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ECOLOGÍA

Natural History of the Flattened Waterfall Frog *Cycloramphus boraceiensis* (Anura, Cycloramphidae)

Historia natural de la Rana de Cascada Aplanada *Cycloramphus boraceiensis* (Anura, Cycloramphidae)

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ABSTRACT

Cycloramphus boraceiensis is an endemic frog of the Atlantic Forest of southeastern Brazil. Although relatively easy to find and distributed over a well-sampled region in southeast Brazil, little is known about its natural history, breeding activity, and vocal repertoire. In the present study, we provide new information on pre-and post-hatching larval development, describe new traits of their advertisement calls, describe its aggressive call for the first time, and provide new data about adults' and tadpoles' defensive strategies. We found individuals on rocks on cascaded streams or within rocky crevices along streams inside forested habitats. Males concentrated their calling activity between 03:00 and 5:00 h and between 19:00 and 23:00 h. The aggressive call is shorter than the advertisement call and has greater variation in the number of pulses and emission rate. The eggs hatched at Gosner's stage 25, after seven and eleven days of oviposition, and tadpoles took between eight and ten days to complete metamorphosis. This study contributes to the knowledge of the Flattened Waterfall Frog by filling natural history gaps that can be useful for species conservation and bringing attention to traits that still need further investigation, such as color plasticity and microhabitat selection.

Keywords: Atlantic Forest, bioacoustics, tadpoles, development, growth, microhabitat selection

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RESUMEN

Cycloramphus boraceiensis es una rana endémica del Bosque Atlántico del sureste de Brasil. A pesar de que es relativamente fácil de encontrar y se distribuye en una región bien muestreada en el sureste de Brasil, se sabe poco sobre su historia natural, actividad reproductiva y repertorio vocal. En el presente estudio, estudiamos una población de *C. boraceiensis* y proporcionamos nueva información sobre el desarrollo larvario antes y después de la eclosión. Describimos también nuevos rasgos de sus vocalizaciones de anuncio, además realizamos por primera vez la descripción de su vocalización agresiva el cual aporta nuevos datos sobre el mecanismo de defensa de adultos y renacuajos. Encontramos individuos sobre rocas en arroyos en cascada y dentro de grietas rocosas. Los machos concentraron su actividad de canto entre las 03:00 y las 5:00 h, y entre las 19:00 y las 23:00 h. La vocalización agresiva es más corta que la vocalización de anuncio y tiene una mayor variación en el número de pulsos y en la tasa de emisión. Los huevos eclosionaron en la etapa 25 de Gosner, después de siete y doce días de la oviposición, y los renacuajos tardaron entre ocho y diez días en completar la metamorfosis. Este estudio contribuye al conocimiento de la rana de cascada aplanada al llenar los vacíos de la historia natural que pueden ser útiles para la conservación de especies y llamar la atención sobre los rasgos que aún necesitan atención, como la plasticidad del color y la selección del hábitat

Palabras clave: Bosque Atlántico, bioacústica, renacuajos, desarrollo, crecimiento, selección de microhábitat

INTRODUCTION

Cycloramphus is the most specious genus of the family Cycloramphidae (Frost c2022). The genus is exclusive to the Atlantic Forest in southeastern Brazil (Heyer 1983) and is associated with leaf litter and fast-flowing streams (Bokermann 1951, Heyer and Maxson 1983, Verdade and Rodrigues 2003). *Cycloramphus boraceiensis* Heyer, 1983, the Flattened Waterfall Frog, is endemic to forested habitats from the southern coast of the state of Rio de Janeiro to the northern coast of the state of São Paulo, including some islands, such as Ilha Grande and Ilha de São Sebastião (Heyer 1983, Frost c2022). The species is classified as Least Concern (LC) on the official Brazilian red list (Brasil 2022). Although common and not endangered, the species declined in the late 1970s in Boracéia (Tol edo *et al.* 2023), most likely due to a chytrid outbreak (Carvalho *et al.* 2017), and information about the life history, population size, distribution, and autecology of *C. boraceiensis* is still lacking (Carvalho-e-Silva and Pimenta 2004).

Cycloramphus spp. can be divided into aquatic and terrestrial breeding species according to their reproductive modes (Lutz 1947, Lutz 1948, Heyer 1983, Nunes-de-Almeida *et al.* 2021, Colaço and Silva 2022). In the first case, and the one exhibited by most species, females lay their eggs on wet rocks, rock crevices, or tree roots above water; tadpoles are exotrophic and semiterrestrial (e.g., Heyer 1983, Lima *et al.* 2010, Verdade *et al.* 2019, Nunes-de-Almeida *et al.* 2021), living on rocks or rock crevices in a water film or on the water-land interface (mode 17) (Nunes-de-Almeida *et al.* 2021). Colaço and Silva (2022) suggest that those tadpoles that stay in the water film until metamorphosis should be classified as "quasi-terrestrial", instead of "semiterrestrial". In the latter case, females lay their eggs on land (reproductive mode 32) (Nunes-de-Almeida *et al.* 2021), usually concealed in cavities; the mother remains in the nest, and the endotrophic tadpoles complete their development on her dorsum (Lutz 1943, Heyer and Crombie 1979, Zocca *et al.* 2014, Verdade *et al.* 2019).

Heyer (1983) provided a simple description of the tadpole and the advertisement call. Later, Dias *et al.* (2021) described the external morphology, buccopharyngeal anatomy, and musculoskeletal morphology of several cycloramphid species larvae, including that of *Cycloramphus boraceiensis*. In the same year, Colaço *et al.* (2021) redescribed the tadpole of *C. boraceiensis* based on individuals collected in Ilha Grande, municipality of Angra dos Reis, Rio de Janeiro, presenting new traits for the species larvae. Both Dias *et al.* (2021) and Colaço *et al.* (2021) suggested the need for an extensive literature review of the larval characters of *Cycloramphus* species, once many of them are absent or were mistakenly reported, and new traits have been revealed to be important in the last decade (Lima *et al.* 2010, Da Silva and Ouvernay 2012, Verdade *et al.* 2019, Colaço *et al.* 2021). Other authors also described additional, but anecdotal, information on the natural history of *C. boraceiensis*. For example, Hartmann *et al.* (2003) described crypsis as the *C. boraceiensis* primary defense, while death feigning and biting were considered secondary defense mechanisms (Toledo *et al.* 2011). Giaretta and Nunes (1997) provided information about its predation by a pit viper and Giaretta and Facure (2003) recorded male attendance to the egg clutch. Herein, we present new data on the natural history of the Flattened Waterfall Frog, including breeding activity, ontogenetic development, and vocalizations.

MATERIALS AND METHODS

We collected data during weekly routine field expeditions from February 2014 to March 2021, at the Projeto Dacnis private reserve in the municipality of Ubatuba, São Paulo, southeastern Brazil (23°27'46" South, 45°07'58" West, WGS-84, 34 m above sea level). The Projeto Dacnis reserve is inserted in a secondary lowland Atlantic Forest region, with some primary forest patches. Also, recordings from a field trip to the municipality of Ilhabela, São Paulo (23°53'4" South, 45°26'57" West, WGS-84), made on 20 November 2015 by L. F. Toledo, were included in the analyses.

To observe the species' ontogenetic development, we photographed and recorded egg development daily with a digital camera (Canon 80D) and a smartphone camera (Xiaomi Redmi 8). We observed clutches in different periods of the day, for approximately two hours per day. We also surveyed the surrounding area to evaluate potential predators and to find out whether parental care was observed. Measurements of the developing embryo were carried out with the aid of a digital caliper (Sagyma plus, 0.1 mm). We defined the larval development stages according to Gosner (1960), with adaptations proposed by Colaço and Silva (2022).

To monitor the periods of vocal activity at the Projeto Dacnis reserve, we used an autonomous recorder (Song Meter SM3, Wildlife Acoustics) and analyzed over 360 recording hours using the Raven Pro v 1.6 software (Center for Conservation Bioacoustics 2019). We analyzed the advertisement call records from three males (20 notes) from the Projeto Dacnis reserve (FNJV 51541–43). We made the records using a Zoom H2n recorder with 16 bits of resolution and 44.1 kHz. We performed sound analyses with the following spectrogram settings: window type = Hann, window size = 512 samples, hop size = 2.9 ms, overlap = 75%, DFT size = 1024 samples, grid spacing = 43.1 Hz. We measured temporal and spectral parameters directly from the oscillogram and spectrogram, using Raven Pro. Call parameters follow the proposal by Köhler *et al.* (2017): call duration, inter-call interval, call rate, dominant frequency, minimum frequency, and maximum frequency.

We obtained the sound graphics using Seewave (Sueur *et al.* 2008) and tuneR (Ligges *et al.* c2014) packages from the R platform (R Core Team c2022) and featured the following spectrogram parameters: Hanning window, FFT = 512, and 70% overlap. We also analyzed an aggressive call (FNJV 32270) from Ilhabela, São Paulo, in Raven Pro using the following spectrogram settings: window type = Hann, window size = 512 samples, hop size = 1.33 ms, overlap = 75%, DFT size = 1024 samples, grid spacing = 93.8 Hz. We deposited the recorded calls at Fonoteca Neotropical Jacques Vielliard (FNJV), Museu de Diversidade Biológica (Bibo), Universidade Estadual de Campinas (Unicamp), Campinas, Brazil.

RESULTS

During the entire monitoring period, individuals of *Cycloramphus boraceiensis* were found on stream edges, rock crevices, or on rocks in the stream. The calling occurred throughout the year without a clear peak activity in any season. Males called mostly at night, with peak of activity a few hours after the sunset (19:00–23:00 h) and a few hours before sunrise (03:00–5:00 h) (Fig. 1). In the Projeto Dacnis area, males of *C. boraceiensis* shared the stream as a calling site with *Thoropa taophora* (Miranda-Ribeiro, 1923) and *Hylodes phyllodes* Heyer & Cocroft, 1986. However, the latter species activity was diurnal.

Cycloramphus boraceiensis egg clutches were laid on humid rocks or land crevices next to a waterfall's spray zone all year long, indicating prolonged and continuous reproduction activity. The number of eggs varied from 38 to 44 and male attendance was not always observed. All tadpoles hatched at Gosner's stage (GS) 25 and we did not ob-

Table 1. Development changes in *Cycloramphus boraceiensis* embryos recorded from a clutch found on April 2015 on a rocky substrate in a small waterfall in the municipality of Ubatuba, São Paulo, Brazil. GS= Gosner´s (1960) stages

2015	2021	Life form	GS	Embryological changes
April 23rd	February 10th	Embryo	07–09	Yolk-rich eggs, each in a transparent gelatinous capsule and with a diameter of 5 mm; superior half of the egg gray with some blood vessels, inferior half beige
April 24th	February 11th	Embryo	10–12	Increase in the gray area and in the number of vessels irrigating the egg
April 27th	February 13th	Embryo	17–19	Formation of small embryos; tail bud elongated; development and appearance of the gill bud
April 28th	February 14th	Embryo	19-20	The tail is longer; ramification of external gill filaments; heartbeat is visible
April 29th	February 15th	Embryo	21	Embryos' eyes visible; olfactory pits are clearly visible; mouth opening visible; ventral and dorsal fins present
May 1st	February 16th	Pre-hatching	23	Opercular fold covering the base of gill stalks giving the perception of reduction of external gills; lightly pigmented embryos
May 2nd		Pre-hatching	24	Reduction of external gills; more pigmented embryos; hindlimb bud
May 4th	February 17th	Pre-hatching	25	Opercular fold closes and external gills fully disappear; larvae characteristically pigmented
	February 21th	larval	26	Photosensitive tadpoles; tail reduction
May 9th		Larval	>30	Tadpole pigmented and more active, angle of mouth between midpoint and posterior margin of eye, the tail is reduced.
	February 26th	Larval	34	Legs apparent
May 16th		Metamorphic	45	Tail regression is complete

serve them eating until the yolk was not visible in the gut. After hatching, the tadpoles looked for shelter and moved around by fixating their mouths on the rock or soil surface and making abdominal contractions.

We found a clutch containing 38 eggs close to a male on 23 April 2015 and monitored it until 16 May 2015. The intracapsular development lasted seven days and took six days to reach GS20, nine to reach GS23, and twelve to reach GS25. At GS07–GS09 we were able to observe an increase in the diameter of the eggs and in the number of blood vessels. At GS18 a small protuberance, which would differentiate in the gill bud, was visible on each side of the head. At GS19–GS20 a small gill bud was present on each side of the head, with three to four secondary filaments. At GS21 the mouth opening was discernible anteriorly oriented, with a ventral notch; the olfactory pits and the dorsally oriented eyes became apparent. The ventral and dorsal fins were present at GS21. At GS23-24 tadpoles were found inside the eggs, while eggs that hatched early already had tadpoles at GS25 outside the egg capsules, on the mucilaginous mass. The eggs hatched after the tadpoles began moving intensely. At GS24–GS25 the operculum expanded and closed later, with the absorption of the gills. At GS25 the body form changed becoming more triangular; the dorsal and ventral fins were differentiated; the tail length was about 3/4 of the body length and the spiracle was visible. In the subsequent larval stages, the changes happened fast and we could observe the eyes becoming dorsolaterally oriented, mouth and olfactory pits moving at GS30; tail reduction, fore and hindlimbs fully developing, and change of mouth angle until GS46, when the metamorphosis was complete (Table 1, Fig. 2).

On 10 February 2021, we followed the development of another clutch with 44 eggs laid on a crevice filled with moss, 91.5 cm above a stream with shallow water and sandy substrate. The eggs were between GS07–GS09 and had a diameter of 5.5 mm, yolk-rich, and wrapped in a transparent gelatinous capsule, similar to the spawn found in 2015. The next day, we found a male close to the clutch. In the following four days we observed an increase in the

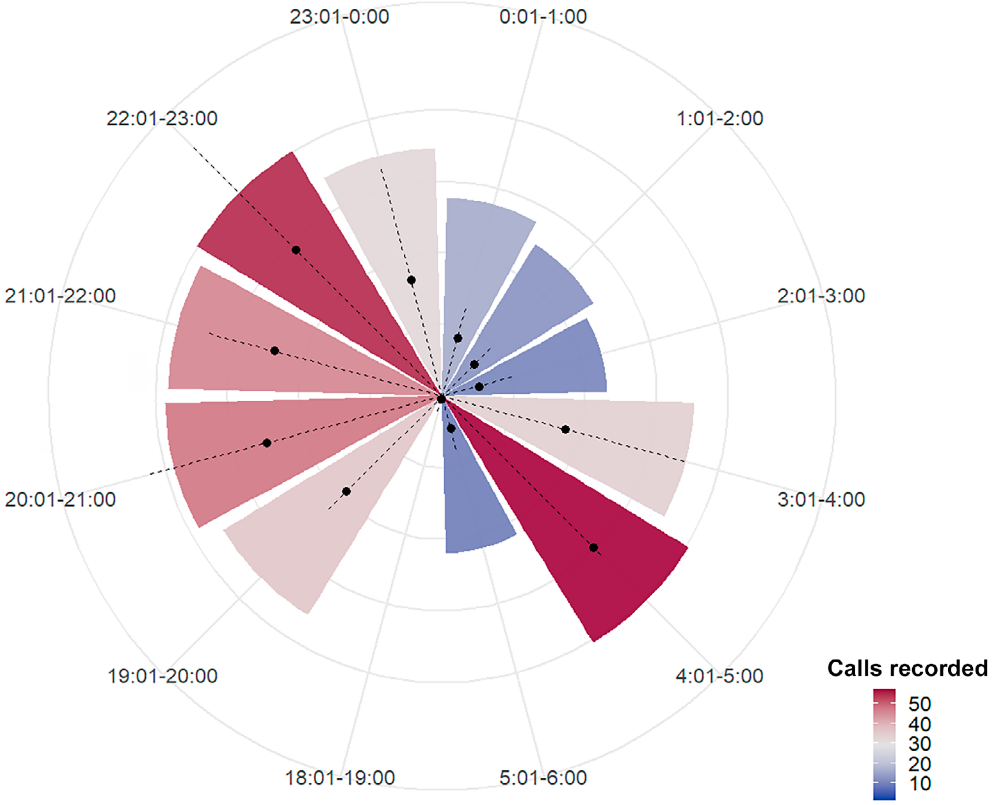

Figure 1. Circular graph of the vocal activity of ***Cycloramphus boraceiensis***. Bars indicate the number of calls recorded, black point indicates the mean, and dashed lines indicate the standard deviation.

diameter of the eggs (6.4–7.8 mm); tadpoles reached GS21 and it was possible to see a gill bud on each side of the head, with three to four secondary long filaments; the olfactory pits and the dorsally oriented eyes became apparent. On 17 February 2021, we observed an increase in the diameter of the eggs (10.1–11.3 mm); at GS23 the embryos' bodies were pigmented and their eyes were clearly visible we also observed the beginning of the hatching of the eggs at GS25 after the tadpoles began moving intensely. At GS26–GS27 tadpoles were photosensitive, seeking shelter in cracks and mosses nearby. At GS34 the legs began to appear, the tail shortened and tadpoles became more active, but always hidden in rock cracks. On March 1st, we could not find any tadpoles nearby, except an individual preyed on by a spider from the Trechaleidae family (Fig. 3).

Both adults and tadpoles were cryptic and their coloration often matched the surrounding background where they were detected (Fig. 4). When found, adults remained motionless and many times adopted a crouching posture in response to our approach (Fig. 4d-e). When handled, the individuals usually bit the researcher's fingers (Fig. 4f). We did not observe any individual displaying thanatosis. Beyond crypsis, tadpoles can also hide in rock cracks; as we approached them, they often broke loose from the rocks, throwing themselves towards the water in an attempt to escape.

The advertisement call of *Cycloramphus boraceiensis* in Ubatuba was a short simple metallic sound (Fig. 5). The call was composed of a single pulsed note. Notes lasted in mean for 0.06 ± 0.02 (0.03–0.10) seconds, mean repeated at a rate of 17.8 ± 6.5 (10.1–35.5) notes/second. The mean dominant frequency of the call was 1.9 ± 0.3 (1.3–2.3) kHz, while the mean minimum frequency was 1.4 ± 0.4 (0.9–1.8) kHz and the maximum frequency was 2.4 ± 0.3 (1.7–2.8) kHz. The aggressive call was emitted by a male before trying to bite the researcher's hand. The call consisted of a single note with a variable structure (pulsed and not pulsed) and duration emitted at irregular intervals (Fig. 6). Mean call duration lasted 19 ± 31 (3–139) ms. The mean peak of the dominant frequency was 2.5 ± 2.2 (1.1–8.5 kHz). Mean low-frequency notes were 1.0 ± 0.3 (0.2–1.3) kHz, and mean high-frequency notes were 7.5 ± 1.9 (3.8–9.9) kHz. The mean pulse number was 3 ± 4 (1–20), and notes were separated by intervals of 451 ± 912 (8–3.63) ms, irregularly or regularly spaced throughout the call.

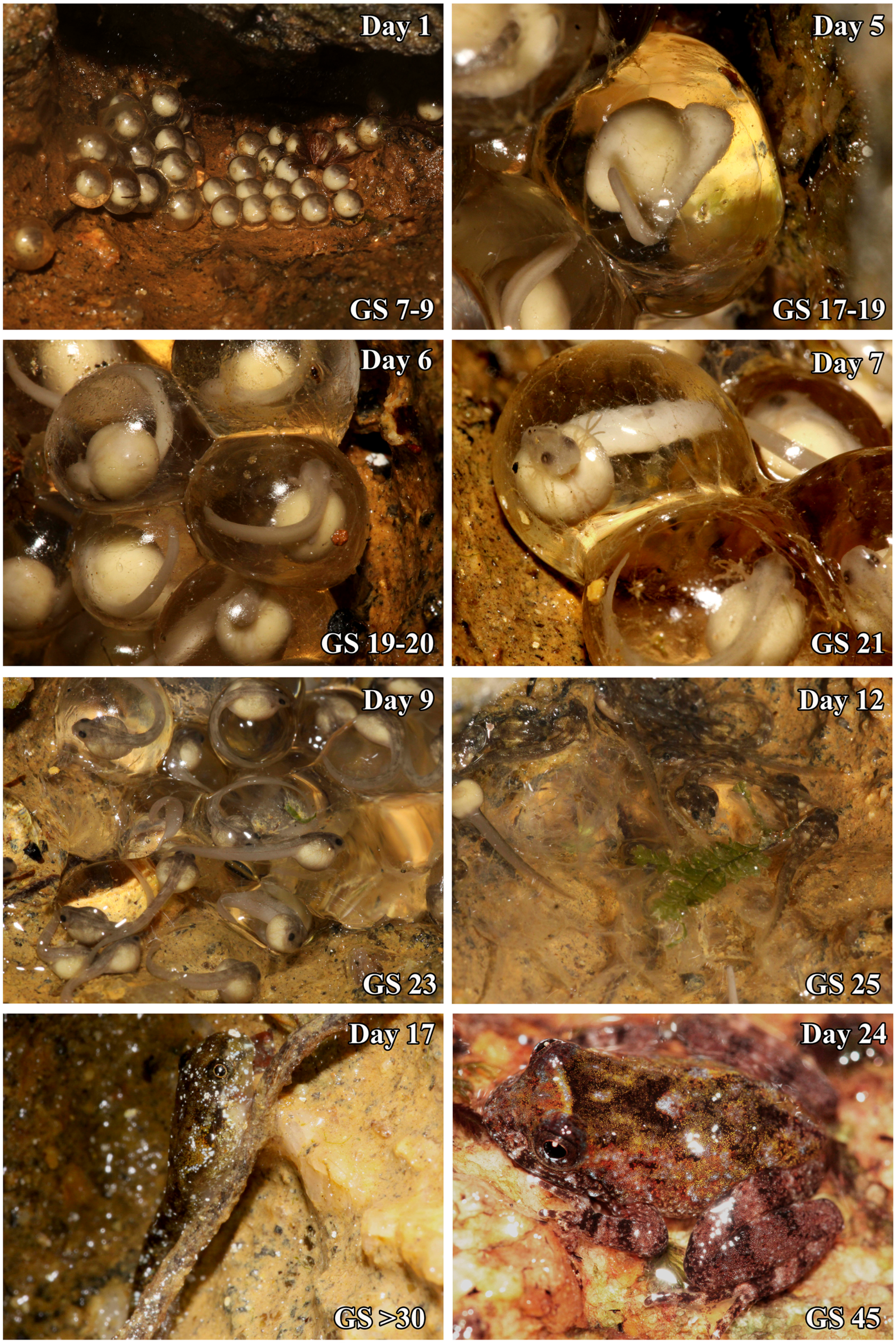

Figure 2. Views of the different detailed development stages of Cycloramphus boraceiensis larvae in the Projeto Dacnis private reserve, Ubatuba, São Paulo, Brazil. GS = Gosner's (1960) stage.

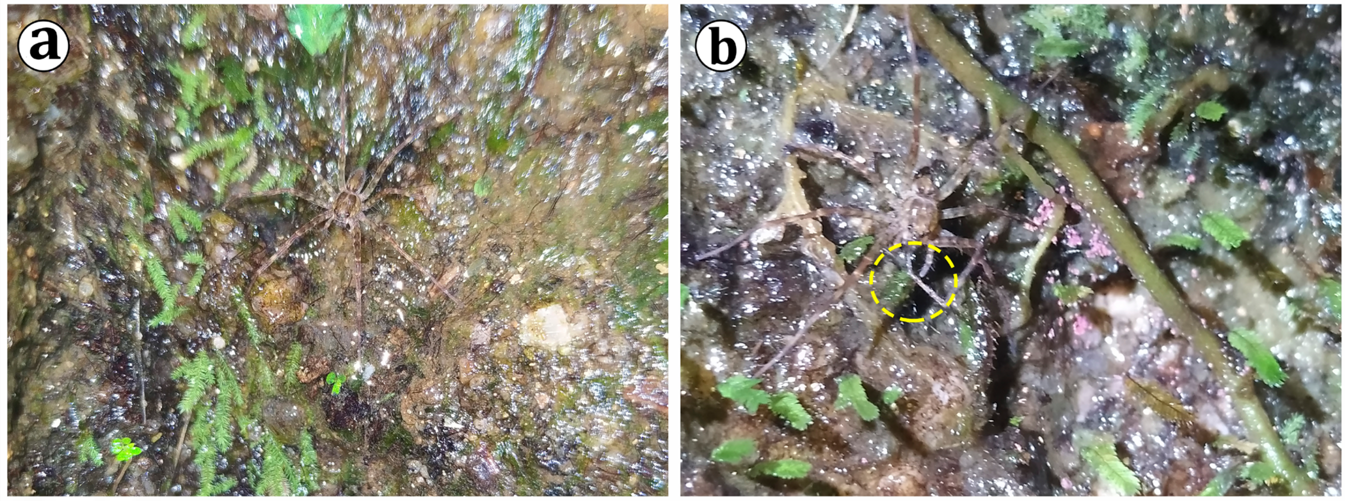

Figure 3. Predation of a ***Cycloramphus boraceiensis*** tadpole by a spider of the Trechaleidae family. The tadpole is indicated by the dashed yellow circle.

DISCUSSION

We observed *Cycloramphus boraceiensis* breeding throughout the year in Ubatuba, in accordance with information available for other congeners that also breed in streams, such as *Cycloramphus dubius* (Miranda-Ribeiro, 1920) (Giaretta and Cardoso 1995). Streams are more stable when it comes to temperature and humidity variations, which can be favorable for prolonged breeding (Afonso and Eterovick 2007). Anurans depend on the environment to obtain energy (Narins 2001) and to perform basic functions such as eating, breeding, and calling (Navas 1996). Calling demands great expenditure of energy and time, and can advertise to a possible predator the presence and location of calling males (Ryan *et al.* 1981, Duellman and Trueb 1994). Therefore, males may have their calling period selected to reduce predation risk (Brooke *et al.* 2000), and these can be directly related to the peak of activity found in our study.

The number of eggs in the spawns of *Cycloramphus boraceiensis* we observed is similar to the 50 eggs previously reported by Heyer *et al.* (1990). *Cycloramphus boraceiensis* has a smaller spawn size when compared to *C. bandeirensis* Heyer, 1983, which may lay up to 130 eggs (Verdade *et al.* 2019); 80–100 in *C. fuliginosus* (Lutz 1929); and 70–80 in *C. dubius* (Giaretta and Cardoso 1995). However, the clutch size was also similar to other congeners with 30–40 eggs, such as *C. faustoi* (Brasileiro *et al.* 2007), *C. stejnegeri* (Heyer and Crombie 1979) and *C. carvalhoi* (Coelho-Augusto 2013, Zocca *et al.* 2014), 36 eggs in *C. lutzorum* (Lima 2011), 10–30 eggs in *C. parvulus* (Lutz 1943, Van Sluys *et al.* 2001), 30-40 in *C. brasiliensis* (Lutz 1929), and 29–33 eggs in *C. lithomimeticus*, (Colaço and Silva 2022). The complete embryonic development (until the last embryo hatched) of *C. boraceiensis* lasted between eleven and twelve days, once embryos hatched, they began moving across the rock, feeding, and seeking shelter. This period is like *in-situ* records for *C. lithomimeticus* (seven days, Colaço and Silva 2022) and *ex-situ* records for *C. lutzorum* (twelve days, Lima 2011) and *C. bandeirensis* (eleven days, Verdade *et al.* 2019). As was observed here, *C. lutzorum*, *C. lithomimeticus* and *C. bandeirensis* eggs hatch at stages 25 and 26, respectively (Lima 2011, Verdade *et al.* 2019, Colaço and Silva 2022). By providing ontogenetic and development information, as recently reported for *C. lithomimeticus* (Colaço and Silva 2022), pre-hatching comparative studies will be possible once more species have their trait descriptions available. This kind of study could elucidate whether tadpoles breathe through the skin, lungs, or branches, a topic that is still being debated for the group (see Verdade *et al.* 2019, Dias *et al.* 2021).

During our monitoring, we found that both adults and tadpoles of *Cycloramphus boraceiensis* matched the background color. This was also observed for *C. rhyakonastes* (Nunes-de-Almeida *et al.* 2016) and may be a common pattern in those saxicolous frogs from the Cycloramphidae family. Wente and Phillips (2005) also observed this pattern in other species of anurans, suggesting a preference for microhabitats that would enhance their camouflage. Avoiding calling a possible predator's attention through their cryptic coloration and using a crouching posture sy-

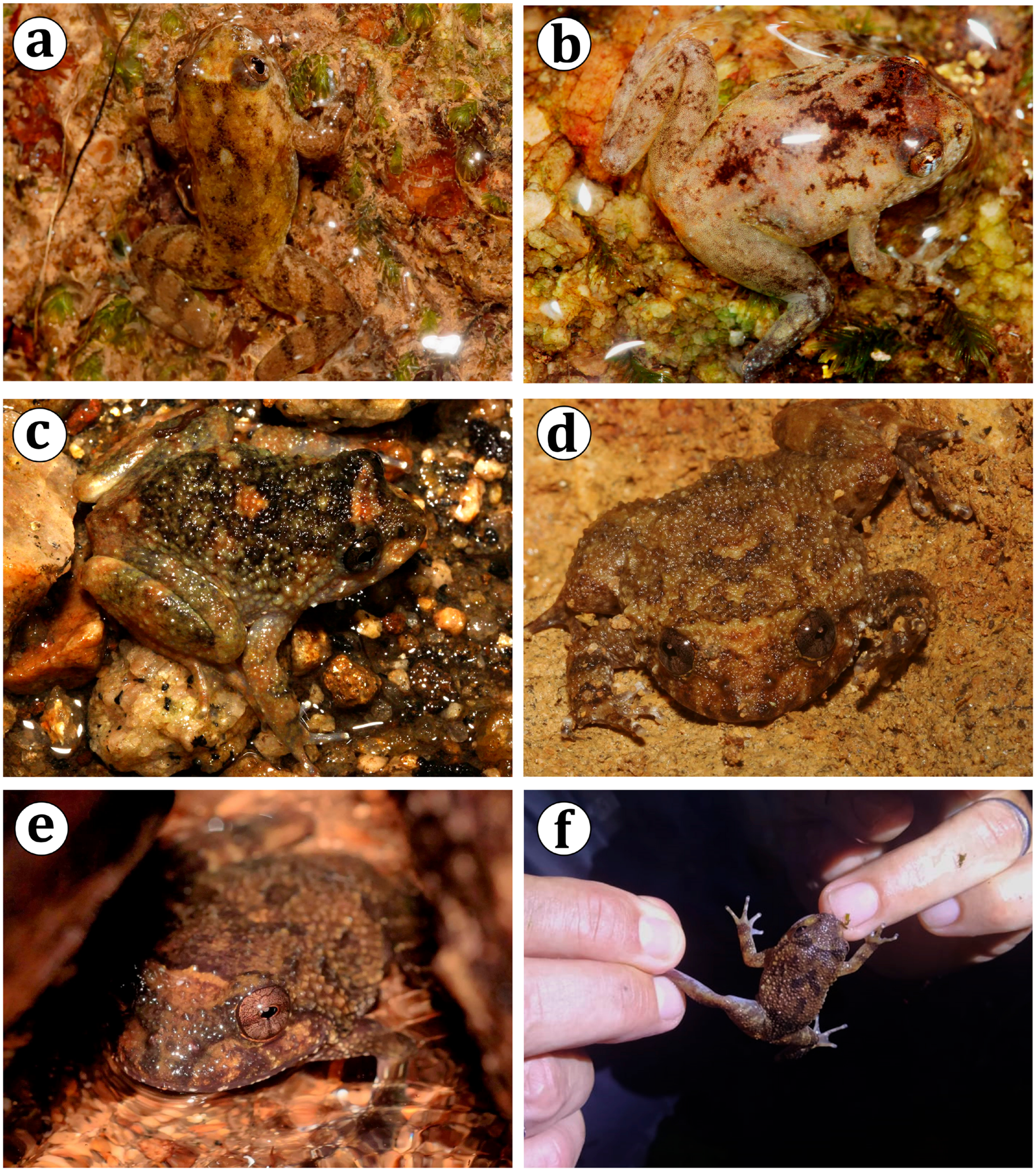

Figure 4. *Cycloramphus boraceiensis* individuals from the Projeto Dacnis private reserve, Ubatuba, São Paulo, Brazil. A-C) Polymorphic and cryptic coloration matching the background. D-E) Individual performing crouching down, and F) Individual biting the researcher's finger.

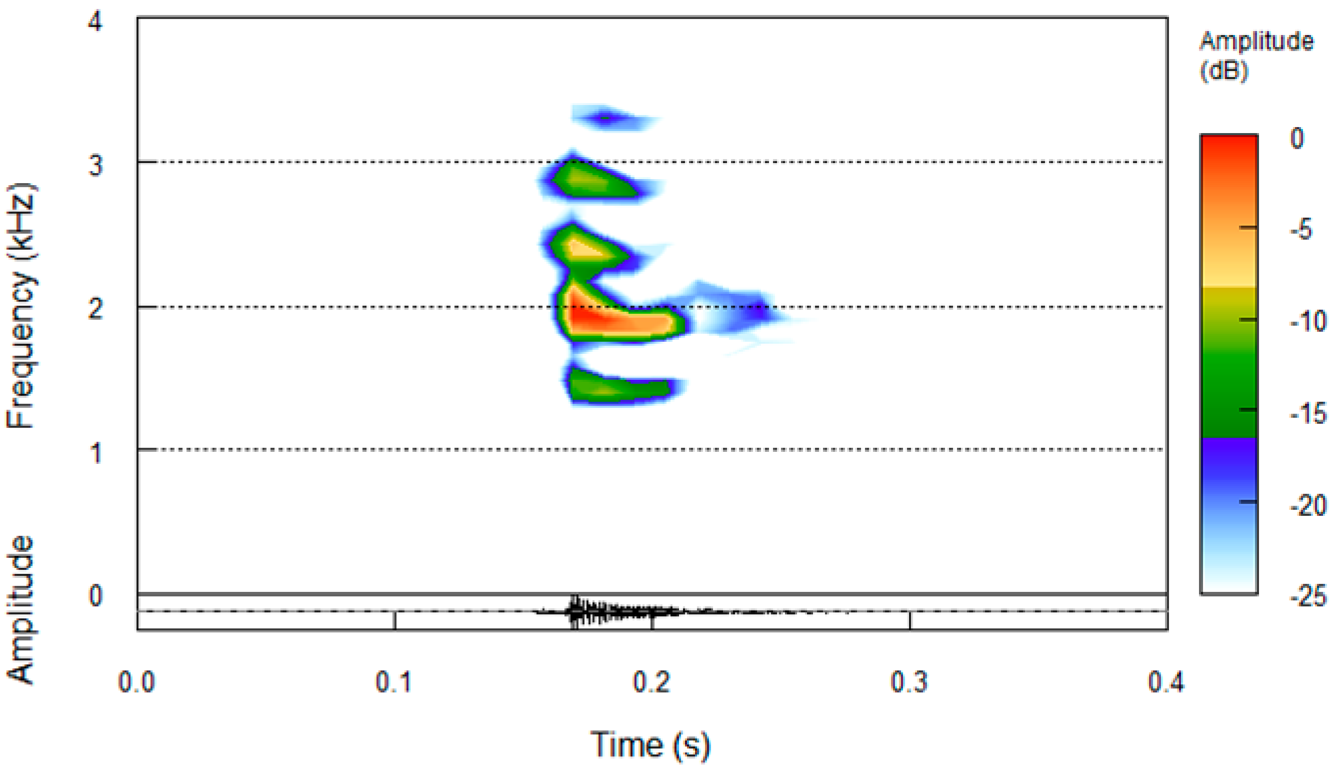

Figure 5. Advertisement call of ***Cycloramphus boraceiensis*** from the Projeto Dacnis private reserve, Ubatuba, São Paulo (FNJV 51541). Unvouchered male recorded on 1 February 2021, air temperature 23.3 °C.

nergistically may reduce the energy expended in escape or fight, saving energy that can be directed to growth and reproduction (Endler 1991, Toledo and Haddad 2009, Toledo *et al.* 2011). Besides that, *C. boraceiensis* can bite in an attempt to intimidate the predator and, thus, avoid predation. Some authors related the biting behavior to the frogs' diet (animals with strong cranial architecture could feed on larger prey) or to parental care (Duellman and Lizana 1994, Scott and Aquino 2005, Toledo *et al.* 2011). Unlike what was suggested for *Cycloramphus* (Hartmann *et al.* 2003, Toledo *et al.* 2011), the biting behavior in *C. boraceiensis* can be triggered not to defend the egg clutches. Tadpoles may present some defensive behavior as well. Additionally, to crypsis and hiding, tadpoles can also break loose from the rocks, throwing themselves towards the water. We noticed this when we approached, and it is possible that the behavior would be repeated to evade the presence of a potential predator. These observations match those made for other Cycloramphidae (Rocha *et al.* 2002, Verdade *et al.* 2019, Colaço *et al.* 2021, Dias *et al.* 2021, Colaço and Silva 2022, Sabbag *et al.* 2022). We also observed tadpoles moving across the rocks, similar to what was described by Colaço *et al.* (2021) and Verdade *et al.* (2019).

The advertisement call of *Cycloramphus boraceiensis* in Ubatuba is composed of a single pulsed note with a metallic sound, as described by Heyer (1983) and classified as "Type-A" by the same author. The aggressive call seems to have a greater variation in note duration and rate of emission. This was also true for *C. dubius* during a response to a male intruder (Giaretta and Cardoso 1995). The aggressive calls can be influenced by the behavioral context, such as the presence of an intruding male or even a predator (Giaretta and Cardoso 1995), but the lengthening of call duration and the increased rate of emission seem to be common in this kind of call, which we confirmed in our study. The lack of information about the aggressive call in *Cycloramphus* precludes us from making comparisons and advancing further in this topic. This kind of data would be useful for taxonomic and phylogenetic purposes (Köhler *et al.* 2017).

We now add new data about the natural history of *Cycloramphus boraceiensis*, such as development in its breeding biology, new acoustic parameters in the advertisement call, and the description of the aggressive call. Further studies could test if there is an active selection of

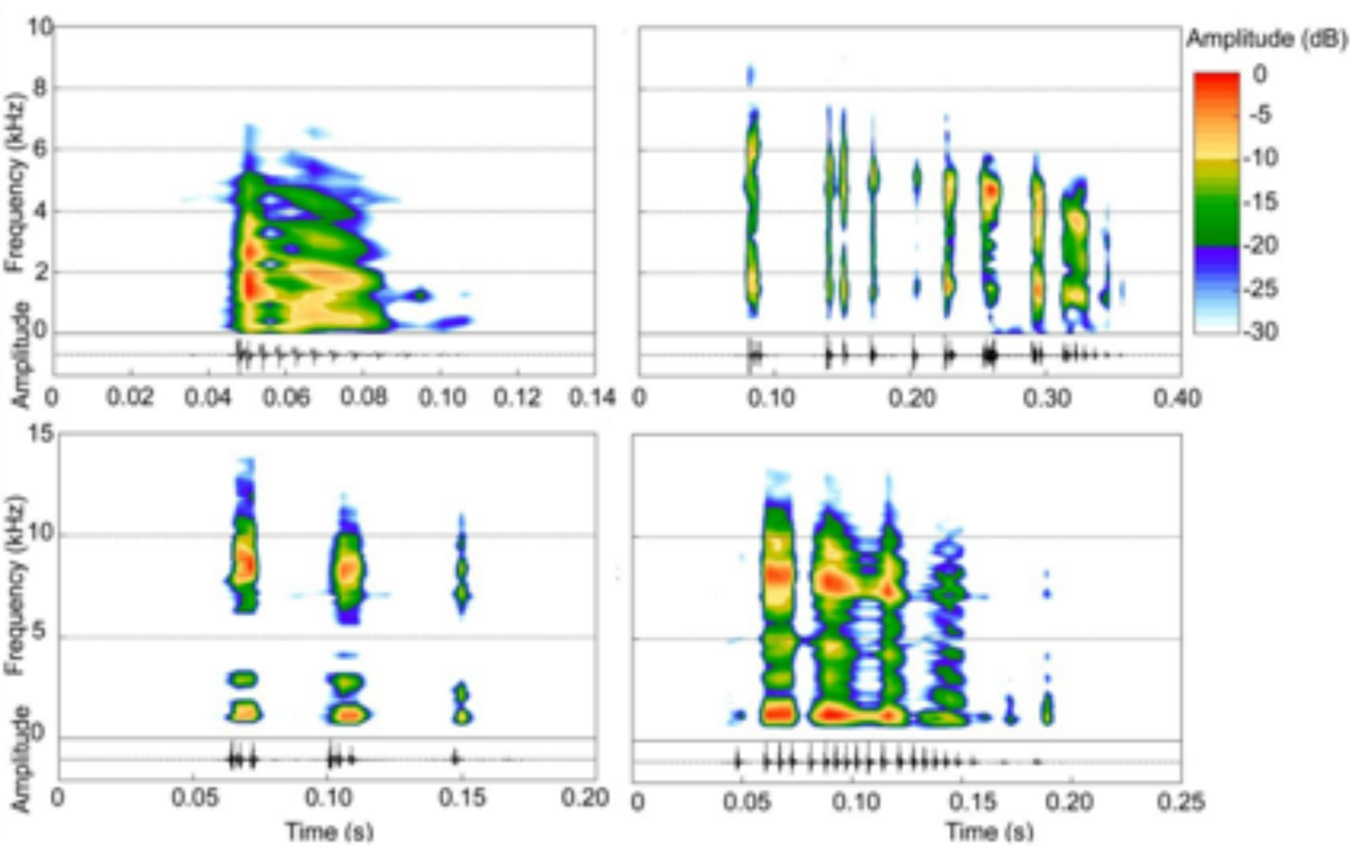

Figure 6. Variation in the aggressive call of ***Cycloramphus boraceiensis*** from Ilhabela, São Paulo (FNJV 32270). Call recorded on 20 November 2015, air temperature 25 °C.

microhabitat according to the general dorsal coloration of each individual, as observed for *Pseudacris regilla* (Baird and Girard, 1852) (Wente and Phillips 2005)

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AUTHORS' PARTICIPATION

EM and ELR conception and design; LMB, LFT, and EM data acquisition; MP and MTM data analysis. All authors contributed equally to writing and reviewing the document.

CONFLICT OF INTEREST

The author's declare that there is not conflict of interest.

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