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Aggressive behaviour, courtship and mating call description of the neotropical poison frog *Phyllobates aurotaenia* (Anura: Dendrobatidae)

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Frogs of the Dendrobatidae family have been documented as notably territorial (Summers, 2000; Pröhl, 2005; Méndez-Narváez and Amézquita, 2014). For many species, a good territory can be characterized by a high density of potential mates, suitable oviposition sites, access to trophic resources and/or land extension (Crump, 1972; Silverstone, 1973; Summers, 1992; Meuche et al., 2013). Moreover, successful territorial defence has been associated to mating success in males (Roithmair, 1992, 1994; Pröhl, 1997; Ringler et al., 2012; Yang and Richards-Zawacki, 2021). Therefore, although female territoriality has been documented (Weygoldt, 1987; Pröhl et al., 2019), typically males show a series of behaviours related to the defence of a territory (reviewed in Pröhl, 2005). Vocal activity combined with visual displays have been strongly linked to the latter (reviewed in Hödl and Amézquita, 2001). Recently, physical combat has also been reported as a mediator of social interactions in dendrobatid frogs (e.g., Summers, 2000; Méndez-Narváez and Amézquita, 2014; Duarte-Marín et al., 2020). Within the genus *Phyllobates* (Duméril and Bibron, 1841), there are few reports on aggressive or courtship behaviours (e.g., Summers, 2000), some of them based on individuals in captivity, which may not mirror the conditions of natural populations (Zimmermann and Zimmermann, 1985; Zimmermann, 1989). Additionally, the only known description of a mating call in *Phyllobates* was done for *P. bicolor* (presumably misidentified as *P. terribilis*) in captivity by Zimmermann and Zimmermann (1985) (Lötters et al., 2007; Kahn et al., 2016). The scarce information available for the genus hinders the understanding of the role of acoustic communication and agonistic behaviours in the defence of a territory and subsequent reproductive success. Here, we report the aggressive behaviour, courtship, and the description of a mating call for *P. aurotaenia*.

Phyllobates aurotaenia (Boulenger, 1913) is a dendrobatid frog native to Colombia, South America, restricted to the pacific lowland rainforests of the western versant of the West Andes (Silverstone, 1976; Kahn et al., 2016) (Fig. 1A). Males actively defend their territory with advertisement calls (Fig. 1B, 2A) and are responsible for transporting the larvae to breeding sites. Females of this species are known to roam around without actively defending a territory and approach calling males when ready to reproduce (Kahn et al., 2016). Recently, we visited two natural populations currently described as *Phyllobates aurotaenia* (Silverstone, 1976; Márquez et al., 2020). Field work was conducted between June and July of 2019, in the municipality of Cantón de San Pablo, Chocó, Colombia (5.32194°N, 76.62861°W; 264 m elevation) and Vereda Bochoromá (5.30557°N, 76.39426°W; 85 m elevation). Physical combat and courtship, which included a mating call undescribed for *P. aurotaenia* to our knowledge, occurred while we observed several resident males that were followed constantly during the previous days.

Aggressive behaviour. We noted that aggressive behaviour in *P. aurotaenia* is triggered by the acoustic activity and intrusion of a conspecific male in an established territory, similar to other dendrobatid frogs (Pröhl, 2005). The territory owner immediately responds by increasing the advertisement call activity (frequency of calls), followed by the search of the intruder. Once the owner has located its target, he lunges into it and hugs his opponent in such a position that the owner's vocal sac presses over the intruder's head, and the owner's anterior extremities tighten the intruder's vocal sac (Fig. 1C). At this point, the owner is preventing the intruder from calling and at the same time the former is emitting advertisement calls. This creates strong vibrations in

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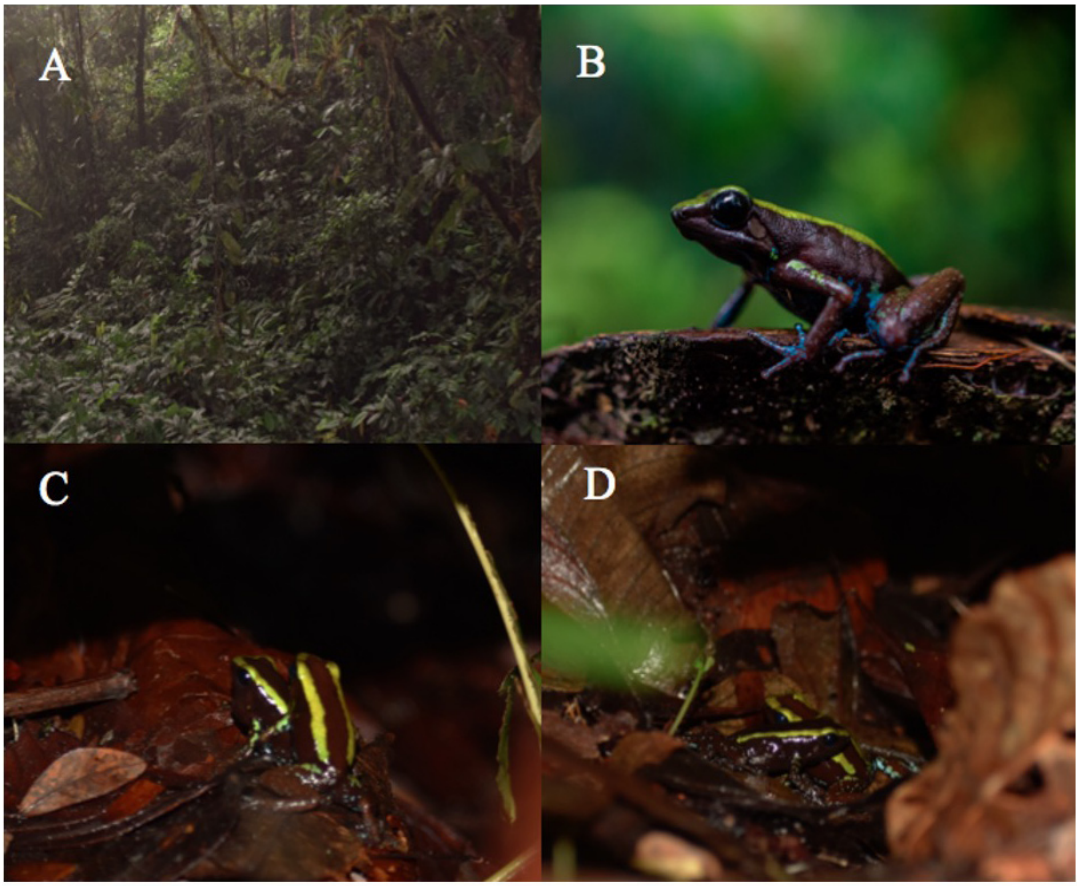

Figure 1. (A) Typical habitat of *P. aurotaenia* characterized by a slope in primary or slightly disturbed lowland rainforests. (B) male in an exposed site during peak acoustic activity. (C) Physical combat between two males, the territory owner embraces an intruder, preventing the latter from calling effectively. (D) Female in the back and male in the front in mating behaviour.

the intruder's head as the owner's vocal sac is pressed against it. The opponent struggles to escape and once he achieves his purpose, he jumps away a few meters, hiding from the owner. The owner is then agitated wandering around his territory, looking for the intruder while emitting advertisement calls, which in this case act as territorial calls. The intruder, however, does not leave the foreign territory, which generates the same response from the territory owner. After three physical combats, the intruder finally gives up invading and leaves the territory. The owner, still stimulated, continues emitting calls for a short period of time. The interaction lasted for about 25 minutes (Footage of this interaction can be seen at https://youtu.be/hNMQyy4tJNo).

This behaviour demonstrates the energy that this species invests towards the defence of its territory. Eventually, this action fulfils its purpose: the territory owner receives the visit of an interested female attracted by his acoustic activity. Evidence in several species of dendrobatid frogs has shown that females usually mate with the closest territory owner without performing an active search, a behaviour that is apparently associated with reducing energy costs (Meuche et al., 2013). Therefore, females may roam around the male's territory for other reasons, such as size, which may include oviposition sites and food, as suggested in Meuche et al. (2013).

Courtship. Neotropical poison frogs may perform complex and long courtships (Montanarin et al., 2011; Souza et al., 2017), during which, males and females use a broad range of cues to evaluate the mating partner's quality (Stückler et al., 2019). In this case, the courtship begins when a female enters a male's territory. Once the male recognizes the female, he approaches

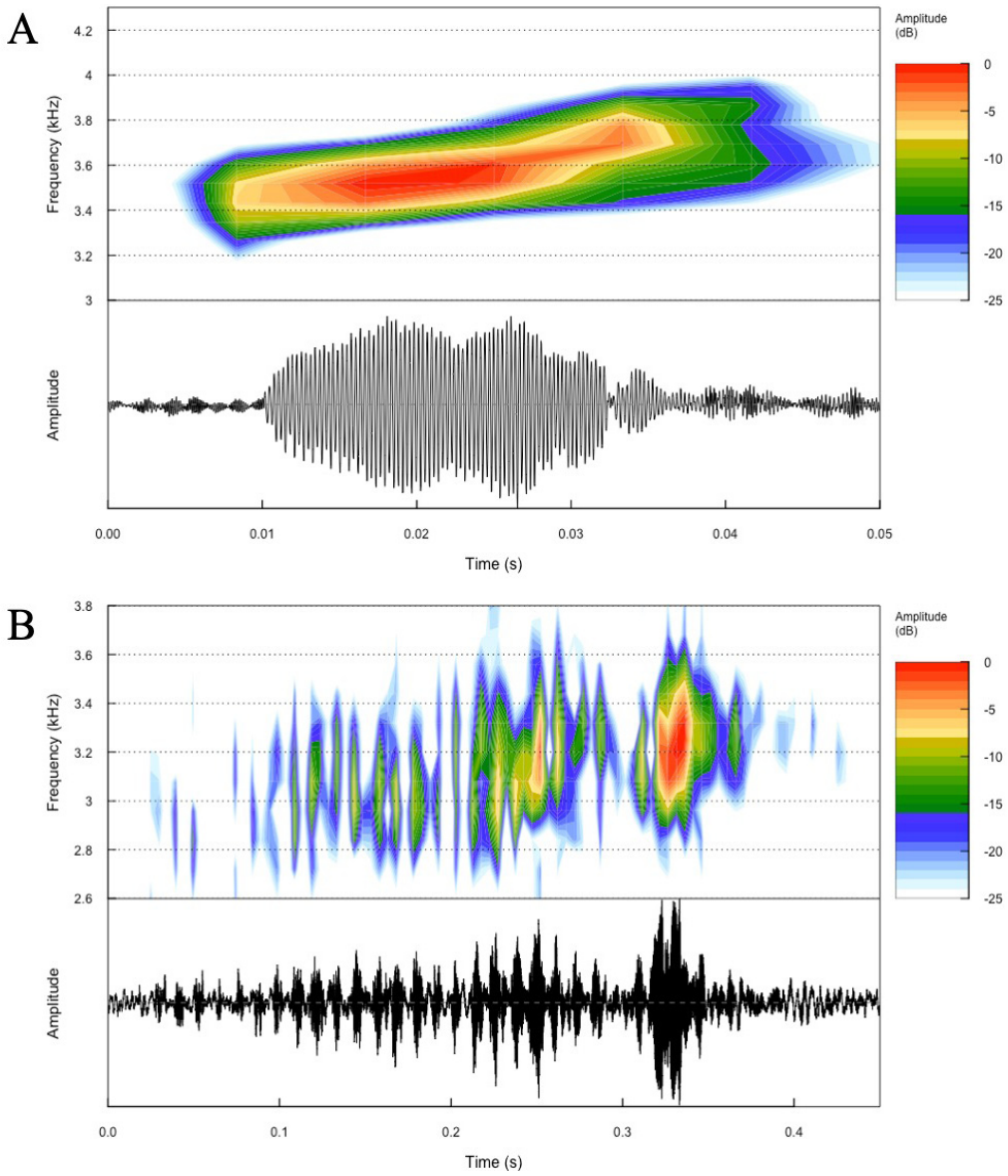

Figure 2. (A) Spectrogram and oscillogram of a single note of the advertisement call, used for territory defence and the first stage of courtship in *P. aurotaenia.* (B) Spectrogram and oscillogram of a mating call of *P. aurotaenia*. The mating call of B is differentiated from A, as it is emitted at a short-range in the presence of a female after several minutes of stimulation.

her while increasing the vocal activity. Each vocal trill stimulates the female to the point that both individuals hold physical contact (Fig. 1D). At this point, the male heads towards another direction and jumps two meters away. The male then starts calling again, to what the female immediately responds, reaching the male's location. This chasing behaviour continues for about ten minutes, apparently outside the territory in which the male emits his typical advertisement calls (used for the territorial defence). The difference between a territory and home range has been largely studied, normally incorporating the territory as a location which the male defends aggressively inside his home range. The latter is still being used for other behaviours, such as foraging and oviposition, and usually overlaps among other males (reviewed in Burt, 1943). Once the male arrives

Table 1. Spectral and temporal traits of the mating call of *Phyllobates aurotaenia*. Abbreviations: Ind (Individuals), CD (call duration), CDF (call dominant frequency), CMINF (call minimum frequency), CMAXF (call maximum frequency), PN (pulse number), PD (pulse duration), PDF (pulse dominant frequency), PMINF (minimum frequency of the pulse), and PMAXF (maximum frequency of the pulse). A single call both for the advertisement and mating call description is based on a single trunk contraction.

Species	**Ind /calls**	**CD (ms)**	**CDF (Hz)**	**CMINF (Hz)**	**CMAXF (Hz)**	**PN**	**PD (ms)**	**PDF (Hz)**	**PMINF (Hz)**	**PMAXF (Hz)**
P. bicolor Mating call (Zimmermann and Zimmermann, 1985)	-/12	606 ± 243	2375 ± 84	1739 ±162	2875 ± 296	-	-	-	-	-
P. aurotaenia Mating call (This study)	1/1	364	3101	2842	3359	30	13.6 ± 2.3 (11.9-19.1)	3015 ± 114 (2842-3187)	2728 ± 155 (2498-3015)	3350 ± 100 (3273-3531)
P. aurotaenia Advertisement call (Erdtmann and Amézquita, 2009)	2/6	31	3587	3355	3893	-	-	-	-	-

at a suitable oviposition site, usually under the leaf litter, he stands still, emitting the typical advertisement calls (presumably acting as a mating call in this case) for a couple of minutes.

Finally, before the female decides to explore the oviposition site, the male emits a short-range mating call that triggers a quick chasing response by the female. We used the software Raven Pro 1.3 to measure three temporal (call duration, pulse number and pulse duration) and six spectral (call and pulse dominant frequency, call and pulse minimum frequency, and call and pulse maximum frequency) traits of the mating call, based on Köhler et al. (2017). The recordings were analysed using a sampling rate of 44.1 kHz with a FFT of 512 points, allowing 50% of overlap between points, using the Blackman window type. Using identical parameters, the R package *Seewave* (Sueur et al., 2008) was used to create the spectrograms and oscillograms (Fig. 2). The mating call of *P. aurotaenia* differs from the advertisement call of the species because a single trunk contraction generates a much longer call at a lower frequency. In comparison to the mating call of *P. bicolor*, the mating call of *P. aurotaenia* is shorter and has a higher frequency (Table 1), most likely related to the larger body size of *P. bicolor*, a trait negatively correlated with call frequency (reviewed in Duellman and Trueb, 1994). The mating calls for both species, however, were emitted in similar courtship contexts (Zimmermann and Zimmermann, 1985). Therefore, they may be common for the rest of the genus. The mating call was deposited at the Colección de Sonidos Ambientales of the Instituto Alexander Von Humboldt, Colombia (IAvH-CSA-34457) and at the Macaulay library at the Cornell Laboratory of Ornithology. We reported measurements as mean ± standard deviation (range).

Our results are of great importance as frogs can detect a wide range of acoustic signals that may be generated by conspecifics, heterospecifics, predators or preys. Nevertheless, the detection of conspecifics is mediated by specific brain centres and pathways (Ringler et al., 2019). The existence of two different acoustic signals suggests different behavioural contexts. Therefore, it is imperative to perform behavioural and physiological experiments that lead us to understanding the differential role that advertisement and mating calls may be playing in agonistic and courtship events. Footage including the advertisement call, aggressive and courtship behaviours, and the mating call can be seen at https://youtu.be/Ej1oPKnGLsE with a version in Spanish at https://youtu.be/HN45T8GayVg.

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