes within the species group. The *Leptodactylus bolivianus* complex currently contains one or two species, depending on author. Based on evaluation of specimens throughout its distributional range, this complex consists of three species (Heyer & de Sá, pers. obs.). There are four species names in current use for members of the *Leptodactylus ocellatus* complex: *L. chaquensis*, *L. macrosternum*, *L. ocellatus*, and *L. viridis*. *Leptodactylus viridis* is morphologically distinctive (within the entire genus *Leptodactylus*) and may not be closely related to the other members of the *L. ocellatus* complex (Heyer, pers. obs.). *Leptodactylus ocellatus* contains at least two species and probably more (Heyer, pers. obs.). The nomenclatural status of both *Rana ocellata* Linnaeus, 1758 and *Leptodactylus ocellatus macrosternum* Miranda-Ribeiro, 1926 are unclear and need clarification. The nomenclature of *Rana ocellata* is complicated (Heyer, pers. obs.). Suffice it to say, the taxon that represents *Leptodactylus ocellatus* is unknown at present. The name *Leptodactylus macrosternum* has been applied in recent years to specimens occurring throughout Amazonia. The type locality of *Leptodactylus ocellatus macrosternum* Miranda-Ribeiro, 1926 is ''procedente da Bahia pelo Snr. Bicego (XI – 1896).'' Miranda-Ribeiro repeated the species description almost verbatim in 1927, but the date given for Bicego's sojourn in the Salvador region is ''(VI 1896)'' (Miranda-Ribeiro 1927:125). Bo-

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kermann (1966:73) suggested the type locality was ''provavelmente Salvador,'' as the collector, Benjamino Bicego, collected other materials for what is now the Museu de Zoologia da Universidade de São Paulo in May of 1896 in the environs of Salvador, Bahia. There are two major morphoclimatic domains in or near Salvador – Atlantic Forest and Caatinga. It is highly unlikely that if *L. macrosternum* is a valid species, it applies to Amazon members of the *L. ocellatus* group. Further research is needed to determine whether *L. macrosternum* is a valid species and what its distribution is. *Leptodactylus chaquensis* Cei, 1950 was described from specimens occurring in the Gran Chaco of Argentina. Cei (1950) differentiated his new species from Argentine specimens considered to be *L. ocellatus*. The two species in Argentina are readily distinguished from each other morphologically (Cei 1950) and by advertisement calls (Barrio 1966) and often occur together in the same ponds. These same two species are also readily distinguished from each other in Uruguay, Paraguay (Heyer & de Sá, pers. obs.), and southern Brasil (Santos & Cechin 2008). The taxonomy of the *L. ocellatus* species complex in Bolivia is not at all clear, as vividly described by De la Riva & Maldonado (1999). *Leptodactylus chaquensis* occurs throughout the Gran Chaco of Argentina and Paraguay, as well as in some adjacent intergrading biomes. Within Bolivia, members of the *Leptodactylus ocellatus* complex occur in the Amazon Forest, Cerrado, Gran Chaco, and Pantanal Flooded Savannas ecoregions (Reichle 2006). The number of species of this complex in Bolivia and their ecoregion distributions are unknown at present (De la Riva & Maldonado 1999, Reichle 2006). Bolivian members of this complex that occur in the Gran Chaco ecoregion may reasonably be assumed to be conspecific with *L. chaquensis* from the Gran Chaco of Argentina and Paraguay.

One purpose of this paper is to evaluate the advertisement call data to determine whether specimens from the Brasilian Cerrado ecoregion are conspecific with *Leptodactylus chaquensis* from the Gran Chaco of Argentina. A second purpose is to report on new natural history observations of *L. chaquensis*.

Materials and Methods

Advertisement calls.—Calls of two individuals of *Leptodactylus* were recorded on 18 Oct 2006 from Brasil, State of Minas Gerais, Municipality of Araguari. Voucher specimens and AAG sound files are in the collection of frogs of the Universidade Federal de Uberlândia (AAG-UFU). The data for voucher specimen AAG-UFU 4096 (99.7 mm SVL) (Fig. 1), recording LeptochaquMG1bAAGm (hereafter referred to as MG1b) and LeptochaquMG1cAAGm (hereafter MG1c), are 03:30h, 24°C water temperature, and 22°C air temperature. The data for voucher specimen AAG-UFU 4108 (74.2 mm SVL), recording LeptochaquMG2bAAGm (hereafter MG2), are 08:45h, 25°C water temperature, and 31°C air temperature. The recordings were made with a Marantz PMD670 digital recorder set at 44,100 Hz and 16 bit resolution and a Sennheiser K6ME66 microphone. The calls were analyzed using Raven (Charif et al. 2004) and Soundruler (Gridi-Papp 2004).

Recording MG1c includes the calls of several other species of frogs and makes detailed analyses of the calls of the focal *Leptodactylus* individual difficult. Recording MG1b has less background sounds than MG1c. Recording MG2 was made early in the morning when most of the other frogs had stopped calling, but there are many bird sounds in the background. Recording MG2 is the cleanest with respect to the *Leptodactylus* calls and was used for the note/pulse duration and individual note/pulse frequency analyses.

Fig. 1. Male *Leptodactylus chaquensis* (voucher specimen AAG-UFU 4108). Municipality of Araguari, State of Minas Gerais, Brasil.

There is cycle to cycle change in fundamental frequencies within the calls. The frequencies of individual pulses and notes were measured from printouts of appropriately expanded wave forms and only well-defined cycles were measured. The fundamental frequency data were sampled from beginning, middle, and ends of calls for 57 grunt, 48 growl, and 127 trill cycles. All quantitative data were taken from calls filtered below about 250 Hz and above about 2000 Hz. Terminology follows Heyer et al. (1990).

Tadpoles.—Tadpoles were preserved in 5% formalin at the moment of collection; they were identified by association with their mother. The description was based on a sample of seven specimens (35–37 mm TL, stage 28). Measurements were taken on a representative specimen with a stereomicroscope coupled to a micrometric ocular.

Parental care observations were made on a female and associated tadpole school on two occasions (1 and 20 Aug 2008) for 300 min scattered throughout the day and night. Maternal defensive behavior was induced by noisily disturbing the water surface with the finger tip near (20 cm) the tadpole school. This female was identified by collecting and photographing her; details of the dorsal pattern confirmed that it was the same individual involved on 1 and 20 August.

Habitat.—The studied site is in the steep and eroded banks of the Paranaíba River. The original vegetation includes tropical forest (which can still be found as small patches along rain drainage channels and rivulets) and typical Cerrado (Brasilian savanna) vegetation. Most of the original vegetation was removed for raising cattle. The specimens were found at the margins of artificial permanent ponds (30 × 10 m or less). Vegetation around these ponds includes buriti palms (*Mauritia flexuosa*), shrubs, and/or grasslike plants. Fish

occur in and cattle regularly drink from these ponds.

Advertisement Calls

Three kinds of calls occur that can be described as growls, grunts, and trills. In addition, there are calls that combine growl and trill elements. Recording MG2 vocalizations (smaller male recorded in the morning) are described in the greatest detail, followed by briefer descriptions for recordings MG1b and MG1c (larger male, with considerable background calls).

Recording MG2 growls.—Growls are the most frequent (12) call type in the recording (Fig. 2, Table 1). Calls are intensity modulated, beginning and ending quieter than the middle portion of the call (Fig. 2). Growls have at least one harmonic. Call durations range from 0.448–0.659 s. Each call contains from 21–30 notes, given at rates of 46–49/s. The first note consists of either a single pulse ($n = 5$) or two pulses ($n = 7$). All remaining notes are single-pulsed. Double-pulsed first notes range from 0.023–0.028 s (mean 0.026), single-pulsed first notes range from 0.012–0.015 s (mean 0.013). For single-pulsed first notes, the next note usually is given in a shorter time interval than occurs among the remaining notes. The average duration of the next 4–5 notes at the beginning of the call ranges from 0.013–0.016 s (mean 0.014). The average duration of 5 sequential notes from the middle of the call ranges from 0.014–0.018 s (mean 0.017). The average duration of the penultimate 4–5 notes of the call ranges from 0.013–0.017 s (mean 0.015). The final note is sometimes shorter or longer than the rest of the notes, ranging from 0.010–0.019 s (mean 0.014). Within calls, there is great variation of note beginning (excluding initial note), middle, and ending (excluding final note) duration, with beginning, middle, and ending notes either having the shortest or longest durations, occurring in all possible sequences among the three categories with one exception – the middle notes are never the shortest notes in the call. Many of the beginning and ending cycles of notes are unclear in expanded wave forms: the following data are based mostly on cycles between the beginning and ending cycles of the note. There is frequency modulation within every note. Overall, the fundamental frequencies evaluated range between 274–650 Hz. The total range of frequency modulation for evaluated notes, 376 Hz, is considerably greater than the largest frequency range observed in any single note (193 Hz). In five notes analyzed, the frequencies rose through the entire note.

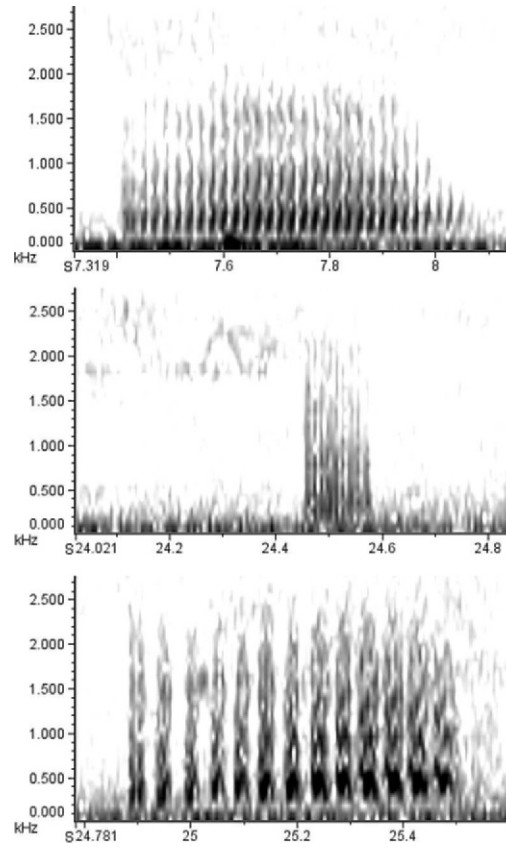

Fig. 2. Audiospectrograms of growl (above), grunt (middle), and trill (below) calls of *Leptodactylus chaquensis*, recording MG2, voucher specimen AAG-UFU 4108.

Only one note had frequencies that fell throughout the entire note. The remainder of the notes had rising and falling frequencies in adjacent cycles throughout the note. The most complex pattern of adjacent frequency cycles observed is (first cycle unclear)–475-337–435-282–298-337–402 Hz (Fig. 4). The average fundamental frequency of all growl notes analyzed is 395 Hz and the dominant frequency ranges from 343–348 Hz.

Recording MG2 grunts.—Grunts are noticeably intensity modulated, starting and finishing quieter than the middle of the call to relatively non-modulated, with slightly less intensity in the latter half of the call (Fig. 3 middle, Table 1). Grunts have at least one harmonic. The durations of the six grunts analyzed range from 0.102–0.122 s. The grunt is made up of individual elements that are intermediate between the definitions of pulses and notes. The six calls are comprised of 8–10 pulses/notes, given at rates of 71–100/s (Figs. 2, 3 both middle). There is less distinction in variation among pulses/notes in the grunt calls when compared to the growl calls. Within calls, the minimum note/pulse duration is 0.005–0.009 s (overall mean 0.008), the average is 0.010–0.011 s, and the maximum is 0.012–0.014 s (overall mean 0.013). Perhaps due to the lower overall intensity of the grunts, the expanded wave forms were not as clear as to where individual cycles begin and end within each note/pulse. Only one or two cycles could be evaluated for most notes/pulses. Beginning, middle, and ending notes/pulses were analyzed for three grunts. In the first, the individual cycles ranged from 209–628 Hz (mean 361), in the second, 255–638 Hz (mean 362), and for the third, 278–619 Hz (mean 436), with an overall mean value of 389 Hz. The dominant frequency ranges from 263–343 Hz.

Recording MG2 trills.—There are six trill calls in the recording (Table 1). The calls are intensity modulated, with the

Table 1.—Comparison of major call parameters for growl, grunt, and trill calls of *Leptodactylus chaquensis* recording MG2. Means ± standard deviation in parentheses. Calls of specimen from Municipality of Araguari, State of Minas Gerais, Brasil.

Call parameters	Call Types		
	Growl	Grunt	Trill
Call duration (s)	0.448–0.659 (0.541 ± 0.075)	0.102–0.122 (0.112 ± 0.008)	0.595–0.663 (0.623 ± 0.025)
Notes/pulses per call	21–30 (25.8 ± 3.3)	8–10 (9.2 ± 0.8)	14–16 (15.0 ± 0.9)
Note/pulse rate/s	46–49 (47.5 ± 1.6)	71–100 (82.8 ± 10.7)	21–26 (23.5 ± 1.9)
Note/pulse duration (s)	0.008–0.029 (0.016 ± 0.003)	0.005–0.014 (0.011 ± 0.002)	0.011–0.042 (0.029 ± 0.007)
Frequency range (Hz)	274–650 (395 ± 84)	209–638 (389 ± 63)	196–613 (433 ± 88)
Dominant frequency (Hz)	343–348 (345 ± 2)	263–343 (291 ± 40)	428–514 (460 ± 41)

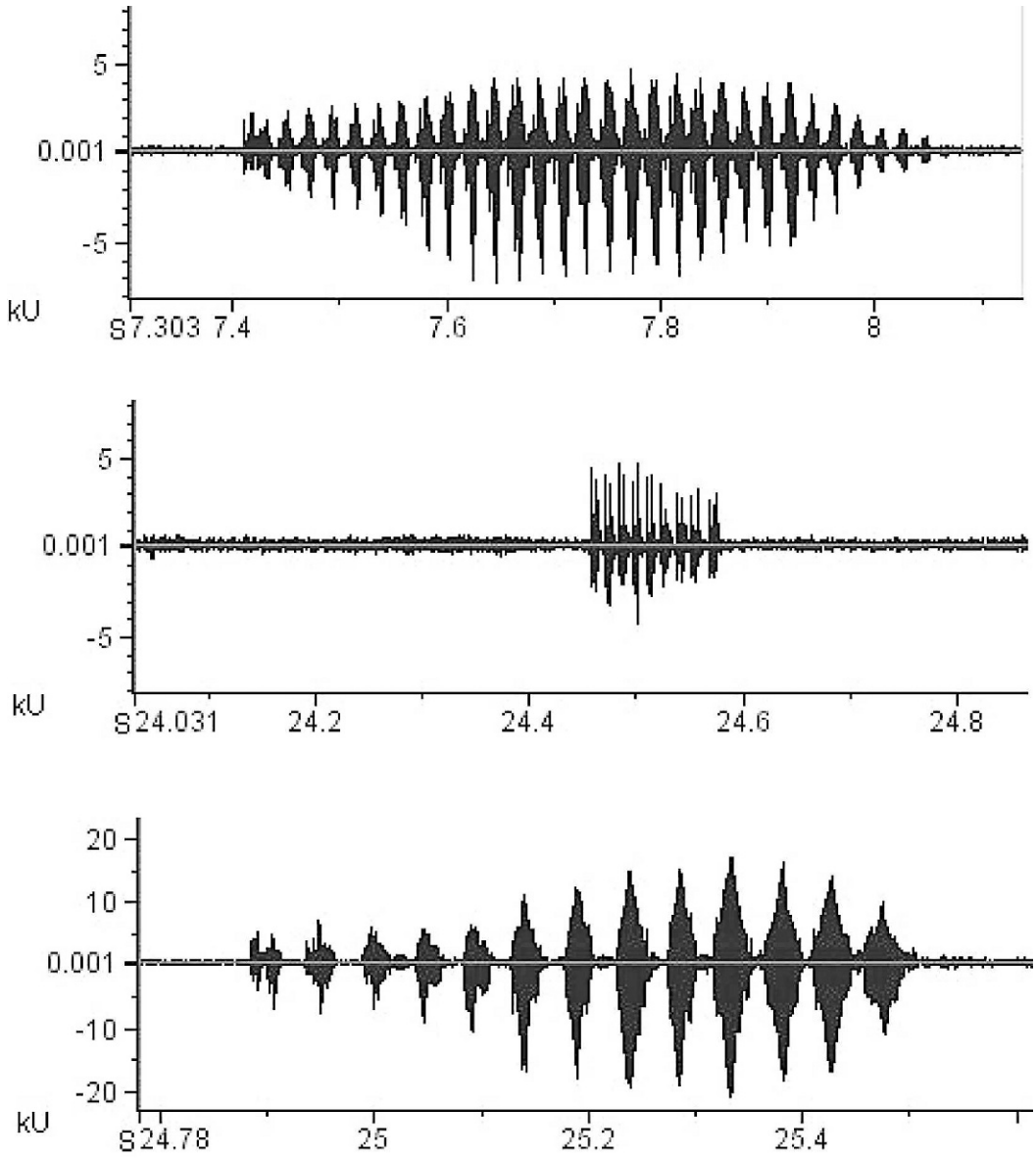

Fig. 3. Wave forms of growl (above), grunt (middle), and trill (below) calls of *Leptodactylus chaquensis*, recording MG2, voucher specimen AAG-UFU 4108.

first 5–6 notes having noticeably less energy than the remaining notes with the exception of the final 2–3 notes which exhibit attenuated intensities. Trills have at least one harmonic. Call durations range from 0.595–0.663 s. Calls consist of 14–16 notes given at rates of 21–26/s. The shortest notes range from 0.011–0.015 s, the average note duration ranges from 0.027–0.030 s, and the longest notes range from 0.035–0.042 s. The shortest notes are either the first (5) or last (1) notes. The longest notes occur from the seventh to the last note. There is frequency modulation within every note. The fundamental frequencies evaluated range between 196–613 Hz. The range of frequency modulation, 417 Hz, is considerably greater than

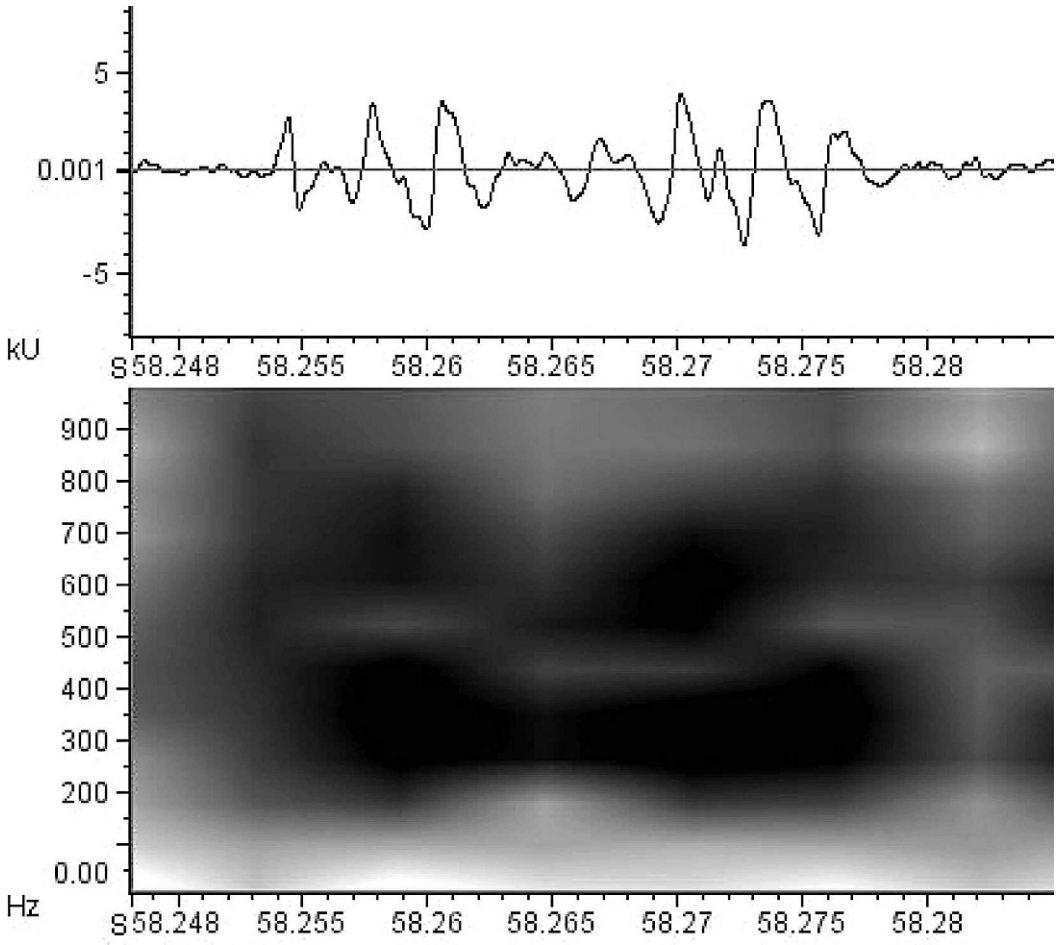

Fig. 4. Expanded wave form and audiospectrogram of an initial growl note of *Leptodactylus chaquensis* with two pulses, recording MG2, voucher specimen AAG-UFU 4108.

the largest frequency range observed in any single note (219 Hz). In only one note (an initial note) did the frequency rise throughout the entire note. In all other notes the frequencies had different patterns of rising and falling throughout the notes. One of the more complex patterns of consecutive cycles is a penultimate note: (first one or two cycles not measurable)-532–591-591–591-532–532-444–444-444–444-484–484-444–380-380–(last cycle not measurable) Hz. The average fundamental frequency of all trill notes evaluated is 433 Hz. The dominant frequency ranges from 428–514 Hz.

The three types of calls described above are quite distinctive from one another, particularly in temporal parameters (Table 1).

Recording MG2 other calls.—There are two calls that are most similar to growls. The two calls differ from growls in that the calls are shorter (0.233, 0.336 s). One note of one call is shorter (0.007 s), and one call rate is just greater (51 notes/s) than found in the analyzed growl calls. The two calls are identical to the growl calls in all other respects and are considered to be growl calls, even though they are relatively short.

There are seven calls that demonstrate transitions from growls to trills. In each case, the call starts with growls and ends with trills. The calls range from mostly growls to mostly trills. One call contains some unusual short notes while another has an unusually long last note (0.051 s). Three of the calls have growl note rates of 51, 53, 54/s, and one call has a trill rate of 20/s. These transition calls do not contain any grunt or grunt-like elements.

Calls of MG1b and MG1c recordings.—Grunt Calls. Recording MG1b has one grunt call and a possible second grunt call. The unambiguous grunt call duration is 0.234 s with about 18 pulses/notes, a dominant frequency of 863 Hz with a slightly quieter frequency peak at 434 Hz. The ambiguous grunt call is 0.094 s long (call not clear enough for further quantitative evaluation). Recording MG1c has three possible grunt calls for which the lack of clarity disallow quantitative evaluations.

Growl and trill calls.—The descriptive information of growl and trill calls for recordings MB1b and MG1c are the same as described for recording MG2. The quantitative data that could be analyzed for the two recordings are presented in Table 2.

Call type organization.—Recording MG1b has the following sequence of calls: 1 trill – 1 growl/trill – 3 grunts – 4 growl/trills – 10 trills – 1 grunt? – 1 trill – 2 growl/trills – 1 trill – 1 grunt. The call sequence for recording MG1c is: 1 grunt? – 1 trill – 1 grunt – 1 trill – 1 grunt – 1 trill – 1 grunt – 3 trills – 2 grunt?s – 5 growls – 1 growl/trill – 1 growl – 1 growl/trill – 3 trills – 1 growl/trill. The call sequence for recording MG2 is: 4 growls – 2 growl/trills – 1 grunt – 1 trill – 1 grunt – 1 trill – 1 grunt – 1 trill – 1 growl/grill – 1 grunt – 1 trill – 1 grunt – 1 trill – 1 grunt – 1 trill – 6 growls – 1 growl/trill – 3 growls – 3 growl/trills – 1 growl.

The only evident pattern is that grunts usually precede trills; otherwise, we find

Table 2.—Comparison of call parameters for growl and trill calls of *Leptodactylus chaquensis* recordings MG1b and MG1c. Means ± standard deviation in parentheses for parameters with more than three values. Calls of specimen from Municipality of Araguari, State of Minas Gerais, Brasil.

Call parameters	Call Types			
	Growl		Trill	
	MG1b	MG1c	MG1b	MG1c
Call duration (s)	0.560–0.616	0.414–0.552 (0.486 ± 0.049)	0.677–0.807 (0.732 ± 0.040)	0.480–0.683 (0.607 ± 0.067)
Notes per call	22–25	16–22 (19.0 ± 2.1)	13–16 (14.1 ± 1.3)	11–14 (12.0 ± 1.2)
Note rate/s	37–39	38–39 (38.4 ± 0.5)	17–22 (19.2 ± 1.5)	17–22 (19.6 ± 2.2)
Dominant frequency	428–432	434–515	424–520 (484 ± 43)	434–515 (469 ± 43)

no obvious pattern to the sequences of grunts, growls, growl/trills, and trills.

The call rates of all calls for the three recordings (MG1b, MG1c, MG2) are 16.8, 19.5, and 24.6 calls/min, respectively. Alternating grunt and trill sequence rates are 48.4 calls/min for MG1c and 63.8 calls/min for MG2.

Individual differences.—The marked size differences of the two *L. chaquensis* individuals recorded would predict that dominant frequencies, in particular, would differ (Tables 1, 2). The dominant frequencies of the trill calls of the two individuals are essentially identical, whereas the dominant frequency of the growl call for the larger individual is actually higher than that for the smaller individual, which runs counter to the situation for virtually all other species of frogs for which there are data. The number of notes per call is essentially the same for trill calls, but the smaller individual produced a greater number of notes/s than the larger individual.

The call differences between the two individuals have no obvious explanations. Both males that were calling sat on the ground (not floating in deep water). The calling individuals were not observed for a sufficient time to determine the behavioral contexts and meanings of the suite of vocalizations involved. Perhaps the growl call is not used to attract females but has some other function.

Call discussion.—The grunt and growl calls sound similar to the human ear, except that the grunt is perceived as of shorter duration than the growl. The trill call sounds very different from the growl and grunt calls because the note rate of the trill is slow enough that the human ear perceives each note individually. The growls are at the edge of the rate at which humans are able to discern the notes as individual entities. Based on what is known about signal recognition and processing in frogs (Fritzsch et al. 1988), *L. chaquensis* likely do not perceive the clear difference between the trill versus grunt and growl calls, as humans do, as frogs can discern temporal patterns much better than humans. Some microhylid frogs produce calls at a rate of 200 pulses/s (Nelson 1973, harmonic interval values in Table 1, p. 165 are actually pulse rates) and presumably can discern each pulse while humans can discriminate temporal features at about 50–60 features/s. To *L. chaquensis*, the grunts, growls, and trills sound the same, but the three call types are recognized as different from each other on the basis of distinct note/pulse rates for each call type. In other words, the frogs likely recognize that all call types are based on packaging differences of the same basic unit, which is the note for the growls and trills and the note/pulse for the grunts. The basic call unit is typically 0.012–0.019 s in duration, is frequency modulated within the unit in a variable pattern of at least some adjacent cycles having different frequencies, and has at least one harmonic frequency.

Calls of the species of the *Leptodactylus ocellatus* complex are notoriously difficult to record. The frogs often call from within water in the shallower portions of bodies of water usually in dense vegetation. The frogs are extremely wary and stop calling and dive into the water when approached close enough to obtain good recordings. It is even more difficult to actually capture the frog after it has been recorded to serve as a voucher specimen (in the present case, both specimens were captured). The difficulty of obtaining vouchered recordings for these abundant, geographically widespread frogs is reflected by the very few recordings that are available. The following are comparisons of the calls we describe herein with all recordings that we are aware of for *Leptodactylus chaquensis*.

The Araguari calls compare well with the two different call types of *L. chaquensis* described and illustrated by Barrio

(1966) for specimens from Helvecia, Santa Fe, Argentina. The shorter call described by Barrio is most similar to the grunt calls analysed herein. The longer call Barrio described matches the trill call of the Araguari specimens (the differences in appearance of the trill call in Barrio's and our figures are probably due to different analytic equipment). De la Riva et al. (2002) published a compact disk recording of *L. chaquensis*. Their recording is of a loud chorus of many individuals of *L. chaquensis* for which it is impossible to analyze individual calls. The recording seems to contain only growl calls.

The only other published recording for *L. chaquensis* that we are aware of is the distress call recorded from the Bolivian Cerrado by Padial et al. (2006). As is true for other species, the distress calls of related species are rather similar to each other as discussed for *L. chaquensis* and *L. ocellatus* by Padial et al. (2006).

The Axel Kwet web page <http://www.herpetologie.naturkundemuseum-bw.de/album.php?species=Leptodactylus+chaquensis&welt=album&land=rio_grande&region=rio_grande> has a recording of two trill calls of *L. chaquensis*. The calls sound different from the Araguari calls to the human ear, perhaps due to dominant frequency differences or geographic variation. The human perceived differences in calls are likely not the result of recording/file format differences.

Given the paucity of recordings for *L. chaquensis*, we do not know whether the Araguari population differs from the other populations of *L. chaquensis* in having three distinct advertisement calls (we presume the three call types are advertisement calls, but one or more of them may be response calls). We suspect that better quality and longer recordings of *L. chaquensis* from throughout its distributional range will reveal the same diversity of calls we report in this paper.

Tadpole Description

Measurements (mm) of a well preserved tadpole [Gosner (1960), stage 28] were 36.7 TL, 14.2 body length, 7.5 maximal height of tail, 8.2 maximal body height, 1.1 eye diameter, 1.2 eye-nostril distance, 2.0 interocular distance, 1.8 internasal distance, 8.0 snout- external border of spiracle distance, 3.0 oral disk width. Tooth row formulae 2/3[1]; P1 interruption very short when present. Upper jaw sheath arched, lower jaw sheath V-shaped. Marginal papillae broadly interrupted anteriorly, 1–2 lateral series and 1 ventral series. Spiracle sinistral, directed posterodorsally, posterior border forming a short free tube. Vent medial, broad, not forming a free tube. Living and preserved tadpoles (stage 25–28) were black; in life (stage 28) there is a discrete orange line (8 mm long) at the border of the upper fin at its insertion to the body.

The tadpoles described herein are in accordance with those described by Cei (1980:352) from Argentina.

Natural History Observations

Habitat.—Four specimens (two males, one female, one juvenile) were found at the margins of artificial ponds. The two males were heard in the rainy season (18 October 2006) and the female (Fig. 5) was found beside her schooling tadpoles in the dry season on 1 August 2008, with water temperatures 18–28°C, and again on 21 August 2008.

Both males called among short (< 1 m height) grass-like plants. Terrestrial frogs calling syntopically included *Leptodactylus fuscus*, *L. labyrinthicus*, *L. ocellatus*, *Elachistocleis bicolor*, and *Physalaemus centralis*. One male called during the night and the other called after dawn the following morning.

Prey.—The smaller male (74.2 mm SVL) regurgitated an adult male *Physa-*

Fig. 5. A female *Leptodactylus chaquensis* beside her tadpole school. Her pelvic girdle is slightly raised because she was photographed while performing pumping behavior. Municipality of Araguari, State of Minas Gerais, Brasil. 20 August 2008, about 20:30h.

laemus centralis (Anura, Leiuperidae) (37 mm SVL) in the plastic bag in which he was held overnight.

Parental care.—The female mentioned above (Fig. 5) was found with her tadpoles during both the day and the night. The tadpoles formed a dense school comprised of hundreds of individuals. The female and larvae were found among short (30–60 cm height) sparse grass-like plants in a well-illuminated and shallow (ca. 15 cm deep) portion of the pond. When approached by humans, the female often dove into the water and reemerged 30–70 min. later. On another occasion during the day, she slowly approached and suddenly attacked by jumping toward the hand of the individual who was disturbing the water. The female performed pumping behavior [periodic raising of the pelvic girdle as described by Wells & Bard (1988) for *L. bolivianus* (= *L. insularum*)] during the night when she was close (0–20 cm) to her school. The female and her larvae were observed within the same 2–4 m area of the pond at both observation periods. On August 20 we also found a female *L. ocellatus* tending her school in a nearby (< 100 m) pond.

Natural history discussion.—Batrachophagy has been also reported for an Argentine population of *L. chaquensis* (Gallardo 1964) and seems to be a frequent behavior among the large sized species of *Leptodactylus* (Gallardo 1964, França et al. 2004).

Our data suggest that at our study site both *L. chaquensis* and *L. ocellatus* can reproduce sympatrically and throughout the year. Cei (1965) reported that in Argentina *L. chaquensis* did not reproduce between December and March, whereas *L. ocellatus* reproduced yearround. Gallardo (1964) and Prado et al. (2005) found that *L. chaquensis* reproduced only during rainy months. Maternal care has been reported for some *Leptodactylus* of the *L. ocellatus* group such as *L. ocellatus* (Vaz-Ferreira &

Gehrau 1975), *L. chaquensis* (Prado et al. 2000), and *L. insularum* (Wells & Bard 1988). In contrast to Prado et al. (2000), we found both aggressive and pumping behaviors in *L. chaquensis*. Our report on aggressive behavior toward potential predators by a female *L. chaquensis* while guarding her young has been reported for *L. ocellatus* (Vaz-Ferreira & Gehrau 1975) and *L. insularum* (Ponssa 2001). While other species within the *L. melanonotus* group are known to exhibit maternal care of their schooling tadpoles (Downie 1996; Martins 2001; Santos & Amorim 2005, 2006; Hoffmann 2006; Lima et al. 2006; de Sá et al. 2007), only *L. podicipinus* exhibited aggressive behavior toward potential predators (Prado et al. 2002).

The Distribution of *Leptodactylus chaquensis* in Brasil

Leptodactylus chaquensis has been reported from two major ecoregions [= biomes or morphoclimatic domains (see Ab'Saber 1977 for a map of morphoclimatic domains in South America)] in Brasil – the Pantanal of the states of Mato Grosso and Mato Grosso do Sul (e.g., Strüssmann 2000; Strüssmann et al. 2000; Gordo & Campos 2004, 2005; Prado & Haddad 2003, 2005; Prado et al. 2005) and the Cerrado in the states of Mato Grosso (Heyer & Muñoz 1999), Mato Grosso do Sul (Uetanabaro et al. 2007), and Minas Gerais (Silveira 2007, Giaretta et al. 2008). *Leptodactylus chaquensis* has also been reported from transitional ecoregions in the states of Rio Grande do Sul (Garcia & Vinciprova 1998, Santos & Cechin 2008) and the interior portion of the State of São Paulo near the border of Mato Grosso do Sul (Santos et al. 2007). Souza and Cardoso (2002) reported *L.* aff. *chaquensis* from the State of Rondônia but did not include the ecoregion type in which the specimens occurred. All of the Brasilian records for *L. chaquensis* did not report advertisement call information. Presumably, identifications were based on morphological attributes when the authors realized that the specimens were not *L.* "*ocellatus.*" The specimens were likely identified as *L. chaquensis* more by default than by comparison of the reported specimens with specimens of *L. chaquensis* from the Gran Chaco of Argentina.

The similarity of advertisement calls that are described herein with those described by Barrio (1966) is the strongest evidence to date that the *L. chaquensis* specimens reported from the Cerrado domain of Brasil are conspecific with *L. chaquensis* of the Gran Chaco of Argentina. All reports of *L. chaquensis* from the Brasilian Cerrado domain are from its southern portion only. Further field work is necessary to establish whether the species is restricted to the Cerrado domain in the states of Mato Grosso, Mato Grosso do Sul, and Minas Gerais, or whether the species occurs in the northern portions of the Cerrado as well (states of Bahia, Distrito Federal, Maranhão, Pará, Tocantins).

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