



Like other frogs in the family Craugastoridae, the young of the semiarboreal *Pristimantis cruentus* undergo direct development. Consequently, adults do not utilize streams or ponds for breeding, and gravid females rely on vocalizations and possibly other cues to locate males dispersed throughout the understory vegetation. Axillary amplexus is utilized (as in this photo) until the female finds a suitable moist microhabitat for egg deposition. This amplexic pair was photographed on 2 June 2014 in the Reserva Biológica Bosque Nuboso de Monteverde, Provincia de Puntarenas, Costa Rica. 📷 © John O. Cossel, Jr.



Vocalizations of *Pristimantis cruentus* (Anura: Craugastoridae) in Costa Rica

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ABSTRACT: The frog genus *Pristimantis*, in the family Craugastoridae, consists of nearly 500 species, but the vocalizations of many species remain unknown. An example is the semiarboreal *P. cruentus*, found in Costa Rica and Panama. We recorded the vocalizations of this species at Reserva Biológica Bosque Nuboso Monteverde and Bosque Eterno de los Niños, Costa Rica. Typical calls were of short (0.063 s), pulsed, buzz-like notes with a dominant frequency of 2,129.4 Hz, and similar sounding multi-note calls occasionally were produced. These calls differ from the only two known vocalizations of the *Pristimantis ridens* species series, *P. ridens*, and *P. altae*, in that the dominant frequency is lower, and was pulsed (*P. altae* non-pulsed). Cryptic species possibly occur within *P. cruentus* and our results might lead to future taxonomic efforts, and facilitate field identification and call surveys.

Key Words: Advertisement call, bioacoustics, frog, *Pristimantis ridens* species series

RESUMEN: El género de las ranas *Pristimantis* dentro de la familia Craugastoridae tiene casi 500 especies, sin embargo, no se conocen las vocalizaciones de muchas especies. Un ejemplo, es la rana de hojarasca, *P. cruentus*, encontrada en Costa Rica y Panamá. Grabamos vocalizaciones en sitios dentro de Reserva Biológica Bosque Nuboso Monteverde y el Bosque Eterno de los Niños, Costa Rica. Las llamadas típicas fueron notas cortas (0.063 s), pulsadas, notas parecidas a zumbidos con una frecuencia dominante de 2,129.4 Hz y llamadas con multinotas de sonido similar ocasionalmente fueron producidas. Estas llamadas difieren de la única vocalización conocida de esta serie de especies, *Pristimantis ridens* y *Pristimantis altae*, en que la frecuencia dominante es más baja, y fue pulsada (*P. altae* sin pulsar). Posibles especies crípticas ocurren dentro de *P. cruentus* y nuestros resultados pueden agregarse a futuros esfuerzos taxonómicos, así como facilitar identificaciones de campo y muestreos de llamadas.

Palabras Claves: Bioacústicas, llamadas de aviso, rana, serie de especies *Pristimantis ridens*

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INTRODUCTION

Craugastoridae is a species-rich family of New World anurans (Hedges et al., 2008), and within this family the genus *Pristimantis* contains nearly 500 species (Frost, 2016). The greatest diversity of *Pristimantis* is in the tropical Andes (Hutter et al., 2016) and species richness declines northward in Central America, with only six species known to occur in Costa Rica. Among the numerous groups in this family is the *Pristimantis ridens* series (*sensu* Hedges et al., 2008), which includes *P. adnus*, *P. altae*, *P. bicolor*, *P. caryophyllaceus*, *P. colomai*, *P. cremnobates*, *P. cruentus*, *P. jorgevelosai*, *P. laticlavus*, *P. latidiscus*, *P. moro*, *P. museosus*, *P. pardalis*, *P. pirrensis*, *P. ridens*, *P. rosadoi*, and *P. sanguineus* (Hedges et al., 2008; Crawford et al. 2010; Padial et al., 2014). Basic natural history details, such as vocalizations, are lacking for many of these species. For example, the vocalizations of only two species in the *P. ridens* species series have been described; Ibáñez et al. (1999) described the call of *P. ridens*, and recently Cossel et al. (2016) described the advertisement call of *P. altae*. Within the *P. ridens* species series, little information is available on the vocal apparatus morphology of several species; for instance, Savage (2002) described both *P. altae* and *P. pardalis* as lacking vocal slits and vocal sacs, whereas Taylor (1952) did not address the presence of a vocal sac in *P. pardalis*, but described the presence of a subgular vocal sac in *P. altae*. Vocal sacs are present in both species, as confirmed by specimen examination (Cossel et al., 2016) and field observations (JOC, pers. observ.). Ibáñez and Crawford (2004) suggested that *P. pirrensis* is closely related to *P. altae* and *P. pardalis*, but did not comment on the vocal apparatus or vocalizations in this species. Further, some species in the *P. ridens* species series, such as *P. bicolor* (Rueda and Lynch, 1983) and *P. cruentus*, lack vocal slits and a vocal sac but still can vocalize. This study provides additional natural history information on *P. cruentus*, a common and locally abundant anuran.

Pristimantis cruentus occurs in Costa Rica and Panama, within humid to wet forests at elevations from 40 to 1,800 m (Savage, 2002). These nocturnal frogs can be found perched on low vegetation, and occasionally in leaf litter. Similar to other species of *Pristimantis*, *P. cruentus* reproduces by direct development, laying its eggs in moist microhabitats such as tree trunk crevices (Myers, 1969) and moss banks (Savage, 2002). These small- to medium-sized frogs exhibit sexual size dimorphism (adult males 11–28 mm in snout–vent length [SVL] and adult females 25–42 mm SVL; Savage, 2002; JOC, pers. observ.). The dorsal coloration is variable, but usually is mottled brown or green, and the skin is tuberculate with supraocular tubercles (Fig. 1). Although *P. cruentus* was described over a century ago (Peters, 1873), little is known about this species. For example, Savage (2002) stated that the species apparently is mute. Nevertheless, Taylor (1952) documented calling males of *P. dubitus*, a species later synonymized with *P. cruentus* (Savage, 1981). Despite conflicting reports, herein we describe vocalizations of *P. cruentus*.

MATERIALS AND METHODS

We made *in situ* recordings of *Pristimantis cruentus* on seven evenings (1700 to 2330 h) between 4 and 13 June 2015. Our recording sites were in Tropical Lower Montane Wet Forest at Reserva Biológica Bosque Nuboso Monteverde and Bosque Eterno de los Niños, in the provinces of Alajuela and Puntarenas, Costa Rica (Fig. 2). The weather conditions varied among the seven nights of data collection, with little to no wind, intermittent periods of light fog, and precipitation ranging from none to heavy. The temperature and humidity ranged from 18.0 to 22.0°C and 84 to 100%, respectively (measured with a digital Merlin® 3000). We made audio recordings with two different portable digital recorders: a Tascam® DR-100 with two built-in cardioid unidirectional microphones, and a Tascam® HD-P2 digital recorder with a Sennheiser® MKH-416 short shotgun microphone. We recorded the calls as WAV files, at a sampling rate of 44.1 kHz/s, 24 bits/sample. We archived the recordings at Fonoteca Zoológica, the animal sound library at the Museo Nacional de Ciencias Naturales in Madrid, Spain (www.fonozoo.com; accessions #9844, #9845). We made most recordings under ambient light conditions, but used a red LED light to visually confirm that the calls originated from *P. cruentus*.

We recorded 134 vocalizations from 11 males at distances ranging from ~0.05 to 5 m. We did not inspect for the presence of nuptial pads or the absence of annulus tympanicus to confirm their sex, but instead assumed that sampled individuals were males based on their calling behavior and size. Of the calls recorded, 51 from seven individuals were of particularly high quality, as they were obtained at distances of ≤ 1 m, and we limited spectral analyses to this subset of high quality vocalizations. All vocalizations ($n = 134$) were analyzed and graphically

constructed using Raven Pro 64 v1.5 (Cornell University Bioacoustics Research Program). We determined vocalization type based on definitions by Wells (2007), and call variables are those defined by Heyer et al. (1990). We constructed time waveforms and spectrograms to determine temporal parameters of calls, whereas we used spectrograms to determine spectral call parameters. We constructed audio spectrogram slices with the use of fast Fourier transform, and time grids with a hop size of 128 samples, with 50% overlap, and frequency grid DFT size of 256 samples with grid spacing of 172 Hz, Hann's sampling window (256 samples), and a 3 dB filter bandwidth of 248 Hz. We captured eight calling males after recording their vocalizations to obtain photos and record body size (SVL; dial caliper) and mass (g; Pesola ® 10g spring scale). One individual was collected as a voucher and deposited in the Museo de Zoología at the Universidad de Costa Rica (accession # UCR 22517).



Fig. 1. A male *Pristimantis cruentus* (Craugastoridae), collected as a voucher (photo Fonozoo #9844 and #9845; preserved specimen # UCR 22517), from Reserva Biológica Bosque Nuboso Monteverde, Provincia de Puntarenas, Costa Rica, after obtaining digital audio recordings of advertisement calls (units cm).

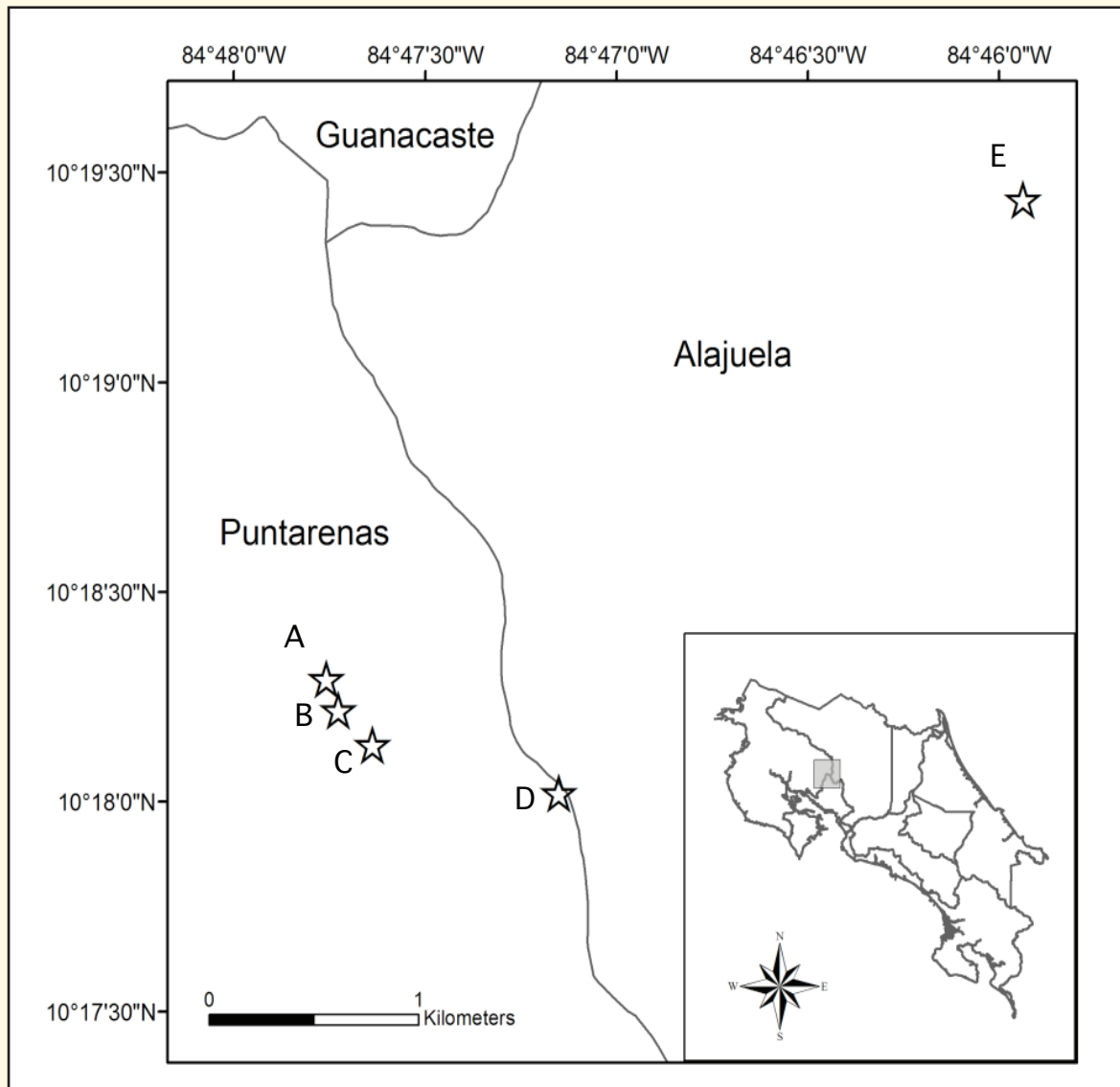


Fig. 2. Map of sampling locations of male *Pristimantis cruentus* vocalizations within Reserva Biológica Bosque Nuboso Monteverde and Bosque Eterno de los Niños, in the provinces of Alajuela and Puntarenas, Costa Rica (A) = 10°18'17.568"N, 84°47'45.312"W; (B) = 10°18'13.068"N 84°47'43.476"W; (C) = 10°18'08.172"N 84°47'38.076"W; (D) = 10°18'01.296"N 84°47'08.880"W; and (E) = 10°19'26.256"N 84°45'56.268"W. Coordinates in Lat./Long., map datum WGS 84.

RESULTS

We found male *Pristimantis cruentus* calling from the upper surfaces of leaves and branches at heights ranging from 0.1 m to ~3 m. Calling males often were widely dispersed throughout the vegetation, but in three instances we observed two males calling in close proximity (< 1 m). When disturbed by investigators, either by moving vegetation or using excessive white light, the frogs ceased calling. Extended periods (in one instance > 50 min) of silence and no white light were necessary for frogs to resume calling.

The most common vocalizations recorded were single buzz-like notes ($n = 134$) (Table 1, Fig. 3); on occasion we heard multi-note buzz-like calls (three recorded), usually at the end of call bouts. Both single- and multi-note calls were of pulsed intensity, with a mean \pm standard deviation ($\bar{x} \pm SD$) of 13.8 (± 1.6) pulses/call for single-note, high quality calls ($n = 51$). The single-note calls were short, with a mean note length of 0.063 (± 0.009) s. Short

Table 1. Variation in morphometry and vocalizations of male *Pristimantis cruentus* recorded in Reserva Biológica Bosque Nuboso Monteverde and the Bosque Eterno de los Niños, in the provinces of Alajuela and Puntarenas, Costa Rica.

ID	Morphometric			Temporal					Spectral			
	SVL (mm)	Mass (g)	# Calls (n)	Bout Length (s) $\bar{x} \pm SD$	# Single Notes / Bout $\bar{x} \pm SD$	Call Length (s) $\bar{x} \pm SD$	Call Intervals (s) $\bar{x} \pm SD$	# Calls (n)	Low Frequency (Hz) $\bar{x} \pm SD$	High Frequency (Hz) $\bar{x} \pm SD$	Dominant Frequency (Hz) $\bar{x} \pm SD$	# Pulses $\bar{x} \pm SD$
1	17.00	0.90	44	49.4 (16.3)	5.0 (2.3)	0.065 (0.006)	10.4 (5.8)	29	1263.6 (138.2)	9306.8 (2050.1)	2188.5 (282.3)	14.3 (0.8)
2	14.82	1.00	15	40.3 (2.8)	6.5 (2.1)	0.061 (0.015)	7.3 (2.4)	-	-	-	-	-
3	-	-	17	36.1 (11.6)	4.7 (1.2)	0.057 (0.009)	10.9 (4.9)	-	-	-	-	-
4	10.70	0.70	5	-	-	0.074 (0.004)	9.9 (4.7)	5	1478.1 (129.3)	8167.9 (1047.4)	2001.3 (42.0)	15.4 (0.9)
5	-	-	16	37.7 (10.3)	5.3 (1.2)	0.066 (0.011)	8.3 (2.1)	-	-	-	-	-
6	14.60	0.25	1	-	-	0.071	-	1	1388.0	3807.2	1894.1	-
7	17.80	0.50	5	54.9	5.0	0.058 (0.005)	13.7 (4.2)	5	1502.5 (114.3)	6312.0 (1480.1)	2022.3 (37.7)	10.8 (0.8)
8	-	-	2	-	-	0.067	-	1	1482.9	4384.2	1792.2	-
9	17.48	0.45	19	42.4 (2.2)	5.7 (2.5)	0.064 (0.005)	12.1 (5.6)	8	1594.2 (166.8)	8869.4 (1764.2)	2128.3 (92.9)	12.2 (1.5)
10	18.30	0.50	6	17.8 (3.8)	-	0.060 (0.008)	10.6 (6.5)	2	1594.3 (114.7)	8674.1 (1031.8)	2148.7 (100.8)	12
11	-	-	4	-	-	0.050 (0.009)	14.4 (0.2)	-	-	-	-	-
	$\bar{x} \pm SD$	$\bar{x} \pm SD$	Total	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	Total	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$
	15.81 (2.67)	0.61 (0.27)	134	39.4 (16.3)	5.1 (1.9)	0.063 (0.009)	9.9 (5.0)	51	1353.1 (269.9)	8603.7 (2175.4)	2129.4 (233.4)	13.8 (1.6)

intervals between single note calls lasted a mean of $9.9 (\pm 5.0)$ s. Multi-note calls commonly were produced at the end of a call bout and consisted of a mean of $6.33 (\pm 2.08)$ notes/call, and were longer than single-note calls with a mean call length of $1.57 (\pm 0.69)$ s. These multi-note calls occurred in bouts lasting a mean of $39.4 (\pm 16.3)$ s. Pauses between bouts varied greatly and might have been influenced by weather and/or disturbance.

Calls had little frequency modulation, and the dominant frequency ranged from 1,722.7–3,540.9 Hz, with a mean dominant frequency of 2,129.4 (± 233.4) Hz. Low frequency was a mean of 1,353.1 (± 269.9) Hz, whereas the high frequency mean was 8,603.7 ($\pm 2,175.4$) Hz. We detected three harmonics in most single-note calls; nevertheless, one call exhibited four harmonics. The first harmonic was emphasized on nearly all calls, with only a single call emphasizing the second harmonic.

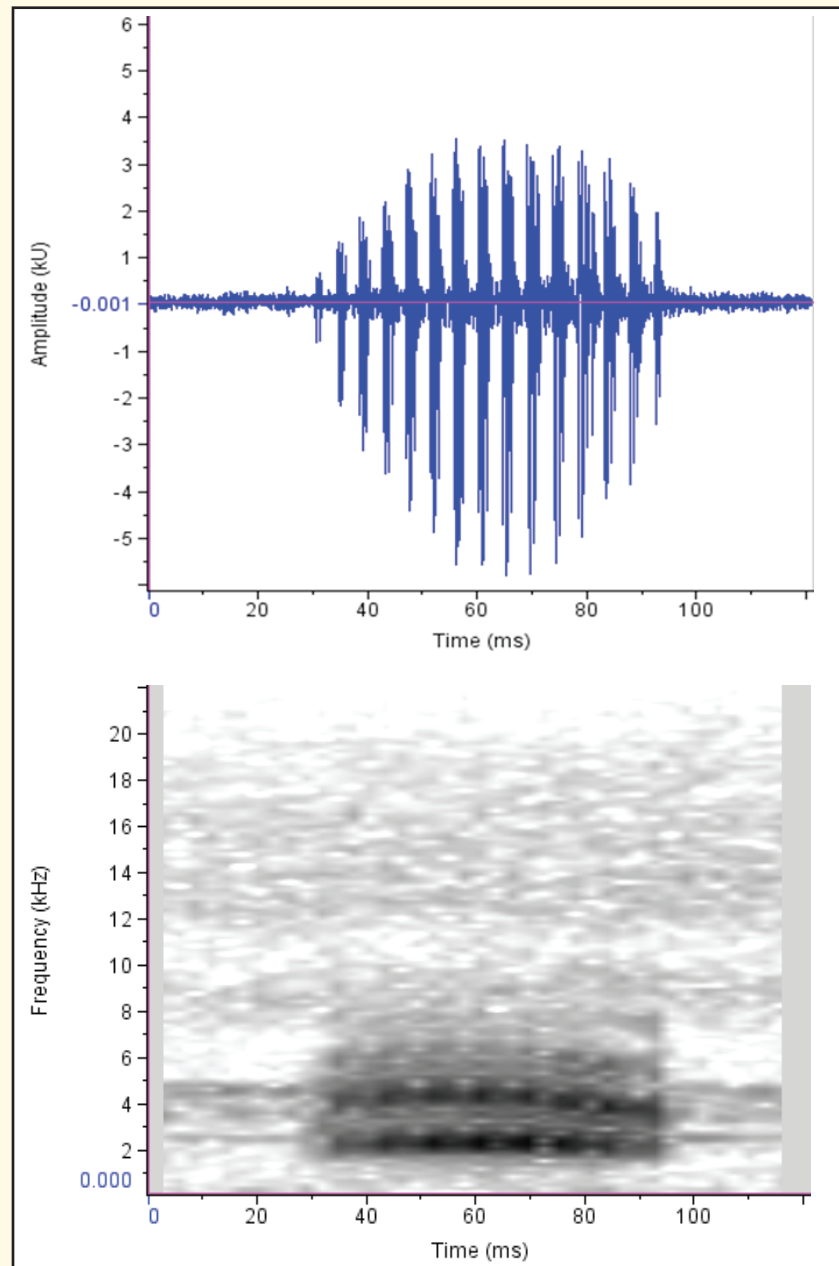


Fig. 3. Time waveform (top) and frequency spectrogram (bottom) of a typical call from male *Pristimantis cruentus* recorded *in situ* at Reserva Biológica Bosque Nuboso Monteverde, Provincia de Puntarenas, Costa Rica.

DISCUSSION

The vocalizations of *Pristimantis cruentus* appeared standardized, and relatively little variation was evident in call parameters among individuals. The calls of each individual also were consistent; for example, the first harmonic was emphasized in 28 of 29 calls in the call group of one male. Our observations suggest that the high frequency value was sensitive to the quality of the call recording, and perhaps resulted in an underestimate of the high frequency limit for this species. Within temporal call parameters, call length was highly standardized, whereas other parameters such as bout length and the interval between calls displayed more variability. Differences in temperature (Gayou, 1984) or other environmental factors, disturbance, or intraspecific interactions might have caused this variability.

In the *P. ridens* species series, formal descriptions of vocalizations only exist for *P. altae* and *P. ridens*. The advertisement call of *P. altae* differs greatly from that of *P. cruentus*, and has been described as a sharp knocking sound consisting of 2–4 notes, with a mode of three (Cossel et al., 2016). Although the mean call length differed between the two species, *P. cruentus* was 0.063 s and *P. altae* 0.35 s, the note length was comparable (*P. cruentus* 0.063 s and *P. altae* 0.051 s). Both calls were of relatively low frequency, with dominant frequencies of 2,129.4 Hz (*P. cruentus*) and 2,813.7 Hz (*P. altae*). Ibáñez et al. (1999) described the advertisement call of *P. ridens* as a short, high-pitched trill, and although these authors provided a qualitative description and a spectrogram, it lacked a detailed quantitative description. Based on the spectrogram provided, the dominant frequency appeared to be around 3–4 kHz, with multiple harmonics and note intervals of less than 0.1 s.

Morphological variation is present in the vocal apparatus of frogs in the *Pristimantis ridens* species series. Vocal slits and sacs are present in the two species of this series that have had their calls described (*P. altae* and *P. ridens*), as well as in the following species: *P. caryophyllaceus* (Savage, 2002), *P. colomai* (Lynch and Duellman, 1997), *P. jorgevelosai* (Lynch, 1994), and *P. moro* (Savage, 2002). In contrast, vocal slits and sacs are lacking in *P. adnus* (Crawford et al., 2010), *P. cremnobates* (Lynch and Duellman, 1980), *P. cruentus* (Savage, 2002), *P. lativallatus* (Lynch and Burrowes, 1990), *P. latidiscus* (Lynch et al., 1994), *P. museosus* (Ibáñez et al., 1994), *P. pardalis* (Savage, 2002), *P. rosadoi* (Flores, 1988), and *P. sanguineus* (Lynch, 1998). Our data demonstrate that species lacking these structures indeed might vocalize, and bioacoustical studies on other species lacking these vocal structures are warranted.

We presume that the vocalizations we described are advertisement calls. Additional work is necessary, however, to determine if there is a functional difference between single- and multi-note calls. Future work also may clarify whether other vocalizations are used for courtship, male spacing, territoriality, or reciprocal calling by females (Schlaepfer and Figueroa-Sandí, 1998). Additional data from across the range of *P. cruentus* are necessary, as calling behavior might vary among populations. If geographic variability were confirmed, this finding would corroborate taxonomic uncertainty (Savage, 1981) and possibly cryptic species (Crawford et al., 2013). Vocalizations in *P. cruentus* likely had not been noted because males appear timid during calling activity, and their vocalizations are relatively weak. In addition, their vocalizations might have gone unnoticed, as they sound similar to those of some insects. Variation in weather, and/or the lunar cycle (V. Acosta-Chaves, pers. comm.) could influence nightly calling activity in *P. cruentus*, and further work might elucidate these patterns. Our formal description of vocalizations in *P. cruentus* adds to the basic behavioral knowledge of this species, and can be used to provide a positive species identification in calling surveys. These data also can be utilized to facilitate future investigations on the taxonomic status of this species.

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