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Geographical variation of advertisement and release calls in toads referred to as *Rhinella diptycha* (Anura: Bufonidae)

Ismael E. di Tada[1,2] & Ulrich Sinsch[2]

[1] Ecología, Departamento de Ciencias Naturales, Facultad de Ciencias Exactas, Físico–Químicas y Naturales, Universidad Nacional de Río Cuarto, Ruta Nacional N° 36 – km 601, (X5804BYA) Río Cuarto, Argentina
[2] Institute of Integrated Sciences, Department of Biology, University of Koblenz-Landau, 56070 Koblenz, Germany

Corresponding author: Ulrich Sinsch, ORCID-ID: 0000-0001-8735-8723, e-mail: sinsch@uni-koblenz.de

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The geographical range of the Neotropical giant toad *Rhinella diptycha*, a member of the *R. marina* species group (sensu Pereyra et al. 2021), seems to be poorly understood, as recent taxonomic re-arrangements and molecular re-assignments of populations provide a complex taxonomic and phylogenetic history (see Frost 2022). Currently, the formerly widely used names *paracnemis*, *schneideri* and *jimi* are considered junior synonyms of *R. diptycha* (Lavilla & Brusquetti 2018, Pereyra et al. 2021, Frost 2022). The situation is further complicated by mitochondrial introgression and hybridization between *R. diptycha* and *R. marina* which might have occurred in the area south of the Amazon River (Sequeira et al. 2011, Vallinoto et al. 2017). The close phylogenetic relationship to the nuclear genome of *R. horribilis* from Ecuador is currently not understood (Pereyra et al. 2021). To make confusion complete, a recent study suggests that the synonymy of *R. schneideri* and *R. diptycha* may be in error (Rivera et al. 2022).

According to Frost (2022), the species' range, including any locality from which *R. diptycha* or one of its junior synonyms have been reported, includes northeastern Brazil from Pará (Municipality of Bujaru) and Maranhão to Piauí, Ceará, Rio Grande do Norte, and Alagoas, south to Rio Grande do Sul and Espíritu Santo, Brazil, inland through Paraguay to Amazonian and eastern Bolivia, and southwest to northern and central Argentina and northern Uruguay at 15–1500 m elevation. For a respective impression, we compiled a dot map of the published localities, in which the presence of this taxon has been detected based on morphological and molecular features (Fig. 1; Köhler et al. 1997, Stevaux 2002, Núñez et al. 2004, Mulcahy et al. 2006, Da Silva et al. 2007, Silva et al. 2008, Garda et al. 2010, Jansen et al. 2011, Sequeira et al. 2011, Vallinoto et al. 2017, Valencia-Zuleta & Maciel 2017, Caballero-Gini et al. 2019, López & Grassi 2019, Neves et al. 2019, Moreira et al. 2020, Peixoto-Couto et al. 2020, Silva-Alves et al. 2020, Duarte et al. 2021, Dubeux et al. 2021, Pereyra et al. 2021, Santos 2021, Oda et al. 2022, Palmeira et al. 2022, Rivera et al. 2022).

Independent from morphological and molecular evidence, we use bioacoustic characters (male advertisement and release calls) to test the assumed geographical distribution range for taxonomic homogeneity. We hypothesize that the advertisement calls of conspecific populations should share common features, even considering intra-specific variation introduced by the variation of snout–vent length of recorded individuals and of ambient temperatures during recording. We provide new call recordings from one of the southernmost populations of the range in the province of Córdoba, Argentina and compare them with published recordings from Bolivia and Brazil (localities marked with blue circles in Fig. 1). Published call data originate from Bolivia, Santa Rosa de la Roca, Nuflo de Chavez province, Santa Cruz department (15°46' S, 61°27' W, 360 m a.s.l.; Köhler et al. 1997), and Brazil, Costa Marques, Rondônia (12°27' S, 64°13' W, 140 m a.s.l.; Santos 2021), municipality of Icém, Sao Paulo (20°20' S, 49°11' W, 449 m a.s.l.; Silva et al. 2008), Serra da Piedade, municipality of Caeté, Minas Gerais (19°48' S, 43°41' W, 1300 m a.s.l.; Duarte et al. 2021), Araguari, Minas Gerais (18°39' S, 48°11' W; 940 m a.s.l.; Santos 2021), Ituiutaba, Minas Gerais (18°58' S, 49°28' W, 531 m a.s.l.; Santos 2021), and Ponta Negra, municipality of Natal, Rio Grande Norte (5°53' S, 35°10' W, 34 m a.s.l.; Garda et al. 2010). Unfortunately, call recordings from the assumed type locality of *R. diptycha* in San Salvador, Concepcion province, Paraguay (22°49' S, 57°48' W, 80 m a.s.l.) are unavailable (Lavilla & Brusquetti 2018).

Our bioacoustic survey was done at night (23:00–24:00 h) during the austral summer in Lucio V. Mansilla, Tulumba department, Córdoba province, Argentina, 5–6 December 2003, in a permanent pond (29°48' S, 64°43' W, 201 m a.s.l.; Fig. 2). The pond was shallow with a maximal water depth of 20–30 cm. Air temperature during call recordings was 24 ± 1°C, water temperature 22°C in a depth of 10 cm. Series of advertisement calls of six undisturbed males were recorded in situ. Following advertisement call recording, we captured these and another 11 specimens to obtain snout–vent length (to the nearest mm), body mass (to the nearest g) and evoked release calls by gently compressing the sides of a male held between thumb and forefinger directly above a microphone (= artificial amplexus; Leary 1999, di Tada et al. 2001). Only slight pressure was necessary to elicit a series of release calls of different duration, but we constrained recording time to 60 s. Then, the toads were released again within the pond. Calls were recorded with a Sony DAT recorder TCD-D8.

For quantitative call descriptions, we analysed the spectral and the temporal structure of advertisement calls using ADOBE Audition 1.0. Stereo recordings were converted to mono using a sampling rate of 44.1 kHz and resolution of 16 bits. Audio spectrograms and frequency analyses were prepared applying Blackman-Harris Fast Fourier transformation with a FFT width of 1024 points. Advertisement calls were characterized by 11 variables (definitions according to Köhler et al. 2017): (1) call duration [ms]; (2) inter-call interval [ms]; (3) call repetition rate [N/min]; (4) pulse groups (= notes) per call [N]; (5) pulse group duration [ms]; (6) inter-pulse group interval [ms]; (7) pulse group repetition rate = ratio of the absolute number of pulse groups and call duration [N/s]; (8) pulses per pulse group [N]; (9) pulse duration [ms]; (10) inter-pulse interval [ms]; (11) dominant frequency of complete call [Hz]. Depending on the structure of the release call, we used a subset of the advertisement call parameters for description. Data are given as mean, standard deviation, and the range of variation among calls per species. All calculations were performed using the statistical package Statgraphics Centurion, version XVIII (Statpoint Inc. 2018).

Size and body mass of the 17 male *R. diptycha* from Argentina ranged between 158 mm and 211 mm (average:

Figure 1. Schematic map of eastern South America, showing the geographical localities at which *Rhinella diptycha* has been detected. References to *Bufo paracnemis, B. schneideri,* and *R. jimi* are included. The map base (available at www. freeworldmaps. net) has been modified to indicate type localities (*R. diptycha*: black star, *R. jimi*: grey star), other localities (red star) and populations with records of vocalizations (blue circle). The locality with the deviating advertisement call (Garda et al. 2010) is indicated by the dotted circle at the Atlantic coast.

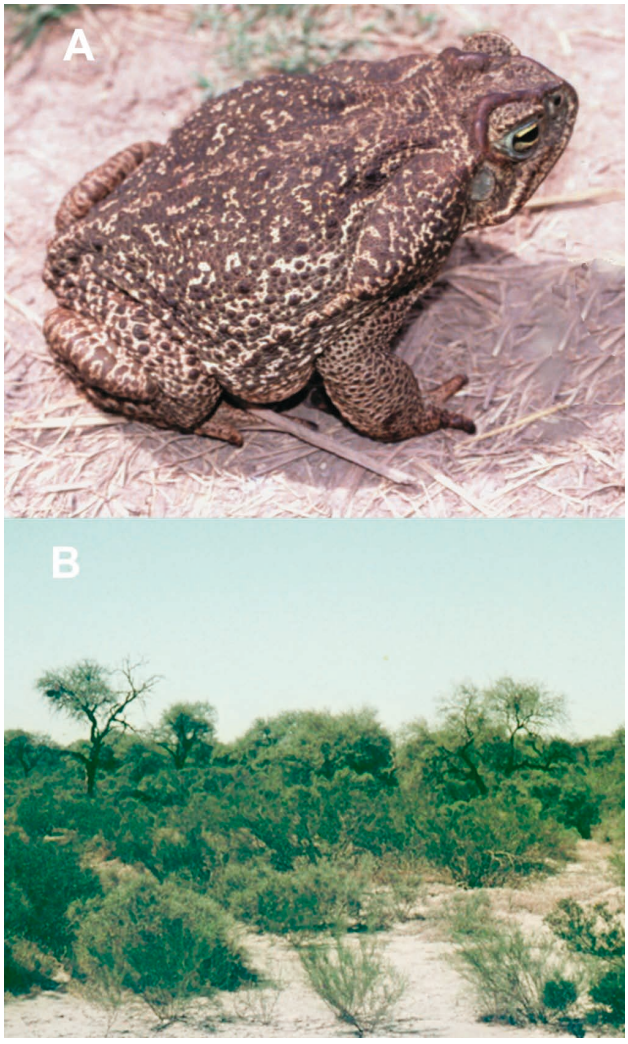

Figure 2. (A) Male *R. diptycha* collected in Lucio V. Mansilla, Cordoba, Argentina. The individual had a SVL of 198 mm and a body mass of 978 g and was released again in the pond. (B) Dry Chaco habitat in northern part of the Cordoba province. Photographs by I. E. di Tada.

192.4 ± 13.8 mm) and between 609 g and 1144 g (average: 917.4 ± 142 g), respectively. Advertisement calls were given in series of 3–14 calls and included 18–46 pulse groups per call that were spaced by regular intervals and included 2–3 pulses per pulse group (Table 1, Fig. 3). The first three pulse groups rose gradually in amplitude to reach a maximum at the fourth or fifth, which was maintained throughout the remaining call duration. The first pulse groups consisted of 2 pulses. Most individuals switched later to 3-pulses pulse groups, but occasionally maintained the 2-pulses structure.

General call features were like those reported for specimens in Bolivia and four out of five localities in Brazil (Köhler et al. 1999, Silva et al. 2008, Duarte et al. 2021, Santos 2021). Minor differences among the localities are probably attributable to the larger size of toads recorded in Argentina and to variation of temperatures during recording. Geographic variation of advertisement calls given by toads referred to as *R. diptycha* in Argentina, Bolivia and most of Brazil indicate that these giant toads are indeed taxonomically homogeneous, disagreeing with Rivera et al. (2022) that *R. diptycha* (= their *R. schneideri*) and *R. jimi* are distinct species. Yet, advertisement calls of toads at the northeastern range limit at the Atlantic Coast and originally identified as those of *R. jimi* (Garda et al. 2010), differed markedly from all other populations (Table 1). Call duration, number of pulse groups per call and call repetition rate rather resemble advertisement calls of *R. marina* in its southeastern range at Pará and Amapá, Brazil (Santos 2021). The taxonomic status of the populations at the Atlantic Coast south of the Amazonas should be re-evaluated, the deviating call features might be associated with mitochondrial introgression and hybridization between *R. diptycha* and *R. marina*, as indicated by molecular data (Sequeira et al. 2011, Vallinoto et al. 2017).

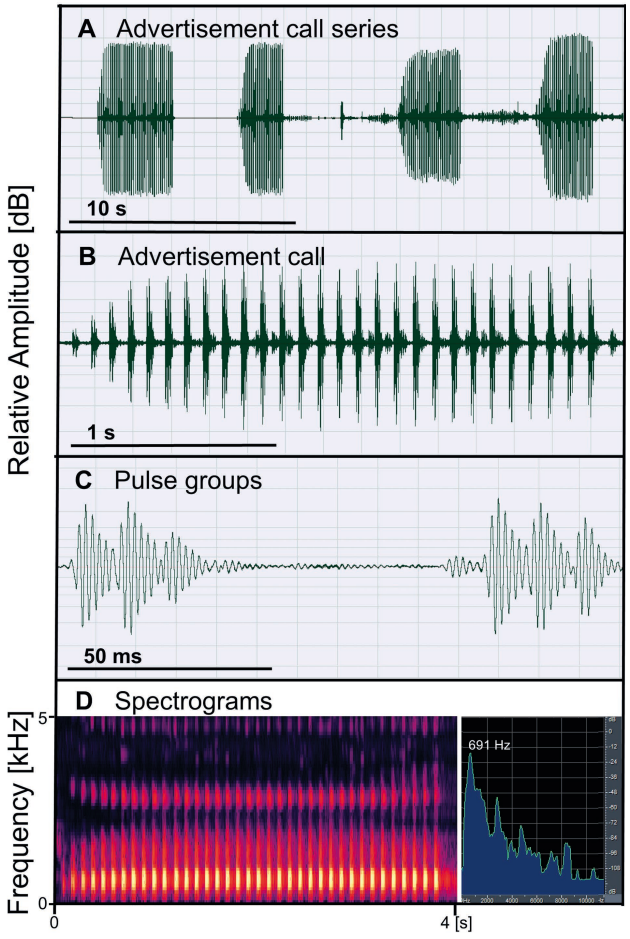

Figure 3. Advertisement call features of *Rhinella diptycha* from Lucio V. Mansilla, Córdoba province, Argentina. (A) Oscillogram of four consecutive calls. (B) Oscillogram of a single call. (C) Oscillogram of two consecutive pulse groups (= notes) with 3 pulses each. (D) Audio and power spectrograms of the call shown in (B). Calls recorded at 24°C air temperature.

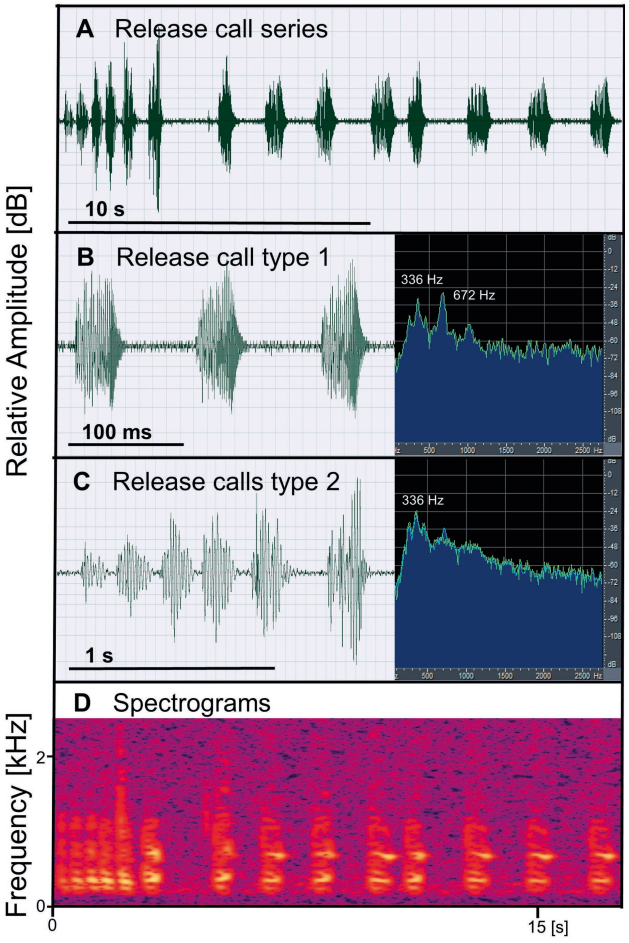

Figure 4. Release call features of *Rhinella diptycha* from Lucio V. Mansilla, Córdoba province, Argentina. (A) Oscillogram of the first 17 s of calling following the start of artificial amplexus. (B) Oscillogram of three consecutive uniform release calls and the corresponding power spectrogram. (C) Oscillogram of the pulsed release call and the corresponding power spectrogram. (D) Audio and power spectrograms of the call series shown in (A). Calls recorded at 24°C air temperature.

Table 1. Numerical parameters of the advertisement calls of *Rhinella diptycha* recorded in the province of Cordoba, Argentina, in comparison to other localities. Data are given as arithmetic means and corresponding standard deviation. In parentheses the range of data measured in single calls is given. Data on the individual from Bolivia have been published in Köhler et al. (1997; as *B. paracnemis*), those on individuals from Brazil (Sao Paulo, Rio Grande do Norte) in Silva et al. (2008; as *R. schneideri*) and in Garda et al. (2010; as *R. jimi*), respectively. The data on the specimens from Brazil (Rondônia, Minas Gerais) are cited from an unpublished Bachelor thesis (Santos 2021).

Advertisement call parameter	Argentina Cordoba	Bolivia Santa Cruz	Brazil Rondônia	Brazil Minas Gerais	Brazil Sao Paulo	Brazil Rio Grande do Norte
	N=6 (n=66 calls) 24±1°C	N=1 (n=13 calls) 25.2°C	N=6 (n=43 calls) 24°C	N=6 (n=79 calls) 23.7–27°C	N=9 (n calls ?) 23.7–27°C	N=4 (n calls ?) 27.1–28.6°C
Call duration [ms]	2810±589 (1440–3950)	2379±276 (1747–2912)	2600±1500 (1600–7200)	2200±700 (600–3700)	1700 (800–2800)	6290±2290 (3830–13970)
Inter–call interval [ms]	2841±891 (1240–4600)	1072±119 (753–1249)	4100±2400 (1200–13300)	2300±1300 (1000–8200)	–	8510±14180 (1730–95970)
Call repetition rate [N/min]	11.4±2.0 (8.2–16.5)	13.2±2.8 (11.2–18.1)	–	–	14.5±0.9 (13.3–15.5)	4.3 (1.4–5.8)
Pulse groups per call [N]	32±7 (18–46)	32±4 (24–40)	31±19 (14–93)	24±10 (7–43)	–	95±34 (52–201)
Pulse group duration [ms]	30±4 (23–37)	35±1 (33–40)	34±3 (25–42)	36±5 (26–49)	30±4 (20–30)	ca. 30
Inter-Pulse group interval [ms]	60±5 (48–71)	19±2 (18–21)	50±4 (37–63)	49±8 (30–67)	–	ca. 45
Pulse group repetition rate [N/s]	11.4±0.9 (9.9–13.8)	14.1±0.1 (14.0–14.2)	11.8±0.8 (11–14)	12.0±1.6 (10–15)	–	–
Pulses per pulse group [N]	2.5±0.5 (2–3)	3	3.6±0.5 (2–5)	3.2±0.4 (2–4)	3	2
Pulse duration [ms]	11.9±1.2 (7.8–15.6)	5±1 (4–6)	–	–	–	–
Inter-pulse interval [ms]	0.2±0.2 (0–2.5)	0	–	–	–	–
Dominant frequency [Hz]	573±26 (552–653)	700 –	770±39 (750–844)	772±38 (750–861)	790±50 (690–870)	600±52 (517–689)

We describe for the first time experimentally evoked release call series including two types of vocalizations in this species (Fig. 4). The uniform release call type 1 had no distinguishable pulses and two co-dominant frequency bands as detected in the terminal pulse groups of release call type 2 as well (Table 2, Fig. 4B). Type 1 calls were given singly, in groups of 2–4 with short inter-call intervals or in discrete groups including up to 9 calls with irregular inter-call intervals (Table 2). The pulsed release call type 2 consisted of 4–9 pulse groups, which started with 3–6 pulse groups with 1–3 pulses per pulse group, a low dominant frequency (398 Hz) and continuously increasing amplitude (Table 2, Fig. 4C). This pulse group train was followed by 1–3 terminal pulse groups with 3–6 pulses per pulse group that differed from the proceeding ones by two co-dominant frequency bands like in release call type 1. The complex release call type 2 was usually given during the first 15 s of the artificial amplexus, always followed by type 1 calls and represented only 5 % of all release calls. The dominant frequency of type 2 calls did not differ from the lower co-dominant frequency of type 1 calls and was significantly lower than the dominant frequency of the advertisement calls. The dominant frequency of release calls was not significantly related to SVL (linear regression model; R^2 = 21.3%, $F_{1,10}$ = 3.71, P = 0.0862).

The release call structure of the ten species considered to form the *Rhinella marina* group (Pereyra et al. 2021) is poorly known. In fact, the only published descriptions of release vocalizations are those for *R. arenarum* (di Tada et al. 2001), the present one for *R. diptycha* and the one regarding an individual of a toad then referred to as *R. jimi* (Garda et al. 2010). As expected, the release vocalization of *R. diptycha* included a uniform call type that seems to be a common repertoire of many *Rhinella* species (di Tada et al. 2001). We propose that release call type 1 in *R. diptycha* is homologous to the uniform call type of *R. arenarum* and may constitute a signal to non-conspecific *Rhinella* spp. (di Tada et al. 2001). In contrast, release call type 2 differed from all signals given by *R. arenarum*. As it was given most often at the beginning of a release call series, we hypothesize that this signal is directed specifically to conspecific males. The release vocalization of northeastern Brazilian "*R. jimi*" differed in all aspects from that of *R. diptycha* in Argentina, supporting the doubts on conspecificity which originated

Table 2. Numerical parameters of the release calls of *R. diptycha* recorded in the province of Cordoba, Argentina. Data are given as arithmetic means and corresponding standard deviation. In parenthesis the range of data measured in single calls is given. If parameters differed significantly between the first and the terminal pulse groups in release call type 2, they are given separately. * For comparison, we provide the data available for evoked release calls of one "*R. jimi*" male from Natal, Brazil (Garda et al. 2010), now regarded as *R. diptycha* according to Frost (2022).

Release call parameter	Type 1 call	Type 2 call	"*R. jimi*" *
	Argentina N=11 individuals (n=695 calls) 24±1°C	Argentina N=11 individuals (n=38 calls) 24±1°C	Brazil N=1 individual (n=26) 28.6°C
Call duration [ms]	46±19 (9–104)	295±65 (226–411)	ca. 21–44
Inter–call interval [ms]	61±54 (9–165)	–	ca. 10–700
Call repetition rate [N/min]	56±42 (22–166)	–	5.2
Pulse groups per call [N]	–	6±2 (4–9)	1
Pulse group duration [ms]	–	23±8 (8–39) 47±10 (31–64)	–
Inter-Pulse group interval [ms]	–	21±7 (8–37)	–
Pulses per pulse group [N]	–	1.5±0.7 (1–3) 4.4±1.1 (3–6)	2–5
Dominant frequency [Hz]	381±63 (300–452)	398±61 (325–489)	512
Co-Dominant frequency [Hz]	682±57 (603–804)	–	–

from advertisement call structure (Garda et al. 2010). In conclusion, our study demonstrates that the vocalization behaviour of *Rhinella* toads referred to as *R. diptycha* confirms conspecificity of most populations formerly referred to as "*R. schneideri*" or "*R. jimi*", but also pinpoints to the still unresolved taxonomic status of the populations at the Brazilian Atlantic coast southeast of the Amazonas River.

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