Taylor & Francis
Taylor & Francis Group

Bioacoustics

The International Journal of Animal Sound and its Recording

ISSN: 0952-4622 (Print) 2165-0586 (Online) Journal homepage: http://www.tandfonline.com/loi/tbio20

The advertisement calls of three Eleutherodactylus species from Hispaniola (Anura: Eleutherodactylidae)

Pedro A. Galvis, Valentina Zaffaroni Caorsi, Santiago J. Sánchez-Pacheco & Marco Rada

To cite this article: Pedro A. Galvis, Valentina Zaffaroni Caorsi, Santiago J. Sánchez-Pacheco & Marco Rada (2016): The advertisement calls of three Eleutherodactylus species from Hispaniola (Anura: Eleutherodactylidae), Bioacoustics, DOI: 10.1080/09524622.2016.1260053

To link to this article: http://dx.doi.org/10.1080/09524622.2016.1260053

Published online: 07 Dec 2016.

BIOACOUSTICS, 2016
http://dx.doi.org/10.1080/09524622.2016.1260053

The advertisement calls of three *Eleutherodactylus* species from Hispaniola (Anura: Eleutherodactylidae)

Pedro A. Galvis[a], Valentina Zaffaroni Caorsi[b], Santiago J. Sánchez-Pacheco[c] and Marco Rada[d]

[a]Barrick, Pueblo Viejo Dominicana Corporation, Pueblo Viejo, Dominican Republic; [b]Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; [c]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Canada; [d]Departamento de Zoologia, Instituto de Biociências; Universidade de São Paulo, São Paulo, Brazil

ABSTRACT
We provide detailed descriptions of the poorly known advertisement calls of *Eleutherodactylus abbotti, E. flavescens* and *E. inoptatus*, three rain frogs endemic to the Caribbean island of Hispaniola. We compare these three advertisement calls to those of closely related and/or geographically proximate *Eleutherodactylus* species. The call of *E. abbotti* lasts 0.5–6 s and consists of four notes that differ in amplitude and duration, with a mean dominant frequency of 4527 Hz. In turn, the call of *E. flavescens*, endemic to the Dominican Republic, lasts 0.02–0.09 s and consists of two different notes with dominant frequencies of 2288 and 3025 Hz. In contrast, the call of *E. inoptatus* lasts 0.25–0.39 s and is composed of a single multi-pulsed note with two harmonics, the first one with a dominant frequency of 660 Hz and the second one with a dominant frequency of 1220 Hz. These congeneric species occur sympatrically over large areas below 1000 m elevation and are commonly encountered together, which suggests that, in addition to interspecific variation (e.g. body size), the remarkable differences in their calls (e.g. dominant frequency) may be due to partitioning of the acoustic environment.

ARTICLE HISTORY
Received 25 February 2016
Accepted 4 October 2016

KEYWORDS
Bioacoustics; Hispaniola; Dominican Republic; Haiti; *Eleutherodactylus abbotti*; *E. flavescens*; *E. inoptatus*; rain frogs; vocalizations

Introduction

The Antillean-Middle American frog genus *Eleutherodactylus* Duméril and Bibron is currently composed of 191 species, 65 of which are distributed throughout the island of Hispaniola (all endemic; Frost 2016). The monophyly of *Eleutherodactylus* has been corroborated on the basis of molecular evidence, and the relationships among its species have been studied in a quantitative phylogenetic framework (Hedges et al. 2008; Alexander Pyron & Wiens 2011; Padial et al. 2014). Therefore, the content of previously proposed species series and groups has been reviewed (Hedges et al. 2008; Canedo & Haddad 2012; Padial et al. 2014).

The description of anuran advertisement calls facilitates species-level taxonomy and provides information both phylogenetically and ecologically relevant (Wen et al. 2012;

CONTACT Marco Rada radamarco@gmail.com

Galvis et al. 2016; and citations therein). Nevertheless, the vocalizations of Hispaniolan *Eleutherodactylus* frogs remain largely unknown. Available information is limited to the brief descriptions, including only a few acoustic properties, provided by Schwartz (1966, 1969, 1973), Hedges and Thomas (1987), Hedges (1991), or more complete descriptions, (Incháustegui et al. 2015) for 14 species. During recent field work at the Dominican Republic, the vocalizations of males from three sympatric *Eleutherodactylus* species, *E. abbotti* Cochran 1923, *E. flavescens* Noble 1923 and *E. inoptatus* (Barbour 1914), were recorded. The former two are part of the subgenus *Eleutherodactylus*, but are included in different species series and groups (*auriculatus* series [*abbotti* group] and *antillensis* series [*flavescens* group], respectively), while the latter is part of the subgenus *Pelorius* (*inoptatus* series) (Padial et al. 2014; Frost 2016). As part of our ongoing contribution to the knowledge of Hispaniolan frogs (Galvis et al. 2014, 2015, 2016), in the present study we provide for the first time quantitative and detailed descriptions of the advertisement calls of *E. abbotti, E. flavescens* and *E. inoptatus*. In addition, we compare these vocalizations with available descriptions of closely related and/or geographically proximate *Eleutherodactylus* species.

Materials and methods

Data collection

Fieldwork was conducted at Municipalities of Cotui, Province of Sánchez Ramirez, and Bonao, Province of Monseñor Nouel, Dominican Republic during November 2011, May 2015 and September 2015. Advertisement calls of five adult males of *Eleutherodactylus abbotti*, five of *E. flavescens*, and six of *E. inoptatus* were recorded. Body size (snout–vent length, SVL) was measured using a digital Mitutoyo caliper (±0.1 mm). Specimens collected in this study and snout–vent length for each specimen are reported in Appendix 1. Calls were recorded at night using a Sony PCM-M10 and a Fostex FR2LE recorders coupled to a Sennheiser ME-66 microphone at a distance of 0.5–2 m from the calling frog. The recording level was adjusted manually and kept constant during each session to obtain the best signal-to-noise ratio and to avoid distortion. Sounds were recorded using sampling rates of 44000, 48000 and 98000 Hz and a resolution of 16 or 24 bit, and saved in an uncompressed .wav (wave) format. Air temperature was measured at the time of recording using a Sony Pathfinder thermometer (accuracy 0.1ºC) and ranged between 22.0 and 23.5 °C (*E. abbotti*), between 22.0 and 25.5 °C (*E. flavescens*), and between 22.0 and 26.6 °C (*E. inoptatus*).

Bioacoustics analysis

Advertisement calls were analysed using the software Raven Pro v. 1.4 for Mac OS X (Bioacoustics Research Program 2011). Temporal properties were obtained from oscillograms (temporal resolution = 5.33 ms), and frequency information was obtained using Fast Fourier Transformation (512 points Hann window; frequency resolution = 93.8 Hz). Descriptions of both temporal and spectral structure of calls for all species were based on seven variables: (1) call duration [s], (2) interval between calls [s], (3) call rate (calls/min), (4) presence and number of harmonics [Hz], (5) dominant frequency of the entire call including all signals emitted in it [Hz], (6) peak time and (7) amplitude modulation. Additional variables were included according to each species' call characteristics. *Eleutherodactylus* *abbotti*: (i) number of notes per call, (ii) note duration [s], (iii) interval between notes [s] and (iv) dominant frequency of each harmonic [Hz]; *E. flavescens*: (i) note duration [s], (ii) dominant frequency of each note [Hz]; *E. inoptatus*: (i) pulses per note, (ii) pulse duration [s], (iii) low and high frequency of each harmonic and (iv) dominant frequency of each harmonic. Measurements were calculated as follows: call rate [(total number of calls-1)/time from beginning of first call to beginning of last call]; call duration (time from beginning to end of one call); note duration (time from beginning to end of one note); interval between notes (distance between two consecutive notes); pulses per note (number of pulses found in one note); pulse duration (time from beginning to end of one pulse); peak time (time in the selection when peak amplitude occurs); dominant frequency (frequency in signal emitted containing the greatest energy); peak frequency (frequency at which maximum power occurs within the selection); low frequency (the lower frequency of the selection); high frequency (the upper frequency of the selection). Some of these parameters (mean, standard deviation and range) are shown in Table 1, and were calculated by combining calls from each individual and then per species. Sound figures were generated using the Seewave R package (Sueur et al. 2008). Voucher specimens (see Appendix 1) were deposited at Museo Nacional de Historia Natural Santo Domingo Prof. Eugenio de Jesús Marcano, Dominican Republic (MNHNSD 23.2105–23.2114). Recordings analysed for the descriptions are deposited at Fonoteca Zoológica, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain (http://www.fonozoo.com/; Codes FZ Sound Collection 9725–9737). In order to compare the advertisement calls described in this study, a search for literature containing call descriptions of closely related and/or geographically proximate *Eleutherodactylus* species was conducted. Species that have at least two acoustic parameters of their advertisement call described, as well as the sources, were included in Table 1.

Results

Eleutherodactylus abbotti (Cochran, 1923)

Recorded adult males (five) were calling on leaves of small shrubs inside the forest (about 30–60 cm above the ground, Figure 1(a)). Call site ranges from 50 to at least 100 cm high. The advertisement call of *Eleutherodactylus abbotti* (Figure 2(a) and (b)) consists of four notes that differ in amplitude and duration, denoted herein as notes A, B, C and D. The call has a mean duration of 1.5 ± 1.2 s (ranging from 0.5 to 6 s), and is emitted at intervals of 6.6 ± 6.9 s. The average call rate is 7.9 calls per minute, and the dominant frequency of the whole call is 4527 Hz, which is also the dominant frequency band of all notes described below. The number of notes per call ranges from 1 to 14 ($\bar{x}$ = 6.8; SD = 2.5), with an average interval between notes of 0.17 s (SD = 0.14 s). Only one instance of one-note call, which was composed by a note A, was recorded. Note A (Figure 2(b)) is the most frequent one ($\bar{x}$ = 4.6 notes per call). It appears at the beginning of the call and sometimes after the other notes. It is also the shortest note, with a mean duration of 0.02 s and a peak amplitude that is reached short after the beginning of the call. Note A has three well-defined harmonics, and a forth one with low energy (Figure 2(b)). The mean peak frequency of the fundamental band is 2025.9 Hz (SD = 86.5 Hz), whereas those of the other two well-defined harmonics are 4536 Hz (SD = 142.6 Hz) and 7247 Hz (SD = 340.7 Hz). The forth harmonic of low energy has a peak frequency on average of 9009 Hz (SD = 272.5). Note B (Figure 2(b)) appears after

Table 1. Structural, temporal and spectral characteristics of the advertisement calls of *Eleutherodactylus* species. Mean, ± standard deviation and range (–).

Species/character	Note*	Call duration (sec.)	Call rate (calls/min)	Interval between calls (sec.)	Notes/call	Dominant frequency (kHz)
***antillensis* series**						
E. antillensis[1]	A				1	1.8–2.2
	B				1	2.5–3.6
E. antillensis[2]	A				1	2.0 ± 0.99
	B				1	2.8 ± 0.1
E. brittoni[3]					1	4.6–6.4
E. brittoni[1]					1	4.5–6.0
E. cochranae[3,4]					1	3.7–4.4
E. cochranae[2]					1	3.8 ± 0.14
E. cochranae[1,**]	A				1	3.7–4.8
	B				0–3	3.7–4.8
E. cooki[1]					3–7	1.5–1.8
E. coqui[5]		3.62 ± 0.02 (3.12–4.12)	1.48 (5.6–22.6)		2	
	A	0.94 ± 0.006 (0.78–1.14)			1	1.46 ± 0.005 (1.32–1.61)
	B	1.29 ± 0.01 (0.91–1.16)			1	2.25 ± 0.008 (2.02–2.46)
E. eneidae[1]	A				1	3.0–3.5
	B				17–33	3.0–3.5
E. flavescens[5]	A,B[***]				2	second note higher than the first
E. flavescens[14] (^{n}males = 5; ^{n}calls = 298)		0.078 ± 0.009 (0.02–0.09)	76	0.73 ± 0.44	2	3.0 ± 0.18
	A	0.04			1	2.3 ± 0.47
	B	0.19			1	3.0 ± 0.18
E. gryllus[1]					1–5	6.7–8
E. hedricki[1]					7–19	2.9–3.4
E. juanariveroi[3]						7.0–9.0
E. locustus[1]	A				1	4.5–5.3
	B				10–16	4.5–5.3
E. portoricensis[1]	A				1	1.5–1.8
	B				1	2.2–3
E. schwartzi[4]	A,B[***]				2	second note higher than the first
***auriculatus* series**						
E. abbotti[14] (^{n}males = 5; ^{n}calls = 44)		1.5 ± 1.2 (0.5–6)	7.9	6.6 ± 6.9	1–14	4.5 ± 0.13
	A	0.02			4.6	4.5 ± 0.14
	B	0.1			1.4	4.5 ± 0.06
	C	0.04			0.5	4.5 ± 0.04
	D	0.06			0.3	4.5 ± 0.04
E. auriculatus[6]		0.0042–0.014	469–981	0.064–0.156	1	4.2 (3.6–4.6)
E. auriculatus[6]		0.0056–0.10	915–1200	0.05–0.093		4.8 (4.6–5.0)
E. auriculatus[6]		0.010–0.12	52–309	0.9–1.5	1–2	4.7 (4.5–4.8)
E. bartonsmithi[6]		0.06–0.56	10–21	1.4–89.7	2–10	3.7 (3.6–3.8)
E. eileenae[6]		0.18–0.29	17–42	1.1–4.2	2	
	A	0.06–0.12			1	1.9 (1.6–2.1)
	B	0.1–0.2			1	3.2 (2.5–3.5)
E. glamyrus[6]		0.08–0.2	69–101	0.6–1.1	1	3.3 (3.1–3.4)
E. mariposa[6]		0.02–0.08	116–365		1	2.9 (1.9–3.9)
E. principalis[6]		0.007–0.012	53–444	0.3–2	1	2.8 (2.7–3.1)
E. ronaldi[6]		0.004–0.016	285–472	0.17–0.436	1	2.9 (1.7–3.5)
***inoptatus* series**						
E. inoptatus[7]					1	Low frequency
E. inoptatus[14]						

(*Continued*)

Table 1. (*Continued*)

Species/character	Note*	Call duration (sec.)	Call rate (calls/min)	Interval between calls (sec.)	Notes/call	Dominant frequency (kHz)
(^{n}males = 5; ^{n}calls =123)		0.29 ± 0.03 (0.25–0.39)	10	5.5 ± 2.0 (3.9–12.8)	1	0.66 ± 0.2
E. nortoni[7]					1	Low frequency
Geographically proximate Eleutherodactylus species						
E. amadeus[8]				30–39	4	Between 2–3.5♦
E. caribe[9]		1.07(0.99–1.25)	19.5 (16.1–22.1)		1	6 (5.85–6.09)
E. corona[10]		0.056 ± 0.0007 (0.055–0.057)	1.58 ± 0.24 (1.43–1.82)		1	2.52 ± 0.08 (2.4–2.6) and rises to 5.40 ± 0.09 (5.3–5.5)
E. dolomedes[10]	A,B***	0.013	0.46	120–130	7	4.71 (4.67–4.75)
E. fowleri[11]	A,B***				2	Second note higher than the first
E. glaphycompus[11,12]					1	2.52–3.28
E. hypostenor[7]					1	Low frequency
E. ligiae[13]		0.028–0.054	5	12–17	1	1.7–2.3
E. neiba[13]		0.035–0.045		12–120	7–9	5.5–6.2
E. parapelates[7]	A,B***			60–600	2	Low frequency
E. wetmorei[4]	A,B***				2	Second note higher than the first

[1]Drewry and Rand (1983).
[2]Ovaska and Caldbeck (1997).
[3]Ríos-López and Villanueva-Rivera (2013).
[4]Schwartz (1969).
[5]Lopez and Narins (1991).
[6]Díaz and Cádiz (2007).
[7]Hedges and Thomas (1987).
[8]Hedges et al. (1987).
[9]Hedges and Thomas (1992a).
[10]Hedges and Thomas (1992b).
[11]Schwartz (1973).
[12]Hedges (1991).
[13]Incháustegui et al. (2015).
[14]This work.
*Notes A and B usually referred to by the authors as "two different notes"; **The author mentions one or two different notes, but does not describe them; ***The authors mention two different notes, but do not describe them; ♦Indicates data inferred from the illustration (audiospectogram) but not stated in the description by the author.

note A and it is the longest note, with a mean duration of 0.1 s and a relatively long peak time beyond the middle of the note; afterwards the amplitude decreases rapidly and steadily. The peak frequency of the fundamental band is on average of 4491.6 Hz (SD = 57.5 Hz), and that of the second harmonic, with low energy, has an average of 8917 Hz (SD = 190 Hz). The third note, C (Figure 2(b)), has a mean duration of 0.04 s and an amplitude that reaches the highest peak in the beginning of the note, and decreases over time. This note is repeated after note B. The peak frequency of the fundamental band is on average 4539 Hz (SD = 35.9 Hz), while that of the second harmonic, with low energy, is on average 8968 Hz (SD = 211). The last note, D (Figure 2(b)), is the least frequent one ($\bar{x}$ = 0.3 notes per call), and it lasts for 0.06 s. This note has abrupt amplitude modulation at its beginning and at its end. The modulation of amplitude is more abrupt at the beginning than at the end of the note. The peak frequency of the fundamental band is on average 4515 Hz (SD = 45 Hz), while that of the second harmonic, with low energy, is on average 9062.2 Hz (SD = 286.6 Hz). Acoustic parameters are summarized in Table 1.

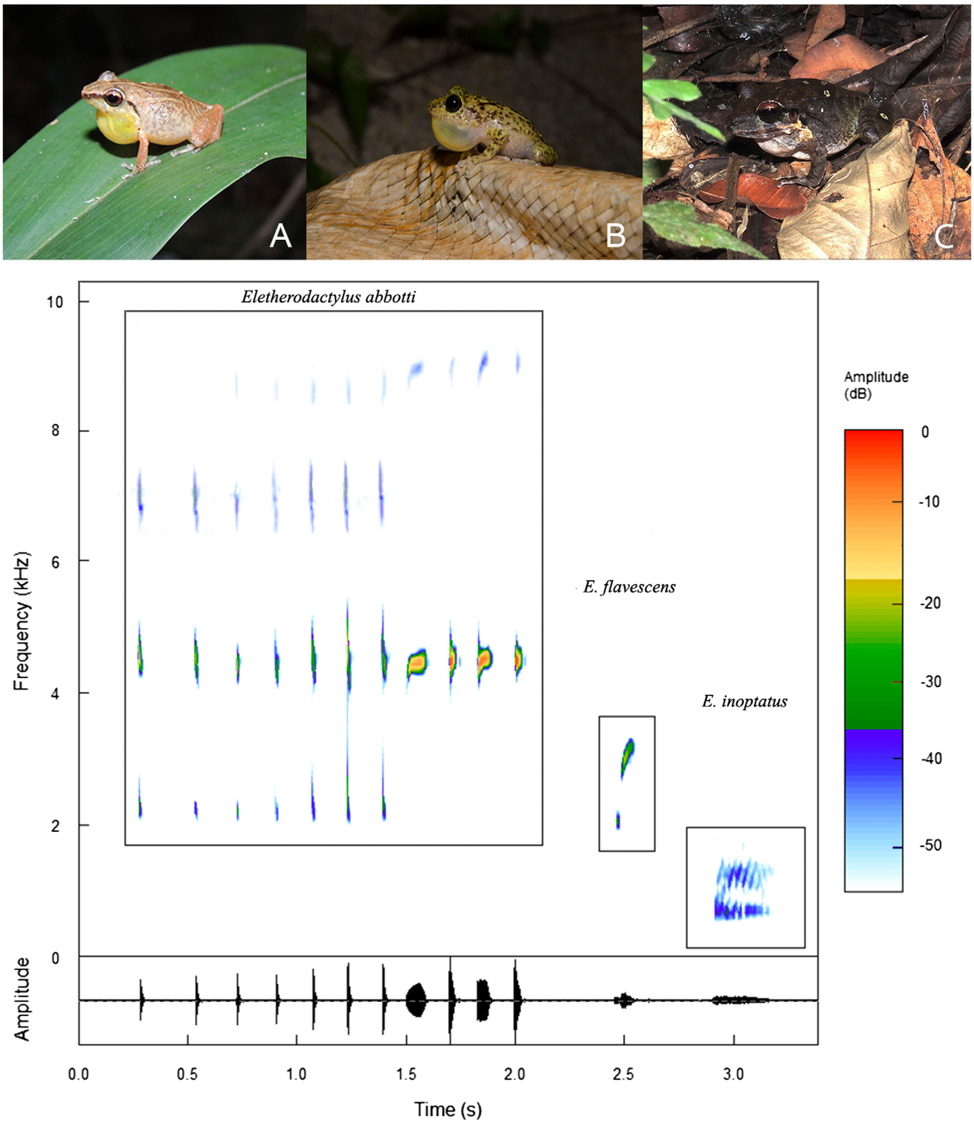

Figure 1. Vocalizing males (top), comparative spectrograms (middle) and oscillograms (bottom) of advertisement calls of (a) *Eleutherodactylus abbotti* (MNHNSD 23.2105; SVL 17.1 mm), (b) *E. flavescens* (MNHNSD 23.2114; SVL 28.1 mm), and (c) *E. inoptatus* (MNHNSD 23.2111; SVL 50.4 mm). Calling male *E. abbotti* corresponds to specimen MNHNSD 23.2112 (SVL 17.5 mm).

Eleutherodactylus flavescens (Noble, 1923)

Recorded adult males (six) were calling from a variety of substrates, including leaves and branches of small shrubs inside the forest, branches of fallen shrubs, and the walls of an intermodal container in a disturbed area (about 10–100 cm above the ground, Figure 1(b)). Call site ranges from 50 to at least 300 cm high. The advertisement call of *Eleutherodactylus flavescens* (Figure 2(c) and (d)) consists of two notes that differ in amplitude and duration,

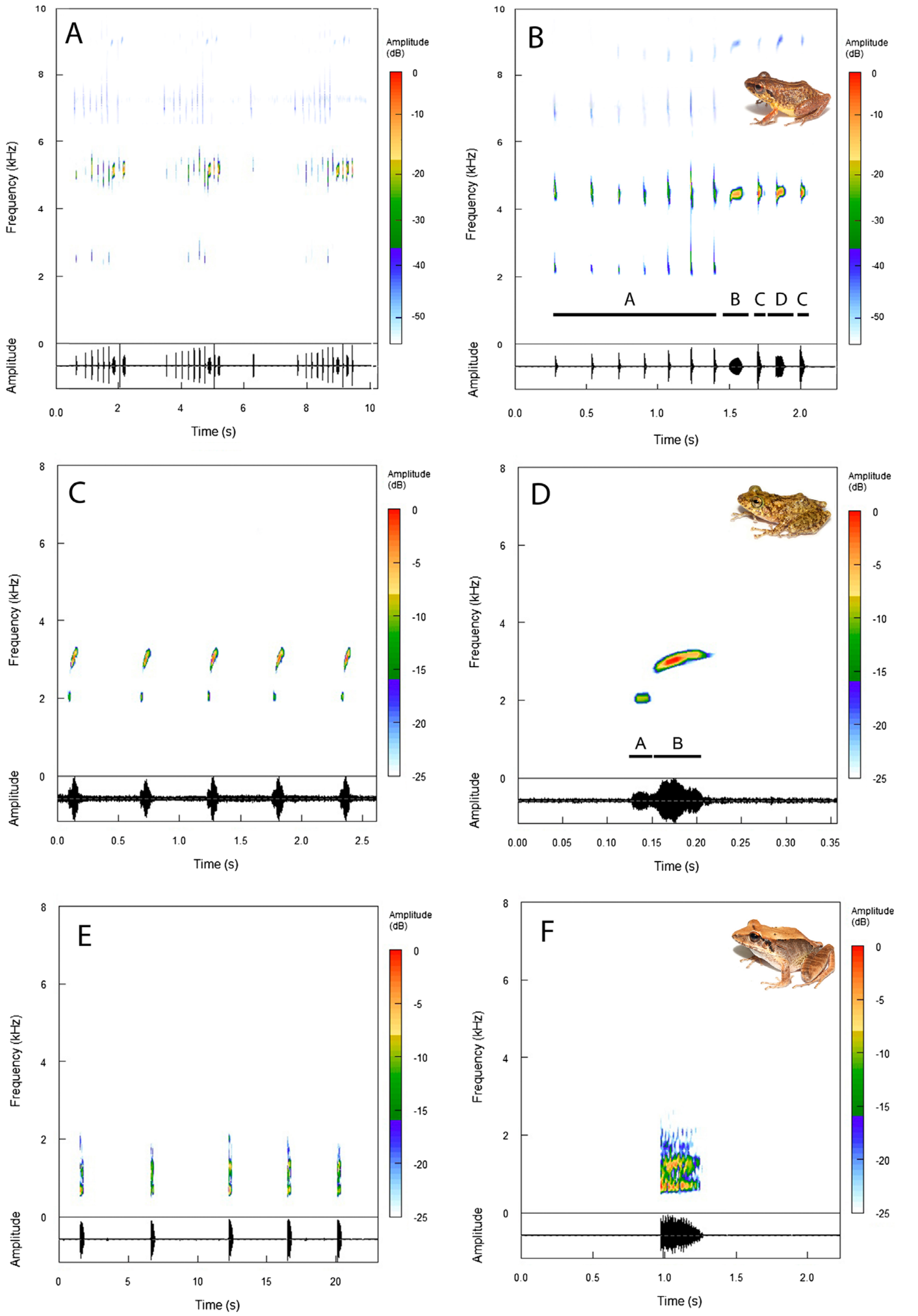

Figure 2. Comparative spectrograms (top) and oscillograms (bottom) of advertisement calls described in this study: (a) three calls of *Eleutherodactylus abbotti* (MNHNSD 23.2105; SVL 17.1 mm) from Dominican Republic, with (b) a closer view (from 7 to 10 s) showing one call. The first seven notes are A, followed by notes B, C, D and C again. (c) five calls of *E. flavescens* (MNHNSD 23.2114; SVL 28.1 mm) from Dominican Republic, with (d) a closer view (from 0 to 0.5 s) showing one call, which is composed by two notes, A and B. (e) five calls of *E. inoptatus* (no voucher) from Dominican Republic, with (f) a closer view (from 0 to 5 s) showing one pulsed call.

denoted herein as notes A and B. Note A is shorter and of lower amplitude than note B. Each call lasts from 0.02 to 0.09 s ($\bar{x}$ = 0.078; SD = 0.009 s), with an interval between calls of 0.73 s on average (SD = 0.44 s), a mean call rate of 76 calls per minute and a mean dominant frequency of 3025 Hz. Note A (Figure 2(d)) lasts 0.024 s on average, with a mean peak frequency of 2288 Hz (SD = 469 Hz). This note has a smooth, round amplitude modulation (its peak time is about one half note duration). It is immediately followed (without a silence gap between them) by note B (Figure 2(d)), which lasts 0.05 s on average. Note B presents frequency modulation, increasing from a mean of 2275 Hz at the beginning to 3234 Hz at the end, with a mean peak frequency of 3025 Hz (SD = 177 Hz). Peak time is about one half note duration. Acoustic parameters are summarized in Table 1.

Eleutherodactylus inoptatus (Barbour, 1914)

Recorded adult males (five) were calling perched on vegetation (about 100–300 cm above the ground) next to a stream; one individual was on the leaf litter in a disturbed forest (Figure 1(c)). The advertisement call of *Eleutherodactylus inoptatus* (Figure 2(e) and (f)) is composed of a single multi-pulsed note, with 14–22 pulses ($\bar{x}$ = 16.8; SD = 1.3). The call lasts from 0.25 to 0.39 s ($\bar{x}$ = 0.29; SD = 0.03 s) and has an average call rate of 10 calls per minute. The interval between calls ranges from 3.9 to 12.8 s ($\bar{x}$ = 5.5; SD = 2.0 s). Each pulse has a mean duration of 0.01 s, and the pulse rate is on average 60.8 pulses per second. The amplitude reaches its highest peak at the onset of the note, then it decreases steadily throughout the call. For last, the dominant frequency of the call is 660.1 Hz and it has two harmonics. The frequency of the fundamental harmonic ranges from 496 Hz (SD = 161.6 Hz) to 910 Hz (SD = 178.4 Hz) and its peak frequency is on average 660 Hz (SD = 213 Hz). The second one ranges from 1037 Hz (SD = 417.2 Hz) to 1856 Hz (SD = 395.8 Hz) and its peak frequency is on average1220 Hz (SD = 68.5 Hz). Acoustic parameters are summarized in Table 1.

Discussion

In this study, we described in detail the advertisement calls of three sympatric frogs, genus *Eleutherodactylus,* from the Caribbean island of Hispaniola, *E. abbotti, E. flavescens* and *E. inoptatus*. Schwartz (1966, p. 372) described the call of *E. abbotti* as a "repeated flat telegraphic clicking", which we interpret as a call composed of more than one note. No other acoustic characteristics of *E. abbotti* were reported by Schwartz (1966). Similarly, Schwartz (1969, p. 105) provided a limited description of the *E. flavescens*'s advertisement call, including only the number of notes per call: two. He also noted that "the second note [is of] higher [frequency] than the first [one]". Likewise, Hedges and Thomas (1987) mentioned the occurrence of a single note with low frequency in the *E. inoptatus*'s advertisement call. Our findings agree with these observations. The advertisement calls of these three congeneric species show several remarkable differences in frequency bands and patterns of structure. For example, the call of *E. abbotti* has a dominant frequency of around 4.5 kHz, whereas that of *E. flavescens* and *E. inoptatus* have dominant frequencies of around 3.0 and 0.66 kHz, respectively. Additionally, the call of *E. abbotti* consists of four notes, whereas that of *E. flavescens* consists of two notes. In contrast, the call of *E. inoptatus* is composed of a single multi-pulsed note. There are also differences in temporal variables such as call duration and interval between calls (see Table 1). These three species occur sympatrically, and even syntopically (i.e. same habitat), over large areas of the island below 1000 m elevation. This is of special importance in understanding the factors that influence mate recognition and the evolution of reproductive isolation. The fact that related species can coexist has been explained by the reduction of interspecific competition (Duellman 1978; i.e. diet divergence, space-temporal partitioning), and the spectral and temporal attributes of the call, as well as the calling site occupancy by males, have been shown to be important for resource partitioning (Crump 1974). Therefore, the remarkable differences observed among the advertisement calls of these three syntopic *Eleutherodactylus* species may be due to partitioning of the acoustic environment. Acoustic partitioning has been observed in other syntopic *Eleutherodactylus* species (Drewry & Rand 1983; Zelick & Narins 1983; Ríos-López & Villanueva-Rivera 2013). In addition, body size data from these three species (see Appendix 1) suggest a qualitative negative relationship between SVL and call dominant frequency. Thus, the observed differences among these three Hispaniolan *Eleutherodactylus* in dominant frequencies may also be associated with major differences between species in body size. A negative correlation between SVL and dominant frequency has been reported in other anurans (e.g. Ryan 1983).

As mentioned above, the advertisement calls of *Eleutherodactylus abbotti* and *E. flavescens* consist of four and two notes, respectively. The four notes of the *E. abbotti*'s call may or may not occur during the call, whereas both notes of the *E. flavescens*'s call are always present (see Results section and Figure 1 for details). Many Neotropical anurans have calls consisting of different notes. Studies of anuran vocal behaviour have suggested that different notes in a species' advertisement call have a distinct communicative significance (e.g. Narins & Capranica 1978). Specifically, some authors have suggested that each note of the male's call has a separate function (Littlejohn and Harrison 1984), and that this could be more general than suspected in animal sound communication (Narins & Capranica 1978). To date, the communicative significance of the two notes of the call in *Eleutherodactylus* has been investigated only in two species: *E. coqui* (Narins & Capranica 1978) and *E. johnstonei* (Tárano & Fuenmayor 2013). Therefore, experimental studies on the relative responses of both sexes to the courtship and advertisement calls may shed light on evolutionary processes that have shaped the vocal communication in these frogs (Ovaska & Caldbeck 1997).

Of the 65 *Eleutherodactylus* species known from Hispaniola, only 19 have their advertisement call described (*E. caribe*, *E. corona* and *E. dolomedes*, Hedges & Thomas 1992a, 1992b; species included in this study), or partially described (i.e. brief descriptions, e.g. species included in Schwartz 1966, 1969, 1973; Hedges 1991; and Hedges & Thomas 1987; see Table 1 for details). Modern, complete and quantitative descriptions of vocalizations are lacking for most species. In this context, the *E. antillensis* and *auriculatus* series (subgenus *Eleutherodactylus*), as well as the *inoptatus* series (subgenus *Pelorius*; sensu Padial et al. 2014) have received considerable attention. *Eleutherodactylus flavescens* is part of the *antillensis* series (which also occur in Puerto Rico and the Lesser Antilles, 15 spp.), *E. abbotti* of the *auriculatus* series (which also occur in Cuba, 16 spp.), and *E. inoptatus* of the *inoptatus* series (endemic to the island of Hispaniola, 3 spp.). Among the species of the *E. antillensis* series, a call composed of a single note has been reported for *E. brittoni*, *E. cochranae* and *E. juanariveroi* (Schwartz 1969; Drewry & Rand 1983; Ríos-López & Villanueva-Rivera 2013), whereas a call composed of two different notes has been reported for *E. antillensis*, *E. coqui*, *E. eneidae*, *E. flavescens*, *E. locustus*, *E. portoricensis*, *E. schwartzi* and *E. cochranae* (Schwartz 1969; Drewry & Rand 1983; Lopez & Narins 1991; Ovaska & Caldbeck 1997;

Ríos-López & Villanueva-Rivera 2013; this study; see Table 1). The advertisement calls of *E. cooki*, *E. gryllus* and *E. heidricki* are composed of the same, repeated notes (Drewry & Rand 1983). Ríos-López and Villanueva-Rivera (2013) reported the dominant frequency for the advertisement calls of *E. brittoni* (4.6–6.4 Hz), *E. cochranae* (3.7–4.4 Hz) and *E. juanariveroi* (7–9 Hz). Ovaska and Caldbeck (1997) and Drewry and Rand (1983) had provided a similar observation for the *E. chocranae*'s call (3.8 Hz). These dominant frequencies are higher than the reported for *E. flavescens* in this work (3.0 Hz). Ovaska and Caldbeck (1997) also reported that the dominant frequency of the *E. antillensis*' call ranges from 2 to 2.8 Hz, lower than in the *E. flavescens*' advertisement call (Table 1). Among the species of the *E. auriculatus* series, an advertisement call composed of a single note has been reported for *E. auriculatus*, *E. glamyrus*, *E. mariposa*, *E. principalis* and *E. ronaldi*, whereas a call composed of two different notes has been reported for *E. eileenae* (Díaz & Cádiz 2007). In contrast, the advertisement call of *E. abbotti* is composed of four different notes (this study; Table 1). Díaz and Cádiz (2007) reported the mean dominant frequency for the advertisement calls of *E. auriculatus* (4.2 kHz), *E. bartonsmithi* (3.7 kHz), *E. eileenae* (1.9–3.2 kHz), *E. glamyrus* (3.3 kHz), *E. mariposa* (2.9 kHz) and *E. pricinpalis* (2.8 kHz). These mean dominant frequencies are lower than the reported for *E. abbotti* in this work (4.5 kHz; Table 1). Finally, the vocalizations of the species in the *E. inoptatus* series and in its sister group sensu Hedges et al. (2008) and Padial et al. (2014), the *E. ruthae* series, consist of a single, multi-pulsed note with a low dominant frequency (Hedges & Thomas 1987; data obtained from the audiospectogram), which was corroborated in this study for *E. inoptatus* (Table 1). Additional comparisons with geographically proximate *Eleutherodactylus* species are included in Table 1.

Acknowledgements

We thank Carlos Tamayo, Jorge Lobato and Jorge Esteva for their support to the "El Llagal Offset Program". We are also grateful to Alejandro Mejia-Tobón, Jose Gil, Emanuel Romero and Jesús Guzmán for field collaboration. Cristian Marte and Carlos Suriel (Museo de Historia Natural de Santo Domingo "Profesor Eugenio de Jesús Marcano" (MHNSD)), and Almudena Gonzáles (Fonoteca Zoológica, Museo Nacional de Ciencias Naturales in Madrid, Spain (CSIC)) kindly provided collection numbers and recordings codes for the voucher specimens used in this study. This manuscript benefited from comments, suggestions and corrections from two anonymous reviewers.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by Barrick-Pueblo Viejo Dominicana Corporation – PVDC, under the "El Llagal Offset Program – ELOP", a comprehensive biodiversity compensation program for the Pueblo Viejo mine in the Dominican Republic.

References

Bioacoustics Research Program. 2011. Raven Pro: interactive sound analysis software [Computer software]. (Version 1.4). Ithaca (NY): The Cornell Lab of Ornithology. Available from http://www.birds.cornell.edu/raven

Canedo C, Haddad CFB. 2012. Phylogenetic relationships within anuran clade Terrarana, with emphasis on the placement of Brazilian Atlantic rainforest frogs genus *Ischnocnema* (Anura: Brachycephalidae). Mol Phylogenet Evol. 65:610–620.

Crump ML. 1974. Reproductive strategies in a Tropical anuran community. Misc Publ Univ Kans Mus Nat Hist. 61:1–68.

Díaz LM, Cádiz A. 2007. Guía descriptiva para la identificación de las llamadas de anuncio de las ranas cubanas del género *Eleutherodactylus* (Anura: Leptodactylidae) [A descriptive guide for the identification of advertisement calls of Cuban frogs of the genus *Eleutherodactylus* (Anura: Leptodactylidae)]. Herpetotropicos. 3:100–122.

Drewry GE, Rand AS. 1983. Characteristics of an acoustic community: Puerto Rican Frogs of the Genus *Eleutherodactylus*. Copeia. 1983(4):941–953.

Duellman WE. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc publ Univ Kans Mus Nat Hist. 65:1–352.

Frost DR. 2016. Amphibian Species of the World: an Online Reference. Version 6.0. New York, NY: American Museum of Natural History; [cited 2016 Jan 25]. Available from: http://research.amnh.org/herpetology/amphibia/index.html.

Galvis PA, Sánchez-Pacheco SJ, Ospina-Sarria JJ, Anganoy-Criollo M, Gil J, Rada M. 2014. Hylid tadpoles from the Caribbean Island of Hispaniola: ontogeny, description and comparison of external morphology. South Am J Herpetol. 9(2):154–169.

Galvis PA, Rada M, Sánchez-Pacheco SJ, Gil J, Mejía A. 2015. Field guide to the hylid tadpoles of Hispaniola. Barrick Pueblo Viejo. Pueblo Viejo Dominicana Corporation. 76pp.

Galvis PA, Caorsi VZ, Sánchez-Pacheco SJ, Rada M. 2016. The advertisement calls of three hylid frogs from Hispaniola. Bioacoustics. 25:89–97.

Hedges SB. 1991. Electrophoretic and morphological variation in *Eleutherodactylus glaphycompus* (Anura: Leptodactylidae) of Hispaniola. J Herpetol. 25:10–17.

Hedges SB, Thomas R. 1987. A new burrowing frog from Hispaniola with comments on the inoptatus group of the genus *Eleutherodactylus* (Anura: Leptodactylidae). Herpetologica. 43:269–279.

Hedges SB, Thomas R, Franz R. 1987. A new species of *Eleutherodactylus* (Anura, Leptodactylidae) from the Massif de la Hotte. Haiti. Copeia. 943–949.

Hedges SB, Thomas R. 1992a. A new marsh-dwelling species of *Eleutherodactylus* from Haiti (Anura: Leptodactylidae). J Herpetol. 26:191–195.

Hedges SB, Thomas R. 1992b. Two new species of *Eleutherodactylus* from remnant cloud forest in Haiti (Anura: Leptodactylidae). Herpetologica. 48:351–358.

Hedges SB, Duellman WE, Heinicke MP. 2008. New World direct-developing frogs (Anura, Terrarana), molecular phylogeny, classification, biogeography, and conservation. Zootaxa. 1737:1–182.

Incháustegui S, Díaz LM, Marte C. 2015. Dos especies nuevas de ranas del género *Eleutherodactylus* (Amphibia: Anura: Eleutherodactylidae) de La Hispaniola. Solenodon, 12: 136–149.

Littlejohn MJ, Harrison PA. 1984. The functional significance of the diphasic advertisement call of *Geocrinia victoriana* (Anura: Leptodactylidae). Behav Ecol Sociobiol. 16:363–373.

Lopez PT, Narins PM. 1991. Mate choice in the neotropical frog *Eleutherodactylus coqui*. Anim Behav. 41:757–772.

Narins PM, Capranica RR. 1978. Communicative significance of the two-note call of the treefrog *Eleutherodactylus coqui*. J Comp Physiol. 127:1–9.

Ovaska KE, Caldbeck J. 1997. Courtship behavior and vocalizations of the frogs *Eleutherodactylus antillensis* and *E. cochranae* on the British Virgin Islands. J Herpetol. 31:149–155.

Padial JM, Grant T, Frost DR. 2014. Molecular systematics of Terraranas (Anura: Brachycephaloidea) with an assessment of the effects of the alignment and optimality criteria. Zootaxa. 3825:1–132.

Pyron RA, Wiens JJ. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol Phylogenet Evol. 61:543–583.

Ríos-López N, Villanueva-Rivera LJ. 2013. Acoustic characteristics of a native anuran (Amphibia) assemblage in a palustrine herbaceous wetland from Puerto Rico. Life Excit Biol. 1:118–135.

Ryan MJ. 1983. Sexual Selection and Communication in a Neotropical Frog, Physalaemus pustulosus. Evolution. 37:261–272.

Schwartz A. 1966. The relationships of four small Hispaniolan *Eleutherodactylus* (Leptodactylidae). Bull Mus Comp Zool. 133:371–399.
Schwartz A. 1969. The Antillean *Eleutherodactylus* of the *auriculatus* group. Stud Fauna Curaçao Caribbean Isl. 30:99–115.
Schwartz A. 1973. Six new species of *Eleutherodactylus* (Anura, Leptodactylidae) from Hispaniola. J Herpetol. 7:249–273.
Sueur J, Aubin T, Simonis C. 2008. Equipment review: seewave, a free modular tool for sound analysis and synthesis. Bioacoustics. 18:213–226. doi:10.1080/09524622.2008.9753600
Tárano Z, Fuenmayor E. 2013. Experimental analysis of the dimorphic function of the biphasic call of *Eleutherodactylus johnstonei* (Anura: Eleutherodactylidae). South Am J Herpetol. 8(2):73–80.
Wen A, Vasquez N, Castroviejo-Fisher S. 2012. Description of the previously unknown advertisement calls of *Hyalinobatrachium fragile*, *H. pellucidum*, and *Vitreorana antisthenesi* (Amphibia: Centrolenidae). Zootaxa. 3480:80–87.
Zelick RD, Narins PM. 1983. Intensity discrimination and the precision of call timing in two species of Neotropical frogs. J Comp Physiol. 153:403–412.

Appendix 1. Specimens recorded

Specimens were recorded and/or collected in the municipalities of Cotui, ca. 450–500 m elevation, Sánchez-Ramirez Province (MNHNSD 23.2105–23.2114), and Bonao, ca. 350–600 m elevation, Monseñor Nouel Province, Complejo Ecoturístico Río Blanco (MNHNSD 23.2112), Dominican Republic.
Eleutherodactylus abbotti. El Llagal, Barrick-Pueblo Viejo Dominicana Corporation mine (18.886789 °N, 70.190832 °W), MNHNSD 23.2105–23.2106 (both individuals SVL = 17.1 mm); Complejo Ecoturistico Río Blanco (18.871356 °N, 70.513577 °W), MNHNSD 23.2112 (SVL = 17.5 mm).
Eleutherodactylus flavescens. El Llagal, Barrick-Pueblo Viejo Dominicana Corporation mine (18.886789 °N, 70.190832 °W), MNHNSD 23.2107 (SVL = 26.0 mm); Hondo, Barrick-Pueblo Viejo Dominicana Corporation mine (18.967070 °N, 70.196059 °W), MNHNSD 23.2113 (SVL = 28.5 mm); Mejita, sector Anfibiario, Barrick-Pueblo Viejo Dominicana Corporation mine (18.929187 °N, 70.169605 °W), MNHNSD 23.2114 (SVL = 28.1 mm).

Eleutherodactylus inoptatus. Hondo, Barrick-Pueblo Viejo Dominicana Corporation mine (18.967070 °N, 70.196059 °W), MNHNDS 23.2108–23.2109 (SVL = 54.5 and 55.6 mm, respectively); Parada de Los Burros, Barrick-Pueblo Viejo Dominicana Corporation mine (18.917220 °N, 70.153169 °W), MNHNDS 23.2110–23.2111 (SVL = 52.8 and 50.4 mm, respectively).