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Vocalizations of three species of *Plectrohyla* (Hylidae: Hylinae), with comments on natural history

WAGNER CHAVES-ACUÑA[1,2,*], JAVIER ZÚNIGA[3] & EDUARDO BOZA-OVIEDO[3]

[1]*División Herpetología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"-Consejo Nacional de Investigaciones Científicas y Técnicas, Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina*
wchaves512@gmail.com; https://orcid.org/0000-0002-6669-5701
[2]*Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina*
javierzuniga54@gmail.com; https://orcid.org/0009-0002-5250-8001
[3]*Proyecto Ixchel, Tegucigalpa, Honduras*
eeboza@gmail.com; https://orcid.org/0009-0002-7935-3732
[*]*Corresponding author*

Abstract

Vocalizations of many species in the genus *Plectrohyla* Brocchi, 1877 remain underexplored. This study provides a description of the vocalizations of *P. catracha* (Porras & Wilson, 1987) and *P. insolita* (McCranie *et al.*, 1993) and the re-description of the call of *P. ixil* Stuart, 1942. The advertisement call of *P. catracha* is a short pulsed call with ascending amplitude modulation, duration of 41 ± 8 ms (20–80 ms), dominant frequency of 2,761 ± 151 Hz (2,411–3,100 Hz), and pulse rate of 101 ± 13 pulses/s (67–150 pulses/s). The territorial call consists of a repertoire of short trills emitted in brief series of 3–6 calls, each with a duration of 15 ± 6 ms (4–20 ms), dominant frequency of 2,725 ± 410 Hz (2,067–3,100 Hz), and pulse rate of 158 ± 55 pulses/s (100–250 pulses/s). The series of territorial calls last 650 ± 110 ms (480–840 ms). *Plectrohyla catracha* vocalizes from vegetation and water surfaces, with peak activity during the rainy season. The advertisement call of *P. insolita* is a short, "click" sound and consists of a single, pulsatile call with descending amplitude modulation, duration of 60 ± 10 ms (50–70 ms), and dominant frequency of 1,894 ± 172 Hz (1,722–2,067 Hz). *Plectrohyla insolita* is less frequently encountered, calling from elevated positions over streams while also displaying egg-attendance of multiple clutches. *Plectrohyla ixil* produces a long, single, pulsatile call with ascending amplitude modulation, duration of 244 ± 28 ms (220–280 ms), and dominant frequency of 1,274 ± 83 Hz (1,125–1,312 Hz). We assessed the variation within the known acoustics of the clade composed by *Plectrohyla*, *Sarcohyla* Duellman *et al.*, 2016 and *Exerodonta* Brocchi, 1879, and discuss some patterns in call parameters among species of these genera and other Hylini.

Key words: Advertisement call, Hylini, Parental care, *Plectrohyla catracha*, *Plectrohyla insolita*, *Plectrohyla ixil*, Territorial call

Introduction

Plectrohyla Brocchi, 1877 is a genus from the tribe Hylini (Hylidae: Hylinae) that contains 21 highland species distributed from the eastern slope of the Isthmus of Tehuantepec in southern Mexico to central Nicaragua (Faivovich *et al*. 2018; Chaves-Acuña *et al*. 2024a; Señaris & Sunyer 2024; Frost 2025). The monophyly of the genus is supported by molecular evidence although a more comprehensive phylogenetic analysis is warranted due to the limited representation of species assessed thus far (Faivovich *et al*. 2005, 2018; Chaves-Acuña *et al.* 2024a).

Knowledge of the biology of *Plectrohyla* is limited, primarily because there have been few field observations conducted on these treefrogs (Duellman 1970, 2001; McCranie *et al.* 1987; Duellman & Campbell 1992). Nevertheless, the available information shows a wide array of peculiar reproductive behaviors, including underwater oviposition in sites such as rock crevices, cavities or roots (McCranie *et al.* 1987; Köhler 2011; Barrio-Amorós *et al.* 2016), subaerial egg clutches in vegetation overhanging water (Wilson *et al.* 1994), unpigmented eggs (Köhler 2011; Barrio-Amorós *et al.* 2016; González-Mollinedo & Mármol-Kattán 2020), site fidelity (González-Mollinedo

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& Mármol-Kattán 2020), egg-attendance (Wilson *et al.* 1994), male-male combats (Barrio-Amorós *et al.* 2016), and the emission of vocalizations in species that lack vocal sacs and vocal slits (Duellman 1970, 2001; McCranie *et al.* 1987; Barrio-Amorós *et al.* 2016; González-Mollinedo & Mármol-Kattán 2020).

To date, vocalizations have been reported for nine species of *Plectrohyla*, including *P. avia* Stuart, 1952, *P. calvata* McCranie *et al.,* 2017, *P. catracha* (Porras & Wilson, 1987), *P. guatemalensis* Brocchi, 1877, *P. insolita* (McCranie *et al.,* 1993), *P. ixil* Stuart, 1942, *P. matudai* Hartweg, 1941, *P. quecchi* Stuart, 1942, and *P. sagorum* Hartweg, 1941 (Stuart 1942; Taylor & Smith 1945; Duellman 1970, 2001; Porras & Wilson 1987; McCranie *et al.* 1987, 1993; Barrio-Amorós *et al.* 2016; McCranie *et al.* 2017; González-Mollinedo & Mármol-Kattán 2020). However, call descriptions with quantitative temporal and spectral parameters are only reported for *P. avia and P. ixil*, although with limited assessment of variation (Duellman 1970; Barrio-Amorós *et al.* 2016).

In this paper we describe the vocalizations of *Plectrohyla catracha* and *P. insolita*, and we report natural history notes based on recent observations. We also re-describe the vocalizations of *P. ixil.* We discuss our findings in the context of the bioacoustic knowledge of the clade including *Exerodonta*, *Plectrohyla*, and *Sarcohyla* (Faivovich *et al.* 2018; Chaves-Acuña *et al.* 2024a).

Materials and Methods

Study site and sampling. During March and October, 2015, September and October, 2016, and August, 2017, we conducted field surveys in the Las Trancas area, Opatoro, La Paz Department, southwestern Honduras (14°7'6.9"N, 87°52'24.8"W; 2,080–2,175 m; see Fig. 1A) to obtain audio recordings of *Plectrohyla catracha*. The site is located in the crest of the Montañas de la Sierra region, 45 km SW from the type locality of *P. catracha* at Zacate Blanco, Intibucá, Honduras (Porras & Wilson 1987). We surveyed a 100 m altitudinal transect around the edges of an artificial lake (ca. 145 m long, 45 m wide; ca. 400 m perimeter; ca. 3885 m^2 of surface; see Fig. 1B) and along puddles on the side of a dirt road, totaling more than 200 person hours of search effort.

During October, 2019 and June, 2022, we conducted fieldwork in a fast-moving stream (approximately 3–4 m wide) with scattered pools of shallow water (up to near 25 cm depth) located in the type locality of *Plectrohyla insolita* near the Texíguat Wildlife Refuge at Fortuna, western end of the Cordillera Nombre de Dios, northern Honduras (15°25'57.1"N, 87°18'34.6"W; 1,520–1,620 m; Fig. 1A). The site is located within canyons surrounded by patches of mature secondary forest and scattered paddocks, farmlands and rustic human settlements of isolated villages (Fig. 1C). We surveyed a transect of 400 m along the stream to record vocalizations of *P. insolita*, totaling 35 person hours of search effort.

We walked around each breeding site to quantify the number of calling males and species composition. We collected voucher specimens that were deposited in the Herpetofauna collection of the Centro Zamorano de Biodiversidad, Escuela Agrícola Panamericana Zamorano (CZB-H) and the Museo de Zoología, Universidad de Costa Rica (UCR). Air relative humidity and air temperature were measured using a digital hygrometer and a standard laboratory thermometer, respectively.

Study species. *Plectrohyla catracha* is a small size frog (SVL males = 22.6–28.7 mm, females = 28.6–32.1 mm) known only from cloud forests of southwestern Honduras between 1,800–2,160 masl along the continental divide of the mountain ranges Opalaca, Montecillos, and Montañas de la Sierra (McCranie & Wilson 2002; Frost 2025). The species is associated with lentic environments and slow-moving streams, where adults and juveniles are often found on low vegetation (up to near 200 cm above the ground) and epiphytic bromeliads (Porras & Wilson 1987; McCranie & Wilson 2002). Calling occurs from reeds, bromeliads, and around ponds and pools (Porras & Wilson 1987; Duellman 2001). Porras & Wilson (1987) and Duellman (2001) provided an onomatopoeic description of the call of *P. catracha* as a "muffled two-toned cackle" emitted repeatedly.

Plectrohyla insolita is a small leaf-dwelling treefrog (SVL males = 31.1–36 mm, females = 34.3–38 mm) known only from cloud forests of the Cordillera Nombre de Dios, in northern Honduras, between 1,520–1,690 masl (McCranie & Wilson 2002). The species has been recorded in few streams across primary and secondary forests in the Texíguat Wildlife Refuge and the Pico Bonito National Park at the east-central portion of this mountain range (Castañeda *et al.* 2019). Information is known on its reproductive biology, including daytime retreats, egg masses, oviposition sites, hatching tadpoles, metamorphs, male-only parental care, and vocal activity (McCranie *et al.* 1993; Wilson *et al.* 1994). Adults use leaves and bryophytes for oviposition and diurnal retreat purposes (Wilson *et al.*

1994; Castañeda & McCranie 2011). McCranie *et al.* (1993) provided an onomatopoeic description of the call of *P. insolita* as a "single, click-like note repeated at intervals of about 1 minute".

Plectrohyla ixil is a small size frog (SVL males = 41 mm, females = 46 mm) known from cloud forests on the Caribbean slopes of the Meseta Central in Chiapas, Mexico, and the highlands of northwestern Guatemala, at elevations of 1,175–1,690 masl (Duellman 1970; Frost 2025). The species is associated with slow-moving streams and rivulets (Duellman 1970). Adults are typically found on rocks within streams or on vegetation stems overhanging the water, where males call at night (Duellman 1970). Individuals have also been observed using the axils of elephant ear plants as daytime retreats (Smith & Brandon 1968; Duellman 1970). The call of *P. ixil*, as originally described by Duellman (1970), consists of a single note with durations ranging from 180 to 260 ms, a fundamental frequency of approximately 700 Hz, and a dominant frequency near 2,100 Hz (see plate 35, fig. 3 in Duellman 1970). While these parameters provide an initial characterization of the species' vocalizations, our analysis indicates discrepancies in the reported values and reveals greater variation across all acoustic traits, as detailed in the Results section (see also Table 1).

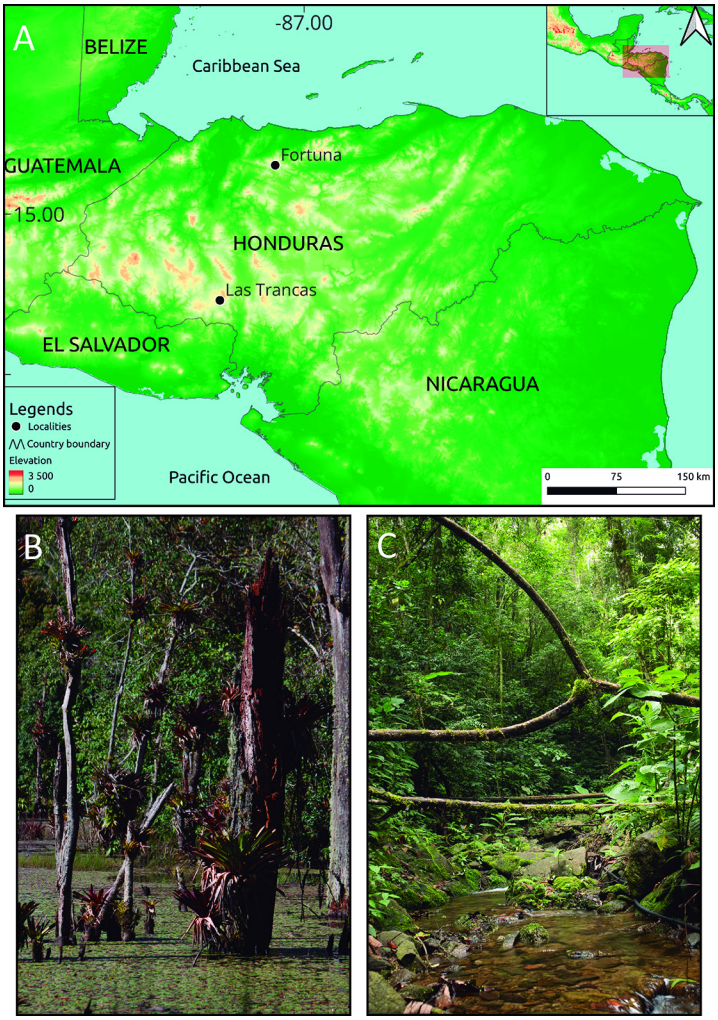

FIGURE 1. Study sites. (A): Map showing study sites where we recorded vocalizations of *Plectrohyla catracha* and *P. insolita* in Honduras. (B): Lentic environment in Las Trancas, southwestern Honduras. Habitat of *P. catracha*. (C): Lotic environment in Fortuna, northern Honduras. Habitat of *P. insolita*.

Vocalizations. To record the calls, we used a digital recorder Zoom H4n with built-in microphones positioned at about 1–2 m from the calling individuals of *Plectrohyla catracha* and about 3–4 m from the calling individuals of *P. insolita*. Call recordings were made in digital format at a sampling rate of 44.1 kHz and a 16-bit resolution. We obtained a sound recording of *P. ixil* (FZ 7461, voucher specimen KU 101027) taken on 24 February 1966, at 6.2 km S of Rayón Mescalapa, Chiapas, Mexico, approximately 120 km NW from the type locality of the species at Finca

TABLE 1. Acoustic parameters (call duration, number of pulses, pulse rate, minimum frequency, maximum frequency, and dominant frequency) of the vocalizations of species of *Exerodonta*, *Plectrohyla*, and *Sarcohyla* species with formal advertisement call descriptions: *Exerodonta bivocata*, *E. melanomma*, *E. sumichrasti*, *P. avia*, *P. catracha*, *P. insolita*, *P. ixil*, *S. cyclada*, *S. hapsa*, *S. hazelae, S. thorectes*, and *S. toyota*. Call vouchers correspond to Fonoteca Zoologica (FZ). Values reported as fundamental frequency in the literature have been included under the minimum frequency category. N/A indicates recordings not available in public repositories, while N/P denotes information not provided in the literature. Number of pulses and pulse rate values are reported only for species with fully pulsed calls; species with partially pulsed or non-pulsed call structures were excluded only from these two columns.

Species	Call voucher(s)	Source	Call duration (ms)	Pulses	Pulse rate (pulses/s)	Minimum Freq (Hz)	Maximum Freq (Hz)	Dominant Freq (Hz)
E. bivocata[1,2]	N/P	Duellman (1970)	70 (4–100)	N/P	240 (220–260)	137 (130–144)	N/P	2,463 (2,456–2,470)
E. bivocata[1,3]	N/P	Duellman (1970)	530	N/P	280	152	N/P	756
E. melanomma[2,4]	N/P	Duellman (1970)	7–8	N/P	300	190 (163–217)	N/P	2,336 (2,286–2,387)
E. melanomma[2,3]	N/P	Duellman (1970)	310–370	N/P	220	139	N/P	2,112
E. sumichrasti	N/P	Duellman (1970)	198 (180–210)	N/P	71 (70–75)	94 (79–115)	N/P	1,830–3,220
P. avia[5]	N/A	Barrio-Amorós *et al.* (2016)	280	7	N/P	N/P	N/P	561.5 (541–572)
P. avia[5]	N/A	Barrio-Amorós *et al.* (2016)	405	9	N/P	N/P	N/P	349.5 (348–353)
P. catracha	FZ 14977–8	This work	41 ± 9 (20–80)	4 ± 1 (2–8)	101 ± 13 (67–150)	1,792 ± 104 (1,535–2,117)	3,525 ± 141 (3,225–3,838)	2,768 ± 145 (2,411–3,100)
P. catracha[6]	FZ 14979–80	This work	15 ± 6 (4–20)	2 ± 1 (1–3)	158 ± 55 (100–250)	1,663 ± 114 (1,360–1,820)	3,693 ± 235 (3,324–4,082)	2,725 ± 410 (2,067–3,100)
P. insolita	FZ 14981–3	This work	60 ± 10 (50–70)	N/P	N/P	1,291 ± 37 (1,258–1,332)	2,265 ± 435 (1,763–2,541)	1,894 ± 172 (1,722–2,067)
P. ixil	N/P	Duellman (1970)	180–260	N/P	200	700	N/P	2,100
P. ixil	FZ 7461	This work	213–281	N/P	N/P	562–937	1,500–1,875	1,125–1,312
S. cyclada[7]	N/P	Duellman (1970)	220-280	N/P	80	74	N/P	2072
S. hapsa	N/A	Campbell *et al.* (2018)	120–250	2–3	12–16	473–559	N/P	947–1,119
S. hazelae	N/P	Duellman (1970)	50–70	N/P	120–140	N/P	N/P	1,800–1,850
S. thorectes	N/P	Duellman (1970)	210 (170–250)	N/P	67 (60–70)	126 (122–134)	N/P	2,062 (2,010–2,108)
S. toyota	N/A	Grünwald *et al.* (2019)	17–20	2–3	N/P	N/P	N/P	4,750

[1] The call of *Exerodonta bivocata* was described as that of *Hyla melanomma bivocata.*

[2] Described as short calls emitted in series.

[3] Described as long, single calls.

[4] The call of *Exerodonta melanomma* was described as that of *Hyla melanomma melanomma.*

[5] Courtship, subaquatic calls.

[6] Territorial call.

[7] The call of *Sarcohyla cyclada* was described as that of *Hyla arborescandens* (see Duellman 2001).

San Francisco, 25 km N of El Nebaj, El Quiché, northwestern Guatemala (Stuart 1942). According to call metadata, the calls of *P. ixil* were recorded at a distance of 1.5 m from the calling individual, which was inside a plastic bag.

We measured spectral and temporal parameters using the software Raven Pro 1.6.1 (Center for Conservation Bioacoustics 2019) with the following settings: window type Hann, window size of 512 samples, 3 dB filter bandwidth of 124 Hz, 50% overlap, hop size of 256 samples, DFT size of 512 samples, and grid spacing at 86.1 Hz. We generated sound figures with the seewave package v. 1.7.6 (Sueur *et al.* 2008) in R software 4.0.2 (R Core Team 2020) using the following settings: window = Hanning, FFT overlap = 90%, FFT size = 512 points. Spectrograms were produced with a relative amplitude color scale of 30 dB (red = maximum amplitude).

Calls were described based on the following the "call centered approach" suggested by Köhler *et al.* (2017). Oscillograms were used to manually count the number of pulses, and to calculate the call duration (s) and the intercall interval (s) using the "delta time" function of Raven. Spectrograms were used to obtain dominant frequency (Hz), minimum frequency (Hz), and maximum frequency (Hz) values using the "peak frequency", "low frequency", and "high frequency" functions, respectively. We estimated the pulse rate as the number of pulses divided by the call duration. We also described the amplitude modulation of calls considering the shape of the call envelope in accordance to the position of amplitude peaks throughout the call duration. We deposited digital vouchers of audio files in the Fonoteca Zoológica of Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, Spain (FZ 14977–83).

Comparisons with other species. For comparisons with advertisement calls of other species, we obtained information from the literature (Duellman 1970; Barrio-Amorós *et al*. 2016; Campbell *et al*. 2018; Grünwald *et al*. 2019). In addition, we analyzed audio recordings obtained from the acoustic repository of the Macaulay Library (ML) at the Cornell Lab of Ornithology, New York (http://www.macaulaylibrary.org/), which include part of the original recordings used by Duellman (1970) to describe the calls of several species. These recordings correspond to *Exerodonta bivocata* (Duellman & Hoyt, 1961; audio recordings ML 193770–2), *E. melanomma* (Taylor, 1940; ML 193978–9), *E. sumichrasti* (Brocchi, 1879; ML 193987–9), *Sarcohyla cyclada* (Campbell & Duellman, 2000; ML 193807–10), *S. hazelae* (Taylor, 1940; ML 193985–6), and *S. thorectes* (Adler, 1965; ML 193982–4), which were originally obtained using Magnemite or Uher portable tape recorders.

Results

Advertisement call of **Plectrohyla catracha** (Fig. 2A–D)**.** We examined a total of 120 calls from four individuals of *Plectrohyla catracha* in a time lapse of 15 minutes recorded at 15ºC and 100% of relative humidity (one calling male collected, CZB-H 023). The vocalization of *P. catracha* is a short, pulsed call composed of 4 ± 1 pulses (2–8 pulses). The call exhibits an ascending amplitude modulation with the peak occurring towards the end of its duration, depicting a triangular wave form (pointed left; see Fig. 2D). Call duration is about 41 ± 9 ms (20–80 ms) and the intercall interval is 13 ± 3 s (10–19 s). The pulse rate is 101 ± 13 pulses/s (67–150 pulses/s). Calls commonly exhibit a slightly ascending frequency modulation (see Fig. 2B). The minimum frequency is 1,792 ± 104 Hz (1,535–2,117 Hz), the maximum frequency is 3,525 ± 141 Hz (3,225–3,838 Hz), and the dominant frequency is 2,768 ± 145 Hz (2,411–3,100 Hz).

Territorial call of **Plectrohyla catracha** (Fig. 2E–H)**.** Territorial calls were recorded when males called concurrently, sometimes overlapping in the timing of calls or alternating with calls from other individuals, including advertisement calls, which served as indicators of aggressive interactions. We examined a total of 46 calls from two individuals of *Plectrohyla catracha* (including CZB-H 023) in a time lapse of 5 minutes recorded at 15ºC and 100% of relative humidity. The territorial call consists of a repertoire of short trills emitted in brief series of 3 to 6 calls. These calls vary in structure, duration, pulse rate, and amplitude modulation compared to the advertisement call (see Discussion below). Territorial calls may exhibit amplitude modulation, with the first and/or second call generally displaying an ascending pattern, where the peak amplitude occurs toward the end of the call duration, forming a left-pointed triangular shape similar to that of the advertisement call. In contrast, subsequent calls typically show a descending pattern, with the peak amplitude occurring at the beginning of the call duration, depicting a right-pointed triangular shape (see Fig. 2H). In some cases, calls lack amplitude modulation (see Fig. 2G). The first call of the series is about 20 ms in duration and consists of 2 to 3 pulses, with a pulse rate of 118 ± 25 pulses/s (100–150 pulses/s). It is usually separated from the second portion of the territorial call by an intercall interval of 238 ± 6 ms

(150–340 ms). From the second call onward, call duration is 15 ± 6 ms (4–20 ms), with each call composed of 2 ± 1 pulses (1–3 pulses), a pulse rate varying from 158 ± 55 pulses/s (100–250 pulses/s), and an intercall interval within the series as of the second call of 100 ± 26 ms (7–170 ms). The series of territorial calls last 650 ± 110 ms (480–840 ms). Calls typically exhibit slightly ascending or descending frequency modulation, but in some cases, calls lack frequency modulation (see Fig. 2E). The minimum frequency is 1,663 ± 114 Hz (1,360–1,820 Hz) and the maximum frequency is 3,693 ± 235 Hz (3,324–4,082 Hz). The dominant frequency is 2,725 ± 410 Hz (2,067–3,100 Hz).

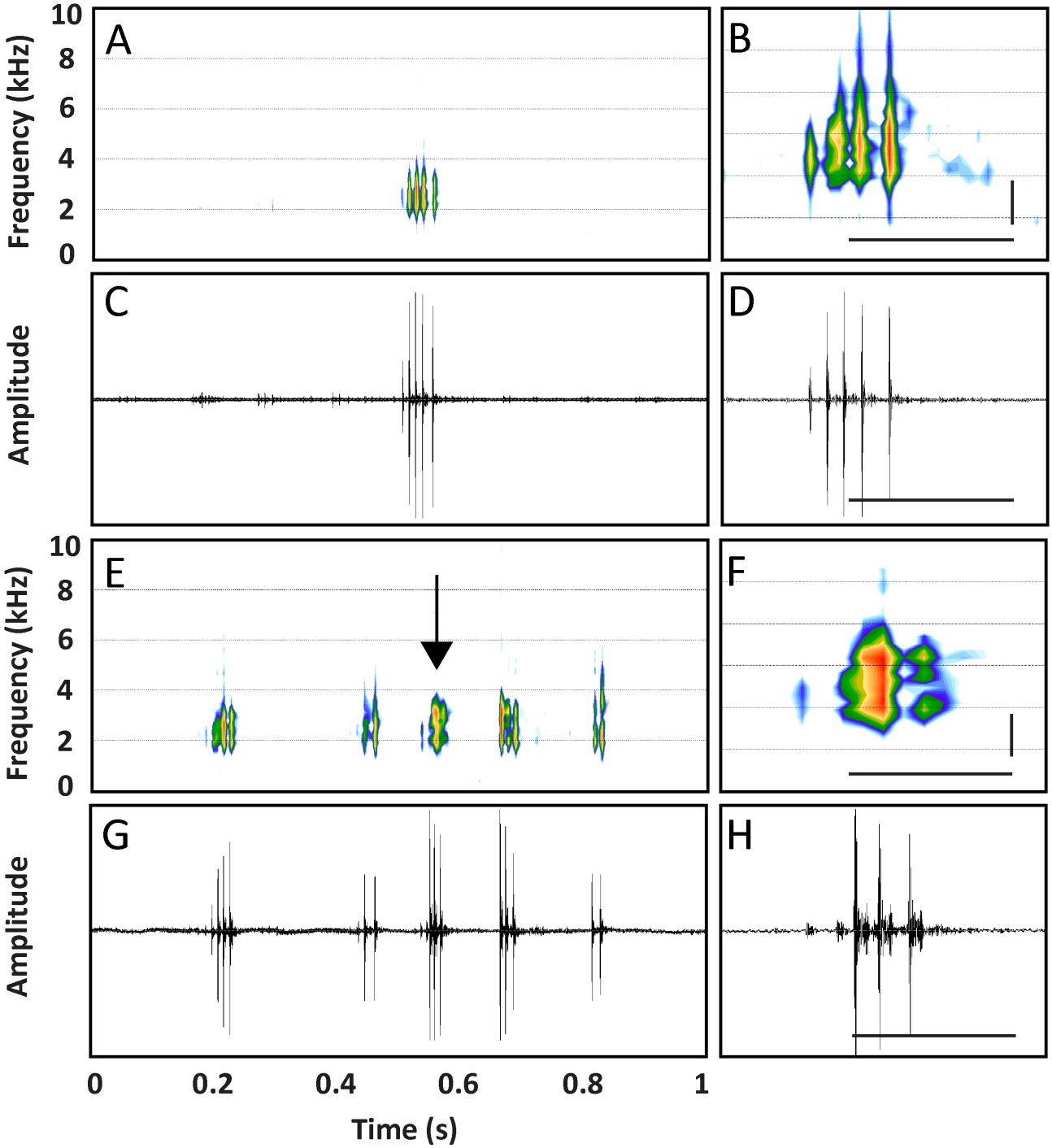

FIGURE 2. Spectrograms (above) and oscillograms (below) of vocalizations of *Plectrohyla catracha* obtained from a male (CZB-H 023) at Las Trancas, Opatoro, La Paz Department, southwestern Honduras. (A–B, E–F): Spectrograms. (C–D, G–H): Oscillograms. (A–D): Advertisement call (FZ 14977). (E–H): Territorial call (FZ 14979). (F, H): Detail of the first vocalization emitted in the territorial call. Scale bar = 100 ms (horizontal), 1 kHz (vertical).

***Natural History of* Plectrohyla catracha** (Fig. 3A–C)**.** The species is common at the study site and was usually detected in densities of tens to hundreds of individuals per night during our study. We found most of them perched on vegetation (leaves or stems) at 40–285 cm above the ground and 0–1.8 m from the nearest water body, but some individuals were found on the ground or floating on the water surface. An adult female was observed during the day in an epiphytic bromeliad, at 1.80 m above the ground and approximately 400 m from the nearest water body. We registered amplectant pairs floating on the water of a pool of a spring used by people to obtain water. On one occasion, we followed one pair for more than five hours but oviposition did not occur (Fig. 3B). For most part of our observation, the pair was partially submerged and floating on water; however, after three hours, it moved to land and stayed there for several minutes before returning back to the water. We noted the highest breeding activity of the species during the rainiest periods (from May to June and September to October). In the Las Trancas area, air temperatures ranged from 11–16ºC during nocturnal surveys.

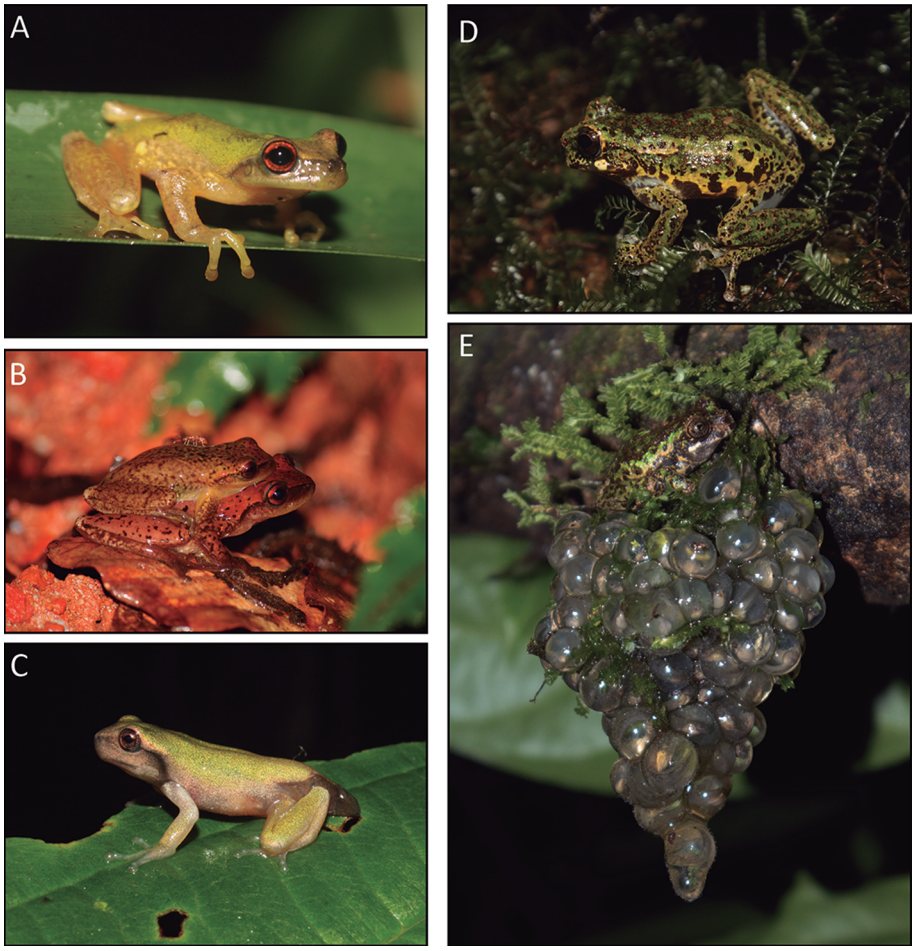

FIGURE 3. Life photographs of *Plectrohyla catracha* from Las Trancas, Opatoro, La Paz Department, southwestern Honduras, and *P. insolita* from the Texíguat Wildlife Refuge at Fortuna, western end of the Cordillera Nombre de Dios, northern Honduras. (A): Adult male (not collected). (B): Amplexus on land (not collected). (C): Metamorph (not collected). (D): Adult male (UCR 23564). (E): Adult male guarding two egg clutches (CZB-H 022).

***Advertisement call of* Plectrohyla insolita** (Fig. 4A–D)**.** We examined a total of three calls from three individuals of *P. insolita* recorded in a time lapse of 125 minutes at air temperature between 15–19.3ºC and 88–100% of relative humidity. The vocalization of *Plectrohyla insolita* is a short "click" call, consisting of 5 to 6 pulses during the first half of its duration, followed by a pulsatile structure in the second half (see Fig. 4D). The call is amplitude modulated with the peak occurring at the beginning of the call duration, depicting a triangular wave form (pointed right; see Fig. 4D). Call duration is 60 ± 10 ms (50–70 ms). Although we obtained only three calls during over two hours of recordings, subsequent auditory surveys of unrecorded individuals indicated that males call every 10–35 minutes.

Calls exhibit no frequency modulation (Fig. 4B). The minimum frequency of the call is 1,291 ± 37 Hz (1,258–1,332 Hz), the maximum frequency is 2,265 ± 435 Hz (1,763–2,541 Hz), and the dominant frequency is 1,894 ± 172 Hz (1,722 to 2,067 Hz).

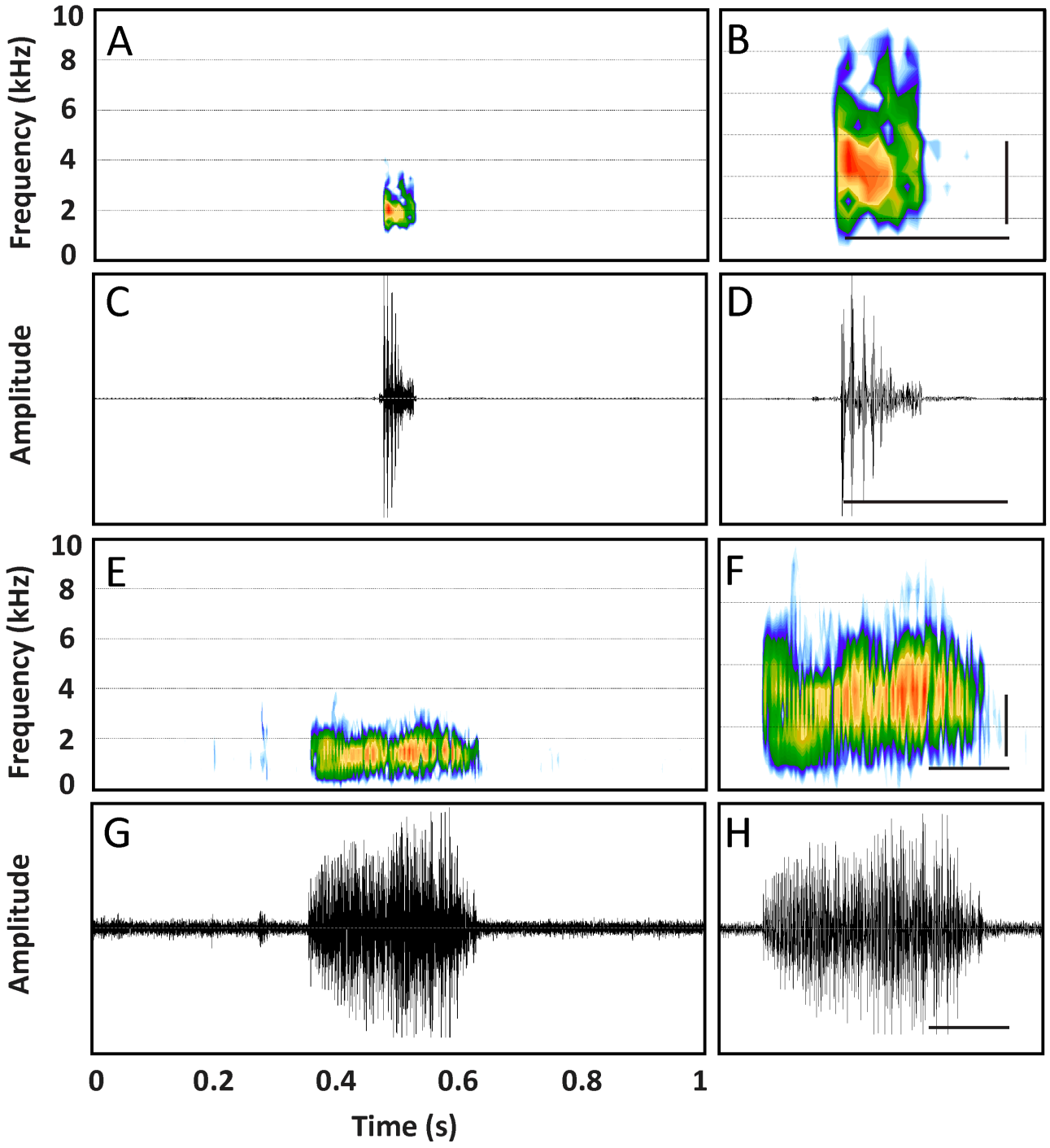

FIGURE 4. Spectrograms (above) and oscillograms (below) of vocalizations of *Plectrohyla insolita* (UCR 23564) from the Texíguat Wildlife Refuge at Fortuna, western end of the Cordillera Nombre de Dios, northern Honduras, and *P. ixil* (KU 101027) from 6.2 km south of Rayón Mescalapa, Chiapas, southern Mexico. (A–B, E–F): Spectrograms. (C–D, G–H): Oscillograms. (A–D): Advertisement call of *P. insolita* (FZ 14981). (E–H): Advertisement call of *P. ixil* (FZ 7461). Scale bar = 100 ms (horizontal), 1 kHz (vertical).

Natural History of **Plectrohyla insolita** (Fig. 3D–E)**.** The species is uncommon and calls sporadically (e.g. 1–2 individuals registered per night). During October 2019, we detected four calling males of *Plectrohyla insolita* between 20:43 and 01:00 h. One adult male (UCR 23564; Fig. 3D) was recorded calling from a bryophyte-covered branch at 2.25 m above the stream, while three uncollected individuals (not recorded) were observed calling at heights of approximately 5 m above the stream. During June 2022, we registered two calling males approximately at 21:35 h. One of the individuals (CZB-H 022) was observed on top of two joint egg masses with a total of 80–100 embryos on different developmental stages (Gosner stages = 22–25; CZB-H 022) positioned at approximately 2.5 m above the stream (Fig. 5B). The egg masses were laid on a bryophyte-covered branch of a fallen tree that crossed the stream bed from side to side. Embryos on the earlier stage of development in the clutch (stage 22) were located in the upper part of the egg mass, with the male on top of them, whereas more developed embryos (stage 25) were at the bottom part of the egg mass. The guarding male was calling at the beginning of our observations but it stopped calling due to our presence. The frog remained on top of the egg mass, changing its orientation to 90° in the vertical plane and to 60° in the horizontal plane. During nighttime surveys in October, 2019, air temperature was 15ºC and the relative humidity was 100%. During nocturnal surveys in June, 2022, air temperature ranged between 15–19.3ºC and the relative humidity varied between 88–100%.

Advertisement call of **Plectrohyla ixil** (Fig. 4E–H). We examined a total of five calls from one individual of *Plectrohyla ixil* recorded in a time lapse of about 1 min at air temperature of 15ºC. The vocalization of *P. ixil* is a long, single call with a fully pulsatile structure. The call is amplitude-modulated, with one or two major peaks occurring throughout the call duration, showing an irregular or asymmetric modulation pattern. Call duration is 244 ± 28 ms (220–280 ms). The intercall interval is 11 ± 5 s (5–18 s). Calls have no frequency modulation. The minimum frequency of the call is 692 ± 139 Hz (496–832 Hz), the maximum frequency is 1,756 ± 208 Hz (1,463–1,987 Hz), and the dominant frequency is 1,274 ± 83 Hz (1,125–1,312 Hz).

Discussion

Vocalizations in *Plectrohyla* remain poorly documented. Of the 21 species of the genus, only nine have known advertisement calls, with quantitative call descriptions limited to only four species: *P. avia* (Barrio-Amorós *et al.* 2016), *P. catracha* (this study), *P. insolita* (this study), and *P. ixil* (Duellman 1970; this study; see Table 1). Earlier studies offer anecdotal insights into the vocal behavior of other species in the genus, but often lack detailed quantitative parameters. Stuart (1942) reported that *P. quecchi* calls. Taylor & Smith (1945) described the call of *P. matudai* as a single note that sounds like "two pebbles struck together underwater" repeated every two minutes. These authors also described the call of *P. sagorum* as a "slightly drawn out, coarsely trilled, nasal quaaaack", with daytime calling emitted from bromeliads (Taylor & Smith 1945; see also Barrio-Amorós *et al.* 2016). McCranie *et al.* (1987) reported the call of *P. calvata* emitted from a bromeliad during the day, but with no reference to its call parameters. *Plectrohyla guatemalensis* is another species that has been reported to call during the day (McCranie *et al.* 1987; González-Mollinedo & Mármol-Kattán 2020). Its call was described as a low-pitched grunt repeated at intervals of about 2 minutes (McCranie *et al.* 1987), often in groups of males located under or within crevices (González-Mollinedo & Mármol-Kattán 2020). The calling repertoire of *P. avia*, recently described by Barrio-Amorós *et al.* (2016), includes two distinct subaquatic calls recorded during amplexus (see Table 1). This species also emits vocalizations from within holes or crevices (Barrio-Amorós *et al*. 2016), though differences between underwater and terrestrial calls remain unspecified.

Considering the known advertisement calls of species of *Plectrohyla*, there is little variation with respect to spectral, temporal, and structural values, with vocalizations consisting of short pulsed calls typically emitted at low dominant frequencies, with call durations ranging from 20 to 281 ms and frequencies from 348 to 3,100 Hz (see Table 1). This pattern is similar to that of advertisement calls known for species in *Exerodonta* and *Sarcohyla*, its more closely related taxa (Faivovich *et al*. 2018; Chaves-Acuña *et al*. 2024a; see Table 1). An exception is *S. toyota* Grünwald *et al*., 2019, with an advertisement call reported to occur at a significantly higher dominant frequency of approximately 4,750 Hz (Grünwald *et al*. 2019), deviating from the generally lower frequencies below 3,500 Hz observed in other species of this clade (see Table 1). Alternatively, short pulsed calls emitted at low frequencies are also noted in many other genera of Hylini, including species with known advertisement calls in most genera of the tribe (e.g. *Acris* Duméril & Bibron, 1841; *Charadrahyla* Faivovich *et al.,* 2005; *Duellmanohyla* Campbell

& Smith, 1992; *Ecnomiohyla* Faivovich *et al.,* 2005; *Exerodonta*; *Hyla* Laurenti, 1768; *Isthmohyla* Faivovich *et al.,* 2005; *Pseudacris* Fitzinger, 1843; *Ptychohyla* Taylor, 1944; *Quilticohyla* Faivovich *et al.,* 2018; *Rheohyla* Duellman *et al.,* 2016; *Smilisca* Cope, 1865; *Tlalocohyla* Faivovich *et al.,* 2005; and *Triprion* Cope, 1866). The pulse-structured vocal repertoire of *Plectrohyla* includes calls with clearly distinct, non-concatenated pulses (e.g. *P. avia*, *P. catracha*); calls with a pulsatile structure composed of continuous, concatenated pulses (e.g. *P. ixil*); and calls that are partially pulsed and partially pulsatile (e.g. *P. insolita*). Similar vocalizations are observed in species of *Exerodonta* and *Sarcohyla* with known advertisement calls (Duellman 1970, 2001). For instance, *S. cyclada*, *S. hapsa* Campbell *et al*., 2018, *S. thorectes*, and *S. toyota* produce calls with clearly distinct, non-concatenated pulses; *Exerodonta bivocata*, *E. melanomma*, and *E. sumichrasti* emit calls with a fully pulsatile structure composed of continuous, concatenated pulses; and *S. hazelae* produces calls that are partially pulsed and partially pulsatile. Calls with distinct pulses generally exhibit ascending or descending amplitude and frequency modulation; fully pulsatile calls typically show amplitude modulation peaking in the middle of the call but lack frequency modulation; and calls that are partially pulsed and pulsatile commonly exhibit amplitude modulation peaking at the start of the call with slightly descending frequency modulation.

While general similarities exist in the calls of *Exerodonta*, *Plectrohyla*, and *Sarcohyla*, their vocalization show variation in structure and emission across taxa. For instance, *E. melanomma*, *E. sumichrasti*, *Sarcohyla cyclada*, and *S. hazelae* typically emit vocalizations in series, with each series consisting of repeated, uniform single vocalizations (in terms of call duration, dominant frequency, and pulse rate) at short and consistent intercall intervals (see Duellman 1970). In contrast, *Plectrohyla avia*, *P. catracha*, *P. insolita*, *P. ixil*, *S. hapsa*, *S. thorectes*, and *S. toyota* produce single calls (Duellman 1970; Barrio-Amorós *et al*. 2016; Campbell *et al*. 2018; Grünwald *et al*., 2019; this study). *Exerodonta sumichrasti* emits two-note calls (Duellman 1970). Intraspecific call variation has been observed in *E. bivocata* and *E. melanomma,* which can emit either short calls in series or single long calls (Duellman 1970; see Table 1). Similarly, in *P. catracha,* single calls function as advertisement calls, whereas calls in series serve as territorial calls (this study; see Table 1).

Plectrohyla catracha defends territories used both as calling and breeding sites, a behavior seldom documented among Hylini (Luría-Manzano *et al*. 2023). Territorial calls are generally similar to advertisement calls in terms of temporal properties, general structure, and frequency (see Köhler *et al*. 2017); however, consistent differences in their acoustic properties can be observed between these two types of calls in *P. catracha*. The territorial call is produced in series of multiple calls (compared to single calls in the advertisement call), and although some parameter ranges overlap, territorial calls generally exhibit shorter durations (4–20 ms vs. 20–80 ms in advertisement calls), fewer pulses per call (1–3 vs. 2–8), and a higher pulse rate (100–250 pulses/s vs. 67–150 pulses/s). Even though the upper values of advertisement call parameters overlap with the lower values of territorial call parameters, their distributions remain largely distinct, with territorial calls predominantly occupying the higher end of the overall range. Additionally, territorial calls exhibit descending amplitude modulation from the second call onward, whereas advertisement calls show ascending modulation.

Plectrohyla insolita is one of the few hylids known for male-only egg attendance (see Chaves-Acuña *et al*. 2024a), a behavior that could significantly impact its calling rate. The limited documentation of advertisement calls observed in this study might be influenced by the male's investment in egg attendance, which is consistent with findings in other anuran species exhibiting similar parental care strategies (e.g. Centrolenidae; see Delia *et al*. 2020), where the dual demands of egg guarding and calling often result in a reduced call rate (Valencia-Aguilar *et al*. 2020; Chaves-Acuña *et al*. 2024b). Despite the energetic demands, our observations indicate that *P. insolita* continues to vocalize while attending multiple egg clutches, which are closely packed and often appear to accumulate atop one another. This ongoing calling behavior likely plays a key role in their reproductive success as it could signal both territorial control and paternal effort (Valencia-Aguilar *et al*. 2020). Future studies should further explore how vocalizations interact with parental care strategies to influence reproductive success in *P. insolita*.

Acoustic communication in Mesoamerican Hylini remains poorly documented, emphasizing the need for further research in this area. Such studies are essential for improving taxonomic assessments and developing more effective conservation strategies.

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References

Barrio-Amorós, C.L., Grünwald, C.I., Franz-Chávez, H., Mendoza, A.M. & La Forest, B.T. (2016) Notes on natural history and call description of the Critically Endangered *Plectrohyla avia* (Anura: Hylidae) from Chiapas, Mexico. *Amphibian & Reptile Conservation*, 10, 11–17.

Campbell, J.A., Brodie, E.D., Caviedes-Solis, I.W., Nieto-Montes de Oca, A., Luja, V.H., Flores-Villela, O., García-Vázquez, U.O., Sarker, G.C., Wostl, E. & Smith, E.N. (2018) Systematics of the frogs allocated to *Sarcohyla bistincta* sensu lato (Cope, 1877), with description of a new species from Western Mexico. *Zootaxa*, 4422 (3), 366–384. https://doi.org/10.11646/zootaxa.4422.3.3

Castañeda, F., Cruz, G. & Wilson, L.D. (2019) Conservation Needs Assessment for *Isthmohyla insolita*, Honduras/AArk/ASG Assessment Workshop. Available from: https://www.conservationneeds.org/assessment/4696 (accessed 14 May 2024)

Center for Conservation Bioacoustics (2019) Raven pro: interactive sound analysis software. Version 1.6.1. Available from: https://www.ravensoundsoftware.com (accessed 24 May 2025)

Chaves-Acuña, W., Boza-Oviedo, E., Zúniga, J., Chaves, G., Bolaños, F., Vásquez-Almazán, C. & Faivovich, J. (2024a) Phylogenetic relationships of two poorly-known Honduran treefrogs (Hylidae: Hylinae: Hylini). *American Museum Novitates*, 2024, 1–17. https://doi.org/10.1206/4016.1

Chaves-Acuña, W., Moreno, E., Salazar-Zúñiga, J.A. & Bolaños, F. (2024b) Acoustics associated with paternal care and territorial behaviors in a glassfrog with prolonged egg-attendance. *South American Journal of Herpetology*, 30, 40–51. https://doi.org/10.2994/SAJH-D-22-00009.1

Delia, J., Bravo-Valencia, L. & Warkentin, K.M. (2020) The evolution of extended parental care in glassfrogs: do egg-clutch phenotypes mediate coevolution between the sexes? *Ecological Monographs*, 90, e01411. https://doi.org/10.1002/ecm.1411

Duellman, W.E. (1970) *Hylid Frogs of Middle America. Monograph of the Museum of Natural History. No. 1*. University of Kansas, Lawrence, Kansas, 753 pp. https://doi.org/10.5962/bhl.title.2835

Duellman, W.E. (2001) *Hylid Frogs of Middle America. Vols. 1 & 2*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, 1158 pp.

Duellman, W.E. & Campbell, J.A. (1992) Hylid frogs of the genus *Plectrohyla*: Systematics and phylogenetic relationships. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 181, 1–32.

Escalona-Sulbarán, M.D., Simões, P.I., Gonzalez-Voyer, A. & Castroviejo-Fisher, S. (2018) Neotropical frogs and mating songs: The evolution of advertisement calls in glassfrogs. *Journal of Evolutionary Biology*, 32, 163–176. https://doi.org/10.1111/jeb.13406

Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A. & Wheeler, W.C. (2005) Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, 294, 1–240. https://doi.org/10.1206/0003-0090(2005)294[0001:SROTFF]2.0.CO;2

Faivovich, J., Pereyra, M.O., Luna, M.C., Hertz, A., Blotto, B., Vásquez-Almazán, C.R., McCranie, J.R., Sanchez-Ramirez, D., Baêta, D., Araujo-Vieira, K., Köhler, G., Kubicki, B., Campbell, J.A., Frost, D.R. & Haddad, C.F.B. (2018) The monophyly and relationships of several genera of Hylinae (Anura: Hylidae: Hylinae) with comments on recent taxonomic changes in hylids. *South American Journal of Herpetology*, 13, 1–32.

Frost, D.R. (2025) *Amphibian Species of the World: an online reference. Version 6.2*. American Museum of Natural History, New York, New York. Available from: https://amphibiansoftheworld.amnh.org/index.php (accessed 15 May 2025)

González-Mollinedo, S. & Mármol-Kattán, A. (2020) The underground sex life of the Guatemalan Spike-Thumb Frog (*Plectrohyla guatemalensis*). *Neotropical Biology and Conservation*, 15, 551–559.

https://doi.org/10.3897/neotropical.15.e57142
Gosner, K.L. (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.
Grünwald, C.I., Franz-Chávez, H., Morales-Flores, K.I., Ahumada-Carrillo, I.T. & Jones, J.M. (2019) A rare new treefrog of the genus *Sarcohyla* (Anura: Hylidae) from Guerrero, Mexico. *Zootaxa*, 4712 (3), 345–364.
https://doi.org/10.11646/zootaxa.4712.3.2
Köhler, G. (2011) *Amphibians of Central America*. Herpeton Verlag, Offenbach, 379 pp.
Köhler, J., Jansen, M., Rodríguez, A., Kok, P.J.R., Toledo, L.F., Emmrich, M., Glaw, F., Haddad, C.F.B., Rödel, M.O. & Vences, M. (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. *Zootaxa*, 4251 (1), 1–124.
https://doi.org/10.11646/zootaxa.4251.1.1
Luría-Manzano, R., Pinheiro, P.D.P., Kohlsdorf, T., Haddad, C.F.B. & Martins, M. (2023) Evolution in territoriality in Hylinae treefrogs: ecological and morphological correlates and lineage diversification. *Journal of Evolutionary Biology*, 2023, 1–12.
https://doi.org/10.1111/jeb.14189
McCranie, J.R. & Wilson, L.D. (2002) *The amphibians of Honduras*. Society for the Study of Amphibians and Reptiles, Ithaca, New York, x + 625 pp.
McCranie, J.R., Wilson, L.D. & Williams, K.L. (1987) *Plectrohyla guatemalensis*. Reproduction. *Herpetological Review*, 18, 72.
McCranie, J.R., Wilson, L.D. & Williams, K.L. (1993) New species of tree frog of the genus *Hyla* (Anura: Hylidae) from northern Honduras. *Copeia*, 1993, 1057–1062.
https://doi.org/10.2307/1447084
McCranie, J.R. (2017) Specific status of the Montaña de Celaque Honduran frogs previously referred to as *Plectrohyla guatemalensis* (Anura: Hylidae: Hylinae). *Mesoamerican Herpetology*, 4, 390–401.
Porras, L. & Wilson, L.D. (1987) A new species of *Hyla* from the highlands of Honduras and El Salvador. *Copeia*, 1987, 478–482.
https://doi.org/10.2307/1445786
R Core Team (2020) R Software: Version 4.0.2. Available from: http://www.r-project.org (accessed 15 November 2023)
Señaris, C. & Sunyer, J. (2024) First record of *Plectrohyla guatemalensis* Brocchi, 1877 (Anura, Hylidae) from Nicaragua. *Checklist*, 20, 721–727.
https://doi.org/10.15560/20.3.721
Stuart, L.C. (1942) Description of two new species of *Plectrohyla* Brocchi with comments on several forms of tadpoles. *Occasional Papers of the Museum of Zoology, University of Michigan*, 455, 1–14.
Sueur, J., Aubin, T. & Simonis, C. (2008) Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, 18, 213–226.
https://doi.org/10.1080/09524622.2008.9753600
Taylor, E.H. & Smith, H.M. (1945) Summary of the collection of amphibians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. *Proceedings of the United States National Museum*, 95, 521–613.
https://doi.org/10.5479/si.00963801.95-3185.521
Valencia-Aguilar, A., Zamudio, K.R., Haddad, C.F.B., Bogdanowicz, S.M. & Prado, C. (2020) Show me you care: female mate choice based on egg attendance rather than male or territorial traits. *Behavioral Ecology*, 31, 1054–1064.
https://doi.org/10.1093/beheco/araa051
Wilson, L.D., McCranie, J.R. & Williams, K.L. (1994) Commentary on the reproductive biology and systematic relationships of *Hyla insolita* McCranie, Wilson, and Williams. *Caribbean Journal of Science*, 30, 214–221.