
DESCRIPTION OF VOCALIZATIONS FROM THE ENDEMIC MEXICAN LIZARD, *ASPIDOSCELIS COSTATUS COSTATUS* (BALSAS BASIN WHIPTAIL)

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Abstract.—Acoustic communication has been reported in the order Squamata, although there are still few studies on this behavior, which constrain our understanding of the functionality and evolution of vocalizations produced in Squamates, especially in the clade Unidentata. The Balsas Basin Whiptail (*Aspidoscelis costatus costatus*) is an endemic lizard to the western Mexican area, which has been anecdotally reported to vocalize. We took the first step in understanding the functionality of the sound production of this species by determining when individuals vocalize, characterizing these sounds by measuring the spectro-temporal variables, and assessing the effect of the temperature on vocal production. We collected 19 female and six male *A. c. costatus* and obtained 24 vocalizations from seven females and four males. Vocalizations were tonal, short, and relatively low-pitched with several harmonics. Individuals vocalized when caught or cornered, which we define as distress calls. At high body temperatures, lizards vocalized more than those at lower body temperatures. Finally, we compared the vocalizations produced by *A. c. costatus* with those reported for other lizard species, especially with the anecdotal reports within the genus *Aspidoscelis*.

Key Words.—behavior; distress calls; nonlinear phenomena; predation; Teiidae

INTRODUCTION

Acoustic communication is the transmission of messages through sound waves, which allow organisms to interact over long distances, in the darkness, or under restricted environmental conditions, such as impeded vision (Vergne et al. 2009). This type of communication occurs in all tetrapod groups (Carrington 1973; Ladich and Winkler 2017), as it possesses a common origin among choanate vertebrates from at least the Paleozoic Era, about 407 million years before present (Jorgewich-Cohen et al. 2022). Most of the investigation related to the description and understanding of its functionality, along with the evolution of sound production, has been mainly focused on birds (Baker 2001; Lewis et al. 2021), mammals, and anurans (Köhler et al. 2017). Although the non-avian Sauropsida (Testudines, Crocodylia, Rhynchocephalia, and Squamata) are generally considered to be rather silent animals, it is becoming known that sound production and acoustic communication are present throughout these four orders (Colafrancesco and Gridi-Papp 2016; Capshaw et al. 2021). They produce sounds through various means, such as: (1) the forceful exhalation of air through the

respiratory system, such as hisses and roars recorded in snakes, lizards, and crocodylians; (2) the aspiration and expulsion of air through the cloaca (cloacal pops) in snakes and geckos; (3) scale rubbing in desert vipers; and (4) the vibration of tail rattles, as seen with rattlesnakes (Gans and Maderson 1973). The focus of our study is the vocalizations produced by oral air expulsion and potentially modulated by a vocal system (Gans and Maderson 1973; Fitch et al. 2002; Ladich and Winkler 2017). Animals vocalize under different contexts, ranging from advertisement calls in social interactions (e.g., territorial interactions or mating; Russell and Bauer 2020) to distress calls emitted when an organism is grasped or captured by a predator (Magrath et al. 2014), which can have different functions, including discouraging the predator while struggling for release and escape (Klump and Shalter 1984; Carter et al. 2015).

Among the orders that compose the non-avian Sauropsida clade, Squamata is the most diverse with lizards accounting for more than 7,310 species (Uetz, P., P. Freed, and J. Hosek (Eds). 2022. The Reptile Database. Available from <http://www.reptile-database.org> [Accessed 25 January 2023]). In lizards, the primary knowledge about vocalizations comes from

studies of species belonging to the clade Gekkota, which are notable for vocalizing during intraspecific interactions, producing advertisement, fight, and copulatory calls during territorial, agonistic, and mating interactions, respectively (Capshaw et al. 2021). Some members of the clade Unidentata (Squamates which are neither dibamids nor gekkonids, the term referring to the presence of a sole egg-tooth; Vidal and Hedges 2005), however, vocalize mainly under interspecific interactions (e.g., predation risk; Labra et al. 2013). These vocalizations usually are distress calls, which have been reported to be emitted by species belonging to different families (Reyes-Olivares and Labra 2017; Russell and Bauer 2020; Capshaw et al. 2021).

Two *Aspidoscelis* species nested within the Teiidae family seem capable of producing vocalizations and distress calls. Campbell (1969) indicated that it had been frequently reported that the Tiger Whiptail (*Aspidoscelis tigris*) makes sounds when individuals are handled, which resemble squeaks, even though there are no descriptions of these sounds. In addition, Bowker (1980) described the emission of a short and monosyllabic squeak produced by individual Eastern Spotted Whiptail (*A. gularis*) after being disturbed when they were manipulated or grasped by the tail. Preliminary evidence suggests that individual Balsas Basin Whiptail (*A. costatus costatus*) also emit vocalizations when handled (pers. obs.), even though these have not been described. The study of sound production has been mostly overlooked in Teiidae, with our study being one of the first records of vocalizations produced by a species of *Aspidoscelis*, even though this genus has a high diversity (44 species), especially in Mexico (42 species; Uetz et al. 2022, *op. cit.*). Under this context, our primary goal is to characterize the calls produced by *A. c. costatus* measuring their spectro-temporal characteristics as the first step in understanding the vocal functionality of this endemic Mexican lizard. Our secondary goal is to determine if body temperature influences the production of vocalizations in *A. c. costatus*.

MATERIALS AND METHODS

Study area.—We collected individuals *A. c. costatus* on 4 July 2019 from an urban area of 2,700 m² near an asphaltic road in Ixtapan de la Sal (18°50'34.5"N, 99°40'51.8"W, 1,880 m elevation), Estado de México, México. The vegetation at the study site included a wide variety of grasses, herbaceous annual and perennial plants, the introduced South American *Jacaranda* tree species, and non-native ornamental shrubs (Gómez-Benítez et al. 2020). We did not observe any other whiptail lizards in the area, although the site is a habitat for other herpetofauna taxa (i.e., spiny lizards,

Sceloporus sp., tree lizards, *Urosaurus* sp., anoles, *Anolis*, sp., or rainfrogs, *Eleutherodactylus* sp.).

Capture of specimens and data collection.—We collected lizards by lifting rocks and seizing them (henceforth inactive lizards) or searching for active individuals as they were foraging or thermoregulating (henceforth active lizards). After capturing a lizard, we first measured its body temperature with a Miller and Weber Cloacal Thermometer® (Miller-Weber of Texas, Houston, Texas, USA) to assess if this variable affected vocalizations. Subsequently, we georeferenced the location where we collected the lizard. After that, we stimulated the lizard to vocalize following a modified protocol by Labra et al. (2013). Our protocol consisted of carefully grasping the animal by the torso while gently touching its snout continuously with the index finger of the other hand for 2–3 min, at 10 cm in front of a microphone integrated into a digital recorder (Tascam DR-100MKIII, TEAC Manufacturing Solutions Corporation, Ome, Tokyo, Japan; Fig. 1). After the recordings, we measured the snout-vent length (SVL; mm) of the lizards with a caliper, and determined its sex based on the morphology and number of the post-cloacal scales (Ashton 2003). Finally, we returned each individual to the spot where we collected it as a conservation protocol.

We analyzed the .WAV files generated in the recordings (96 kHz, 16 bits) with Raven Pro 1-5 (K. Lisa Yang Center for Conservation Bioacoustics, Ithaca, New York, USA), using a fast short-term Fourier transformation, with a Hanning window length of 512 points and an overlapping of 50% (Labra et al. 2013). The temporal resolution was 3.54 ms, while the spectral resolution was 86.1 Hz. We measured eight spectro-temporal variables for each vocalization (Table 1).

For the call characterization, we measured the fundamental and dominant frequencies, plus the number of harmonics, at the beginning of the vocalization. Then, by visual inspection (e.g., Eckenweber and Knörnschild



FIGURE 1. Procedure to stimulate the vocalizations of the captured Balsas Basin Whiptails (*Aspidoscelis c. costatus*) from Mexico in the field. The digital recorder was employed to record the vocalizations, which had a protective cover to filter out the wind. (Photographed by Oswaldo Hernández-Gallegos).

TABLE 1. Description of acoustic variables measured in the vocalizations emitted by Balsas Basin Whiptails (*Aspidoscelis c. costatus*) from Mexico. For some variables, a figure showing an example of how the variable was measured is shown in parentheses.

Variable	Description
Duration (s)	Time from the onset to the end of one vocalization obtained in the oscillogram (Fig. 2B).
Fundamental frequency (kHz)	Frequency of the lowest harmonic of the vocalization obtained in the spectrogram or power spectrum slice (Fig. 2B-C).
Dominant frequency (kHz)	The harmonic frequency with the highest energy obtained in the spectrogram or power spectrum slice (Fig. 2B-C).
Maximum frequency (kHz)	The frequency at which maximum power occurs within the vocalization obtained in the spectrogram.
Delta frequency (kHz)	The difference between the upper and lower frequency limits of a vocalization obtained by considering the information from the spectrogram or power spectrum slice.
Aggregate entropy (bits)	Measurement of the disorder in a sound in the spectrogram indicates the energy distribution within the vocalization. Higher values indicate more chaos in the vocalization.
Bandwidth (90%, kHz)	The difference between the 5% and 95% frequencies recorded in vocalization was measured in the spectrogram.
Number of harmonics	The total number of harmonics of a vocalization is identified in a spectrogram and/or the power spectrum slice if necessary (Fig. 2B-C).

2016) and according to the classification made by Labra et al. (2013), we categorized the vocalizations as simple or complex based on the absence or presence of nonlinear phenomena in the spectrograms, respectively. Simple calls varied in modulation patterns, and we classified them by determining the fundamental frequency (F0) at the beginning, middle, and end in each vocalization. Using these three values, we sought to recognize the following patterns (see also Labra et al. 2013): (1) downward - a progressive decline of the F0; (2) upward - a progressive increase of the F0; (3) bell-shape - a noticeable increase of the F0 up to the middle of the vocalization, followed by a fall, giving it a bell shape; (4) invariant - the F0 remains constant for the duration of the vocalization, with F0 deviating less than 4% between any of the three points considered; and (5) u-shape - a significant decrease of the F0 in the middle of the vocalization, followed by an increase.

Complex calls (also called nonlinear phenomena) are vocalizations that possess rapid qualitative acoustic transitions and occur due to instabilities in the vocal-fold oscillations during the production of the sound (Fitch et al. 2002; Tokuda 2018). We looked to identify four types of these phenomena (Fitch et al. 2002; Riede et al. 2004; Labra et al. 2013): (1) deterministic chaos - the vocalization contains additional auditory components, which are not random; (2) frequency-jump - the F0 in the vocalization suddenly changes; (3) biphonation - the vocalization contains two independent, yet concurrent F0s; and, (4) subharmonics - secondary spectral components may manifest interspersed between the primary ones, due differences upon the natural vibratory frequencies of the vocal folds. Finally, vocalizations that exhibited two or more phenomena were called mixes. Besides the previously explained categories, some calls included a silence, a condition termed as the

presence of a break (Labra et al. 2013).

Statistical analyses.—All data submitted, the call spectrotemporal variables, and the morphological information collected of the individuals is presented as mean \pm standard error (SE). For the statistics, each individual was characterized by the average of all its calls. We used a Mann-Whitney test to determine whether body temperature differed between inactive and active lizards. Furthermore, we compared the percentage of inactive lizards that vocalized against that of active lizards that vocalized. We performed the statistics in STATGRAPHICS Centurion XVII and deemed the results significant if $P < 0.05$.

RESULTS

We captured 25 individuals, including 11 inactive and 14 active lizards. Body temperature differed significantly ($U = 4.0$, $P < 0.001$) between eight inactive (median 27° C; range, 25.4°–30.0° C) and 13 active individuals (median 34° C; range, 28.0°–42.0° C). Only 13 lizards (52%) vocalized, three were inactive (two females and one male; 27.3%), and 10 were active individuals (six females, four males; 71.4%). Occasionally, lizards tried to bite when handled (Fig. 1). For the males that vocalized, mean SVL = 99.8 ± 8.5 mm (range, 77–115 mm), while for females, mean SVL = 82.3 ± 1.7 mm (range, 77–90 mm).

Unfortunately, we could not record the vocalizations of two inactive lizards, as one vocalized as soon as it was grasped, and the other did it while measuring its temperature before we could set up the recorder properly; none of these two individuals vocalized further. Consequently, we recorded the vocalizations of seven females and four males (i.e., one inactive and 10 active lizards). A higher percentage of females did not vocalize (63%), although each produced more vocalizations than males (75% of

TABLE 2. Mean values of the spectro-temporal variables of the vocalizations of Balsas Basin Whiptails (*Aspidoscelis c. costatus*) from Mexico. The abbreviations n = sample size (number of individuals that vocalized) and SE = standard error. For some lizards, it was impossible to measure all the call variables (e.g., due to the presence of deterministic chaos), explaining the difference in sample size.

Variable	Mean \pm SE (range)	n
Duration (s)	0.14 \pm 0.03 (0.04–0.36)	11
Fundamental frequency (kHz)	1.65 \pm 0.12 (1.32–2.27)	9
Dominant frequency (kHz)	2.76 \pm 0.35 (1.38–4.31)	9
Maximum frequency (kHz)	2.32 \pm 0.28 (0.95–4.05)	11
Delta frequency (kHz)	12.5 \pm 1.51 (6.89–21.23)	11
Aggregate entropy	4.9 \pm 0.25 (4.18–7.08)	11
Bandwidth (90%, kHz)	3.88 \pm 1.1 (1.1–1.47)	11
N ^o harmonics	7.6 \pm 0.8 (4.0–11.0)	9

vocalizations were from females; see below).

This species produced tonal, short, and relatively low-pitched vocalizations with several harmonics (Table 2, Figs. 2–3); when lizards vocalized, they did sparingly. In total, we obtained 24 vocalizations during the stimulations: one female did it twice, a male and a female did it three times, a female vocalized four times, and finally, a female emitted up to six distress calls during the recording. All other individuals (six) vocalized only once during the experimental procedure, albeit we noted that some individuals vocalized while in

the herpetological bags.

Of the 24 distress calls produced, 80% were complex, and the rest were simple. The only recorded vocalization from an inactive lizard was a mix (a complex call with deterministic chaos and frequency jumps). On the other hand, the vocalizations of active lizards were both simple and complex. We identified three modulation patterns out of five for simple calls. The percentages (based on the total number of vocalizations) and the number of each simple modulation pattern found are as follows: (1) downward (Fig. 3A), 8%, two; (2) upward (Fig. 3B), 4%, one; and (3) bell-shaped (Fig. 2A, 2B and 2C), 8%, two. Meanwhile, we identified three modulation patterns for complex calls. The percentages and number of each complex vocalization were: (1) deterministic chaos (Fig. 3C–3D), 29%, seven; (2) mix (Fig. 3D), 38%, nine; (3) frequency jump (Fig. 3E), 13%, three. One of the complex calls, a frequency jump, exhibited a silent interval at the beginning, with a duration of 0.017 s.

DISCUSSION

Individual *A. c. costatus* mainly vocalized when they were handled or grasped, characteristics that indicate that these sounds are distress calls (Magrath et al. 2014; Wu et al. 2019), as found in other species such as the Weeping Lizard (*Liolaemus chiliensis*; Labra et al. 2013). This conclusion is further strengthened by the presence of other complementary anti-predator behavior,

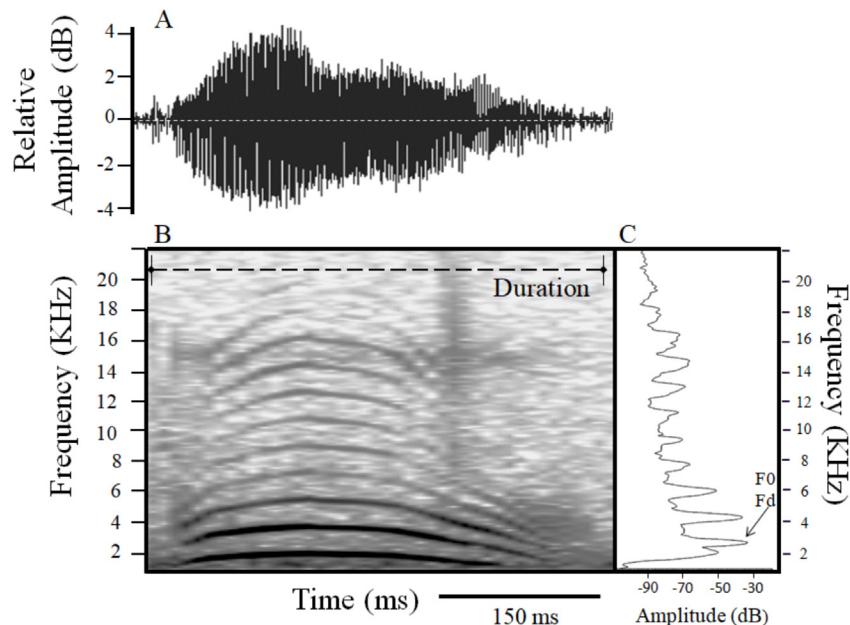


FIGURE 2. (A) Oscillogram, (B) spectrogram, and (C) power spectrum slice of a simple distress call with a bell-modulated pattern emitted by a female Balsas Basin Whiptails (*Aspidoscelis c. costatus*) from Mexico (snout-vent length, 84 mm). The power spectrum presented was taken in the middle of the vocalization, which allows the determination of the fundamental frequencies to characterize the parameters of the vocalization. In this vocalization, the fundamental frequency (F0) and the dominant frequency (Fd) were the same.

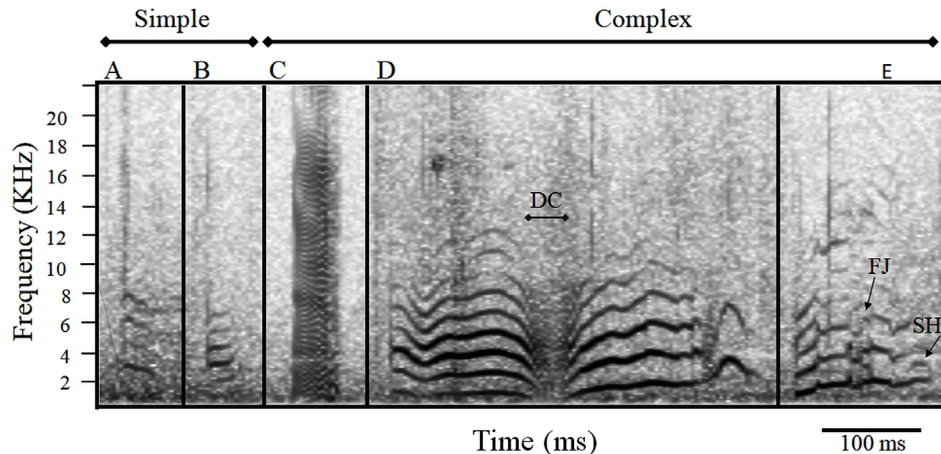


FIGURE 3. Spectrograms of five types of distress calls, two simple, and three complex (i.e., with nonlinear phenomena) of Balsas Basin Whiptails (*Aspidoscelis c. costatus*) from Mexico. Simple: (A) downward and (B) upward. Complex: (C) deterministic chaos, (D) a mix of deterministic chaos and frequency jump, and (E) a mix of frequency jump and subharmonic. We have abbreviated the following phenomena within the figure: deterministic chaos (DC), frequency jump (FJ), and subharmonic (SH).

such as attempted biting, which is also involved during the emission of distress calls (Zuberbühler 2009). The emission of vocalizations by lizards when grasped has been mentioned in the Tiger Whiptail (*Aspidoscelis tigris*; Campbell 1969) and the Eastern Spotted Whiptail (*Aspidoscelis gularis*; Bowker 1980). The vocalization of *A. gularis* had a fundamental frequency between 2.0 to 5.7 kHz (Bowker 1980), with a similar range found for *A. c. costatus*. The hearing sensitivity of Teiid lizards may be found in middle-frequency ranges (Bowker 1980), from 2.7 to 6.3 kHz in the subfamily Teiinae (Wever et al. 1963; Wever 1978; Manley et al. 2018), which includes *Aspidoscelis* (Harvey et al. 2012). Therefore, the vocalizations of at least *A. gularis* and *A. c. costatus* may be heard by conspecifics and potentially act as a warning signal to them, such as in the case of *L. chiliensis* (Hoare and Labra 2013; Ruiz-Monachesi and Labra 2020).

The vocalizations emitted by *A. c. costatus* are complex, exhibiting different modulated patterns and nonlinear phenomena, a variation that potentially may have an informative value as the vocalizations of *L. chiliensis* (Ruiz-Monachesi and Labra 2020). This vocal complexity suggests the existence of a specialized vocal structure that modulates air movements, as described in other taxa, through anatomical specializations in the larynx, such as vocal cords or other oscillators (e.g., Fitch et al. 2002; Russell and Bauer 2020). It is, therefore, unlikely that vocalizations are just involuntary responses to the handle. In addition, if handling was the cause of vocalizations in *A. c. costatus*, most likely, all lizards would have emitted sounds.

Aspidoscelis c. costatus emitted tonal vocalizations, typically isolated in a period of two to three minutes. Thus, these sounds cannot be considered pulse

repetitions, such as those found in the Gekkonid genera, consisting of a sequence of clicks emitted quickly (Gans and Maderson 1973; Haacke 1976). Moreover, the vocalizations of *A. c. costatus* had no similar pattern, frequency, or duration or were set in clearly defined intervals as the vocalizations produced by the geckos, such as the Common Barking Gecko (*Ptenopus garrulus*) and Koch's Barking Gecko (*Ptenopus kochi*; Haacke 1976).

Few inactive individuals vocalized compared to the proportion of active lizards that vocalized. Although a bigger sample size is necessary, the differences in body temperatures between the inactive and active individuals most likely determined the dissimilarity in sound production. Defensive behaviors of various reptile species are modulated by body temperature (Huey 1987). For example, Ladich (2018) states that in ectothermic vertebrates, temperature plays an important role in physiological and metabolic processes, affecting neuromuscular and sensory systems alongside behavior; within anurans, body temperature may modulate the acoustic properties of sounds significantly, as is the case with pulse rate, or moderately, as with call length and carrier frequency. Marcellini (1974) identified that call rates in insects, anurans, and the Common House Gecko (*Hemidactylus frenatus*) suffer a significant increase at temperature elevation, and this rate is significantly reduced at low temperatures in the barking geckos (genus *Ptenopus*). In contrast, individual Long-nosed Leopard Lizards (*Gambelia wislizenii*) at high body temperatures attempted a rapid escape from predators, while those at lower body temperatures adopted a protective stance in which defensive postures, vocalizations, and attacks were involved (Crowley and Pietruzka 1983). Because active *A. c. costatus costatus* vocalized more, we postulate

that high energy is necessary for this species to emit calls. Vocalizations may be sparse or non-existent in *A. c. costatus* when lizards are at low body temperature ($\leq 30^\circ\text{C}$), which is lower than the field body temperature of this species, about $38.7^\circ \pm 0.18^\circ\text{C}$ (Rubio-Blanco 2007).

No lizards vocalized once they detected a potential predator (e.g., a human), and active lizards opted for a rapid escape (pers. obs.). Instead, vocalizations were only produced after lizards were captured and usually not immediately after being seized, except in previously explained instances (e.g., cloacal temperature measurement). Therefore, if vocalizations are antipredator responses, these are not a primary defense; potentially, these could be a warning signal to conspecifics, as in *L. chiliensis* (Hoare and Labra 2013). The emission of vocalizations by some individuals that vocalized inside the herpetological bags may be a last-ditch effort to coax or surprise the predator, as they would find themselves restrained and unable to escape back into their habitat. Likewise, it might be possible that these calls also function as a discouraging signal toward predators. In this context, a discouraging signal would be one that improves the survivability of a species or its conspecifics by instigating behavioral changes within a predator and/or conspecifics (Hoare and Labra 2013). These signals may take many forms when it comes to distress calls, such as: (1) startling the predator; (2) inducing mobbing behavior by attracting conspecifics to attack the predator; (3) inducing a dispute among predators that allow the organism a chance to escape; or (4) a warning and allowing kin to escape from potential predation (Klump and Shalter 1984). These functions are not mutually exclusive (Hoare and Labra 2013).

Distress calls can function as a deterrent mechanism against predators (Magrath et al. 2014; Carter et al. 2015; Wu et al. 2019), although it is unknown if this can be the case for *A. c. costatus*. Among the possible predators against which *A. c. costatus* could employ its vocalizations as a defensive mechanism are snakes, such as coachwhips (*Masticophis* spp.; Hernández-Gallegos and Domínguez-Vega 2012), the Thornscrub Vine Snake (*Oxybelis microphthalmos*), which is known to prey upon species of *Aspidoscelis* (Bucio-Jiménez and Flores-Loyola 2021), and mammals, like the Ringtail (*Bassariscus astutus*), as this species occasionally feeds upon lizards (Herrera-Flores 2018). Baeckens et al. (2019) postulated that distress calls from the Algerian Psammodromus (*Psammodromus algirus*) convey honest information about the body size and maximum bite performance of a lizard, which could be employed as a deterrent signal against Least Weasels (*Mustela nivalis*) and Red Foxes (*Vulpes vulpes*). Thus, it is possible that distress calls of *A. c. costatus* could have a similar effect on their predators.

The study of vocalizations in the clade Unidentata is

a relatively novel field of investigation in herpetology. Hopefully, studies such as the present might be a steppingstone to inspire more behavioral studies that explore the functionality of sound production and acoustic communication, tackle some of the questions raised here, and determine whether vocalizations may occur in social contexts (Milton and Jenssen 1979). As Jorgewich-Cohen et al. (2022) stated, the study of poorly investigated groups is important to better understand the development of acoustic communication throughout vertebrate history, as their recent phylogenetic study revealed that acoustic communication is a homologous trait, which evolved at least since the last common ancestor of all choanate vertebrates. Previous studies inferred that acoustic communication had evolved independently on numerous clades due to the lack of available data concerning several groups which were not thought to produce sounds (Jorgewich-Cohen et al. 2022).

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