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Original Article

Distress vocalizations of *Aspidoscelis costatus costatus* (Squamata: Teiidae): when does this behavior occur in the ontogeny?

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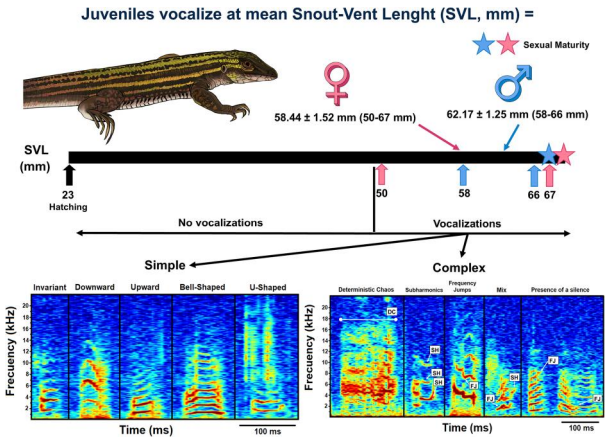
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Abstract

Vocal sound production has been reported in juveniles of mammalian, avian, and nonavian sauropsid lineages. In this last taxon, studies concerning the ontogenetic development of vocalizations have mainly been focused on Crocodylia and Testudines. Less is known about Squamata, though this behavior has been recognized in a few juvenile gecko species, albeit only characterized in the Mediterranean House Gecko (*Hemidactylus turcicus*). In the present study, we identified the vocalizations emitted by the juvenile Balsas Basin Whiptail lizard (*Aspidoscelis costatus costatus*), a species endemic to Mexico. We sought to characterize the spectro-temporal variables of the juveniles' calls and determine whether these vocalizations occur during early ontogeny or are associated with a minimum snout-vent length. The study included 74 individuals (41 hatchlings, 33 juveniles); only 21 juveniles vocalized (16 females and 5 males). The calls possessed simple and complex modulation patterns and were only emitted when the individuals were seized. Thus, we classified them as distress calls. Sound production occurs before the first year of life. However, hatchlings did not vocalize, and individuals required a minimum snout-vent length to emit sound. Three nonmutually exclusive hypotheses are proposed to interpret these findings: 1) the vocal structure responsible for sound production develops during ontogeny; 2) juveniles do not have enough energy to vocalize, as this energy is primarily allocated for growth and maturation; and 3) juveniles only vocalize once an adequate size has been obtained, which allows calls to reach an effective intensity and/or duration.

Keywords behavior, development, distress calls, juveniles, predation

Graphical abstract



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Vocal sound production in tetrapods is a feature present in all its lineages (Bradbury and Vehrencamp 1998), amphibians, avian and nonavian sauropsids (hereafter reptiles), as well as mammals (Köhler et al. 2017; Lewis et al. 2021; Russell and Bauer 2021). This sound production is innate (Nieder and Mooney 2020; Zhang et al. 2023), although in some bird and mammal lineages, certain types of vocalizations need to be learned, allowing animals to incorporate sounds with specific characteristics of the group/population in their repertoire, which facilitates their communication (Mooney 2020). This behavior has been reported in parrots (Pepperberg 2010) and cetaceans (Zamorano-Abramson et al. 2023), to mention a few examples.

Among reptiles, significant attention has been given to sound production across the ontogeny in Crocodylia (Mathevon et al. 2013; Chabert et al. 2015; Russell and Bauer 2021). These ubiquitous calls occur while hatchlings are still inside the egg and are especially prevalent during the early stages of their life. Vocal activity decreases throughout ontogeny, although juvenile calls continue shortly before sexual maturity is reached, giving way to adult vocalizations (Vergne et al. 2009; Reber 2018). The juvenile calls can be divided into 3 types: 1) hatching calls: produced just before and after egg emergence, which provide hatchlings with cues that aid in synchronizing their hatching, triggering a response in the mother to assist them by digging the nest (Vergne et al. 2009; Delbosc et al. 2025); 2) contact calls: allow hatchlings and juveniles to maintain cohesion while moving in groups or foraging (Campbell 1973; Vergne et al. 2009, 2012), and 3) distress calls: emitted by young crocodilians to summon the mother so that she may protect them from a potential predator (Reber 2018). It is worth noting that distress calls may also be found in other taxa and are produced by the organism when a predator seizes, captures, or attacks it (Magrath et al. 2015; Wu et al. 2018; Hörmann et al. 2021).

Vocalizations have also been reported early in the ontogeny of different taxa within the order Testudines (Ferrara et al. 2019; Charrier et al. 2022; Jorgewich-Cohen et al. 2022). These occur in embryos, hatchlings, and juveniles of marine (Ferrara et al. 2014a, 2014b; Ferrara et al. 2019; McKenna et al. 2019; Monteiro et al. 2019), as well as freshwater turtles (Giles et al. 2009; Ferrara et al. 2013; Jorgewich-Cohen et al. 2024, 2025). As per Ferrara et al. (2019) and Jorgewich-Cohen et al. (2024), vocalizations found in turtle embryos and hatchlings could serve different functions: 1) prehatch vocalizations could synchronize hatching behavior; 2) after hatching, sounds may synchronize the digging efforts to reduce energy expenditure; and 3) once underwater, vocalizations may be used by hatchlings to gather close together.

Much less information is available on this behavior during early ontogeny in the order Squamata (Russell and Bauer 2021). In the clade Gekkota, it is known that juveniles of the Asian House Gecko (*Hemidactylus frenatus*; Hopkins et al. 2020) and the Leopard Gecko (*Eublepharis macularius*; Landová et al. 2013) vocalize, with the latter doing so after being disturbed and unable to flee from a predator. Frankenberg (1982) indicated that juveniles of the Mediterranean House Gecko (*Hemidactylus turcicus*) vocalize when approached by adults; these vocalizations are loud, lacking both modulation patterns and harmonics, although they become increasingly harmonious as the threat, adults, get closer to the young.

In contrast, and as far as we know, no reports or analyses of calls emitted by hatchlings or juveniles exist in the clade Unidentata. It is no surprise, however, as vocalizations found in adults of this clade are already quite cryptic and seldom studied. Reports for adults of a few species of some families of the Unidentata clade show that they may exhibit this behavior during social encounters (Russell and Bauer 2021). For example, during agonistic encounters between males, the Argentine Black and White Tegu (*Salvator merianae*) emits sibilated sounds (Winck and Cechin 2008), whereas the Graham's Anole (*Anolis grahammi*) utters squeaks (Milton and Jenssen 1979).

Oral sound production in Unidentata, however, is mainly exhibited under predation risk (Labra et al. 2013). In Crotaphytidae, the Long-nosed Leopard Lizard (*Gambelia wislizenii*) produces vocal sounds described as similar to moans or wails when alarmed or threatened by a predator, especially if individuals have a low body temperature, leaving them unable to rapidly escape to avoid predation (Wever 1966; Crowley and Pietruzka 1983). In Dactyloidae, at least 6 species of *Anolis* emit vocalizations when captured or handled (10 other species vocalize under uncertain contexts; Ruibal 1964; Williams et al. 1965; Myers 1971; Milton and Jenssen 1979), and *A. grahammi* utters grunts and wails at being seized (Milton and Jenssen 1979). Hartdegen et al. (2001) report the calls emitted by the Red-Eyed Crocodile Skink (*Tribolonotus gracilis*; Scincidae) when caught; females were also observed vocalizing when detecting a potential threat to their eggs, showcasing parental care. Then, the Liolaemidae's Weeping Lizard (*Liolaemus chiliensis*) vocalizes after being captured (Labra et al. 2013), as well as members of other lizard families, including Lacertidae (e.g., the Algerian *Psammodromus*, *Psammodromus algirus*; Baeckens et al. 2019), and Teiidae, such as *Aspidoscelis* (e.g., Milstead 1961; Campbell 1969; Bowker 1980; De La Rosa-Silva et al. 2023; Rivera et al. 2024).

All individuals of the Balsas Basin Whiptail, *Aspidoscelis costatus costatus*, incited to vocalize by De La Rosa-Silva et al. (2023), were adults. We recently, however, noted that some juveniles emit calls when grasped. Based on these observations, we intend to analyze the spectro-temporal variables of juvenile vocalizations in this species and determine whether vocalizations occur early in ontogeny or whether sound production is associated with a minimum snout-vent length (SVL). Additionally, we evaluate the effect of SVL on calls, considering data from juveniles and adults (using information from De La Rosa-Silva et al. 2023). Finally, given that temperature influences the vocalizations of the species, as observed by De La Rosa-Silva et al. (2023), we aim to assess whether it has any impact on juvenile calls.

Materials and methods

Study area

The research was conducted within an urban zone spanning approximately 2,700 m^2, located next to a bitumen driveway (Federal Highway 55) in the municipality of Ixtapan de la Sal, Estado de México, México. This area was chosen as it had previously been sampled to capture adult specimens of *A. costatus costatus* (De La Rosa-Silva et al. 2023). The study site has a well-defined seasonality characterized by a wet season from June to mid-September and a dry season from around mid-September to May (Hernández-Gallegos and Domínguez-Vega 2012).

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Gravid females of *A. costatus costatus* lay eggs seasonally from June to September during the wet season (Hernández-Gallegos et al. 2020). Hatchlings emerge mainly from August to November, with juveniles present from September to May (Rubio-Blanco 2007). We collected lizards in November 2022 (2 days), April 2023 (3 days), May 2023 (1 day), and September 2023 (1 day). In addition, we included individuals collected as eggs from several wild nests that hatched in the laboratory in August 2019.

Capture of juveniles and procurement of biometric data

On each field trip, we searched for lizards from 8 AM to 2 PM. The team consisted of 5 people; thus, our study involved 210 h of exploration. We only considered sexually immature individuals of both sexes of 2 developmental stages. The hatchling stage (hereby class I) corresponds to a SVL of less than 45 mm (Gómez-Benitez et al. 2020), with a prominent ventral scar. Conversely, the juvenile stage (hereby class II) has a SVL of 46–66 mm for males and 46–67 mm for females (Gómez-Benitez et al. 2020). We considered an adult to be an individual with a SVL equal to or larger than 67 mm for males and 68 mm for females (Granados-González et al. 2015; López-Moreno et al. 2016). We captured lizards by hand, seizing them underneath rocks early in the morning or while they were active, foraging, or thermoregulating. After capture, each lizard was placed individually in a herpetological bag and rested on a warm surface for 10 min before inducing vocalizations, avoiding overheating it.

In total, we tested 74 individuals: class I = 41: 12 in August (hereby 1-month-old; 7 ♀, five ♂), 7 during September (2-month-old; 4 ♀, 3 ♂), 22 in November (4-month-old; 9 ♀, 13 ♂), and class II = 33: 4 in November (1 ♀, 3 ♂), and 29 in April–May (9- and 10-months-old; 21 ♀, 8 ♂). Lizard age was proposed under the assumption that hatching took place in August due to the 12 individuals that hatched in the laboratory during that month. It should be noted that age could vary mildly, as hatchlings are reported to be present from August to November (Rubio-Blanco 2007).

We stimulated individuals to vocalize using a modified protocol of De La Rosa-Silva et al. (2023). It entails carefully gripping an individual by the torso before giving gentle strokes to its snout and head for 3 min. To reduce stress, we made 2 short pauses of 10 s, after 50 s of stimulation; thus, the total recording time was 2 min, 40 s. A Tascam® DR-05 digital recorder with a protective cover over the microphone to muffle external sounds was placed about 10 cm from the lizard's snout to register the vocalizations. All recordings were made inside a motorized vehicle to minimize the effects of external sounds. In the case of those individuals hatched in the laboratory, we kept the protective cover of the microphone to standardize the technique, even though the recordings were done in the laboratory. We minimized extrinsic noise by proceeding in the mornings (9–10 AM) when there was little or no human activity.

At the end of the call acquisition session, we registered the lizard's body temperature using a Miller and Weber® cloacal thermometer. We sought to keep the temperature within an optimal threshold (30–38 °C, Rubio-Blanco 2007 for *A. costatus costatus*) to prevent shifts in behavior stemming from the temperature (De La Rosa-Silva et al. 2023). Nevertheless, we tested whether temperature modulated the acoustic variables recorded. We then measured the lizard's SVL with a plastic ruler. Individuals were sexed using the technique detailed by Ashton (2003), determining the presence of post-cloacal scales, as these are only visible in males. After all the measurements were taken, individuals were released in healthy conditions at their exact collection points no later than 1 h after their capture. The hatchlings from August 2019 were also freed in the area where we found their nests.

To reduce stress or potential harm to the lizards, they were not grasped by the tail, preventing autotomy. Then, letting them rest on a herpetological bag after being seized sought to reduce stress due to handling (Labra 2011). The stimulation protocol was based on Labra et al. (2013), who reported no ill effects on the *L. chiliensis* individuals recorded. Additionally, the same investigator (E.R-S) performed the vocal stimulation in all instances. Although an accurate measure of the force applied cannot be provided, contact with the lizards was kept to a minimum in strength and surface area to avoid altering the lizard's body temperature. We chose a total stimulation period of 3 min to maximize data acquisition while minimizing distress for the animal. Although we did not detect any anomalies during this process, we were prepared to suspend the stimulation if any change in the lizard was detected.

Analysis of vocalizations

We characterized the vocalizations stored in .WAV files (96 kHz, 16 bits) using Raven® Pro 1.6, employing a short-time Fourier transformation, with a Hanning window length of 512 points and an overlap of 50% (Díaz and Labra 2023). Following the classification established by De La Rosa-Silva et al. (2023), we measured different spectro-temporal variables at the beginning of the vocalization (see Table 1 for definitions): fundamental frequency (FF; kHz), dominant frequency (DF; kHz), and the number of harmonics. The remaining variables, duration (s), maximum frequency (kHz), delta frequency (kHz), aggregate entropy (bits), and bandwidth (90%, kHz), were quantified considering the entire vocalization (for more details, see De La Rosa-Silva et al. 2023). Calls were characterized as simple or complex based on the absence or presence of nonlinear phenomena (NLP), respectively. The modulation patterns of simple calls were classified by measuring the FF at the beginning, middle, and end of the call (see Figure 1 for a description of the simple modulation patterns considered). Complex calls, on the other hand, are vocalizations which contain NLPs: acoustic transitions both rapid and qualitative, which occur when the vocal folds, or similar structures, vibrate asynchronously as sound is emitted (Fitch et al. 2002; Tokuda 2018). The categorization of each complex modulation pattern was based on the NLP type observed (see Figure 2).

Statistical analysis

Call variables and the morphological data are presented as mean ± standard error (*SE*). To standardize each individual for the call statistical tests, we used the average of each of its calls. We

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conducted a parametric 2-way ANOVA considering the 74 individuals to determine differences in SVL across months and sexes, followed by a Tukey's multiple range test. A non-parametric Mann–Whitney test was used to determine whether the SVL averages of the juveniles that vocalized differed between sexes. Additionally, Pearson's correlation coefficients were used to determine whether SVL modulates the acoustic variables, considering juvenile and adult vocalizations, the latter obtained from De La Rosa-Silva et al. (2023). This test was also implemented to explore whether temperature could influence the vocal behavior. The statistical tests were performed using STATGRAPHICS® Centurion XVII and were considered significant if $P < 0.05$.

Table 1 Definitions of the acoustic variables measured in the calls of juvenile Balsas Basin Whiptails (*Aspidoscelis costatus costatus*), endemic to México

Variable	Definition
Duration (s)	The amount of time during which a vocalization lasts
Fundamental frequency (kHz)	The basal or lowest harmonic found in a vocalization, from which all other harmonics are multiples of
Dominant frequency (kHz)	The harmonic which contains the most amount of energy in the vocalization
Maximum frequency (kHz)	The maximum power in a vocalization transpires in this harmonic
Delta frequency (kHz)	Contrasts the lower and upper frequency limits within a vocalization
Aggregate entropy (bits)	Evaluates the energy distribution within a vocalization by assessing the disorder in the sound. The higher the values, the more chaos within the vocalization
Bandwidth (90%, kHz)	Contrasts the 5% and 95% frequencies found in a vocalization
Number of harmonics	Refers to the sum of all harmonics within a vocalization

Results

Of the 74 juveniles tested, only the 9- to 10-month-old juveniles vocalized: from the 29 collected individuals of this age, 21 emitted sounds (72.4%), corresponding to 16 females (76.2%) and 5 males (23.8%). Some of these individuals also vocalized directly after being captured or while we measured their morphological variables, and a male emitted a call a few seconds after the 3 min of recordings. None of these vocalizations were included in the analyses. During stimulation, most emissions (97.8%) occurred when the juveniles had their mouths closed, except for 1 female, which vocalized with her mouth open. Lizards also attempted to escape, writhing and threshing on the investigator's grasp and using their tails to lash out; bite attempts were rarely observed.

Juveniles emitted a total of 46 vocalizations. Most individuals produced more than 1 vocalization (52.4%), with a female uttering up to 7 calls. As shown in Table 2, the calls had a short duration and few harmonics. Furthermore, calls exhibited simple (Figure 1; Supplementary Audio 1) and complex modulation patterns (Figure 2; Supplementary Audio 2), although most of the 46 calls (69.6%) were complex. As shown in Table 3, the most frequent patterns observed in simple and complex calls were downward and deterministic chaos, respectively. We discerned that 15 (11 females, 4 males) out of 21 lizards emitted at least 1 complex vocalization. One complex call exhibited a brief break of 0.019 s (Figure 2E).

Lizards grew over the months (Figure 3; $F_{3,73} = 135.25$, $P < 0.0001$), without difference between sexes ($F_{1,73} = 0.21$, $P = 0.65$), and there was no interaction between these 2 factors ($F_{3,73} = 0.52$, $P = 0.67$). On average, lizards began vocalizing when they reached a mean SVL of 58.44 ± 1.52 mm (range, 50–67) for females and 62.17 ± 1.25 mm (range, 58–66) for males. This mean size, however, was similar between the sexes ($U = 32.0$, $P = 0.25$).

Considering the data for juveniles and adults, as recorded by De La Rosa-Silva et al. (2023), SVL modulates certain spectrotemporal variables. SVL showed a negative relation with fundamental and maximum frequency, whereas a positive relation

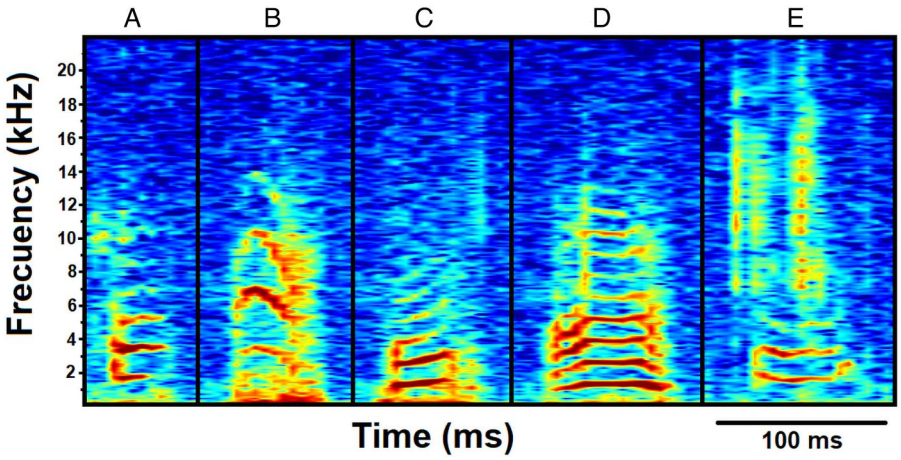


Figure 1 Spectrograms showing the 5 simple modulation patterns identified in the juveniles' calls of the Balsas Basin Whiptail (*Aspidoscelis costatus costatus*). (A) invariant (the FF remains constant; deviation of less than 4% in the FF), (B) downward (the FF diminishes progressively), (C) upward (the FF increases progressively), (D) bell-shaped (the FF has its highest increase up to the middle of the call, then decreases), and (E) u-shaped (the FF decreases significantly up to the middle of the call, then increases).

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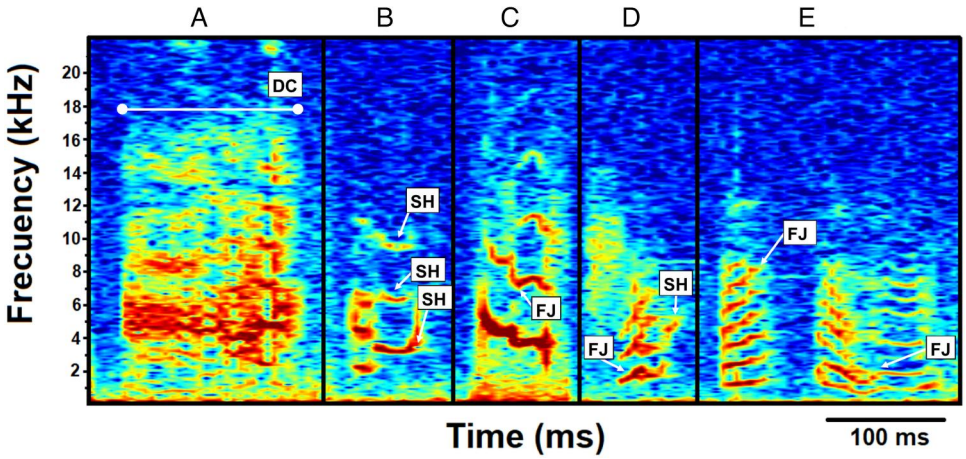


Figure 2 Spectrograms showing 3 complex modulation patterns identified in the juveniles' calls of the Balsas Basin Whiptail (*Aspidoscelis costatus costatus*). (A) deterministic chaos (DC; the call has additional, non-arbitrary auditory elements), (B) subharmonics (SH; the main spectral components possess secondary constituents among them) indicated by the arrows, (C) frequency jump (FJ; sudden change of the frequency in the call). Some vocalizations had more than 1 pattern, (D) a mix with frequency jumps and subharmonics. In addition, 1 call included a silence (E), a break in between a frequency jump.

Table 2 Mean (± *SE*, standard error; Range, minimal and maximal value) of the spectro-temporal variables recorded in the distress calls emitted by juveniles and adults of the Balsas Basin Whiptail (*Aspidoscelis costatus costatus*). The statistical values (*r* and *P*) of the correlations with SVL and spectro-temporal variables of both juveniles and adults are also presented. Statistically significant values are highlighted in bold.

Variable	Juveniles mean ± *SE* (range)	N	Adults mean ± *SE* (range)	N	Statistical values
Duration (s)	0.05 ± 0.01 (0.03–0.16)	21	0.14 ± 0.03 (0.04–0.36)	11	$r = 0.349$, $P = 0.05$
Fundamental Frequency (kHz)	3.11 ± 0.48 (0.17–5.86)	13	1.65 ± 0.12 (1.32–2.27)	9	**$r = -0.482$, $P = 0.02$**
Dominant Frequency (kHz)	3.89 ± 0.54 (0.17–6.8)	13	2.76 ± 0.35 (1.38–4.31)	9	$r = -0.330$, $P = 0.13$
Maximum Frequency (kHz)	4.04 ± 0.30 (1.81–7.15)	21	2.32 ± 0.28 (0.95–4.05)	11	**$r = -0.491$, $P = 0.004$**
Delta Frequency (kHz)	8.95 ± 0.87 (1.18–15.20)	21	12.5 ± 1.51 (6.89–21.23)	11	**$r = 0.370$, $P = 0.04$**
Aggregated Entropy (bits)	4.67 ± 0.16 (3.05–5.93)	21	4.9 ± 0.25 (4.18–7.08)	11	$r = 0.026$, $P = 0.89$
Bandwidth (90%, kHz)	3.98 ± 0.42 (0.60–6.55)	21	3.88 ± 1.1 (1.1–1.47)	11	$r = -0.018$, $P = 0.92$
Number of Harmonics	2.80 ± 0.39 (1–6)	13	7.6 ± 0.8 (4.0–11.0)	9	**$r = 0.759$, $P < 0.001$**
Number of Complex Vocalizations	1.52 ± 0.29 (0–5) Percentage: 69.6%	21	1.73 ± 0.38 (1–5) Percentage: 79.2%	11	$r = 0.156$, $P = 0.40$

N = sample size (number of individuals that vocalized). The sample size differs in several instances due to the unfeasibility of estimating these variables in calls with complex modulation patterns (e.g., deterministic chaos). The adult data were obtained from De La Rosa-Silva et al. (2023). Finally, the percentages indicate the amount of complex modulation patterns observed when compared to the total number of recorded vocalizations.

with delta frequency and the number of harmonics was seen. The duration, DF, aggregated entropy, bandwidth, and number of complex vocalizations showed no association with SVL (Table 2). On the other hand, temperature showed a positive correlation with DF ($r = 0.684$; $P = 0.01$); no other variable correlated with temperature ($P > 0.05$ in all cases).

Discussion

Our study confirms that juveniles, but not hatchlings, of *A. costatus costatus* vocalize; thus, oral sound production in this species is not an exclusive behavior of adults (De La Rosa-Silva et al. 2023). Due to the presence of both simple and complex modulation patterns, we can infer that there are anatomical structures that modulate sound production in juveniles, since these modulations require a vocal structure (e.g., oscillators such as air sacs, vocal folds, or membranes) to regulate the air release (Fitch et al. 2002; Russell and Bauer 2021).

We classify the vocal production of the juvenile lizards as distress calls because 1) individuals were only observed to emit sounds when seized or captured, never showcasing other antipredator vocal responses, such as alarm calls (i.e., vocalizations emitted upon detecting a potential danger, such as a predator; Berthet and Zuberbühler 2020) and 2) lizards display antipredator behavior like escape attempts during sound production. Both characteristics are consistent with what has been reported in other species that exhibit distress calls (Labra et al. 2013; Magrath et al. 2015; Hörmann et al. 2021).

The presence of NLPs in vertebrates has been linked to high arousal levels, which primarily stem from stressful contexts (Massenet et al. 2025), coding aggressive (Anikin et al. 2021),

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Table 3 Number and percentage in which the simple and complex modulation patterns were registered in the 46 distress calls produced by juveniles of the Balsas Basin Whiptail (*Aspidoscelis costatus costatus*)

Simple modulation patterns	Number of instances	Percentages
Invariant	2	4.4
Downward	5	10.8
Upward	1	2.2
Bell-shaped	3	6.5
U-shaped	3	6.5
Total	**14**	**30.4**
Complex modulation patterns	**Number of instances**	**Percentages**
Deterministic Chaos	22	47.8
Subharmonics	5	10.9
Frequency Jump	4	8.7
Mix	1	2.2
Total	**32**	**69.6**

For more information on these patterns, see Figures 1 and 2, respectively.

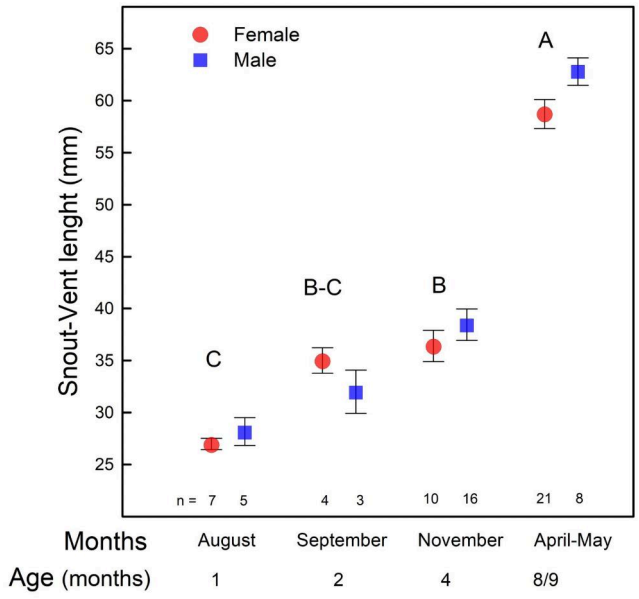


Figure 3 Mean (± *SE*, standard error) snout-vent length (SVL, mm) per month (and age) of the hatchlings and juveniles of the Balsas Basin Whiptail (*Aspidoscelis costatus costatus*). *n* = sample size; number of females and males per month. The 9- and 10-month-old juveniles were the largest (April–May; letter A; $P < 0.0001$) and significantly different from the younger individuals: 4-month-olds (November; letter B), 2-month-olds (September; letters B–C), and 1-month-olds (August; letter C).

pain (Corvin et al. 2025), and/or fearful (Blesdoe and Blumstein 2014) responses. These become especially alarming if deterministic chaos is involved (Terrade et al. 2025). The higher number of complex vocalizations compared with simple calls, with most of the modulation patterns being deterministic chaos, suggests a fear reaction of *A. costatus costatus* to the stimulation. Ruiz-Monachesi and Labra (2020), for example, observed heightened fear responses in *L. chiliensis* lizards when exposed to complex calls of conspecifics, in contrast to simple calls.

Individuals of *A. costatus costatus* exhibit vocal sound production under predation risk, although the exact function of this behavior remains unclear; whether it benefits the sender, conspecifics, or modulates the response of the potential predator (e.g., Branch and Freeberg 2012; Hoare and Labra 2013). Beyond this unresolved question, another must be addressed: why do lizards not emit distress calls earlier in the ontogeny? We propose 3 nonmutually exclusive hypotheses to explain these observations.

First, we propose that the vocal structure involved in the sound production of *A. costatus costatus*, regardless of its nature, does not fully mature until the individuals reach a specific body size. For example, in green-rumped parrotlets (*Forpus passerinus*), Berg et al. (2013) examined the physiological and vocal ontogeny, noticing short, high-pitched vocalizations that featured more NLPs from 0 to 13 days of age, when the neural pathways, skeleton, and muscles are still developing in the functional structures they have as adults. Moreover, in the case of the studied species, the short duration of the juvenile calls could also be explained by the relatively small size of the respiratory system, which is still developing as the lizard grows, as seen in bird chicks (Vleck and Bucher 1998).

The second hypothesis is related to the energy involved in sound production. Van Zele et al. (2024) determined that the emission of warning hisses by the long-nosed viper (*Vipera ammodytes*) entailed an increment in energy expenditure and water loss due to the muscular activity involved during this behavior. Under this context, juveniles of *A. costatus costatus* may not have sufficient energy availability to vocalize, unlike adults. Previous studies that explored the development of *A. costatus costatus* found that juveniles reach sexual maturity 1 year after hatching, experiencing an increased growth rate (0.317 mm per day) during the wet season (June to mid-September), when resources (e.g., basking sites, food, water) are better and/or more abundant for lizards (Rubio-Blanco 2007; Hernández-Gallegos and Domínguez-Vega 2012). The growth rate decreases during the dry season (mid-September to May), likely due to depletion in resource availability (Rubio-Blanco 2007). In this context, we propose that juveniles allocate energy to mature into reproductive adults as fast as possible and that the development of the vocal structure is delayed until later in the ontogeny; thus, energy is only allocated toward vocal sound production late during the dry season, once the juveniles are at least 8 to 9 months of age. A fast growth rate is a strategy observed in different *Aspidoscelis* species (Ramírez-Bautista et al. 2000; Hernández-Gallegos 2004), including *A. costatus costatus*, which exhibits low annual survival rates, with an average lifespan in the wild of 1 to 2 years (Rubio-Blanco 2007). Nevertheless, individuals in the studied population have been recorded to live up to 5 years (Hernández-Gallegos et al. 2023).

A final hypothesis is that the studied lizard may only vocalize until juveniles reach a specific size, when calls are loud enough or have enough duration to be effective. Forti et al. (2018) determined that body size in anuran species correlated with the occurrence of distress calls; small species are unable to sustain vocal sound production for a sufficient duration and/or at high enough intensity, so they either lose or never develop this behavior.

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Albeit it was determined not to be statistically significant, it is interesting that the minimum SVL at which juvenile females of *A. costatus costatus* start to vocalize is lower than in males (i.e., 50 and 58 mm, respectively). Moreover, a female produced the most vocalizations during stimulation, a total of 7, and comparatively, more females than males vocalized. These observations may imply that juvenile females physiologically mature and develop a vocal system faster than males. Thus, calls could possess a greater significance in the behavior of the former. Nevertheless, there is insufficient information to validate such hypotheses, which must be tested in future research.

A general comparison between the vocal characteristics of the juveniles and adults of *A. costatus costatus* (De La Rosa-Silva et al. 2023) showed some differences. In contrast to adults, the distress calls of juveniles contain fewer harmonics. Indeed, some vocalizations contain only the FF. This, in turn, causes a reduction in the delta frequency, as with fewer harmonics, juveniles cannot reach the higher frequencies that adults display. Likewise, we observed that the distress calls of juveniles have a higher pitch than those of adults, as reflected in both the fundamental and the maximum frequencies. These differences may be related to the principle of negative size-frequency allometry, i.e., the production of vocalizations with lower frequencies by larger organisms (Bowling et al. 2017) and could also imply that juvenile vocalizations change as they mature into adulthood. Juveniles and adults exhibited the same trends regarding the most common modulation patterns: downward in the case of the simple and deterministic chaos, for the complex modulation patterns (De La Rosa-Silva et al. 2023). Nevertheless, vocalizations with a mix of complex modulation patterns were less observed in juveniles (2.2%) than in adults (38%; De La Rosa-Silva et al. 2023).

Comparing the juvenile distress calls of *A. costatus costatus* with those of other lizard species is challenging. Although there are reports on the vocalization of juvenile geckos (Landová et al. 2013; Hopkins et al. 2020), only Frankenberg (1982) described the sounds emitted by juveniles of *H. turcicus*. Moreover, our study appears to be the first in the Teiidae, or Autarchoglossa (comprising Scincopmorpha and Anguimorpha; Simões and Pyron 2021) to approach this subject.

Based on Frankenberg's (1982) observations, the main potential distinction between both species is that, unlike the calls of *A. costatus costatus,* which appear as single events, some of the calls of juvenile *H. turcicus* could be sequential, separated by no more than 150 ms. At first glance, it may be argued that a difference in function exists, as *H. turcicus* calls are seemingly involved in social interactions of juveniles with adults (Frankenberg 1982). Indeed, the emission of vocalizations remains a key aspect of communication in geckos, a trait that has evolved in association with their nocturnal habits (Wever et al. 1963; Gamble et al. 2015). However, the calls of *H. turcicus,* although produced in a social setting, appear to be a response to a potential risk, as adults of the species are known to exhibit cannibalism toward both hatchlings and small juveniles (Locey and Stone 2008). Thus, this would be a characteristic shared with *A. costatus costatus.*

As ectothermic vertebrates, a key aspect of reptile behavior is achieving an optimal body temperature, which allows for proper biological function (Raske et al. 2012), with sound production being no exception (Christensen-Dalsgaard et al. 2025). As a result, acoustic characteristics may be modified by this variable (Ladich 2018). Indeed, De La Rosa-Silva et al. (2023) reported that inactive *A. costatus costatus* lizards (mean body temperature 27 °C) vocalized less than active lizards (mean body temperature 34 °C). Thus, in this study, an adequate foraging temperature interval for the species (30–38 °C; Rubio-Blanco 2007) was chosen to prevent shifts in behavior in the individuals tested. Although most spectro-temporal characteristics evaluated showed no statistical association with temperature, this was not the case with the DF. This is interesting, as in other ectothermic vertebrates, such as fish and amphibians, a similar relationship has been reported, i.e., the Weakfish (*Cynoscion regalis*; Connaughton et al. 2000), the Striped Raphael Catfish (*Platydoras armatulus*; Papes and Ladich 2011), the Tiger Perch (*Terapon jarbua*; Amron et al. 2017), and the Gray Treefrog (*Hyla versicolor*; Gerhardt 2005; Humfeld and Grunert 2015). It is postulated that this increase in DF is caused by an increment in activation rate and contraction speed of the muscles responsible for sound production at elevated temperatures, at least in the Roche's blenny (*Ophidion rochei*; Kéver et al. 2015). Under this context, we propose that a similar effect takes place in *A. costatus costatus*, though the novelty of this discovery merits further research.

In conclusion, juveniles of *A. costatus costatus* display audible distress calls as a response to predation risk, although the exact function of these calls remains unknown. Although vocalizations with simple modulation patterns were observed, most showed complex patterns, i.e., with NLP. Both sexes began to vocalize at a similar mean body size when they were 9- to 10-month-old, which suggests that vocalizations do not occur until a certain point during development. Juvenile calls are shorter and higher pitched than those emitted by adults.

Observations such as these deepen our understanding concerning sound production in lizards, especially those belonging to the clade Unidentata. Furthermore, the present investigation seeks to bridge the pronounced gap in our knowledge of Squamata's bioacoustics, as a significant portion of ontogenetic studies on this topic primarily focus on crocodiles and turtles (Vergne et al. 2009; Mathevon et al. 2013; Chabert et al. 2015; Ferrara et al. 2019; Russell and Bauer 2021; Charrier et al. 2022; Jorgewich-Cohen et al. 2024). Analyzing the physiological and developmental mechanisms responsible for innate vocalizations would help to determine why species such as *A. costatus costatus* do not vocalize until they reach a specific size. Finally, future studies should investigate the functionality of vocalizations in this and other lizard species.

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Authors' contributions

All the authors undertook the planning phases of the study. Conception of study: E.R.-S., A.L., and O.H.-G. Fieldwork: E.R.-S. and O.H.-G. Data analysis: E.R.-S., revised by A.L. and O.H.-G. E.R.-S. wrote the original manuscript, revised by A.L. and O.H.-G. All authors thoroughly read and approved the final draft of the manuscript.

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Conflict of interest statement

The authors declare they have no conflict of interest.

Ethics statement

The collection permit (SGPA/DGVS/002491/18) was provided by the Mexican government (Secretaría de Medio Ambiente y Recursos Naturales; SEMARNAT) to conduct the study.

Supplementary material

Supplementary material can be found at https://academic.oup.com/cz.

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