Official journal website:
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Amphibian & Reptile Conservation
14(3) [General Section]: 177–188 (e265).

Forensic bioacoustics? The advertisement calls of two locally extinct frogs from Colombia

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***Abstract.*—Analyses of vocalizations are an important tool for anuran species taxonomy and identification, and can become especially important for detecting rare or threatened species. Based on recordings obtained in 1986 in the Reserva Natural La Planada (Department of Nariño, southern Colombia), we describe the acoustic characteristics of the advertisement calls of *Paruwrobates andinus* (Dendrobatidae) and *Gastrotheca guentheri* (Hemiphractidae), two Andean anuran species not seen since the 1990s and considered locally extinct. The call of *P. andinus* consists of a rapid series of short notes emitted in three call groups. The first two groups have five notes with 6–7 pulses each and a duration of about 2 sec, while the third call group contains 50 notes or more, with 5–8 pulses each and a duration of about 30 sec. On average, the notes have a fundamental frequency of 2.2 kHz and a dominant frequency of 4.4 kHz. This call differs from that of its likely most closely-related species, *P. erythromos,* in having shorter notes repeated at a higher rate. The call of *G. guentheri* has a single loud, short note (average duration, 0.262 sec) composed of 3–4 pulses, with negative frequency modulation, a fundamental frequency of 0.9 kHz, and a dominant frequency of 1.8 kHz. Advertisement calls of members of the *Gastrotheca longipes* group (to which *G. guentheri* belongs) are poorly known and seem to be quite variable, making it difficult to establish reliable comparisons.**

Keywords. Amphibia, Andes, Dendrobatidae, extinction, *Gastrotheca guentheri*, Hemiphractidae, *Paruwrobates andinus*, vocalizations

***Resumen.*—Los análisis de las vocalizaciones son una importante herramienta en la taxonomía e identificación de anuros, y pueden ser especialmente importantes para detectar especies raras o amenazadas. A partir de grabaciones obtenidas en 1986 en la Reserva Natural La Planada (Departamento de Nariño, sur de Colombia), describimos las características de los cantos de *Paruwrobates andinus* (Dendrobatidae) y *Gastrotheca guentheri* (Hemiphractidae), dos especies de anuros andinos que no han sido observadas desde 1990 y se consideran extintas localmente. El canto de *P. andinus* consiste en series rápidas de notas cortas emitidas en tres grupos de llamadas, las dos primeras conteniendo 5 notas con 6–7 pulsos cada una, y una duración de cerca de 2 segundos, mientras que el tercer grupo contiene 50 notas o más, con 5–8 pulsos cada una y una duración de cerca de 30 segundos; en promedio, la frecuencia fundamental es de 2.2 kHz y la frecuencia dominante es de 4.4 kHz. Este canto difiere del de la que probablemente es la especie más próxima, *P. erythromos*, por tener notas más cortas repetidas a un ritmo más rápido. El canto de *G. guentheri* tiene una sola nota alta y corta (duración media, 0.262 segundos) compuesta por 3–4 pulsos, con modulación de frecuencia negativa, frecuencia fundamental de 0.9 kHz y frecuencia dominante de 1.8 kHz. Los cantos dentro del grupo de especies de *Gastrotheca longipes* (al cual pertenece *G. guentheri*) no se conocen bien y parecen ser muy variables, por lo que no se pueden hacer comparaciones fiables.**

Palabras clave. Amphibia, Andes, Dendrobatidae, extinción, *Gastrotheca guentheri*, Hemiphractidae, *Paruwrobates andinus*, vocalizaciones

Citation: De la Riva I, Lansac C, Cepeda B, Cantillo G, De Luca J, González L, Márquez R, Burrowes P. 2020. Forensic bioacoustics? The advertisement calls of two locally extinct frogs from Colombia. *Amphibian & Reptile Conservation* 14(3) [General Section]: 177–188 (e265).

Accepted: 11 October 2020; **Published:** 9 November 2020

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Introduction

"Extinction is forever" is a famous sentence often quoted in texts on evolution and conservation biology, but deciding when a species is extinct is not an easy task. Empirical data, either on the existence of surviving individuals or their disappearance, are often difficult to obtain, especially for poorly known, rare, widespread, or elusive species. While the conservation status of species with small or restricted distributions can be more easily evaluated, surveying the entire range of species with large and/or patchy distributions in order to know whether they are extant or extinct is a much greater challenge. For this reason, a more conservative and less compromising approach is simply to refer to local extinctions or extirpations, instead of extinction (see Smith-Paten et al. 2015).

Within the current Sixth Mass Extinction crisis, amphibians are the most threatened class of vertebrates due to several factors (Wake and Vredenburg 2008). In particular, chytridiomycosis has been linked to the extinction of at least 90 species of amphibians and the decline of 501 others (Scheele et al. 2019). The amphibian crisis is especially severe in the American tropics, where mountain forest ecosystems, even pristine ones, have suffered the collapse of entire amphibian communities (e.g., Lips 1998, 1999; Lips et al., 2006, 2008; Catenazzi et al. 2011, 2014), usually including precipitous declines of many species and the extirpation of others. Because the beta-diversity is high and many amphibian species have reduced distributions in tropical mountains, in many cases local extirpation equals the extinction of the species altogether.

One case of amphibian community collapse in the tropical Andes which remains poorly documented is that of the Reserva Natural La Planada, in southern Colombia (Fig. 1A–B). In 1986, during a three-month period from April to June, Patricia Burrowes carried out the first (and hitherto only) comprehensive study of the amphibian community of La Planada (Burrowes 1987). A total of 42 species of amphibians were reported, including 12 species of anurans new to science (Myers and Burrowes 1987; Duellman and Burrowes 1989; Lynch and Burrowes 1990). After 1986, further amphibian monitoring and inventory in La Planada has been anecdotal and intermittent, mostly carried out by G. Cantillo and field parties from the Universidad de Nariño (e.g., Muñoz-Arcos et al. 2016). In April 2019, four of the authors of this article (IDlR, PAB, GC, and BC) and several students returned to La Planada to carry out amphibian surveys. Although the temporal sampling effort was much shorter than in 1986, that brevity was partially compensated by having a large team instead of a single person doing the fieldwork. Preliminary data indicated that massive declines in numbers and species diversity have taken place in La Planada, suggesting chytridiomycosis and climate change as potential factors involved in the observed collapse (De la Riva and Burrowes 2019; data not shown).

Two of the most iconic anurans studied in La Planada by Burrowes in 1986 were the poison arrow frog, *Paruwrobates andinus* (Myers and Burrowes, 1987) [Fig. 1C], and the marsupial frog, *Gastrotheca guentheri* (Boulenger, 1882) [Fig. 1D]. *Paruwrobates andinus* was described (as *Epipedobates andinus*) by Myers and Burrowes (1987) based on nine specimens. This small species (snout-to-vent length [SVL] of males 19.5–20.1 mm; females, 20.7–21.5 mm) is considered diurnal, terrestrial, and semiarboreal, being observed near water-filled bromeliads in trees and near fallen tree branches (Myers and Burrowes 1987). The species is only known from La Planada, where it was observed across an elevation range of 1,700–2,020 m asl (Myers and Burrowes 1987; Lötters et al. 2007; Kahn et al. 2016; Frost 2020). It has not been seen at the type locality since the 1990s (G. Cantillo, field notes), and its conservation status is "Critically Endangered (Possibly Extinct)" according to IUCN (2019a). While it is possible that the species still occurs somewhere in southwestern Colombia or even nearby northwestern Ecuador, it has not been found despite several search attempts, both in La Planada since 2013 and at nearby Río Ñambí Natural Reserve (IUCN 2019a). Thus, this is an example of a species extirpated locally, and perhaps extinct.

The case of *Gastrotheca guentheri* is quite different. The species has been known since its original description as the only anuran with true teeth in the lower jaw, which led Boulenger (1882) to place it in its own genus, *Amphignathodon*, meaning "teeth in both jaws," a phenomenon studied and discussed by Wiens (2011). Despite this exceptional peculiarity, different phylogenetic analyses have consistently placed the species deeply nested in the genus *Gastrotheca* (e.g., Duellman et al. 1988; Wiens et al. 2007; Castroviejo-Fisher et al. 2015). This moderately large species (SVL of males 67.8–76 mm; females, 69.9–82 mm) is nocturnal and usually associated with canopy vegetation, including bromeliads, and frequently found next to rivers (Arteaga et al. 2013; Duellman 2015). It preys on small vertebrates, such as frogs and lizards, and large insects, such as orthopterans (Arteaga et al. 2013; Paluh et al. 2019), a feeding behavior expected by Wiens (2011) based on the functional teeth in the lower jaw which enable the species to catch and swallow large prey. *Gastrotheca guentheri* occurs between 1,200–2,010 m asl in Andean cloud forests along the Cordillera Occidental from provinces Cotopaxi, Imbabura, and Pichincha in northwestern Ecuador to the Department of Antioquia in northwestern Colombia. A distribution gap of about 500 km has been noted between a Nariño-Cauca nucleus in the south of Colombia and a nucleus in the north comprising the departments of Risaralda-Chocó-Antioquia. However, based on specimen IND 4853, collected by J.V. Rueda on 3 December 1989 and examined by two of the authors

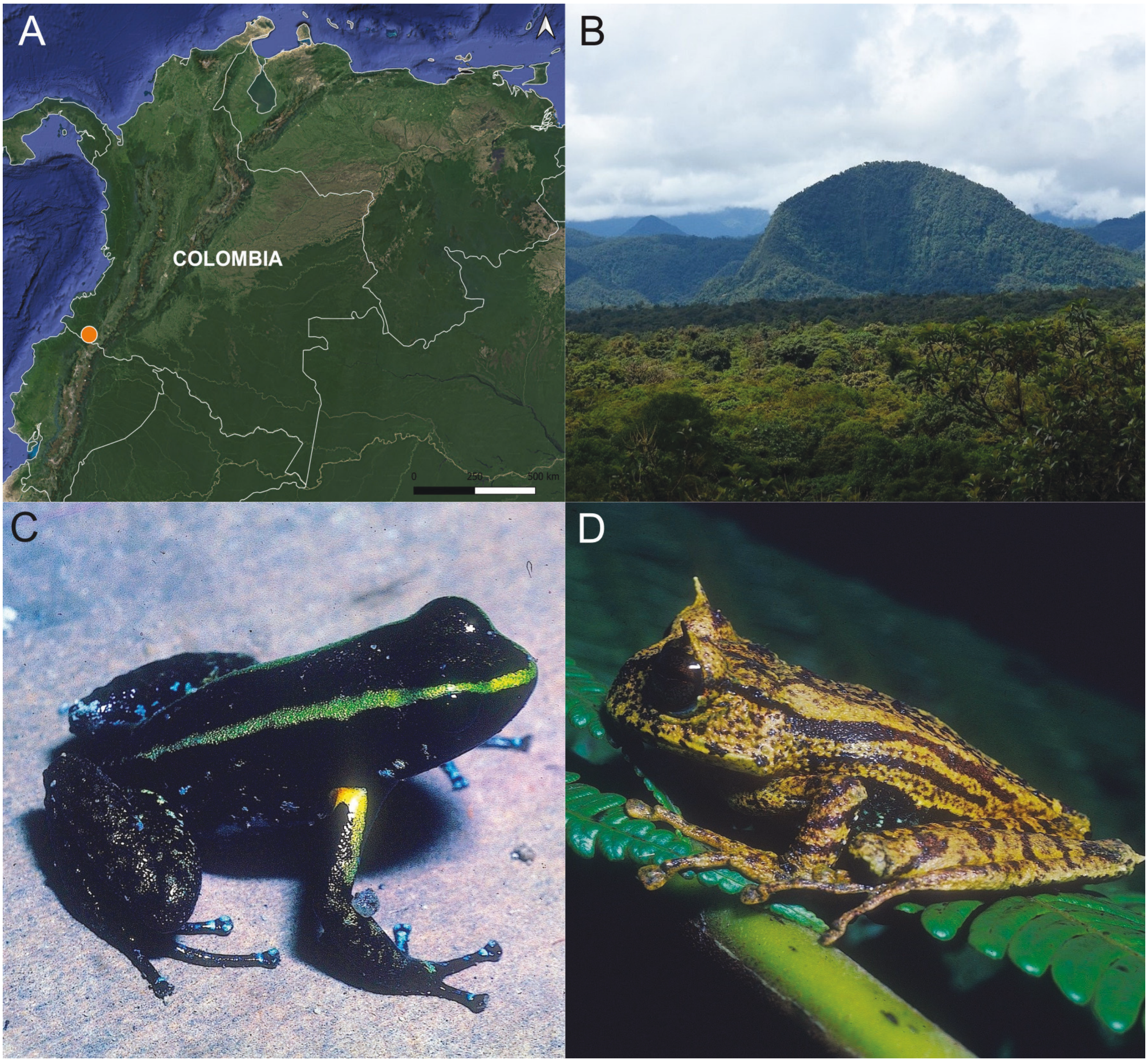

Fig. 1. Geographic location (A) and general view (B) of Reserva Natural La Planada (Department of Nariño, Colombia; (C) *Paruwrobates andinus* and (D) *Gastrotheca guentheri* from Reserva Natural La Planada, Colombia. *Photos by I. De la Riva (B) and P.A. Burrowes (C–D).*

(PAB and IDlR) at the herpetological collection of the Institute Von Humboldt, the species is also recorded in Risaralda (see below). A dubious record exists from the Amazonian slopes of northeastern Ecuador (Duellman 2015; IUCN 2019b; Frost 2020).

Gastrotheca guentheri is globally considered as Data Deficient, although its situation differs in Ecuador and Colombia (IUCN 2019b). In Ecuador, the species is considered as possibly extinct, because it has not been observed since 1996 despite active searches at known localities (Arteaga et al. 2013; IUCN 2019b), and the most recent specimen was collected on 1 January 1991 (L. Coloma, pers. comm.). In Colombia, its conservation status is difficult to assess due to its broader and apparently patchy distribution. It was last seen in 1990, and was not found in surveys carried out in La Planada in 2005 or in Parque Nacional Natural Munchique (Department of Cauca) in 2014–2016 (IUCN 2019b). Two specimens deposited at the Instituto de Ciencias Naturales-Universidad Nacional de Colombia [ICN 50102–3] were collected in Munchique in 1990 (A. Acosta, pers. comm.), although the species was not reported in the park by Pisso et al. (2018). The disappearances of the species at some locations may be explained by pollution and habitat loss, but those at pristine habitats are attributed to climate change or/and chytridiomycosis (IUCN 2019b).

In 1986, P. Burrowes and G. Cantillo obtained recordings in La Planada of *P. andinus* and *G. guentheri*, two species for which the advertisement calls were then unknown. Later, the general vocal behavior of *P. andinus* was outlined by Myers and Burrowes (1987), who described the vocalizations of the species as “a distinctive call comprised of a series of well-spaced ‘creek’ notes” often emitted from bromeliads at different heights in the trees. As for *G. guentheri,* the call was described by Duellman (2015) as "a single loud 'bop,' usually repeated at intervals of several minutes," although "some individuals have been heard to produce two or three calls in quick succession."

This paper provides the first comprehensive analyses, including the first numerical descriptions, of the advertisement calls of these two species, which are now apparently extirpated from La Planada, and might be extinct altogether. Because observing frogs is usually harder than hearing them, this case study of what can be termed "forensic bioacoustics" may prove useful in future surveys and acoustic monitoring of anurans in the Pacific Andean forests of Colombia and Ecuador.

Materials and Methods

The study site, Reserva Natural La Planada, is a protected area of 3,200 hectares at 1,700–2,010 m asl, in the cloud forests of the Pacific slopes of the Andes, Department of Nariño, Colombia (1º09'29"N, 77º58'36"W), near the Ecuadorian border (Fig. 1A).

The recordings were obtained from individuals (adult males in both cases) kept in captivity on 7 May 1986 at 1915 h for *G. guentheri*, and on 5 June 1986 at 1030 h for *P. andinus*. Unfortunately, records were not made of the air temperature or the size of the recorded specimens. The sound files were originally obtained by means of a Sony stereo cassette recorder TCS-350 and stored in analog cassettes, then digitized in a lossy compressed format (mp3). Because the cassettes were not available at the time of our study, the *.mp3 files were finally converted to *.wav for analyses with Raven 1.05 software (Cornell Lab of Ornithology 2014). Figures were generated with the R package Seewave (Suerur et al. 2008). Temporal data were obtained from the oscillograms and frequency information was obtained using fast Fourier transforms (FFTs; frame width: 1,024 points).

The terminology used for the call descriptions is based on Köhler et al. (2017) and the oscillograms and audiospectrograms presented follow the format of Bosch et al. (2000). Due to the compression imposed by the MP3 format, some of the properties of the recordings could be affected as reported by Araya-Salas et al. (2019). Several parameters were considered for the analyses of the calls: call group duration, intercall group duration, note repetition rate, internote duration, dominant frequency, and fundamental frequency. To determine the point in which the amplitude is maximum within each call/note three points were used: at the beginning of the call (t1), at the middle section (t2), and at the end (t3); thus, providing some information about frequency modulation (t3 minus t1). In addition, the delta harmonic energy (dB) was measured as the difference between the peak intensity of the dominant frequency minus the peak intensity of the fundamental frequency. This parameter provides information about the energy distribution in the spectrum. The number of pulses within calls/notes and pulse rate (pulses per sec) within calls/notes were difficult to estimate because the pulses were not clearly delimited due to their incomplete amplitude modulation. The numerical parameters of the advertisement calls are shown in Tables 1 and 2. The acoustic characteristics of the advertisement calls of *P. andinus* and *G. guentheri* were compared with those of other species which are phylogenetically closely related to them.

The original recordings are deposited in the scientific collection of the Fonoteca Zoológica of the Museo Nacional de Ciencias Naturales-CSIC, with collection numbers 11998 (*P. andinus* call) and 11997 (*G. guentheri* call) and are available in the web checklist *Frog Calls of the World* at the following links for *P. andinus* (http://www.fonozoo.com/fnz_detalles_registro_eng.php?tipo_registro=2&id=22942&id_sonido=1116) and *G. guentheri* (http://www.fonozoo.com/fnz_detalles_registro_eng.php?tipo_registro=2&id=22943&id_sonido=1117).

Results

The description of the call of *P. andinus* is based on the analysis of two call sequences. Only one type of call was heard, and three call groups were identified: A and B are similar to each other, while C is markedly different regarding the number of notes. Call groups A and B are composed of five notes with 6–7 pulses each, while call group C is longer, encompassing 53 notes with 5–8 pulses each (Fig. 2). For the analyses, only 50 notes were considered due to the background noise. The sounds of these individual notes are very similar in all call groups, having an average duration of 0.118 sec per note and an average inter-note duration of 0.450 sec (*n* = 73). The envelope shape of the audiospectogram is slightly asymmetrical, with rise time faster than fall time. An average call group duration of 2.089 sec (*n* = 2) was registered for call groups A and B, and a call duration of 30.139 sec for call group C. The inter-call group duration between A and B is 2.247 sec (*n* = 2), and 1.778 sec between B and C. Inter-call group durations were considered from the end of one call group to the beginning of the next call group. The note repetition rate in group C is 1.76 notes/sec. Inter-note durations were measured from the end of one note to the beginning of the next one. All of the call groups contain a series of notes with an average fundamental frequency around 2.2 kHz, a dominant frequency of 4.3 kHz, and one harmonic around 6.5 kHz. The presence and relative power of other harmonics were difficult to ascertain because of the MP3 format compression and the likely automatic gain control used in the recorder. The average delta harmonic energy is 29.9 dB (SD $\pm$ 8.246, range 17.1–46.4) and the average frequency modulation is 222.2 Hz (SD $\pm$ 129.6, range 129.2–344.5). In call group C, there is an increase in the amplitude level possibly due to a closer approach of the

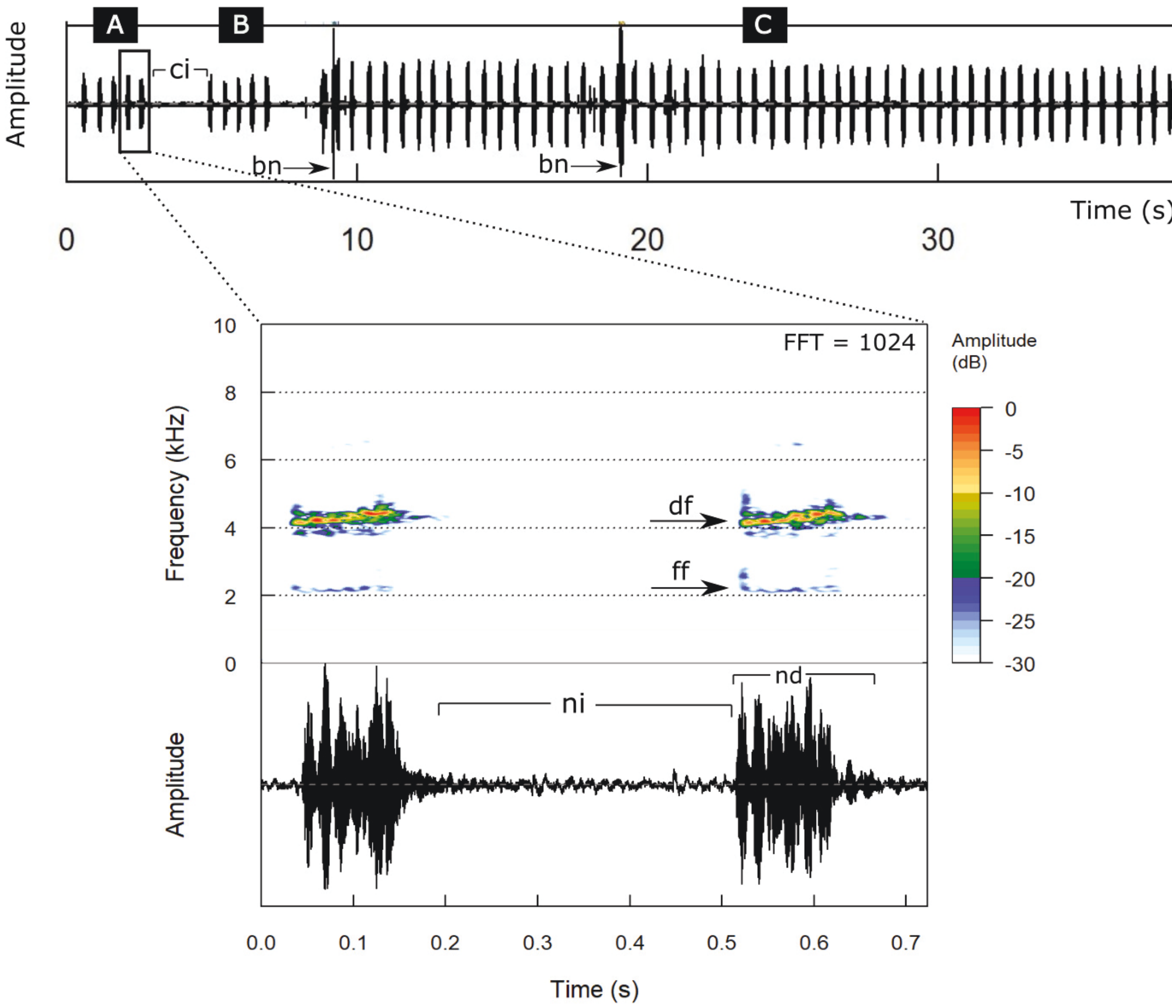

Fig. 2. Full-scale oscillogram (top), and expanded oscillogram and its audiospectrogram (bottom) of the advertisement call of *Paruwrobates andinus.* Call groups (A, B, and C), inter-call group interval (ci), and background noise (bn) are represented in the full-scale oscillogram. The note duration (nd), inter note interval (ni), dominant frequency (df), and fundamental frequency (ff) are indicated in the expanded box.

recorder to the sound source. The numerical data of the advertisement calls are summarized in Table 1.

At La Planada, the loud call of *G. guentheri* could be heard coming from the canopy and, despite it being a mostly nocturnal species, some individuals started to vocalize as early as 1400 h when raining (data not shown). The analyses here are based on two recorded calls. Only one type of call was heard, and each call was composed by only one note constituted by 3–4 pulses (Fig. 3). The envelope shape of the audiospectogram is asymmetrical, with a fast rise time and a more extended fall time. Notes have an average duration of 0.262 sec, an average fundamental frequency around 0.9 kHz, and a dominant frequency of 1.8 kHz. The presence of other harmonics was difficult to measure due to the same issue as in the *P. andinus* recordings. Frequency modulation is negative, and amplitude modulation is also predominately negative (see the descendant envelope shape in the oscillogram, Fig. 3). The inter-call duration, considered between the end of the first call and the beginning of the second one, was 20.4 sec. However, due to the fact that only a sequence of two calls was recorded, we cannot consider that this inter-call duration is representative. The average delta harmonic energy is 6.4 dB and the average frequency modulation is -0.2 kHz. The numerical data of the advertisement calls are summarized in Table 2.

Discussion

Recordings and knowledge of anuran advertisement calls not only constitute a powerful taxonomic tool, but call parameters can also contain valuable phylogenetic information. However, anuran advertisement calls are subjected to strong sexual selection, which can promote rapid character differentiation even in species which are closely related, especially if they occur in sympatry (see Goicoechea et al. 2010, and references therein). On the other hand, similar selective pressures affecting the evolution of advertisement calls of non-related species can lead to high levels of homoplasy in particular bioacoustic parameters. Thus, when comparing anuran vocalizations, determining which similarities are due to

Table 1. Summary of numerical parameters of vocalizations of *Paruwrobates andinus* and some other species of dendrobatoid frogs (mean ± SD, range). Acoustic data of *P. erythromos* were extracted from Myers and Burrowes (1987); of *E. atopoglossus* from Grant et al. (1997); of *E. isthminus* from Myers et al. (2012); and of the species within the *Ameerega picta* group from Serrano-Rojas et al. (2017). *Note: In *P. andinus*, the inter-call interval represents the value of the mean inter-call group interval of this species.

	Note duration (s)	Inter-note interval (s)	Note repetition rate (notes/s)	Inter-call interval (s)	Dominant frequency (Hz)	Fundamental frequency (Hz)
Paruwrobates andinus						
Mean ± SD	0.118 ± 0.011	0.45 ± 0.113	1.76	2.013 ± 0.331	4,323.8 ± 774.0	2,169.1 ± 405.0
Range	0.105– 0.157	0.31–0.58	-	1.778–2.247*	4,134.4–4,478.9	2,067.2–2,756.2
	n = 60	*n* = 60	-	*n* = 2	-	-
Paruwrobates erythromos						
Mean ± SD	0.135 ± 0.007	1.3 ± 0.141	0.63	-	4,166.7 ± 611.0	-
Range	0.13–0.14	1.2–1.4	-	-	3,500–4,700	
Ectopoglossus atopoglossus						
Mean ± SD	≤ 0.03	-	14.8	-	4,733.3 ± 924.6	-
Range	-	-	-	-	4,160–5,800	
Ectopoglossus isthminus						
Mean ± SD	0.085 ± 0.007	-	1.3	-	4,166.7 ± 642.9	-
Range	0.08–0.09	-	-	-	3,700–4,900	
Amereega shihuemoy						
Mean ± SD	0.098 ± 0.007	1.04 ± 0.19	0.9 ± 0.1	1.04 ± 0.187	4,672.7 ± 251	4,237 ± 281.9
Range	0.084–0.12	0.97–1.2	0.8–1.0	-	4,478.9–4,909.6	-
Amereega simulans						
Mean ± SD	0.105 ± 0.01	-	1.3 ± 0.1	0.691 ± 0.163	4,460.3 ± 157.7	4,060.9 ± 74.6
Amereega picta						
Mean ± SD	0.046 ± 0.002	-	2.2 ± 0.1	0.430 ± 0.045	4,044.2 ± 94.7	3,770.7 ± 76.7
Amereega hahneli						
Mean ± SD	0.013 ± 0.003	-	8.5 ± 0.1	0.107 ± 0.013	4,550 ± 49.1	2,516.8 ± 83.7
Amereega boliviana						
Mean ± SD	0.081 ± 0.009	-	1.2 ± 0.1	0.783 ± 0.089	3,846 ± 46.3	3,416.1 ± 68.2
Amereega yungicola						
Mean ± SD	0.048 ± 0.005	-	5.2 ± 0.0	0.148 ± 0.007	3,703.7 ± 0.0	3,475.7 ± 43.5
Amereega macero						
Mean ± SD	0.038 ± 0.001	-	8.7 ± 0.0	0.076 ± 0.003	3,617.6 ± 0.0	3,353.7 ± 38.1

convergence and which ones represent a phylogenetic signal can be contentious. In any case, it is useful to make call comparisons of species that are closely related and, if they have allopatric distributions, the observed similarities may support hypotheses of relatedness based on other sources of evidence. The two species studied herein are rare and their closest relatives are also poorly known; as a consequence, they have not been thoroughly studied from a bioacoustics standpoint. However, some inferences can be made from comparing the data available at hand.

Parubrowates andinus was originally described by Myers and Burrowes (1987) in the genus *Epipedobates*, which was then a diverse and broadly distributed group in South America; however, it was later split into various genera, one of them being *Ameerega*, in which the species was included as *Ameerega andina* (Frost et al. 2006; Grant et al. 2006). The genus *Ameerega* was subsequently rearranged by Grant et al. (2017), and *Paruwrobates* (a genus described by Bauer [1994] to include the species from La Planada) was resurrected from its synonymy to accommodate only three trans-Andean species: the Colombian *P. andinus* (type species), and the Ecuadorian *P. erythromos*, and *P. whymperi*. Edwards (1971) included *P. whymperi* in the genus *Colosthetus*, and Coloma (1995), in his review of Ecuadorian species of this genus, had already pointed out the similarity of this species with *P. erythromos* (then in the genus *Epipedobates*). Unfortunately, the call of *P. whymperi* is unknown. Finally, Grant et al. (2017) suggested that the colorful, aposematic Colombian species *Colosthetus ucumari* might belong to *Paruwrobates*, but its call is also unknown.

At the moment, phylogenetic hypotheses of dendrobatoid frogs are mostly based on morphological and genetic characters, with the occasional support of

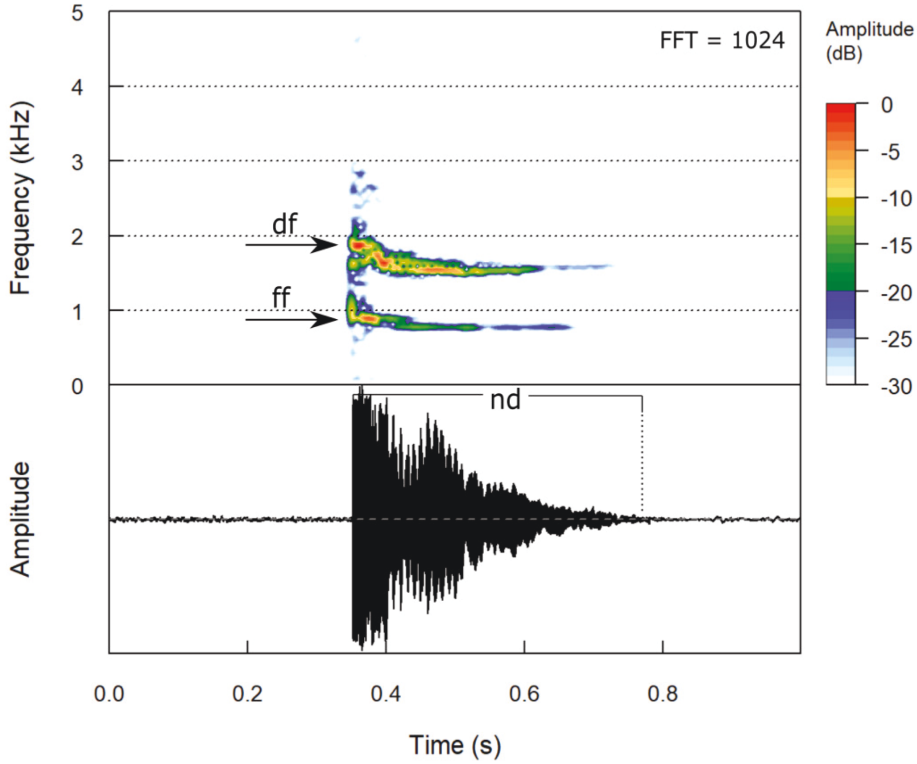

Fig. 3. Full-scale audiospectrogram (top) and oscillogram (bottom) of the advertisement call of *Gastrotheca guentheri.* The note duration (nd), dominant frequency (df), and fundamental frequency (ff) are indicated.

data from skin alkaloids (see Grant et al. 2006, 2017, and references therein). Myers and Burrowes (1987) described the call of *P. erythromos* (as *Dendrobates erythromos*) and opportunely considered it useful to compare this call with that of the new species from La Planada, whenever recordings were available. In fact, the recordings analyzed here had been obtained by the time of the description of *P. andinus*, but they were then "in storage" and only now available to be formally described. They now provide an opportunity to make the desired comparisons in order to ascertain whether the allocation of *P. andinus* and *P. erythromos* in the same genus is somehow supported by bioacoustical data as an additional source of evidence. This study also compares the call of *P. andinus* with those of two (out of seven) representatives of *Ectopoglossus* (*E. atopoglossus* and *E. isthminus*), another trans-Andean and Panamanian genus which is the sister group of *Paruwrobates* (Grant et al. 2017; Frost 2020). At the end of the convoluted taxonomic trajectory of many groups of dendrobatid frogs, *Ameerega* and *Paruwrobates* have ended up in different subfamilies, Colosthetinae and Hyloxalinae, respectively, within the family Dendrobatidae (Grant et al. 2017; Guillory et al. 2019; Frost 2020). Because of this distant phylogenetic relatedness, the calls of *P. andinus* are compared with those of some representatives of *Amereega* for descriptive purposes only; searching for possible shared character states, either as a result of having a common ancestor or of convergence, is beyond the scope of this paper.

Comparing the calls of *P. erythromos* and *P. andinus*. The call of *P. erythromos* was verbally described as a series of well-spaced "short repetitive chips" (Vigle and Miyata 1980), and then a 3.6 min sequence was analyzed and figured by Myers and Burrowes (1987). These authors described it as follows:

> "The advertisement call is a long train of harsh but not very loud 'chirps,' given continuously for many seconds. The one recording made includes an unbroken sequence of 136 notes given in 3 min, 35 s, for an overall repetition rate of 0.63 notes/s. Spacing between notes varied from 1 to 4 s, with an internote interval of about 1.2–1.4 s being most typical. Individual notes are 0.13–0.14 s duration and have a median frequency of about 4.5 kHz. Frequency is modulated within the note, there being a slow rise and more rapid fall, as indicated by the frequency-time

Table 2. Mean ± standard deviation (SD) and range of call parameters of *Gastrotheca guentheri* (*n* = 2).

Note duration (s)	Intercall (s)	Dominant frequency (Hz)	Fundamental frequency (Hz)	Delta harmonic energy (dB)	Frequency modulation (Hz)
0.262 ± 0.015	20.411	1,765.7 ± 182.716	861.3 ± 0.00	6.4 ± 2.121	-215.3 ± 182.716
0.273–0.251		1,636.5–1,894.9	861.3–861.3	4.9–7.9	(-344.5)–(-86.1)

curvature on spectrograms […]; sections of a few notes show the dominant frequency starting at about 4,300 Hz, rising to about 4,700 Hz, then dropping back below 4,500 Hz. The individual note is strongly pulsed at a rate of 131 pulses/s; the first several pulses are produced more rapidly than subsequent ones."

Comparisons of anuran calls among different studies would be easier if the same terminology and forms of graphical representation were used, but we are still far from reaching this desirable standardization (see Köhler et al. 2017). The terminology and type of figure that Myers and Burrowes (1987) used to describe the call of *P. erythromos* differ from those presented herein. However, a careful reading of their description of the call, and a visual comparison of their Fig. 12 (Myers and Burrowes [1987, p. 15]) with the audiospectrogram in Fig. 2 of this paper, allows for useful comparisons. Both calls consist of a rapid succession of short notes. In the temporal domain, the call of *P. andinus* has slightly shorter notes (0.118 sec on average, vs. 0.13–0.14 sec in *P. erythromos*), they are composed by fewer pulses (5–8 vs. 17, in the figure by Myers and Burrowes cited above), the inter-note intervals are shorter (0.45 sec on average vs. 1–4 sec, but most often 1.2–1.4 sec), and notes are repeated at a higher rate (note repetition rate 1.76 notes/sec vs. 0.63 notes/sec). Data are not available on the temperatures at the times of recording in either species. However, despite the known general effect of temperature on the behavioral and physiologically-induced variation of gross temporal parameters of anuran calls (the higher the temperature, the faster the call [Gerhardt 1994]), the differences found here are sufficiently remarkable to affirm that the call of *P. andinus* is notably faster than that of *P. erythromos*. In the spectral component, both species have a similar dominant frequency around 4.3 kHz, but *P. andinus* shows a narrower frequency modulation (0.2 kHz vs. 0.4 kHz in *P. erythromos*), and the envelope of the audiospectrogram shows a more complex call in *P. erythromos*, with a slow rise at the beginning of the note and a more rapid fall at the end.

Comparison with calls of *Ectopoglossus* species. Advertisement calls have been described for two species of the genus *Ectopoglossus*, the sister group of the genus *Paruwrobates* (Grant et al. 2017). The calls of those two species are quite different from each other, and also differ noticeably from those of *P. andinus* and *P. erythromos*. The call of *E. atopoglossus* was described by Grant et al. (1997). It consists of a fast succession of 12–14 short notes (note duration < 0.03 sec) repeated at a high rate (note repetition rate 14.8 notes/sec, as deduced from call duration and notes per call), emitted with a rising frequency from 4.16–4.24 kHz in the first notes of the call to 5.80 kHz in subsequent notes and with a decline in the last notes. The call of *E. isthminus* was described by Myers et al. (2012), and consists of a long train of weakly pulsed (3 pulses/note) short notes (note duration 0.08–0.09 sec) repeated at a much lower rate than in *E. atopoglossus* (1.3 notes/sec); frequency is also modulated, rising sharply from 3.7–3.9 kHz to 4.9 kHz.

In summary, the calls of species of *Parubrowates* and *Ectopoglossus* share the common feature of being composed of long trains of pulsed notes; in *Paruwrobates* notes are moderately long (one order of magnitude longer than those of *Ectoploglossus*) and frequency modulation is not very marked. In contrast, species of *Ectopoglossus* share calls composed of short notes with remarkable frequency modulation but highly variable note repetition rates. Whether these similarities and differences can be explained by phylogenetic relatedness is difficult to ascertain.

Comparison with calls of *Amereega* species. Species of *Paruwrobates* were formerly placed in the genus *Ameerega* (Grant et al. 2017; Guillory et al. 2019). Serrano-Rojas et al. (2017) provided call analyses of several species of *Ameerega* in the *A. picta* group (a group not recognized by Guillory et al. 2019). In comparison to those species of *Ameerega* analyzed by Serrano-Rojas et al. (2017), the advertisement call of *P. andinus* has, in general, a longer note duration and inter-call duration, sustains the highest fundamental frequency, and has a dominant frequency which falls within the dominant frequency range (Table 1). However, considering the great heterogeneity of call characteristics shown even by closely related species of *Ameerega*, comparing their calls with those of *P. andinus* does not shed much light on their phylogenetic relationships.

Comparisons of calls of *G. guentheri* with those of other *Gastrotheca* species. *Gastrotheca guentheri* was included by Castroviejo-Fisher et al. (2015) in the *Gastrotheca longipes* group (equivalent to the subgenus *Amphignathodon* used by Duellman [2015]), which also comprises *G. andaquiensis*, *G. angustifrons*, *G. antomia*, *G. bufona*, *G. cornuta*, *G. dendronastes*, *G. helenae, G. longipes*, *G. walkeri*, *G. weinlandii*, and *G. williamsoni.* According to Castroviejo-Fisher et al. (2015), the species most closely related to *G. guentheri* is *G. weinlandii.* However, as far as we know, the only one of these species for which bioacoustic characteristics have been comprehensively described and analyzed is *G. cornuta,* which occurs in the Pacific lowlands of Ecuador and Colombia, reaching the Caribbean slopes of Costa Rica across Panama. According to Duellman (1970), males of this rare species (as *G. ceratophrys*) vocalize from the canopy, and the call sounds like a loud "bop" reminiscent of the sound of uncorking a bottle of champagne. It consists of one to three notes emitted at long intervals, usually between 8–12 min. The note duration is approximately 0.08 sec, and the inter-note interval is 0.6 sec (when the call is composed by more than one note). The note consists of three harmonics of 0.8 kHz (dominant frequency), 1.6 kHz, and 2.4 kHz and there is frequency modulation, with each note diminishing abruptly from the beginning to the end. Comparisons of the numerical parameters of Duellman (1970) and the accompanying audiospectrogram of the call of *G. cornuta* (Plate 36.1) with those of *G. guentheri* presented herein (Fig. 3) show that *G. cornuta* emits shorter notes (0.08 sec vs. 0.262 sec in *G. guentheri*), with a lower dominant frequency (0.8 kHz vs. 1.8 kHz) and a much more pronounced, descending frequency modulation. Duellman (2015) briefly described the call of some other species of the *G. longipes* group. The calls of *G. dendronastes* is a loud chuckle-like sound followed by three to four "clucks;" *G. helenae* generates a call of 12–15 monosyllabic notes in a period of about five sec, and the call is repeated every 20–30 min; and the call of *G. weinlandii* is characterized by an explosive "wrock" usually followed by one or two shorter notes, "rock-rock" (Duellman 2015). Thus, the call characteristics within the *G. longipes* group seem quite variable, with short "bop" or "wrock"-like calls, either followed by short notes or not, and there are also calls composed by a succession of many monosyllabic notes like that of *G. helenae.*

Unfortunately, analyses of *Gastrotheca* vocalizations remain too scarce to make sound comparisons that would be sufficient to detect general inter- and intra-species group patterns. However, some patterns in vocalization characters variation seem to be detectable among several groups. For example, Sinsch and Juraske (2006) found consistent differences in calls of members of the *G. plumbea* group in relation to those of the *G. marsupiata* group (although all these species are now included in the broader *G. marsupiata* group of Castroviejo et al. [2015]). In general, these authors found that members of the *G. marsupiata* group emitted long pulsed advertisement calls in contrast to the more erratic, shorter calls of some members of their *G. plumbea* group. They even found distinctive call features among two clades within such a *G. plumbea* group, supporting a previous phylogenetic hypothesis by Duellman and Hillis (1987) based on allozymes. The short, erratic calls with frequency modulation often described as "bop" or "wrock" might be distinctive of members of the *G. longipes* group, although more research on *Gastrotheca* bioacoustics is needed to confirm this.

Conclusions

In cases of vanishing anuran species, description of the calls can be extremely useful for detecting remnants of populations, but it is important to record and safely store this type of information in general sound archives. For this reason, the publication of the calls in web checklists, like *Frog Calls of the World* (http://www.fonozoo.com), allows the comparison of any new recordings or hearing events with existing recorded sounds. The information on acoustic signals of *Paruwrobates andinus* and *Gastrotheca guentheri* provided in this study could be useful to researchers and the personnel of local nature reserves or conservation projects, in order to detect these species in nature once again. Several Andean anuran species once considered extinct have been rediscovered in recent years in the form of relict populations (e.g., Barrio-Amorós et al. 2020, and references therein). In particular, rare species inhabiting the forest canopy can be especially difficult to register visually, so they can remain unnoticed for long periods of time even when they are present, e.g., the Colombian large treefrog *Ecnomiohyla phantasmagoria* (Dunn, 1943) reported by Duellman and di Domenico (2020) after nearly 80 years without any records. This might be the case of *G. guentheri,* but the conspicuous call of the species described herein should be useful in detecting it. Thus, we remain hopeful that, someday, researchers will announce the re-discovery of one of the two species of anurans studied herein, which were once sadly considered to be "extinct forever."

***Acknowledgements.*—**We are indebted to the Awa community in charge of the Reserva Natural La Planada, especially to its former director Byron Guanga, for their support during PAB and IDlR's visit to La Planada in 2019, to Mauricio Zambrano for his help during the fieldwork, and to Andrés Acosta-Galvis for assisting us at the Instituto Alexander Von Humboldt in Villa de Leyva (Colombia). This research was funded by project PGC2018-097421-B-I00 of the Spanish Government (PI: I. De la Riva).

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