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# Acoustic Features of the Weeping Lizard's Distress Call

Antonieta Labra<sup>1,2</sup>, Gabriela Silva<sup>1</sup>, Fernanda Norambuena<sup>1</sup>, Nelson Velásquez<sup>1</sup>, and Mario Penna<sup>1</sup>

**The study of acoustic communication in lizards has been restricted and mainly focused on Gekkota. The rest of the lizards, Unidentata, are generally considered voiceless, although there are sparse reports on vocal sound production in members of different families. We analyzed the spectro-temporal characteristics of the distress calls emitted by the Unidentata lizard, *Liolaemus chiliensis* (the weeping lizard; Liolaemidae), the only species of this highly diverse genus (>220 species) that vocalizes. We also explored the relationships of the call characteristics with the sex and size of the individuals. The vocalizations of *L. chiliensis* are highly diverse and complex compared to any known call produced by Unidentata lizards. They exhibit pronounced frequency modulations, various nonlinear phenomena, and harmonics that extend into the ultrasonic range. Fundamental frequency and call duration are correlated with body size, and males emit louder but simpler calls (i.e., with less nonlinear phenomena) than females. Based on the characteristics of the vocalizations, we discuss their potential role for startling predators and/or alerting conspecifics to predation risk.**

**I**N recent decades, significant progress has taken place in understanding how lizards use chemical and visual senses to assess the environment and to communicate (Pough et al., 1998; Mason and Parker, 2010). Lizards also use the acoustic channel in different contexts, but studies on the function and ecology of this modality are quite scarce (e.g., Javed et al., 2007). This contrasts with extensive research on the morphology and physiology of the lizard auditory system, which include the anatomy of the central auditory system (Browner and Baruch, 1984) and ear (Baird, 1970; Wever, 1978; Manley, 1990), records of the hearing sensitivity (Wever, 1978; Manley, 1990), and records of brain responses to vocalizations (Kennedy, 1975).

Research on lizard bioacoustics have been mostly focused on Gekkota (geckos and pygopos *sensu* Vidal and Hedges, 2009), which vocalize extensively during social interactions, including courtship (Regalado, 2003; Jono and Inui, 2012), conspecific avoidance (Marcellini, 1977a), territory marking (Hibbitts et al., 2007), and agonistic interactions (Regalado, 2003; Jono and Inui, 2012). Gekkota are also unique among lizards in having laryngeal specializations for vocalization (Russell et al., 2000) and well developed auditory sensitivity (Manley, 1990; Manley and Kraus, 2010).

The rest of the lizards, all included in the Unidentata division (Vidal and Hedges, 2009), have largely been considered voiceless (Bradbury and Vehrencamp, 2011). However, there are reports of vocal sound production in members of at least 15 Unidentata families (Crowley and Pietruszka, 1983; Böhme et al., 1985; Ouboter, 1990; Traeholt, 1997; Carothers et al., 2001; Hartdegen et al., 2001; Alonso and Rodríguez, 2004; Bauer et al., 2004; Gienger and Beck, 2007; Labra et al., 2007; Laspiur et al., 2007). Probably, the designation of Unidentata as voiceless is a consequence of the tight association of vocalizations with predation circumstances, which are rarely observed in nature. Lizards vocalize in response to threat (Crowley and Pietruszka, 1983; Wikramanayake and Green, 1989), but mostly when they are seized by a predator (Bowker, 1980; Ouboter, 1990; Alonso and Rodríguez, 2004). In a few species, vocalizations occur during social interactions

(Milton and Jenssen, 1979; Böhme et al., 1985; Gienger and Beck, 2007), and this behavior is considered to have evolved from antipredatory vocalizations (Milton and Jenssen, 1979).

The Unidentata lizard *Liolaemus chiliensis* (Liolaemidae) is known as the weeping lizard because it vocalizes when seized (Donoso-Barros, 1966; Carothers et al., 2001) in a way that corresponds to distress calls or fear screams (*sensu* Caro, 2005). Interestingly, *L. chiliensis* is the only species of this highly diversified genus (>220 species; Breitman et al., 2011) that vocalizes. Carothers et al. (2001) summarily described these calls, reporting that 68% of the individuals vocalized when seized, and that this was independent of their sex and size, while Lamborot et al. (2006) indicated that although all males vocalized, the only females that did were triploid or had mosaic chromosomal conditions. Finally, Carothers et al. (2001) proposed that these calls may startle predators and/or warn conspecifics of predation risk.

In this study, we analyze the spectral and temporal characteristics of the weeping lizard distress calls and explore the relationships of these features to the sex and size of the individuals, to gain an understanding of their potential adaptive value.

## MATERIALS AND METHODS

Lizards were collected in mid-spring and early summer (October–December) of 2009 and in mid-spring (October) of 2010. In 2009 we collected 44 individuals (25 ♂ and 19 ♀) in Central Chile: 37 near Melipilla city (33°41'S, 71°13'W), and seven in El Manzano (33°40'S, 70°20'W). In 2010, we collected 32 individuals (21 ♂ and 11 ♀) in Melipilla. Lizards were transported to the laboratory where their body sizes (snout–vent length, mm) were measured with a caliper and their sexes were determined by observation of the tail base. Thereafter, animals were placed in an indoor vivarium, and housed individually in plastic enclosures (44.5 × 32 × 25 cm) with hermetic lids partially replaced by a plastic mesh. To allow extra light and surface for climbing, the

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front of each enclosure also had an opening ( $10 \times 5$  cm) covered with plastic mesh. Enclosures contained a pot for water, an inverted tile used as shelter and basking place, a wooden stick used as perch, and the floor had a sand layer of 3 cm. Water was provided *ad libitum* and food (mealworms dusted with vitamins) was supplied three times per week. The vivarium had conditions mimicking those recorded in the field during hot summer days, with temperatures ranging between  $33^{\circ}\text{C}$  and  $12^{\circ}\text{C}$  and a 13:11 L:D cycle. These conditions were provided by halogen lights (100 W) installed on the room ceiling. For at least one week prior to acoustic recordings, lizards were undisturbed, except for feeding. Finally, after the recording period, lizards were returned to their collecting sites.

We recorded vocalizations in an acoustically isolated, semi-anechoic room, between 11 and 16 hrs. To reduce variations in body temperature that could potentially affect the emission of vocalizations (Crowley and Pietruszka, 1983), lizards were exposed to a heat source (infrared lamp or sun light) before the recordings. This allowed them to thermoregulate and achieve a body temperature around the selected value of the species ( $35^{\circ}\text{C}$ ; Labra et al., 2009). We checked lizard body temperatures at the end of the recording session, and, if values deviated more than  $\pm 2^{\circ}\text{C}$  from the species selected temperature, the trial was disregarded and repeated after at least two days ( $n = 4$ ).

For two minutes, we evoked the distress calls by gently grasping each animal with the thumb and forefinger and touching their snouts with a finger (Carothers et al., 2001; Bauer et al., 2004). In 2009, lizards were positioned 10 cm in front of a directional microphone (Sennheiser ME 66; frequency response: 40 Hz–22 kHz) connected to a digital recorder (Tascam DR-100). The WAV files generated (44.1 kHz, 16 bits) were filtered (high-pass filter, cutoff: 200 Hz) and analyzed using Raven Pro 1.3 (Cornell Laboratory of Ornithology). For each vocalization, we measured the following spectro-temporal variables: call duration (ms) and the fundamental and dominant frequency (kHz), corresponding to the first harmonic and to the harmonic having the highest energy content, respectively. The number of harmonics that were clearly recognizable in spectrograms was also quantified.

Calls were classified as simple or complex according to the absence or presence of nonlinear phenomena in their spectrograms, respectively. Within the simple calls, five frequency-modulation patterns were recognized (invariant, downward, upward, bell-shaped, and U-shaped). These categories were established by measuring the fundamental frequency at the beginning, middle, and end of each vocalization. A modulation pattern other than invariant was considered to occur if measurements between any of these three points differed by at least 4% (modified from Opazo et al., 2009). Categories within the complex calls were established based on the type of nonlinear phenomena present (subharmonics, frequency jumps, and deterministic chaos), as in previous studies (Wilden et al., 1998; Fitch et al., 2002; Riede et al., 2004; Tyson et al., 2007). We included the mixed category, when more than one nonlinear phenomenon is present. In the complex calls, the fundamental and dominant frequencies and the number of harmonics were measured in a segment free from nonlinear phenomena, preferentially at the beginning of the signal.

Preliminary analyses of the vocalizations recorded in 2009 indicated that some calls contained harmonics above

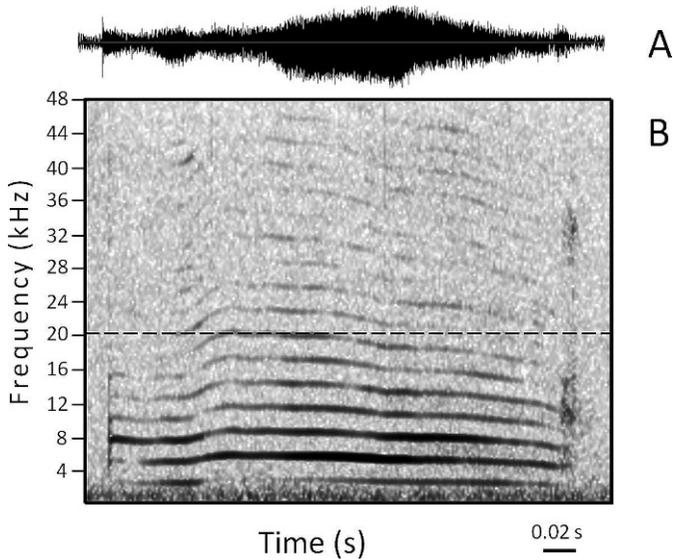
20 kHz. We further explored this in 2010, using a similar setup as in 2009, but changing the microphone to one with a broad frequency range (G.R.A.S. 40 BE, frequency response: 0.2–97 kHz) connected to a preamplifier (G.R.A.S. 26 CB). We determined the percentage of vocalizations having ultrasound components clearly detectable in the spectrograms ( $>20$  kHz). In addition, we measured the sound pressure level (SPL) of these vocalizations, and for that, we taped with the G.R.A.S. microphone the 93.8 dB SPL, 1 kHz pure tone produced by a sound calibrator (Brüel and Kjær, 4230) at the beginning of each recording session using the same recording level for the subsequent registers. To tape this tone, the microphone was fitted with a rubber ring to the 0.5-inch opening of the calibrator.

Each individual was characterized by the average values of each of its acoustic variables. The influence of snout-vent length on call characteristics and the relationships among these variables were analyzed using Pearson correlations. For the statistical analyses, the average values in dB SPLs were converted to Pascal. Sex differences in the variables were analyzed using Student's *t* test or ANCOVA with body size as a covariate for variables that were correlated with body size. To explore differences between simple and complex calls in the spectro-temporal variables analyzed, we used ANCOVA with body size as a covariate. Coefficients of variation (CVs) were calculated to determine the dispersion of each acoustic variable at the intra- (CV<sub>w</sub>) and inter-individual (CV<sub>a</sub>) level:  $\text{CV} = 100 \times \text{standard deviation}/\text{mean}$ ; see Opazo et al., 2009). To determine if distress calls have individual features we performed three analyses (Feng et al., 2009): MANOVA to determine whether calls from different individuals were significantly different, ANOVAs to determine which of the spectro-temporal variables and types and categories of calls were significantly different among individuals, and third, a stepwise discriminant function analysis (DFA). Finally, comparisons between proportions (e.g., simple and complex calls with ultrasound) were analyzed using contingency tables or proportion tests. All statistical analyses were performed using Statistica 6.0 (StatSoft, Inc., 2003), and data are presented as mean  $\pm$  SE.

## RESULTS

In 2009, 39 out of 44 lizards (88.6%) vocalized in response to seizure, producing 403 calls. The subjects did not vocalize spontaneously and very rarely when threatened (e.g., by approaching hand of the experimenter). The five lizards (3  $\sigma$  and 2  $\varphi$ ) that did not vocalize, even after two attempts, were about average size. Because most lizards that vocalized produced a high number of vocalizations (average  $> 10$ ), we excluded from the analysis those that gave fewer than three calls (4  $\sigma$  and 5  $\varphi$ ), which led to a final sample size of 30 individuals (17  $\sigma$  and 13  $\varphi$ ) that produced 390 calls.

The distress call of *L. chiliensis* is short and high-pitched, emitted with the mouth open, exposing the black coloration of the oral structures. The vocalizations contain multiple harmonics encompassing a broad range, extending into the ultrasound range ( $>20$  kHz; Fig. 1). Males and females did not differ in call duration ( $F_{1,27} = 0.44$ ,  $P = 0.51$ ), fundamental frequency ( $F_{1,27} = 0.76$ ,  $P = 0.39$ ), dominant frequency ( $t_{28} = 0.06$ ,  $P = 0.96$ ), or number of harmonics ( $t_{28} = 0.25$ ,  $P = 0.80$ ), and therefore data of both sexes were pooled for the analyses. Averages and measures of dispersion for these variables are listed in Table 1, where it can be noted that variables had higher intra- relative to inter-individual

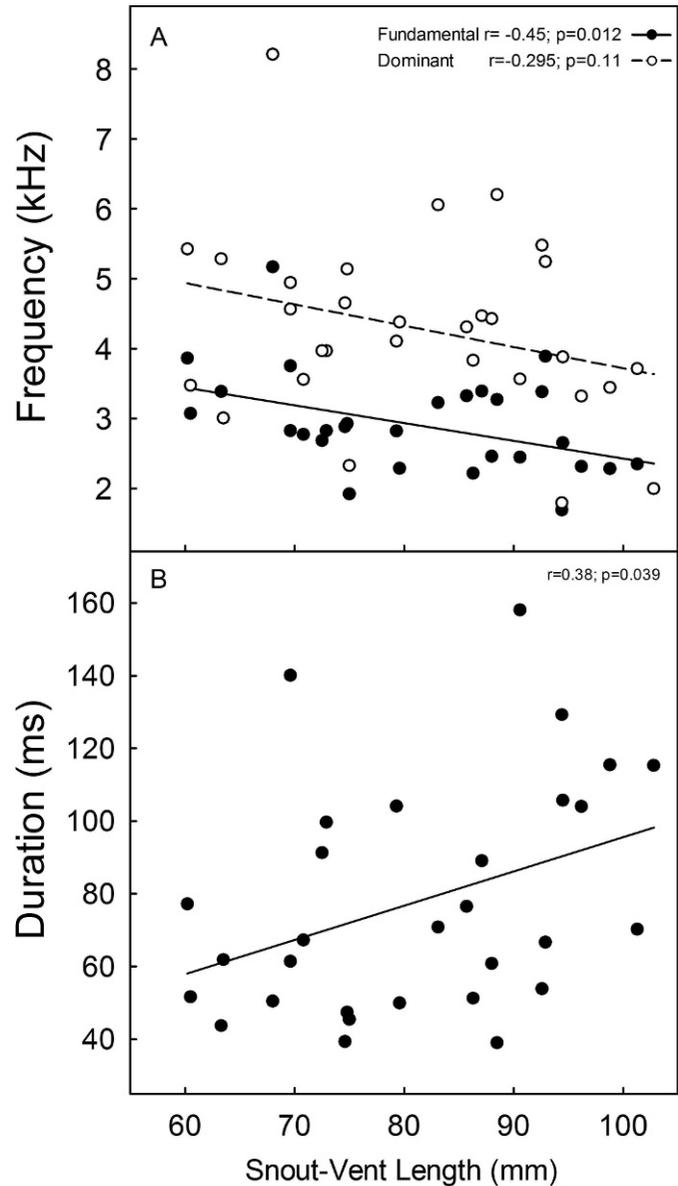


**Fig. 1.** (A) Oscillogram and (B) spectrogram of a representative distress call of a female of *Liolaemus chiliensis* (snout–vent length = 99.8 mm), showing harmonics extending into the ultrasound range (>20 kHz), a limit indicated by the dotted line. Recording made with the G.R.A.S. 40BE microphone.

variability. The MANOVA using these four spectro-temporal variables and types and categories of calls showed significant differences among individuals (Wilks' Lambda = 0.259,  $F_{174,2100} = 3.105$ ,  $P < 0.001$ ). The ANOVAs of the different variables (spectro-temporal variables and types and categories of calls) showed significant differences among individuals ( $P < 0.01$ ). However, the DFA showed that only 20.3% of the calls were correctly assigned to individual lizards.

The dominant frequency corresponded to the fundamental frequency in 65.0% of the vocalizations, which resulted in a high correlation between these two variables ( $r = 0.839$ ,  $P < 0.001$ ). The dominant frequency was the second harmonic in 27.2% of the calls, and the remaining 7.8% corresponded to harmonics ranging from the third to the sixth. Body size was negatively correlated with the fundamental but not with the dominant frequency (Fig. 2A), positively correlated with call duration (Fig. 2B), but uncorrelated with the number of harmonics ( $r = 0.198$ ,  $P = 0.294$ ). Finally, duration was positively correlated with the number of harmonics ( $r = 0.527$ ,  $P = 0.03$ ).

Sixty-three percent of the 390 calls were simple. Five categories were recognized resulting from variation of the fundamental frequency (FF) along the call: invariant (35.8%, Fig. 3A; constant FF), downward (39.4%, Fig. 3B; FF decreases), upward (10.6%, Fig. 3C; FF increases), bell-shaped (11.8% Fig. 3D; highest FF value in the middle of the call), and U-shaped (2.4%, Fig. 3E; lowest FF value in the middle

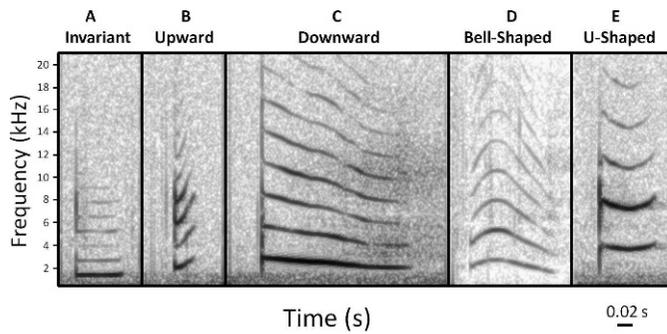


**Fig. 2.** Relationships between body size and (A) dominant and fundamental frequency and (B) duration of the distress call of *Liolaemus chiliensis*.

of the call). The complex calls were divided into four categories considering the nonlinear phenomena present. The subharmonic category (16.7%, Fig. 4A) contains additional tonal components between the harmonics, the deterministic chaos category (21.5%; Fig. 4B) contains broadband components of non-random noise, and the frequency-jump category (46.5%; Fig. 4C) contains abrupt

**Table 1.** Descriptive Statistics for Five Variables of the Distress Call of *Liolaemus chiliensis*, CVw = intra-individual coefficient of variation, CVa = inter-individual coefficient of variation. The snout–vent length of the lizards from  $n = 30$ ,  $81.23 \pm 2.3$  mm, and for the  $n = 32$ ,  $86.25 \pm 1.42$  mm.

	Mean $\pm$ SE (range)	<i>n</i>	CVw	CVa	CVa/CVw
Duration (ms)	77.80 $\pm$ 5.82 (39.00–158.05)	30	71.5	40.9	0.57
Fundamental freq. (kHz)	2.90 $\pm$ 0.13 (1.69–5.17)	30	25.1	24.4	0.97
Dominant freq. (kHz)	4.29 $\pm$ 0.24 (1.79–8.21)	30	42.2	30.4	0.72
No. harmonics	5.21 $\pm$ 0.25 (2.38–8.25)	30	33.0	26.1	0.79
Amplitude (dB SPL)	62.53 $\pm$ 0.61 (55.15–69.27)	32	58.7	5.5	0.09



**Fig. 3.** Spectrograms of the five categories of simple distress calls of *Liolaemus chiliensis*, according to the pattern of frequency modulation: (A) invariant, (B) upward, (C) downward, (D) bell-shaped, and (E) U-shaped. Note that the downward and bell-shaped patterns have harmonics that occur at frequencies higher than 20 kHz. Recordings made with the Sennheiser ME 66 microphone.

changes in the fundamental frequency. We included the mix category (15.3%; Fig. 4D), which exhibits more than one type of nonlinearity.

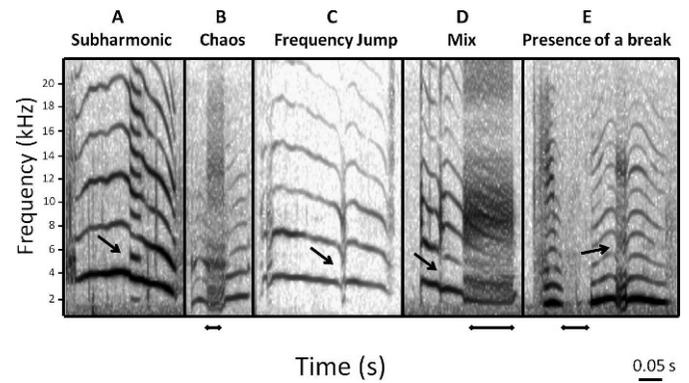
A few calls (6% of the total), most of which corresponded to the complex type (92%), exhibited silent intervals having an average duration of  $0.027 \pm 0.03$  s (Fig. 4E). Simple and complex calls had similar fundamental frequency ( $F_{1,387} = 1.62$ ,  $P = 0.204$ ) and dominant frequency ( $F_{1,387} = 1.60$ ,  $P = 0.207$ ). However, complex calls had more harmonics ( $F_{1,387} = 7.16$ ,  $P = 0.008$ ) and a longer duration ( $F_{1,387} = 76.16$ ,  $P < 0.001$ ) than simple calls. Sexes differed in the proportion of simple and complex calls exhibited ( $\chi^2 = 8.64$ ,  $P = 0.003$ ); males produced more simple calls (70%), while females produced similar proportions of both type of calls (simple [56%], complex [44%]). The first call produced by females in a recording session was mainly complex (62%), while males equally emitted both types (47% simple and 53% complex).

Some vocalizations analyzed in 2009 showed ultrasound, e.g., detectable energy in harmonics extending the 20 kHz (Fig. 3C, 3D). This was confirmed using better equipment in 2010, and we found ultrasound in 18% of the 250 calls recorded (Fig. 1). Ultrasound was proportionally more frequent in complex (27.7%) than in simple calls (14.6%;  $P = 0.02$ ). Sexes showed similar proportion of calls having ultrasound components (males 16.1%; females 19.1%;  $P = 0.55$ ), but they differed in the amplitude of their vocalizations ( $t = 3.127$ ,  $P = 0.004$ ); males had louder calls than females ( $63.85 \pm 0.635$  and  $60.00 \pm 0.932$  dB SPL, respectively). Finally, the intensity of these vocalizations did not correlate with body size ( $r = 0.3107$ ,  $P = 0.083$ ).

## DISCUSSION

The distress call of the weeping lizard shows remarkable variation and complexity, which includes a diversity of frequency-modulation patterns, nonlinear phenomena, and harmonics that extend into the ultrasound range. This high complexity is unique among Unidentata lizards (for comparisons see Milton and Jenssen, 1979; Böhme et al., 1985; Alonso and Rodríguez, 2004), but it is similar to that observed in taxa with well developed acoustic communication such as frogs (Feng and Narins, 2008; Feng et al., 2009; Opazo et al., 2009).

The weeping lizard is one of few species of *Liolaemus* that inhabits bushes (Donoso-Barros, 1966; Cei, 1986, 1993) where the use of vision is limited (e.g., Preininger et al.,



**Fig. 4.** Spectrograms of the four categories of complex frequency-modulated patterns of distress calls of *Liolaemus chiliensis*. (A) Subharmonic. The arrow shows one of the subharmonics. (B) Deterministic chaos. The arrow below the figure shows where the chaos is. (C) Frequency jumps. The arrow points to the jump. (D) Mixed. This category corresponds to the presence of more than one nonlinear phenomenon. This example shows one of the various possible combinations of two nonlinear phenomena in the same vocalization, frequency jump at the first part of the call (shown by the arrow) and deterministic chaos in the second (shown by the arrow below the figure). (E) Example of a break in a complex call (deterministic chaos). The arrow below the figure shows the silent period. Recordings made with the Sennheiser ME 66 microphone.

2009). This visual constraint may act as a selective pressure for the evolution of sound production in Unidentata (Labra et al., 2007). Similarly, sound production in Gekkota is more developed in nocturnal than diurnal species, which have a more restricted use of visual information (Marcellini, 1977b). However, in the case of the Chilean lizard, dense vegetation also imposes constraints on sound communication, since high frequencies are attenuated in these environments (Bradbury and Vehrencamp, 2011), and this acoustic drawback combined with the low intensity of the calls restrict their effectiveness to short distances. In nature, *L. chiliensis* can be observed forming pairs of individuals on the same bush, usually male and female, at distances of about 2–3 m from each other (J. Constanzo, pers. comm.). This proximity would facilitate calls to warn conspecifics of a predation risk that is not readily visible (Carothers et al., 2001).

The main spectral components of the weeping lizard call concentrate in a broad band between 1.8–8.2 kHz, which is within the range of the frequencies recorded in the calls of Unidentata lizards (Milton and Jenssen, 1979; Böhme et al., 1985; Ouboter, 1990), and also within the range of the hearing sensitivity of these lizards (Manley, 2002). High-frequency distress calls by vertebrates have been considered adaptive responses to predators having auditory sensitivity in this spectral range (Caro, 2005), which supports the hypothesis that calls of the weeping lizard may startle predators (Carothers et al., 2001). This lizard is mainly preyed by mammals, raptors, and snakes (Jaksic et al., 1982), and the first two are endowed with hearing sensitivities in the high-frequency range that match the spectral contents of the distress calls of *L. chiliensis* (Manley, 1990). In contrast, the sensitivity of snakes is restricted to low-frequency sounds (<1 kHz; Young, 2003), and snakes would therefore not be able to detect calls of *L. chiliensis*. However, snakes are responsive to sound-induced head vibration (Christensen et al., 2012) and body vibration (Boback et al., 2012), which can be effective mechanisms for

detection of sounds like these calls. Alternatively, the high-frequency distress calls of *L. chiliensis* may serve to attract secondary predators that prey on primary predators, a circumstance may give the lizard a chance to escape (Caro, 2005).

The calls of *L. chiliensis* also contain harmonics extending into the ultrasound range, and so far, this has only been documented in Gekkota (Brown, 1985; Frankenberg and Werner, 1992). Nevertheless, there are no reports of hearing sensitivity in this frequency region for any lizard. The highest hearing limit reported reaches ~14 kHz in pygopod geckos that produce ultrasound (Manley and Kraus, 2010). Therefore, it is unlikely that the weeping lizard is sensitive to ultrasound, and that these high-frequency components are effective for intraspecific communication. However, it is possible that ultrasound is just a byproduct of the emission of these vocalizations (e.g., Blumberg and Sokoloff, 2001).

The presence of nonlinear phenomena in the distress call of *L. chiliensis* is a feature that has not been reported in other lizards, although it has been described in different tetrapod taxa: mammals (e.g., primates: Fitch et al., 2002; whales: Tyson et al., 2007), birds (Fee et al., 1998; Narins et al., 2004), and amphibians (frogs: Narins et al., 2004; Feng and Narins, 2008). In mammals, nonlinearities are produced by the vocal folds and potentially by other oscillators such as air sacs and vocal membranes (Herzel et al., 1995; Fitch et al., 2002). In birds, these phenomena involve the syrinx (Fee et al., 1998), while in frogs, the vocal folds are the most probable emitter structures (Suthers et al., 2006; Feng and Narins, 2008). In Unidentata lizards, however, it is unknown which structures are implicated, and the only attempt to identify the structures involved in the vocal sound production in Unidentata failed to find any specialized structure (Milton and Jenssen, 1979). However, the high complexity of the weeping lizard call, including the nonlinearities, can only be generated by specialized laryngeal structures similar to those found in Gekkota (Russell et al., 2000). It remains unclear, however, if these nonlinearities have any function, such as those reported in other studies, e.g., reducing habituation and keeping the attention of receivers (Fitch et al., 2002; Blumstein and Recapet, 2009; Townsend and Manser, 2011).

The distress calls of *L. chiliensis* contain information about individual characteristics, e.g., the fundamental frequency and duration of the calls are related to body size. Moreover, duration can be a honest signal of stamina (Fischer et al., 2004), as longer calls imply higher energetic demands (Taigen and Wells, 1985). It is likely that other call features like frequency-modulation patterns or nonlinearities also encode relevant information, such as the degree of aggressiveness (Hibbitts et al., 2007) or body condition (Juola and Searcy, 2011), information that can startle predators (e.g., Laiolo et al., 2004), or that can be used to decide if the prey is worthy or not, e.g., easy to eat, without struggles.

The sexes differed in two characteristics of their calls; males produced louder calls and calls with less nonlinear phenomena than females. These differences would probably be irrelevant for predators, and it is unclear if these have significance for conspecifics since we lack information on the species' social structure. However, even if distress calls can give information valuable for sex recognition, they do not convey more information on "who" is the emitter. The spectro-temporal characteristics showed high intra-individual variation, and the DFA assigned only 20% of the calls to

the correct individuals. Such high variability is, however, a feature common to alarm/defensive calls of various vertebrates (see Weber and Werner, 1977). Nevertheless, the observed sexual variation in these distress calls may provide the basis for further evolution of social communication mediated by acoustic signals (Milton and Jenssen, 1979).

In summary, the detailed spectro-temporal analysis of the distress calls of the weeping lizard shows that these vocalizations may attain considerable complexity. The analysis of their characteristics provides insights into the potential adaptive value, fostering further tests of specific hypotheses on the role in the weeping lizard as well as in other Unidentata.

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