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RESEARCH ARTICLE

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Vocalisations, territoriality and aggressive interactions of the Chaco tree frog *Boana raniceps*

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ABSTRACT – Various types of intra and interspecific vocalisation are a primary means of communication among anuran species. In intraspecific interactions, male anurans emit calls to attract females and repel rival males. This study describes new vocalisation types for reproductively active *Boana raniceps* (Anura: Hylidae) and provides a commentary on aggressive intraspecific behaviour that was recorded at ten sites. In addition to advertisement calls, our findings reveal that males emit two types of aggressive call, one territorial call and one encounter call. We identified a sequence of different aggressive behaviours displayed during physical combat between two males. Our findings show that *B. raniceps* exhibits complex intraspecific behaviours in a reproductive context.

INTRODUCTION

Vocalisations in anurans are considered the primary form of communication for most species and a critical reproductive isolation mechanism (Wells, 1977a). During the breeding season, acoustic signalling may enable adult anurans to aggregate; the males emitting advertisement calls to attract females but also to defend territories for the prime purpose of reproduction which leads to aggressive interactions between individual males (Duellman & Trueb, 1986). Most territorial disputes have a sexual context and aggressive behaviours can occur when males are very close to each other, sometimes resulting in physical combat (Bastos & Haddad, 1996; Giasson & Haddad, 2006; Dautel et al., 2011). The mate choice and maintenance of territories by male-male interactions during the breeding season are energetically costly (Guimarães & Bastos, 2003), especially for species with long reproductive life spans (Wells, 1977a). A fundamental characteristic of anuran species with prolonged reproduction is the use of a variety of call types with distinct functions (Wogel et al., 2004; Dautel et al., 2011) and their investment in complex vocal repertoires may positively influence reproductive success (Vilaça et al., 2011). There are several known anuran call types documented for species in the Neotropics (Toledo et al., 2015).

In this study, our focus is on the vocalisations and aggressive behaviours of the Chaco tree frog *Boana raniceps* (Cope, 1862), a wide-ranging species. *Boana raniceps* belongs to the *Boana albopunctata* group and is widely distributed in South America, occurring from the Amazon of Venezuela to Colombia, French Guiana, Brazil, Paraguay, Argentina and Bolivia (Frost, 2023). Male *B. raniceps* typically call during twilight hours whilst situated on elevated surfaces. At nightfall, they tend to migrate towards bodies of water and can be found perched on the branches of shrubs, grasses, trees and bulrushes (Guimarães & Bastos, 2003).

MATERIALS & METHODS

Study area

The study was undertaken in the north of the State of Paraná bordering the State of São Paulo in southern Brazil, at ten sampling sites in the municipalities of Alvorada do Sul, Sertaneja, Porecatu, Centenário do Sul and Rancho Alegre (Fig. 1). According to the Köppen-Geiger climate classification (Peel et al., 2007), the region's climate is categorised as subtropical humid (Cfa) and the vegetation type was originally dominated by semi-deciduous seasonal forests, with only a few fragments of forest remaining today. The region is located along the contact zone between the Atlantic Forest and the open formations of the Cerrado.

We surveyed temporary and permanent water bodies across agropastoral environments and reforestation areas near the Tibagi River during the summer from October 2016–February 2017 on 30 days from 18:00 h to 24:00 h, totalling 180 hours. To minimise disturbance, headlamps with white

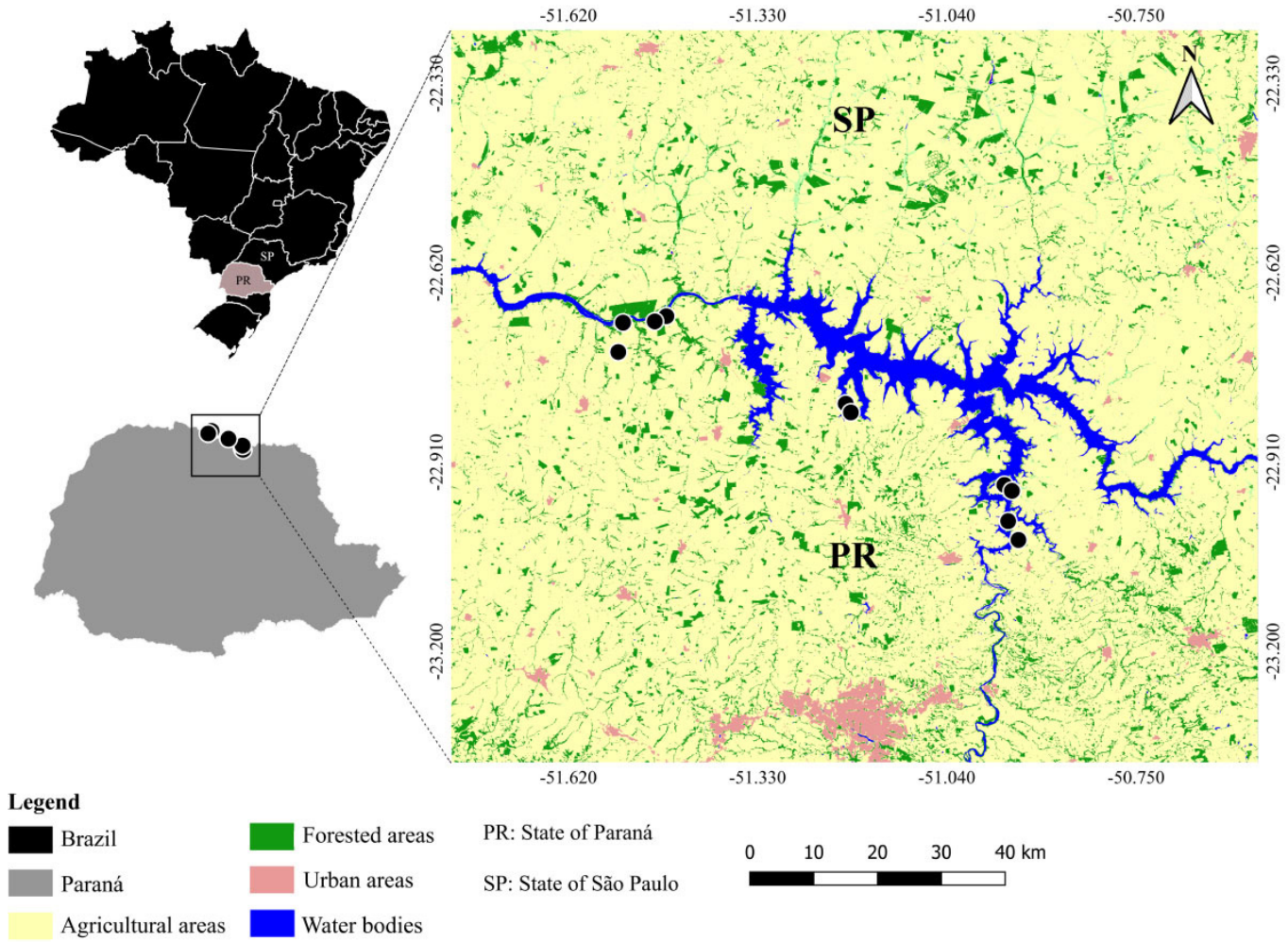

Figure 1. Map of the study area showing the sampled sites (black circles) in the north of the State of Paraná, southern Brazil, the co-ordinates are in WGS84

light were used to search for calling males, and red light (RGB night vision option of the Black Diamond Icon 500 Headlamp) were used to observe males after they had been found and provided the illumination to observe the frequencies of call and aggressive interactions. A straightforward approach was used by locating a focal animal and recording all observed behaviours (Lehner, 1979; Martin & Bateson, 1986). Male frogs were selected for study when they were within a 5-metre range, at which time a digital laser tape measure (model Bosch GLM50C) was used to give accurate and precise measurements of distance from the observer.

Boana raniceps was identified by its morphology in particular by its size (medium to large) and the presence of dark brown to black cross-bands that extend onto the concealed surfaces of its hind limbs (Boulenger, 1889; Duellman, 1970) and by its typical vocal calls (identified by personal field experience). The sex of individuals was determined by the presence or absence of vocal sacs, which are only present in males (Duellman & Trueb, 1986). The resident male was identified by his behaviour during the event. He vocalises while standing on the grass and emits advertisement calls for a time (about 8 minutes), while an invading male subsequently approaches at a distance (< 5 m) from the resident male. The

Figure 2. Vocalising male *Boana raniceps* in a reforestation area near the Tibagi River, State of Paraná, Brazil

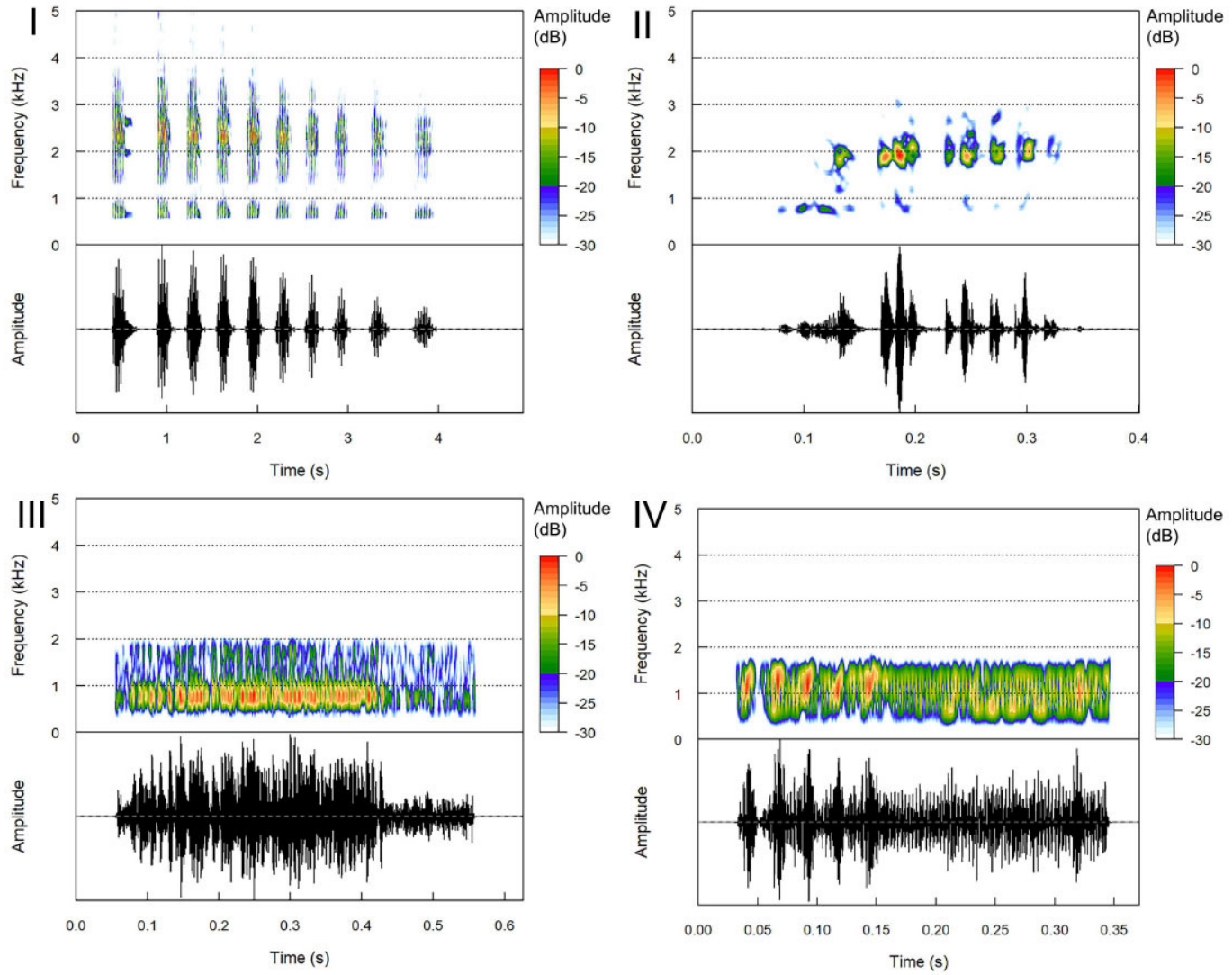

Figure 3. Sound spectrograms and oscillograms of four calls types made by male *Boana raniceps* - **I.** Advertisement call, **II.** Territorial call, **III.** Unidentified call, **IV.** Encounter call. The air temperature at the time of advertisement call was 23.2 °C and the other calls recorded simultaneously was 25.4 °C.

vocalisations of *B. raniceps* males (Fig. 2) were recorded, using a TASCAM DR-05 digital recorder coupled with a YOGA HT-81 unidirectional microphone, in 24-bit wav format, with a 96 kHz sampling rate. A call-based approach was used and the methodology for call description followed the recommended terminology of Köhler et al. (2017). The following parameters were used to describe calls: dominant frequency (kHz), call duration (s), pulses (present or absent) and harmonic (present or absent). The records were edited through the Raven Pro 1.5 software (Cornell Laboratory of Ornithology, Ithaca, NY). The images of the individuals' acoustic activity were assessed in the R statistics program (R Development Core Team 2017), using the Seewave package (Sueur et al., 2008), with the following settings: window name = hanning; window length = 512; overlap = 90%; air temperature = 23.2 °C for the advertisement call and 24.5 °C for the others calls. The calls were vouchered in the Fonoteca Neotropical Jacques Vielliard with number IDs FNJV 74362 to 74369.

RESULTS

Male *B. raniceps* vocalised to attract females and defended their territories through aggressive social interactions. In some instances, resident males displayed aggressive behaviour towards other males entering their territory. The territorial disputes among males were observed at a range of 0.7–3.6 m. The closest pair of males, just 0.7 m apart, were engaged in territorial conflict and emitted territorial and encounter calls before initiating physical combat. More distant males were too far apart to engage in combat.

Vocalisation activities began at dusk around 19:00 h, with the peak of males calling at 21:00 h and declining by 24:00 h. *Boana raniceps* type calls are complex, featuring various note types that can be arranged in both regular and irregular sequences. In some instances, individuals may emit either a territorial call or an advertisement call exclusively, while others emit both territorial and advertisement calls simultaneously within the same call.

Table 1. Four call types of *Boana raniceps* presented as ranges and as mean values ± standard deviation. These values are based on a total of 108 advertisement calls, 75 territorial calls, six unidentified calls and five encounter calls. The air temperature for all advertisement calls was 23.2 °C and the other calls recorded simultaneously was 25.4 °C.

Call type	Dominant frequency (kHz)	Call duration (s)	Pulses	Harmonic
Advertisement call	861.3–2411.7 (1860.86 ± 613.37)	0.214–0.347 (0.224 ± 0.06)	yes	yes
Territorial call	1722.7–2411.7 (2190.23 ± 238.19)	0.182–0.312 (0.240 ± 0.038)	yes	yes
Unidentified call	775.2–861.3 (732.15 ± 72.03)	0.339–0.624 (0.4763 ± 0.113)	yes	yes
Encounter call	1033.5–1205.9 (1162.82 ± 86.15)	0.311–0.643 (0.4 ± 0.16)	yes	yes

Figure 4. Two male *Boana raniceps* **A.** With fully inflated vocal sac, indicated by the white arrow when emitting the territorial call, **B.** Emitting the encounter call, the red arrow indicates the anterior portion of the vocal sac inflated while the posterior portion remains uninflated, indicated by the white arrow

However, we registered the emission of other calls that can vary depending on the specific reproductive context. In total, we examined four types of male vocalisation: 1. Advertisement call (Fig. 3I), 2. Territorial call (Fig. 3II), 3. Unidentified call (Fig. 3III), and 4. Encounter call (Fig. 3IV). We did not record any distress calls in males but we did hear (but not record) this type of defensive call when handling a gravid female. We observed a total of 12 events of physical combat but only one was recorded in detail. Among the males observed in this study, the advertisement call was the most frequently emitted vocalisation. Territorial calls were only produced when two or more males were emitting advertisement calls simultaneously (Fig. 4A). Encounter calls were always produced during interactions between two males before physical combat. During these interactions, it was noted that the encounter calls were emitted by males using only the anterior portion of their vocal sacs while the posterior part was not inflated (Fig. 4B).

We recorded a sequence of distinct aggressive behaviours exhibited during physical combat between two individual males. The intruding male was observed approaching the territory of the resident male while emitting territorial calls. In response, the resident male jumped in a circle and emitted territorial calls (Fig. 5I). When the intruding male entered the territory of the resident male, both began emitting encounter calls (Fig. 5I&II). When the intruding male approached the resident male closely, physical combat was initiated by the intruding male who attempted to jump on the back of the resident male, but this was unsuccessful as the resident male dodged and grabbed the intruder from behind. From that moment on, the resident male initiated a series of aggressive behaviours. These included blows and jerks directed towards the ventrolateral region of the intruding male using its forelimbs, accompanied by territorial calls (Fig. 5III&IV). Then, the resident male applied a blow with the ventral-cephalic part of his body propelled with the hind limbs resting on the floor (Fig. 5V), and shortly after that, he lifted his body and performed two scrapes with the anterior limbs in the ocular region of the intruding male (Fig. 5VI). Subsequently, the resident male grabbed the intruder's cephalic region with the anterior limbs and pulled backward (Fig. 5VII). After that moment, the intruding male escaped (Fig. 5VIII) and jumped straight forward, emitting territorial calls at the resident (Fig. 5IX). In a subsequent phase of the physical combat between the two males, the resident male performed another attack on the intruder. This involved leaping backward (Fig. 5X) and applying a series of strikes with its hind limbs (Fig. 5XI), followed by two additional blows using its forelimbs (Fig. 5XII&XIII). Despite this, the intruding male resisted the resident male's series of behaviours (Fig. 5XIV). Both males remained close to each other and continued to emit territorial calls (Fig. 5XV). Finally, after this sequence of aggressive behaviours the battle ended when the resident male jumped away leaving his territory to the intruder (Fig. 5XVI).

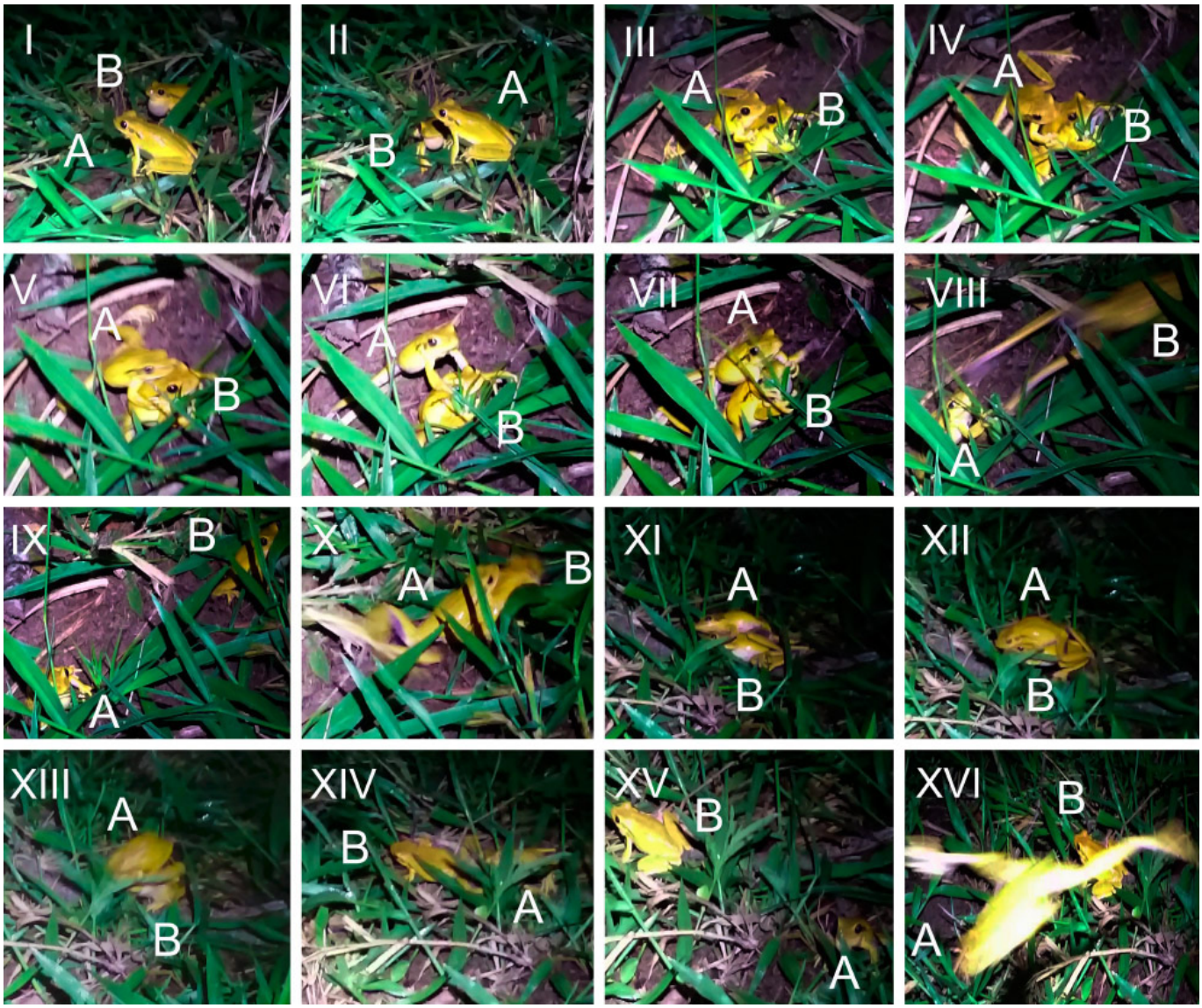

Figure 5. The sequence of aggressive behaviours between two male *Boana raniceps*, **A.** a resident male in its territory and **B.** an intruder. Details on the behaviours are described in the results section.

DISCUSSION

This study shows that *B. raniceps* presents complex intraspecific behaviour that is mediated by at least four types of call made in different contexts. First, individuals make advertisement calls that, in addition to having the function of attracting females, also warn other males about their territory issuing an alternation of advertisement calls and territorial calls. As mentioned in Köhler et al. (2017), for some species the territorial call and advertisement call are part of the same call. When one male intrudes on another's territory and persists, the territorial call is emitted, if this is not enough then physical combat begins preceding a series of different calls (i.e. territorial call and encounter call). The territorial call is emitted from a fully inflated vocal sac whereas the encounter call is emitted from only the anterior portion of the vocal sac while the posterior portion remains uninflated (Fig. 4A&B). It was observed that an unidentified call (Fig. 3III) is made in a territorial context when several males are vocalising. It may be a variation of the territorial call, although it is structurally, parametrically and sonically dissimilar. Therefore, we have referred to it as an unidentified call.

Boana raniceps has a prolonged breeding period (Guimarães et al., 2001) and it is considered that such anuran species generally do not actively search for females during the breeding season but instead tend to use different acoustic signals to attract females to their calling sites (Wells, 1977b). Consequently, such anurans have more complex vocal repertoires, usually associated with their acoustic competition for females, oviposition sites, calling sites and feeding (Wells, 1977a; Duellman & Trueb, 1986). Males can defend their microhabitats with territorial calls, emitting threatening signals, termed 'encounter' calls (Wells, 1977a; Toledo et al., 2015). When the intruding male fails to heed these threats, physical combat typically ensues (Wells, 1977a). This may involve the use of butting and pushing with the forelegs, as well as more aggressive

fighting involving grips and kicks. In some cases, secondary sexual traits (e.g. the prepollex) may also be used as weapons (Bittencourt-Silva et al., 2020).

Physical combat has a high energy cost, and increases the chances of predation, and the risk of injury (Wells, 1977b; Martins et al., 1998; Bastos & Haddad, 2002; Batista et al., 2015). Consequently, physical combat only occurs in extreme cases (Kluge, 1981). As observed in *Boana rosenbergi* (Kluge, 1981) and *Boana faber* (Martins et al., 1998), combat in *B. raniceps* occurs in choruses with large numbers of calling males (Guimarães et al., 2001), where dense aggregation results in aggressive calling responses and offensive or defensive behaviours. Our results suggest that calling sites were faithfully defended against intruding males through acoustic interactions and defensive behaviours. The battles observed in *B. raniceps* for access to females and territories occur within a mating system based on resource defence competition (Guimarães et al., 2001).

The species-specific acoustic repertoire of *B. raniceps* males is an aspect of their ecological niche, defined by acoustic competition amongst species (Krause, 1993). When many males are vocalising in the chorus, the most frequent vocalisation strategy observed is to emit the advertisement call and territorial call simultaneously. The encounter call of *B. raniceps* has also been described. It has a complex acoustic structure comprising a multi-pulsed note with irregular pulses. In addition to the acoustic signals, this study provides evidence that violent aggression within the genus *Boana* is not limited to the *B. faber* group but also occurs in the *B. albopunctata* group. These findings justify further research into the breeding behaviour of *B. raniceps*, in particular, to investigate the function of the unidentified call.

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