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Male release calls of two gladiator treefrog species (Cophomantini, *Boana faber* species group), with an intrageneric acoustic comparison

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Short title: Release calls of two species of *Boana*

Abstract

Anurans emit calls that convey different messages, depending on the context of emission. Reproductive calls mediate intraspecific interactions in reproductive contexts, and among these, the advertisement call is the most conspicuous and best-described type. It serves to attract mates, signal aggression between conspecific males, and maintain spacing between chorus-calling frogs. Another reproductive call, the release call, is emitted by males and females to signal non-receptiveness to a conspecific, or not, amplexus. *Boana* Gray, 1825, is a species-rich genus widely distributed in the Neotropical region, and the *Boana faber* species group comprises nest-building gladiator frogs that use prepollical spines to defend their territory. The advertisement call is known for all species in the *B. faber* species group; however, the male release call is known only for one species of the group. Furthermore, the male release call is only known for five of the 101 species of *Boana*. In this study, we describe for the first time the male release call of *Boana crepitans* and *B. faber*, and we make intrageneric acoustic comparisons among the known male release calls within *Boana*. The male release call of both species is composed of a single type of note. Pulsed notes are ubiquitous in *B. crepitans*, but they can be pulsed, pulsatile, or non-pulsed in *B. faber*. Besides the temporal envelope, notes presented differences in duration: 209–449 ms in *B. crepitans* and 5–80 ms in *B. faber*, and in pulse repetition rate: 19–25 pulses/s in *B. crepitans* and 147–156 pulses/s in *B. faber*. Expanding our acoustic comparisons to *Boana*, we found much variation in the few described release calls for the genus. Our study also highlights the rarity of described male release calls for *Boana*, and, finally, we expanded the known male release calls descriptions to seven of the 101 known *Boana* species.

Keywords: Acoustic communication, Atlantic Forest, Hylidae, Neotropics, vocal repertoire.

Introduction

Acoustic communication plays a major role in the life history of anuran amphibians (Wells 2007), mediating inter- and intraspecific interactions related to reproductive, aggressive, and defensive behaviors (Toledo et al. 2015). Looking at the anuran vocal repertoire, the most conspicuous and commonly reported call type is the advertisement call, emitted mostly in a reproductive context to attract conspecific females; this call also conveys information about species identity and serves as a proxy to maintain spacing between chorus-calling species (Wells 1977; Wilczynski & Brenowitz 1988). Another type of reproductive call is the release call, emitted by males and females when they are not receptive to the amplexus (Bogert 1960; Santana et al. 2025). In the case of males, the release call conveys information to the clasping male that he is not amplexed on a mate, i.e., a female (Martof & Thompson 1958; Bogert 1960; Santana et al. 2025). This behavior could trigger the rapid release in misdirected amplexus and avoid loss of energy (McLister 2003) and reduce fitness costs (Bowcock et al. 2009) associated with the amplexus. Finally, because release calls are typically produced only when individuals are clasped but not receptive, they are reported and recorded less frequently than advertisement calls (e.g., Mângia et al. 2017; Shuck et al. 2024; Lopes et al. 2024).

Boana Gray, 1825, is a species-rich treefrog genus

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in the Neotropical region, with 101 described species to date (Frost 2026). The genus is widely distributed in South and Central America, and some Caribbean islands (Frost 2026). The *Boana faber* species group (sensu Faivovich et al. 2005; Lyra et al. 2020; Pinheiro et al. 2021) consists of nine species of nest-building gladiator treefrogs. Species of the clade have well-developed prepollical spines used to defend their territory, i.e., clay nests or natural basins (Lutz 1960; Martins & Haddad 1988; Faivovich et al. 2005). The advertisement calls of all species of the *B. faber* species group have been described, but the release call has so far been described for only one species of the group (*B. albomarginata*; Velasco et al. 2025). In addition to *B. albomarginata*, release calls have been described only for four other species of the genus: *B. goiana* (Dias et al. 2014), *B. punctata* (Brunetti et al. 2015), *B. raniceps* (Guerra et al. 2018; Siqueira et al. 2025), and *B. semilineata* (Velasco et al. 2025).

In the *Boana faber* group, the vocal repertoire of *B. crepitans* is restricted to its advertisement call (Casal & Juncá 2008; Martins et al. 2009). On the other hand, the vocal repertoire of *B. faber* was described by Martins & Haddad (1988) and includes the advertisement call, two types of territorial calls, and the distress call. In the present study, we describe, for the first time, the male release calls of both species and make an intrageneric acoustic comparison.

Materials and Methods

Study site

We conducted fieldwork in two regions of the Brazilian Atlantic Forest in Minas Gerais: (1) Jaguaraçu (19°38'37.4" S, 42°42'08.2" W; datum WGS84) on 11 November 2024, where some of us (LV, ASG, GCS) recorded and collected one male of *Boana faber*; and (2) Conselheiro Pena (19°17'30.2" S, 41°35'14.4" W; datum WGS84) on 28 October 2025, where some of us (LV, ASG, GCS, LC, TLA) recorded and collected one male of *B. crepitans* under the collection permits SISBIO #95261-1 and #68199, respectively. We euthanized both specimens with the application of topical lidocaine 5%, fixed them in formalin 10%, and preserved them in ethanol 70%. We deposited the vouchers in the Collection of Amphibians (UFMG-AMP) of the Taxonomic Collection Center at Universidade Federal de Minas Gerais (CCT-UFMG), in Belo Horizonte, Brazil, under the following accession numbers: UFMG-AMP 22009 (*B. faber*) and UFMG-AMP 22813 (*B. crepitans*).

Sound recording and acoustic analysis

Release calls were stimulated by gently pressing the axillary region with the thumb and index finger in both males, simulating an amplexus. We recorded the release calls from both males with a Marantz PMD 660 digital recorder coupled with a Sennheiser ME66 (+K6 power module) unidirectional microphone. We set the recorder at a 44.1-kHz sampling rate and a 16-bit depth. We did not measure the temperature at the time of recording. We deposited sound recordings in the acoustic repository of the Herpetology Section of Universidade Federal de Minas Gerais (CBUFMG), Belo Horizonte, Brazil, under the following accession numbers: CBUFMG 1191–1192 (*B. faber*) and CBUFMG 1337–1338 (*B. crepitans*). Before analysis, we screened all recordings and applied a 100-Hz high-pass and a 5000-Hz low-pass filter in Audacity v.3.7.3 (Audacity Team 2024).

We analyzed the calls using Raven Pro v.1.6.5 (Bioacoustics Research Program 2024), employing the following spectrogram parameters: window type = Hann, window size = 512 samples, bandwidth 3dB filter = 124 Hz, overlap = 90%, DFT size = 1024 samples, grid spacing = 43.1 Hz. We quantified temporal and spectral variables of the calls from oscillograms and spectrograms, respectively. From each call, we measured: note duration (s; delta time in Raven Pro), note rise time (%; peak time relative in Raven Pro), pulses per note (pulse number), pulse repetition rate (pulses/s), dominant frequency (Hz; peak frequency in Raven Pro), minimum frequency (Hz; Frequency 5% in Raven Pro) and maximum frequency (Hz; Frequency 95% in Raven Pro). Given the high variability in the rise time of *B. crepitans* calls, we divided the note into four sections: 1 to 25 %, 26 to 50 %, 51 to 75 %, and 76 to 100 %. We based our description on a note-centered approach and followed Köhler et al. (2017) for acoustic definitions and terminology. Finally, we produced sound figures in the R environment v.4.4.2 (R Team Core 2024), using the seewave v.2.2.3 (Sueur et al. 2008) and tuneR v.1.4.7 (Ligges et al. 2023) packages. We applied the following settings: Hann window, FFT size: 512 samples, FFT overlap: 90%, and the level of frequency components was indicated by a relative 36-dB color scale (red = maximum energy).

Results

The males of *Boana crepitans* and *B. faber* emitted release calls with the mouth closed, by expanding and contracting their vocal sacs. They struggled to escape by pushing with their legs against the researcher's hand.

In total, we quantified 33 release calls from one male of *B. crepitans* and seven from one male of *B. faber*; data are presented as minimum and maximum values (mean ± SD). The male release call of *B. crepitans* (Figure 1A) consists of a single pulsed note emitted regularly as stimuli are provided. The note has a stereotyped envelope composed of regularly spaced pulses. Note duration varies from 209 to 449 (306.4 ± 63.0) ms, formed by 5 to 10 (7.0 ± 1.4) pulses, emitted at a rate of 19 to 25 (20.3 ± 1.2) per second. The rise time varied from 1 to 99 (65.2 ± 25.8) % of note duration. The rise time coincided most with the last section (36% of notes), followed by the third and second quarters (33% and 27%, respectively), and lastly, the first quarter of the note (one instance, 3% of the analyzed notes). Notes showed no evident harmonic structure. The dominant frequency ranges from 904 to 991 (971.0 ± 24.3) Hz, the minimum frequency from 474 to 775 Hz (589.9 ± 103.0), and the maximum frequency from 1809 to 2455 Hz (1977.1 ± 177.4).

The male release call of *B. faber* (Figure 1B, C, and D) consists of a single type of note, which can be pulsed (28.57%), pulsatile (28.57%), or nonpulsed (42.86%). Since we have a low number of calls from only one recorded male, we chose to treat these differences as note variants rather than splitting them into two or three different types of notes. Note duration varies from 5 to 80 (42.0 ± 26.2) ms, with a rise time varying from 10 to 64 (35.3 ± 18.9) %. Pulse number, when present, varies from 4 to 10 (7.0 ± 4.2), emitted at a rate of 147 to 156 (151.5 ± 6.7) per second. Pulsed and pulsatile notes showed no evident harmonic structure; nonpulsed notes have an evident harmonic structure. Considering all note variants, the dominant frequency ranges from 560 to 1034 (799.8 ± 148.9) Hz, the minimum frequency from 215 to 732 (430.7 ± 202.0) Hz, and the maximum frequency from 1593 to 1809 (1673.4 ± 84.1) Hz

Discussion

This is the first description of the male release calls of *Boana crepitans* and *B. faber*. Despite the taxonomic diversity of *Boana* (i.e., >100 species), male release calls have rarely been reported. With the two new descriptions in our study, we increased the known male release call descriptions to seven of 101 species of *Boana*, representing 6.9% of the species richness of the genus. However, the rarity of the male release call is not exclusive to *Boana*. Other hylid

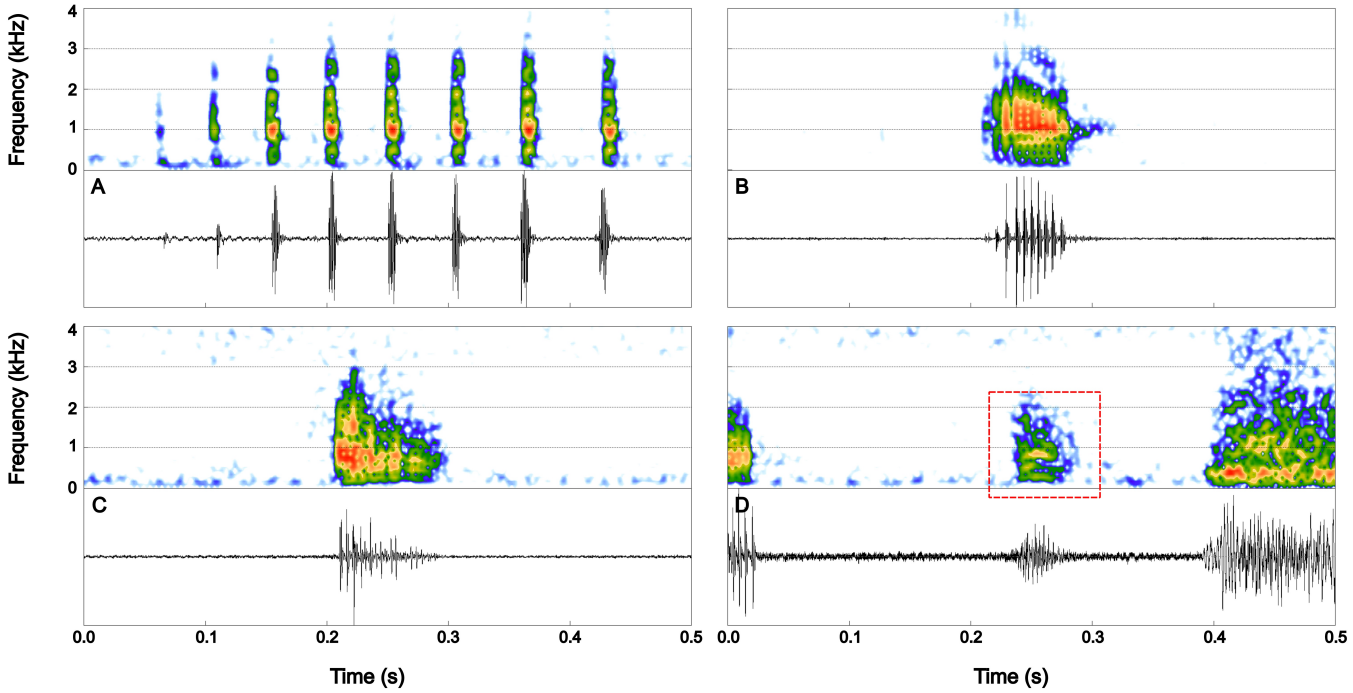

Figure 1: Male release calls of two species of *Boana*. In each panel (A-D), the upper portion shows a spectrogram and the lower portion shows its corresponding oscillogram. (A) Pulsed note of *B. crepitans*; (B) pulsed note of *B. faber*; (C) pulsatile note of *B. faber*; (D) nonpulsed note of *B. faber*, highlighted by a dashed-line red square.

genera follow this pattern, with one or a few papers describing this call type, e.g., *Dendropsophus* (Shuck et al. 2024), *Scinax* (Mângia et al. 2017), and *Trachycephalus* (Lopes et al. 2024). The rarity of this type of call could also be related to the specific context in which it is emitted, during misdirected amplexes between males (Siqueira et al. 2025) or ongoing fights (Guerra et al. 2018), and, although it can be stimulated artificially, male frogs do not necessarily elicit release calls (L. Vilela & T. R. Carvalho, field observation), which hampers the recording and description of male release calls.

Despite their rarity, male release calls exhibit considerable acoustic variation in their structure. Different combinations of these qualitative acoustic characteristics are as follows: (1) pulsed notes and evident harmonic structure present in *B. albomarginata*, *B. goiana*, and *B. semilineata* (Dias et al. 2014; Velasco et al. 2025); (2) nonpulsed notes and evident harmonic structure present in *B. faber* and *B punctata* (present study; Brunetti et al. 2015); and (3) pulsed notes without evident harmonic structure are present in *B. crepitans*, *B. faber*, and *B. raniceps* (present study; Guerra et al. 2018). Besides the variation related to acoustic structure, male release calls in *Boana* also vary in quantitative data (see Table 1). *Boana crepitans* have longer notes (209–449 ms) in comparison with *B. albomarginata* (20 ms on average), *B. faber* (5–80 ms), both notes of *B. goiana* (Note A: 23–79 ms and Note B: 17–43 ms), *B. punctata* (38–48 ms), the Cerrado population of *B. raniceps* (26–109 ms), and *B. semilineata* (50 ms on average), except with the Atlantic Forest population of *B. raniceps* (389 ms on average). Pulse rate is higher in *B. faber* (147–156 pulses/s) than in *B. crepitans* (19–25 pulses/s). Finally, the dominant frequency is lower in *B. albomarginata*, *B. crepitans*, *B. faber*, *B. raniceps*, and *B. semilineata* (861–2584 Hz, 904–991 Hz, 560–1034 Hz, 517–1206 Hz, and 516–2239 Hz, respectively; Table 1) than in both notes of *B. goiana* and *B. punctata* (Note A: 2480–3000 Hz, Note B: 2423–3000 Hz, and 1240–1380 Hz, respectively; Table 1). These differences in male release calls among species could help in species discrimination based on acoustic data.

Martins & Haddad (1988) reported two types of territorial calls in *B. faber*. One type was elicited when a resident male jumped onto an intruder male,

Table 1: Summary of male release call data within *Boana*. Data (when provided) is presented as mean ± SD (range). N = number of recorded males (number of analyzed notes). Abbreviations are as follows: PN = Pulse number, ND = Note duration, NRT = Note rise time, PR = Pulse rate, Min Freq = Minimum frequency, Max Freq = Maximum frequency, Dom Freq = Dominant frequency.

Species	PN	ND (ms)	NRT (%)	PR (pulses/s)	Min Freq (Hz)	Max Freq (Hz)	Dom Freq (Hz)
B. albomarginata (Velasco et al. 2025) N = 3 (57)	6–7	20 ± 10	–	–	1103 ± 207 (775–1550)	2297 ± 508 (1378–3445)	1384 ± 400 (861–2584)
B. crepitans (present study) N = 1 (33)	7 ± 1 (5–10)	306 ± 63 (209–449)	65 ± 26 (1–99)	20 ± 1 (19–25)	590 ± 103 (474–775)	1977 ± 177 (1809–2455)	971 ± 24 (904–991)
B. faber (present study) N = 1 (7)	7 ± 4 (4–10)	42 ± 26 (5–80)	35 ± 19 (10–64)	152 ± 7 (147–156)	431 ± 202 (215–732)	1673 ± 84 (1593–1809)	800 ± 149 (560–1034)
B. goiana Note A (Dias et al. 2014) N = 2 (33)	4 ± 2 (2–10)	35 ± 15 (23–79)	–	–	–	–	2786 ± 196 (2480–3000)
B. goiana Note B (Dias et al. 2014) N = 2 (33)	–	30 ± 7 (17–43)	–	–	–	–	2610 ± 168 (2423–3000)
B. punctata (Brunetti et al. 2015) N = 3 (3)	–	42 ± 4 (38–48)	–	–	–	–	1307 ± 69 (1240–1380)
B. raniceps (Guerra et al. 2018) N = 1 (10)	–	50 ± 27 (26–109)	–	–	517 ± 0 (517–517)	1550 ± 269 (1206–1895)	758 ± 202 (517–1206)
B. raniceps (Siqueira et al. 2025) N = 1 (37)	46 ± 9	389 ± 1	–	–	938 ± 36	3657 ± 684	1594 ± 281
B. semilineata (Velasco et al. 2025) N = 2 (7)	7–12	50 ± 20	–	–	504 ± 59 (431–603)	3802 ± 230 (3445–4221)	800 ± 636 (516–2239)

and the other, formed by two notes, was emitted alternatively by each male during physical combat. We noted that there are similarities between the male release call described in our study and the second type of territorial call reported by Martins & Haddad (1988), both of them consisting of a single type of pulsed note and a similar spectral structure (see our Fig. 1C and Fig. 2b of Martins & Haddad 1988). The emission of release calls during physical combat has been reported in other hylid species. One example is *Pithecopus nordestinus*, whose release call was originally described as a territorial call with a distress function (Vilaça et al. 2011) and was later reassigned to a release call category by Mângia et al. (2019). Within *Boana*, male release calls during physical combats have been reported for at least two species: *B. punctata* (Brunetti et al. 2015) and *B. raniceps* (Guerra et al. 2018). Therefore, based on the note description and spectrogram provided, we suggest the possibility of the second type of territorial call of *B. faber* being actually a male release call emitted during physical combat.

Our study presents remarkable acoustic variation in two species of *Boana*, with novel male release calls. In one species (*B. crepitans*), there is a stereotyped pulsed call, and, in the other (*B. faber*), there are three note variants with respect to the same stimuli. A high degree of variation in call duration was observed in the male release call of *B. raniceps* (Siqueira et al. 2025): a male belonging to a population from the northern Atlantic Forest emitted release calls with a mean duration of 389 ms and a male from a Cerrado population emitted much shorter release calls with a mean duration of 50 ms (Siqueira et al. 2025). Therefore, we emphasize that the collection and description of this type of data is relevant, given its current rarity and possible applications in anuran taxonomy (Grenat & Martino 2013; Köhler et al. 2017). Future descriptions should benefit from an increase in sample size of recorded males and localities, so we can better assess patterns of intraspecific acoustic variation.

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