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Breaking the silence: vocal diversity revealed in four Peruvian gecko species, genus *Phyllodactylus* (Squamata: Phyllodactylidae)

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Abstract. We report the first comprehensive description of vocal repertoires in four Neotropical leaf-toed geckos (*Phyllodactylus clinatus*, *P. kofordi*, *P. microphyllus*, and *P. sentosus*), revealing substantially greater acoustic complexity than previously documented. Our study characterises distinct advertisement and distress calls across the four species, identifying three shared note types that modulate both call categories. Different note types dominated advertisement and distress calls. Our results support some acoustic patterns seen in other Gekkota lineages. Beyond ecology, this work establishes bioacoustics as a new relevant tool for investigating *Phyllodactylus* biology.

Key words. Bioacoustics, vocal repertoires, leaf-toed geckos, acoustic complexity, advertisement calls, distress calls.

Introduction

Among lizards, geckos (Infraorder Gekkota) are distinguished by their skills of producing frequency-modulated vocalisations (Evans 1936, Ganeshina & Vorobyev 2009, Rothla Jr. et al. 2019). This ability stems from specialised elastin-rich structures in the cartilaginous larynx (Rothla Jr. et al. 2019), which share homologous features with vocal organs in other vertebrates (Gans & Maderson 1973, Moore et al. 1991). Vocal geckos typically produce at least two types of calls: (1) advertisement calls, which exhibit greater ranges of structural elements and occur in different intraspecific social contexts (Brillet & Pailette 1991, Tang et al. 2001); and (2) distress calls, consisting of loud notes emitted within defensive contexts (Marcellini 1974, 1977, 1978, Brown 1984, Rothla Jr. et al. 2019). Current knowledge of gecko bioacoustics primarily derives from studies on Gekkonidae species, particularly *Gekko* spp. (tokay geckos), *Hemidactylus* spp. (house geckos), and *Phelsuma* spp. (day geckos) originating from the Old World (Kästle 1964, Marcellini 1974, 1977, Marcellini 1978). Meanwhile, New World taxa, such as *Phyllodactylus* species (leaf-toed geckos), remain understudied in this context.

With 68 currently recognised species in the family Phyllodactylidae (Uetz & Hošek 2025), *Phyllodactylus* represents a diverse group of small and nocturnal lizards distributed across the Americas, occupying both arid and semi-arid environments (Dixon & Huey 1970, Huey 1979, Catenazzi & Donnelly 2007, Venegas et al. 2008, Koch & Beraún 2011, Koch et al. 2016, Uetz & Hošek 2025). They are generally regarded as relatively quiet animals, with only anecdotal mentions of distress calls during handling (Donoso-Barros 1966, Reyes-Olivares & Labra 2017), and vocal repertoire remains poorly documented. Before this study, the only published record of *Phyllodactylus* vocalisations was Marcellini's (1978) description of advertisement calls in *P. tuberculosus* from Central America's Pacific coast. This paucity of data has led to the widespread assumption that most *Phyllodactylus* species are essentially non-vocal.

Peru's western arid and semiarid regions harbour at least 15 species of *Phyllodactylus* (Dixon & Huey 1970, Huey 1979, Catenazzi & Donnelly 2007, Venegas et al. 2008, Koch & Beraún 2011, Koch et al. 2016, Uetz & Hošek 2025). After two years of fieldwork across the Peruvian Pacific coastal desert, we obtained the first recorded evidence of context-dependent vocalisations in four species of leaf-toed geckos. Our analysis reveals two structurally and functionally distinct calls: advertisement calls, used in social communication, and distress calls, emitted during defensive situations. Here, we describe our findings, which fundamentally alter our understanding of ecology in this genus and provide new venues for researching its evolutionary relationships.

Materials and methods

Fieldwork and recordings

We captured adult individuals (males and females) of *Phyllodactylus clinatus* Dixon & Huey 1970, *P. kofordi* Dixon & Huey 1970, *P. microphyllus* Cope 1875, and *P. sentosus* Dixon & Huey 1970 from four different localities, as close as possible to their type localities on the Peruvian Pacific coast (Fig. 1, Table 1). Those individuals were recorded at the time of capture while we handled them. The sounds they made in this context were considered distress calls (Marcellini 1978, Rothla Jr. et al. 2019). These recordings were made using a Marantz PMD 620 recorder and a Marantz SG 5BC gunshot microphone, or cellphones with the Song Meter Touch 2.0 app by Wildlife Acoustics Inc. The distance between the emitter and the recorder was always 50 mm. In the field, we also recorded pairs of different adult males together (*P. kofordi*, *P. microphyllus*, and *P. sentosus*) or three males together (*P. clinatus*) of every species inside cardboard boxes of 60 × 45 × 25 cm (as an experimental arena in semi-captive conditions) during 2–3 nights, eight hours per night (see Table 2) with an Audiomoth 1.2.0. configured to seven minutes of recording and three minutes resting, and placed on a corner of the box. Since there was no capture or predator pressure on individuals in the cardboard boxes, the calls recorded under these conditions were considered advertisement calls (Rothla Jr. et al. 2019). All recordings were stored on SD memory cards as WAV files (WAV files corresponding to every species in this study are digitally archived at www.fonozoo.com). We recorded the air temperature at the time of the recordings with a digital thermometer (± 0.1° precision). Photographs of the specimens were taken in the field by KYVC and GC. Six individuals of *P. clinatus*, five of *P. kofordi* and *P. microphyllus,* and two of *P. sentosus* (Table 1) were euthanised with T61, fixed in formalin 10%, and pre-

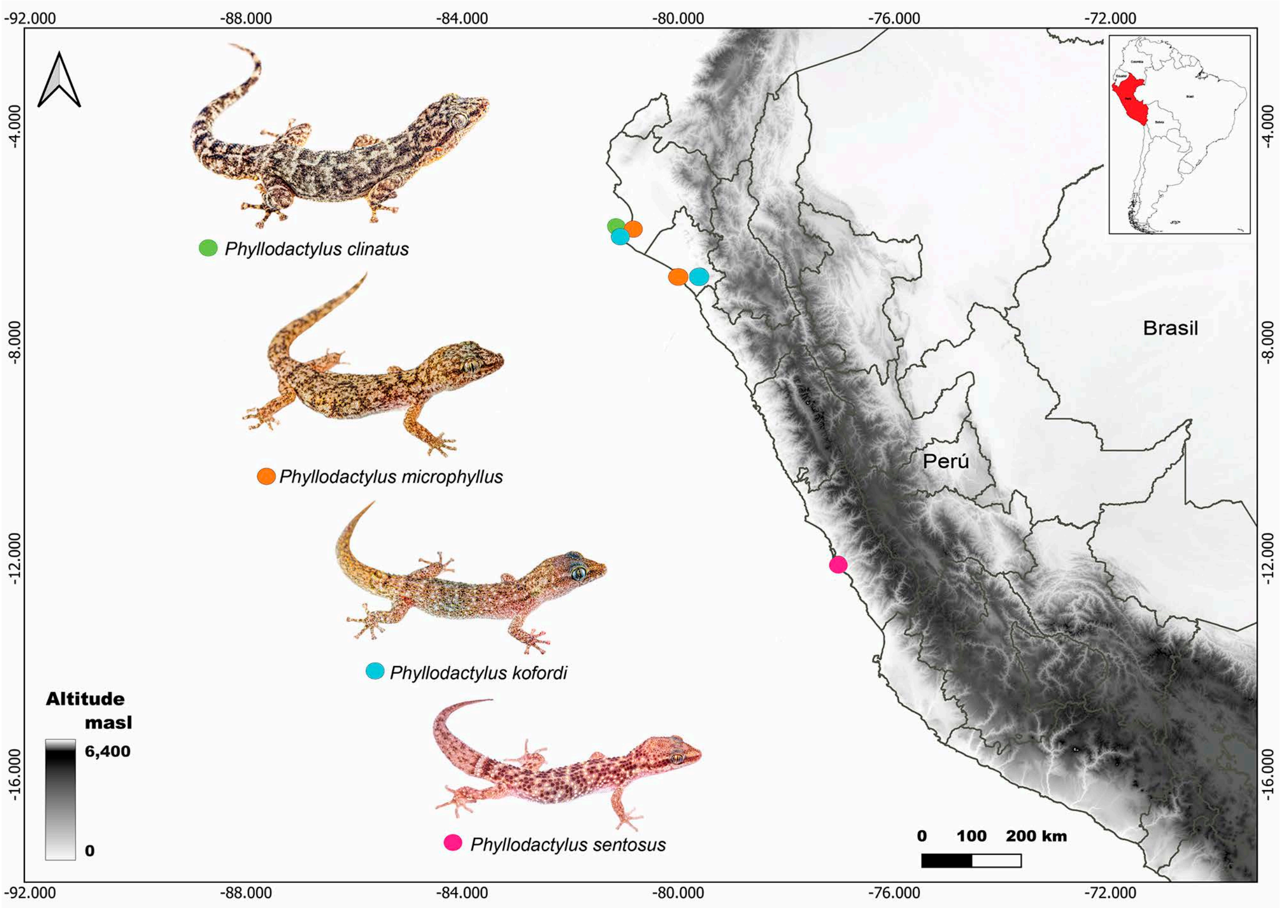

Figure 1. Map indicating localities on the Peruvian coast where fieldwork was conducted. Species correspondence is as follows: green dot = *Phyllodactylus clinatus*; orange dots = *P. microphyllus*; turquoise dots = *P. kofordi*; fuchsia dot = *P. sentosus.*

Table 1. Voucher specimens (CORBIDI) of Peruvian *Phyllodactylus* used in this study. Sex of the specimens is given as follows: F = female, M = male, U = undetermined. Call type recorded (Call) is shown as follows: A = advertisement call, D = distress call. Collection localities are categorized from the most minor (Locality) to broader areas (Region) within Peruvian Territory. Distances from type localities (Dist) are given in kilometres (km). Coordinates Datum WGS84. Type locality of the species is taken from Dixon & Huey (1970).

						Coordinates		
Species	Voucher	Sex	Call	Locality	Region	Latitude	Longitude	Dist
Phyllodactylus clinatus	CORBIDI 26263	F	D	Quebrada Nunura	Piura	-5.871524	-81.067166	7
Phyllodactylus clinatus	CORBIDI 26265	F	D	Quebrada Nunura	Piura	-5.860675	-81.080652	6
Phyllodactylus clinatus	CORBIDI 26267	F	D	Quebrada Nunura	Piura	-5.860675	-81.080652	6
Phyllodactylus clinatus	CORBIDI 26796	M	A	Macizo de Illescas	Piura	-5.899843	-81.014283	12
Phyllodactylus clinatus	CORBIDI 26797	M	A	Macizo de Illescas	Piura	-5.899843	-81.014283	12
Phyllodactylus clinatus	CORBIDI 26803	M	A	Macizo de Illescas	Piura	-5.905533	-81.01319	13
Phyllodactylus kofordi	CORBIDI 26250	F	D	Quebrada Nunura	Piura	-5.860883	-81.080607	157
Phyllodactylus kofordi	CORBIDI 26251	F	D	Quebrada Nunura	Piura	-5.862349	-81.079397	157
Phyllodactylus kofordi	CORBIDI 26264	M	D	Quebrada Nunura	Piura	-5.860675	-81.080652	157
Phyllodactylus kofordi	CORBIDI 28239	M	A	Pucalá	Lambayeque	-6.779984	-79.600522	64
Phyllodactylus kofordi	CORBIDI 28240	M	A	Pucalá	Lambayeque	-6.779984	-79.600522	64
Phyllodactylus microphyllus	CORBIDI 26281	F	D	Punta Faro	Piura	-5.883461	-8.1137805	240
Phyllodactylus microphyllus	CORBIDI 26282	F	D	Punta Faro	Piura	-5.883461	-8.1137805	240
Phyllodactylus microphyllus	CORBIDI 26287	U	D	Punta Faro	Piura	-5.877853	-8.1134705	240
Phyllodactylus microphyllus	CORBIDI 28241	M	A	Humedales de San José	Lambayeque	-6.757314	-79.967216	80
Phyllodactylus microphyllus	CORBIDI 28242	M	A	Humedales de San José	Lambayeque	-6.757314	-79.967216	80
Phyllodactylus sentosus	CORBIDI 28234	M	A/D	Miraflores	Lima	-12.1132	-77.03484	8
Phyllodactylus sentosus	CORBIDI 28235	M	A/D	Miraflores	Lima	-12.1132	-77.03484	8

Table 2. Sampling effort for advertisement calls of *Phyllodactylus* species in this study. Vocal activity rate is defined as the percentage of recordings containing calls.

Species	Nights recorded	Time record (Hrs)	Recording files per hour	Total no. of recording files	Files with calls recorded	Vocal activity rate (%)
P. clinatus	3	16.8	6	144	15	10.41
P. kofordi	2	11.2	6	96	7	7.29
P. microphyllus	2	11.2	6	96	8	8.33
P. sentosus	3	16.8	6	144	48	33.33

served in alcohol 70%. Those specimens are stored in the Herpetological Collection of the Centro de Ornitología y Biodiversidad (CORBIDI) in Lima, Peru.

Taxonomic identification

We identified individuals used in this study through morphological diagnostic characters. We review original descriptions of the four species (Cope 1875, Dixon & Huey 1970), and used external traits described by Dixon & Huey 1970 such as the snout–vent length, the number of rows of tubercles on dorsum, type of tubercles on dorsum (rounded/trihedral), presence or absence of trihedral tubercles on tibia, condition of subdigital lamellae of toes, and presence of tubercles on the base of the tail to confirm our identifications. Due to the scarcity of morphological information on *P. clinatus*, we reviewed photographs of the preserved holotype of this species (MVZ 82227) to enhance our morphological diagnosis. Furthermore, for *P. clinatus* and *P. sentosus*, we collected individuals as close as possible to their type localities to ensure the reliability of our identifications. Additionally, we reviewed museum collections specimens of *P. delsolari*, *P. interandinus*, *P. johnwrigthi*, *P. kofordi*, *P. magister* (holotype), *P. microphyllus*, *P. pachamama* (paratypes), *P. reissi* (lectotype and paralectotypes), *P. sentosus*, and *P. thompsoni* to confirm the results of our comparisons. Museum acronyms are for Academy of Natural Science, Department of Herpetology, Philadelphia (ANSP); Herpetology Collection of Centro de Ornitología y Biodiversidad (CORBIDI); Museo Universidad Nacional Pedro Ruiz Gallo (MUPRG); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Vertebrate Zoology, Berkeley University (MVZ); Museo de Zoología, Pontificia Universidad Católica de Ecuador (QCAZ); Texas Cooperative Wildlife Collection (TCWC); and Museum für Naturkunde (ZMB). Reviewed specimens are detailed in Appendix I.

Bioacoustics and data analyses

Gecko vocalisations have been characterized in various ways and lack a standardised terminology. We consider three note types: chirps, churrs, and clicks. (1) Chirps are frequency modulated and we consider this note to be similar to the harmonious frequency modulated type squeaks described by Frankenberg (1975), at least one of the chirp types in Rothla Jr. et al. (2019), chirp notes in Marcellini (1974), and "squeaky" calls described by Werner et al. (1978); (2) churrs have been described as rapidly strung together short chirps, rattle-like, and a note composed of a series of extremely short sound pulses (Marcellini 1974); (3) clicks are vocalisations of very short duration and can be singular or in a series of multiple clicks (Frankenberg 1975). For distress calls, we measured the following variables (as defined by Araya-Salas & Smith-Vidaurre 2017; K. Lisa Yang Center for Conservation Bioacoustics 2024): mean dominant frequency (DoF; average of dominant frequency measured across the spectrogram) and bandwidth 90% (BW90; the difference between the 5% and 95% frequencies) (Table 3). We did not measure temporal call variables for distress calls because our handling of the animals could have influenced the note or internote duration (Zuberbühler 2009). For advertisement calls, we measured DoF, BW90, note length, and internote length (Table 3). We measured temporal call variables on oscillograms and BW90 using Raven Pro v1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics 2024) and DoF using the warbleR package (Araya-Salas & Smith-Vidaurre 2017), and visualised the spectrograms and oscillograms using the seewave package (Sueur et al. 2008) with a Hanning window, 90% overlap, and window length of 512 in R v4.3.3 (R Core Team 2024). We visually inspected the spectrograms to select notes with minimal background noise for measurement, with the aim of measuring as many notes as possible for each species and note type. We used a low-pass filter with a frequency range of 400–700 Hz, depending on the frequency of the low rumbling background noise in the recordings. For all parameters, we used the average calculated across up to ten notes of each individual for each note type. To test for differences in mean DoF in calls among the four species, we used linear mixed-effects models with individual as a random intercept where DoF ~ Species + (1|individual). We used separate models for churrs, chirps, and clicks. We grouped advertisement and distress notes of the same type due to the low sample size and omitted *P. sentosus* in the analysis for clicks, as we only analysed a single click note for this species. We conducted pairwise comparisons using the Tukey method with a pairwise adjustment. Model assumptions, including linearity, normality of residuals, and homogene-

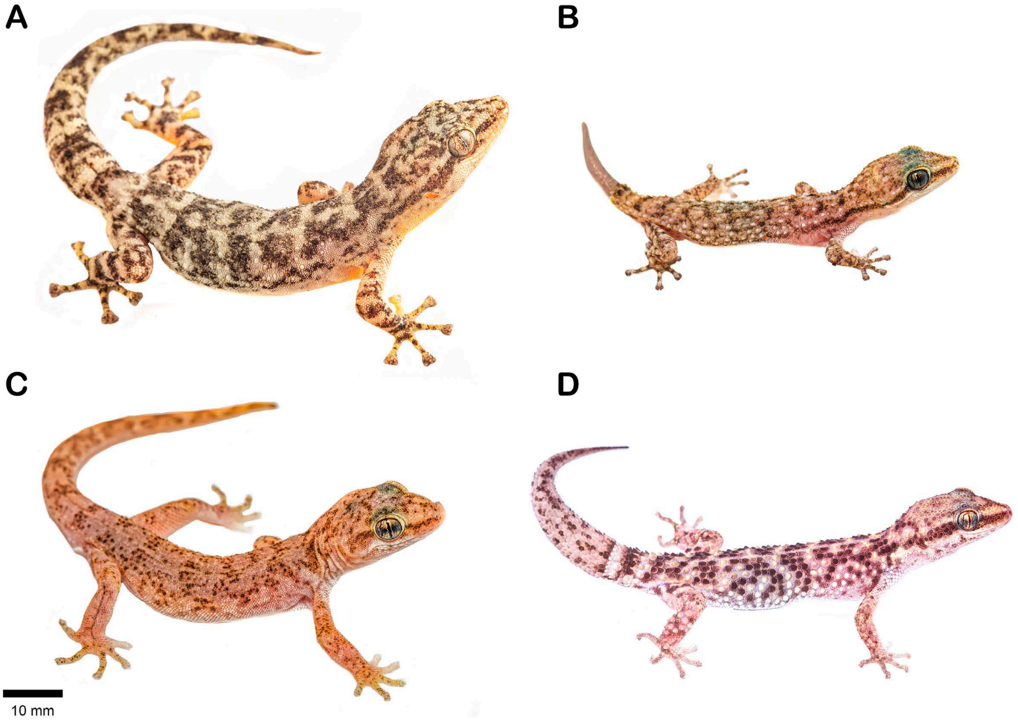

Figure 2. Specimens included in this study represent four species of leaf-toed geckos: (A) *Phyllodactylus clinatus* (CORBIDI 26796); (B) *P. kofordi* (CORBIDI 28239); (C) *P. microphyllus* (CORBIDI 28241); (D) *P. sentosus* (CORBIDI 28234).

ity of variance, were evaluated visually and using diagnostic plots. We analysed the models using the lme4 (Bates et al. 2015) and lsmeans (Lenth 2016) packages in R. The map in this study (Fig. 1) was created using Digital Elevation Models (Verdin 2017) in QGIS, an open-source software (QGIS 2025).

Results

We assigned specimens CORBIDI 26263, 26265, 26267, 26796 (Fig. 2A), 26797, and 26803 to *Phyllodactylus clinatus* by the presence of granular scales on the dorsal surface of tibia, 10–12 rows of trihedral tubercles on dorsum, and terminal lamellae well expanded; specimens CORBIDI 26250, 26251, 26264, 28239 (Fig. 2B), 28240 to *P. kofordi* by the presence of trihedral tubercles on dorsum and dorsal surface of the tibia, tail with a reduction of enlarged tubercles per whorl from base to distal half of the tail, and terminal lamellae of digits moderately enlarged and truncate; specimens CORBIDI 26281, 26282, 26287, 28241 (Fig. 2C), and 28242 to *P. microphyllus* by having a dorsum and dorsal surfaces of tibia without distinct tubercles, only with some small flat, oval scales slightly longer than rest of dorsals, and having very small terminal lamellae on all digits with fingers claws visible beyond the tip of lamellae; finally we assigned specimens CORBIDI 28234 (Fig. 2D) and 28235, and a released individual to *P. sentosus* by the presence of very large trihedral tubercles on dorsum, forearm, thigh, tibia, and tail, by having the terminal lamellae of digits separated, and the claws visible slightly beyond proximal edge of terminal lamellae.

We collected a total number of 480 seven-minute recordings of individuals housed in cardboard boxes under field conditions, yielding a total of 56 hours of audio data. Vocalisations from these records are considered advertisement calls (Table 2, 3A, Fig. 3). It was not always clear when a call started and stopped. Therefore, we focused on describing different notes and note series. We obtained 78 recordings containing advertisement call notes: 15 recordings for *Phyllodactylus clinatus*, seven for *P. kofordi*, eight for *P. microphyllus*, and 48 for *P. sentosus* (Table 2, Fig. 3). We also obtained 43 recordings containing distress call notes (Fig. 4), 20 for *Phyllodactylus clinatus*, 15 for *P. kofordi*, five for *P. microphyllus,* and three for *P. sentosus*. We analysed between 12 and 20 distress call notes per species (Table 3B). Notes fall into Clicks, Chirps, and Churrs categories (Marcellini 1974). Call parameters and note types of the four species analysed are summarised in Table 3.

Description of note types

Chirp: Notes are frequency modulated, contain strong to moderate harmonics and are sometimes very elongated. Of the three types of notes identified, chirps displayed the strongest harmonic components. We found no differences in species pairwise comparisons of mean dominant frequency (Fig. 5) for this note: *P. clinatus* – *P. kofordi* (β = -151, SE = 1070, p = 0.999), *P. clinatus* – *P. microphyllus* (β = -406, SE = 1070, p = 0.981), *P. clinatus* – *P. sentosus* (β = 936, SE = 1010, p = 0.793), *P. kofordi* – *P. microphyllus* (β = -255, SE = 1070, p = 0.995), *P. kofordi* – *P. sentosus* (β = 1087, SE = 1010, p = 0.712), *P. microphyllus* – *P. sentosus* (β =1342, SE= 1010, p = 0.565).

Churr: Notes mainly emitted over a broad band of frequencies, but there may be some weak harmonic structure visible; pulsatile to pulsed; sometimes can be elongated. We found a difference in mean dominant frequency between *P. clinatus* and *P. kofordi* (Fig. 5), with *P. kofordi* exhibiting a higher mean dominant frequency (β = -2134, SE = 686, p = 0.046). We did not find significant differences between other pairwise comparisons: *P. clinatus* – *P. microphyllus* (β = -821, SE = 852, *p* = 0.772), *P. clinatus* – *P. sentosus* (β = -78, SE = 742, p = 0.999), *P. kofordi* – *P. microphyllus* (β = 1313, SE = 887, p = 0.482), *P. kofordi* – *P. sentosus* (β = 2056, SE = 782, p = 0.098), *P. microphyllus* – *P. sentosus* (β = 743, SE = 931, p = 0.854).

Click: Notes very short (less than 0.01 seconds) and relatively quiet. We did not find significant differences between pairwise comparisons (Fig. 5): *P. clinatus* – *P. kofordi* (β = -1903, SE = 885, p = 0.13), *P. clinatus* – *P. microphyllus* (β = 238, SE = 960, p = 0.97), *P. kofordi* – *P. microphyllus* (β = -2140, SE = 1010, p = 0.14).

Description of advertisement calls

We obtained acoustic recordings from four *Phyllodactylus* species under semi-captive conditions during field campaigns in 2023 and 2025. Three adult males of *P. clinatus* (CORBIDI 26796–97, 26803) were recorded on 15, 16, and 17 November 2023 between 23:00 and 05:30 h at air temperatures of 20–23 °C. Two adult males of *P. kofordi* (CORBIDI 28239–40) were recorded on 7 and 8 February 2025 between 22:30 and 01:20 h at 21 °C. Recordings of *P. microphyllus* were obtained from two individuals (CORBIDI 28241–42) on 6 and 7 February 2025, with calling activity between 22:20 and 01:30 h at 22 °C. Finally, two adult males of *P. sentosus* (CORBIDI 28234–35) were recorded on 11, 12, and 13 February 2025, calling between 03:00 and 06:30 h at air temperatures of 19–21 °C. These recordings formed the basis for the acoustic description of advertisement calls (Table 3).

Across species, advertisement calls were composed of click, chirp, and churr notes. Churr notes were often more common than chirps in advertisement recordings. Clicks were present in the four species, but particularly frequent in *P. microphyllus* and *P. clinatus*. Advertisement calls of *P. clinatus* were restricted to chirps and churrs, making it the only species in our sample showing two (and not three) notes. Range of mean dominant frequency across note types and species was 1687–6352 Hz and bandwidth 90% was 1500–13500 Hz. Mean dominant frequency range was 1976–6352 Hz for churrs, 2390–6253 Hz for chirps, and 1687–5872 Hz for clicks. For churr notes, *P. clina-*

Table 3. Call structure of the four species in this study. Parameters for advertisement calls (A) and distress calls (B) are given in hertz (Hz) and seconds (s). Data are reported as mean, standard deviation and range (in parentheses) when available.

Species	Note type	Number of individuals	Number of notes	Mean dominant frequency (Hz)	Bandwidth 90% (Hz)	Note duration (s)	Internote duration (s)
A	Advertisement calls						
Phyllodactylus clinatus	Click	2	7	1960.74±222.19 (1687.50–2272.33)	4619.70±1362.84 (2670.12–6000.00)	0.005±0.001 (0.003–0.007)	0.15±0.06 (0.10–0.24)
	Churr	3	19	2372.00±189.16 (1987.50–2781.25)	2506.58±875.47 (1500.00–4500.00)	0.01±0.01 (0.002–0.02)	0.10±0.03 (0.01–0.15)
Phyllodactylus kofordi	Click	1	1	5872.34	2437.50	0.002	–
	Chirp	1	1	2390.63	7593.75	0.02	–
	Churr	1	8	5037.50±1118.76 (2953.13–6351.56)	8144.53±3909.16 (4031.25–13500.00)	0.03±0.01 (0.02–0.04)	0.91±0.61 (0.36–1.96)
Phyllodactylus microphyllus	Click	1	7	3664.38±169.88 (3410.53–3829.79)	2450.89±288.59 (2156.25–29.06.25)	0.002±0.001 (0.001–0.004)	0.21±0.02 (0.16–0.22)
	Chirp	1	2	4539.21±2423.85 (2825.28–6253.13)	9468.00±4905.55 (6000.00–12937.75)	0.08±0.01 (0.07–0.09)	–
	Churr	1	4	3636.28±1136.50 (1976.56–4476.56)	6609.38±5468.93 (1500.00–12750.00)	0.07±0.01 (0.05–0.08)	1.92±1.39 (0.93–2.90)
Phyllodactylus sentosus	Click	1	1	2359.83	12000.00	0.01	–
	Chirp	2	9	3867.29±968.34 (2713.54–5296.88)	5250.00±587.34 (4781.25–6750.00)	0.11±0.02 (0.08–0.15)	0.13±0.06 (0.08–0.16)
	Churr	2	9	2830.53±292.11 (2318.51–3263.67)	4593.75±2652.89 (2625.00–9187.50)	0.18±0.09 (0.05–0.34)	0.24±0.17 (0.07–0.46)
B	Distress calls						
Phyllodactylus clinatus	Click	2	7	5258.81±596.96 (4537.82–5949.58)	4419.64±1487.67 (3000.00–6093.75)	–	–
	Chirp	3	9	4854.61±1007.36 (3769.30–6031.67)	4541.67±1597.27 (2718.75–6843.75)	–	–
	Churr	1	4	4896.39±739.91 (4154.30–5789.06)	3351.56±594.78 (2625.00–4031.25)	–	–
Phyllodactylus kofordi	Click	2	5	5980.66±817.73 (4851.06–6782.61)	6993.75±3983.33 (4031.25–13875.00)	–	–
	Chirp	3	10	5588.59±852.65 (4517.27–6816.01)	4321.88±846.00 (3093.75–5531.25)	–	–
	Churr	2	2	5512.88±602.21 (5087.05–5938.70)	5671.88±66.29 (5625.00–5718.75)	–	–
Phyllodactylus microphyllus	Click	2	3	3641.72±280.64 (3319.15–3829.79)	6937.50±2030.29 (4781.25–8812.50)	–	–
	Chirp	3	9	5196.09±1802.57 (3709.38–8455.08)	3989.58±1049.32 (2625.00–5812.50)	–	–
	Churr	1	2	3751.04±226.86 (3590.63–3911.46)	2578.13±198.87 (2437.50–2718.75)	–	–
Phyllodactylus sentosus	Chirp	3	11	3382.19±453.58 (2728.84–4155.54)	3459.67±1225.74 (2153.32–6546.09)	–	–
	Churr	1	1	4396.09	2411.72	–	–

tus had the lowest average of mean dominant frequency (2372 Hz), compared to *P. kofordi* (5038 Hz), *P. microphyllus* (3636 Hz), and *P. sentosus* (2831 Hz), though most of their ranges overlapped. Note duration range was 0.002–0.34 s for churrs, 0.02–0.15 s for chirps, and 0.001–0.01 s for clicks.

Description of distress calls

Distress calls were obtained from four *Phyllodactylus* species during captures in 2022 and 2025. In *P. clinatus*, three adult females (CORBIDI 26263, 26265, 26267) produced distress calls on 1 November 2022, at an air temperature of

19 °C. For *P. kofordi*, two adult females (CORBIDI 26250–51) and one male (CORBIDI 26264) were recorded on 3 November 2022 under 20 °C. Distress vocalisations of *P. microphyllus* were documented from two adult females (CORBIDI 26281, 26287) and a juvenile (CORBIDI 26282) on 5 November 2022 at 17 °C. Finally, in *P. sentosus*, three adult males (CORBIDI 28234–35 and one unvouchered individual) were recorded on 11 February 2025 at an air temperature of 22 °C. These recordings formed the basis for the acoustic description of distress calls (Table 3).

As observed in advertisement calls, distress calls were composed of clicks, chirps, and churrs. Chirps were more

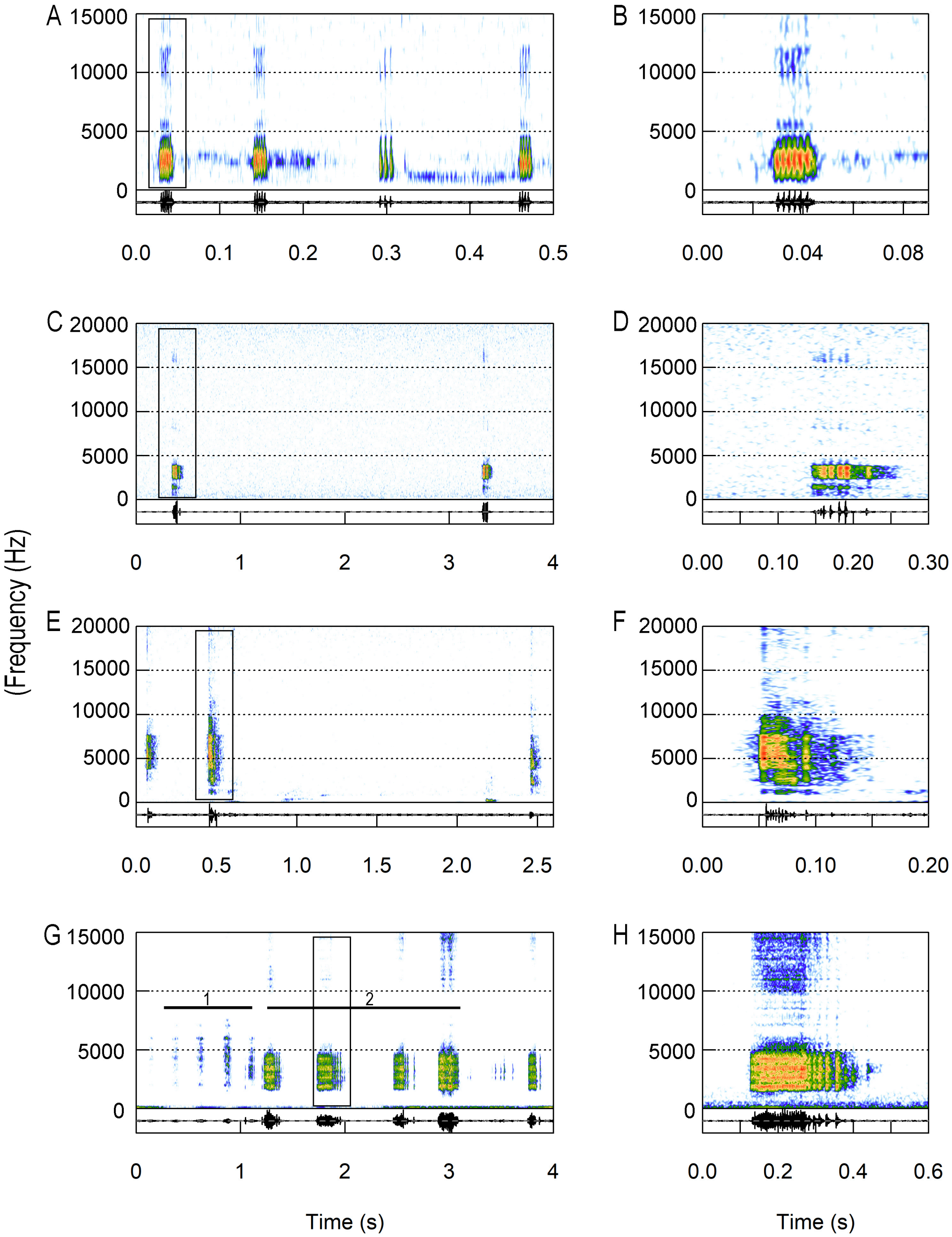

Figure 3. Spectrograms in colours (above) and oscillograms in black (below) of advertisement calls of the species in this study. Churr calls of *P. clinatus* (A, B), *P. kofordi* (C, D), *P. microphyllus* (E, F), and chirp (G1) and churr (G2, H) calls of *P. sentosus*. Black boxes in figures on the left indicate notes used for figures on the right.

prevalent in distress calls than churrs. Distress calls of *P. sentosus* were restricted to chirps and churrs. Across species and note types, range of mean dominant frequency was 2729–8455 Hz and bandwidth 90% was 2153–13875 Hz. The mean dominant frequency was 3591–5939 Hz for churrs, 2729–8455 Hz for chirps, and 3319–6783 Hz for clicks. Ultrasonic components (>20,000 Hz) were detected in three species (*P. clinatus*, *P. kofordi*, and *P. microphyllus*).

Discussion

Our findings reveal a previously undocumented aspect of *Phyllodactylus* biology: their ability for complex acoustic communication. While gekkonid genera (i.e., *Gecko*, *Hemidactylus*, *Phelsuma*, *Ptychodactylus*) are known for loud vocalisations (notably the loud "tokay" calls of male *Gecko gecko*), almost all *Phyllodactylus* species have been assumed to be silent outside of distress calls when handled.

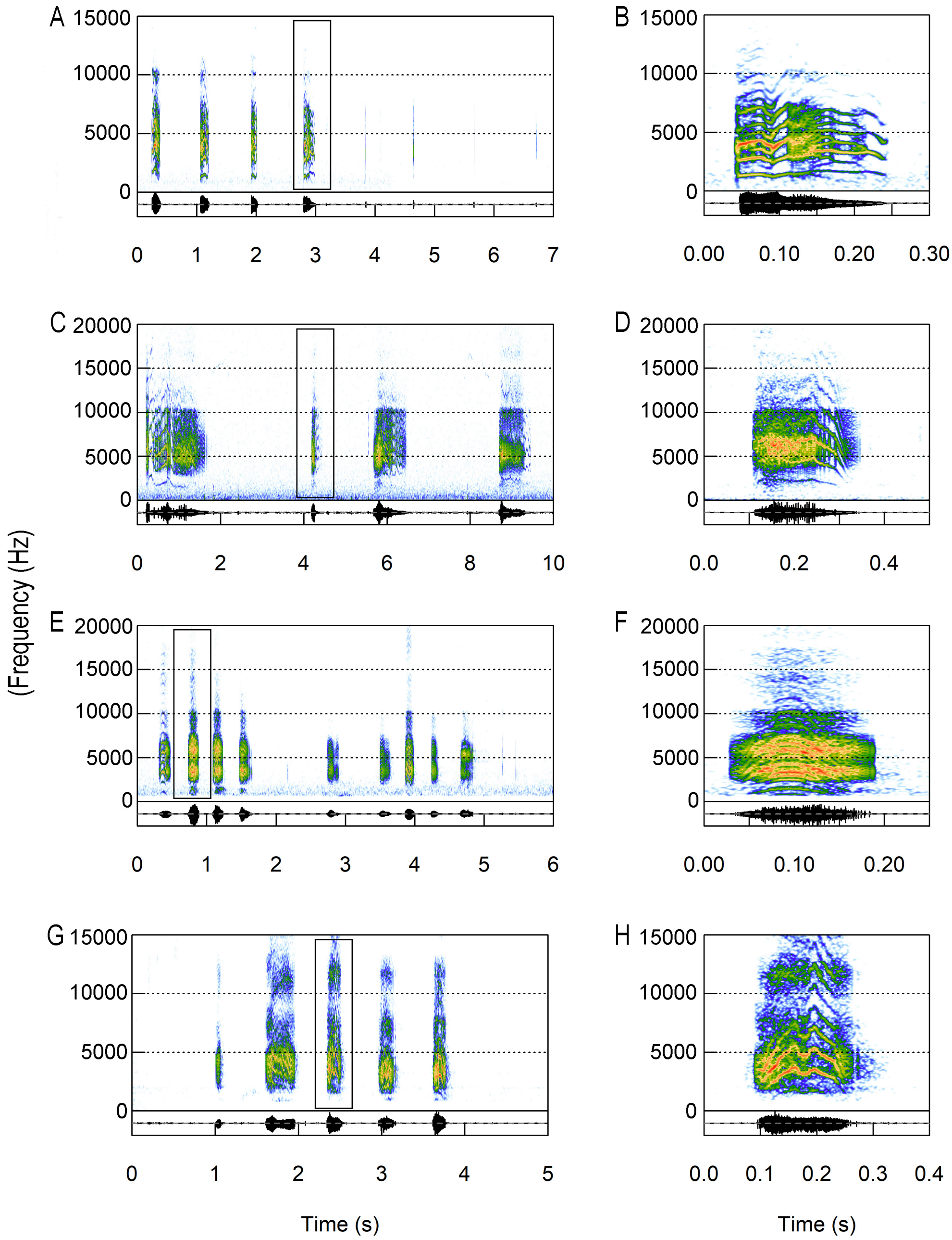

Figure 4. Spectrograms in colour (above) and oscillograms in black (below) of distress calls of the species in this study. *P. clinatus* (A, B) showing clicks and chirps; *P. kofordi* (C, D) showing chirps; *P. microphyllus* (E, F) showing churr (E) and chirps (E, F); *P. sentosus* showing chirps. Black boxes in figures on the left indicate notes used for figures on the right.

This assumption has continued despite their nocturnal lifestyle, where acoustic communication would be highly advantageous, creating a significant gap in our understanding of *Phyllodactylus* biology. Our documentation of both advertisement and distress calls in four Peruvian species fundamentally challenges this long-held belief.

Gecko vocalisations have historically been described with inconsistent terminology, often based more on onomatopoeic impressions or behavioral context than on quantitative acoustic traits. Marcellini (1974) noted that most calls described in the early literature resembled the multiple chirp call of *Hemidactylus frenatus*, although authors variously referred to them as "chirps," "barks", or "clicks" (Beebe 1944, Schmidt & Inger 1957, Brain 1962, Petzold 1965). In some cases, distinct labels were applied to what appear to be the same acoustic structures. For instance, Frankenberg (1974) used the term "squeaks" to describe single chirps typically emitted under handling stress. The churr, in turn, has been inconsistently recognized, reported only in a few species such as *Gekko gecko* (Wever et al. 1963) *Nephrurus asper* (Bustard1967), and *Hemidactylus frenatus* (Marcellini 1974), perhaps overlooked in others due to its low occurrence in other bioacoustic datasets. More recent works, such as Rothla Jr. et al. (2019), continue to emphasize the functional context of vocalisations (advertisement vs. distress calls) but similarly classify note types on the basis of general structure and behavioral setting, rather than standardised acoustic parameters. As a result, current terminology for gecko note types (chirps, churrs, clicks, etc.) still lacks clear quantitative definitions, complicating comparisons among species and studies. Our dataset follows established qualitative categories, but we also add detail and connect descriptions from previous publications with our observations to begin building a more cohesive and standardised terminology for *Phyllodactylus* note types. Given the historical inconsistency in terminology, we expect further research will keep working toward standardised definitions to improve comparability across taxa and advance a unified framework for gekkotan vocalisations.

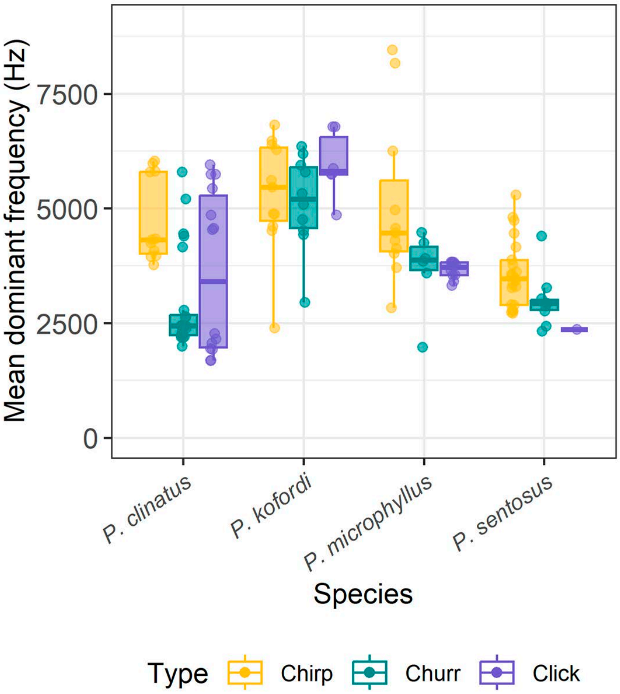

Figure 5. Box plot of mean dominant frequencies of chirps (gold), churrs (green), and clicks (purple) for each species recorded. Dots represent mean dominant frequencies of individual notes measured.

Advertisement calls generally show greater structural complexity than distress calls (Marcellini 1978, Brown 1984, Rothla Jr. et al. 2019). Our study finds a similar level of complexity in the vocalisations of *Phyllodactylus* geckos, with both advertisement and distress calls consisting of two to three note types (chirps, churrs, and clicks; see Table 3). Notably, churrs were more prevalent in advertisement calls (Table 3), while chirps appeared slightly more often in distress calls (Table 3). Our results differ from Marcellini (1974, 1978) and Rothla Jr. et al. (2019), who identified multiple chirps as the main component in the advertisement calls of most Diplodactylidae and Gekkonidae species studied; however, Rothla Jr. et al. (2019) pointed out a few species with more complex vocal repertoires, including multiple chirp types. Our findings agree with Rothla Jr. et al. (2019) in that most advertisement calls consist of distinctly separated, short, countable notes, or note series, while some calls feature very elongated trilled notes. It remains unclear whether these are fused notes in time or separate, elongated notes. *Phyllodactylus sentosus* showed the highest vocal activity rate, with 33.33% of recordings containing call notes, which is notably higher than *P. clinatus* (10.41%), *P. kofordi* (7.29%), and *P. microphyllus* (8.33%) (Table 2). However, our limited sample size prevents further conclusions. Whether this indicates a genus-wide trend or a unique acoustic specialisation in *P. sentosus* is an open question requiring additional research. Overall, there was significant variation in vocal characteristic measurements within each species. Therefore, further studies with a larger sample size and more recordings per species are necessary to determine whether differences in vocal repertoire complexity exist among species.

While advertisement call measurements are limited for most Phyllodactylidae, data are available for *Phyllodactylus tuberculatus* (Marcellini 1978) and *Ptyodactylus hasselquistii* (Rothla Jr. et al. 2019). The range of dominant frequency in *P. tuberculatus* partially overlaps with that of *P. sentosus* (Table 4), which is consistent with their similar body sizes (Table 4). In contrast, *P. hasselquistii*, a larger species than all *Phyllodactylus* in our study, shows lower dominant frequency in its advertisement call without overlapping on any other species (Table 4). Extending our comparison to Diplodactylidae and Gekkonidae species (Table 4), we observe the same pattern: larger species (e.g., *Correlophus ciliatus*, *Chondrodactylus fitzimonsi*, *Gecko gecko*, *Oedura marmorata*) consistently display lower dom-

Table 4. Advertisement call parameters of documented species in the families: Diplodactylidae, Gekkonidae and Phyllodactylidae. The means and ranges (in parentheses) for acoustic values are given in hertz (Hz), and time values are given in seconds (s). Acoustic values for *Phyllodactylus clinatus*, *P. kofordi*, *P. microphyllus* and *P. sentosus* were taken from churr and chirp note types. Acoustic data for other species were taken from Marcellini (1974, 1978) and Rothla Jr. et al. (2019); morphometric data were taken from Bauer et al. (2002), Grismer (2011), Jacobsen et. al. (2014), Branch et al. (2017), Rothla Jr. et al. (2019), Masroor et al. (2020), O'shea (2021).

Taxa	Max SVL (mm)	Dominant frequency (Hz)	Bandwidth 90% (Hz)	Note duration (s)	Internote duration (s)
Diplodactylidae					
Oedura marmorata	93.1	2050 (1500–2670)	7560 (6720–8790)	Fused	Fused
Correlophus ciliatus	109.4	1550 (780–2950)	3190 (1110–9340)	0.03 (0.02–0.08)	0.16 (0.10–0.97)
Gekkonidae					
Afroedura namaquensis	64	3640 (2760–4480)	5020 (2240–6720)	Fused	Fused
Afroedura loveridgei	59	2280 (1550–3790)	5400 (2580–7240)	Fused	Fused
Chondrodactylus fitzimonsi	84.1	1390 (1010–2130)	2430 (660–6720)	0.03 (0.01–0.04)	0.79 (0.23–1.80)
Gekko gecko	200	(500–1000)	–	–	–
Hemidactylus frenatus	61	(1000–2000)	–	1.97 (1.05–3.73)	–
Hemidactylus turcicus	50	3800 (2760–4310)	3980 (3390–4810)	0.07 (0.05–0.08)	0.72 (0.31–1.22)
Lepidodactylus lugubris	35.8	3770 (1900–1275)	4940 (2240–1137)	0.03 (0.01–0.05)	50.31 (0.21–706)
Microgecko persicus	31.8	5920 (4970–6350)	2490 (1590–6350)	0.08 (0.01–0.10)	0.46 (0.11–0.58)
Pachydactylus montanus	43.4	3440 (2580–4650)	2660 (1850–3960)	–	–
Pachydactylus parascutatus	38.40	3440 (2430–4270)	3340 (2310–4220)	–	–
Pachydactylus scutatus	47.9	5060 (2780–5930)	4410 (3450–4820)	–	–
Ptenopus garrulus	49.7	3680 (2930–3960)	2700 (2410–2760)	0.03 (0.02–0.06)	0.09 (0.09–0.11)
Stenodactylus sthenodactylus	43.6	3320 (2410–4590)	2020 (1340–3730)	0.02 (0.02–0.05)	0.26 (0.22–0.31)
Phyllodactylidae					
Phyllodactylus clinatus	75	2372 (1988–2781)	2506.58 (1500–4500)	0.01 (0–0.02)	0.10 (0.01–0.15)
Phyllodactylus kofordi	46	4743 (2391–6352)	8083 (4031–13500)	0.03 (0.02–0.04)	0.91 (0.36–1.96)
Phyllodactylus microphyllus	58	3937 (1977–6253)	7562 (1500–12937)	0.07 (0.05–0.09)	1.92 (0.93–2.90)
Phyllodactylus sentosus	59	3349 (2319–5297)	4922 (2625–9188)	0.07 (0.05–0.34)	0.13 (0.05–0.34)
Phyllodactylus tuberculosus	60	(2000–2500)	–	–	–
Ptyodactylus hasselquistii	96	1490 (1280–1720)	3620 (2970–4310)	0.06 (0.02–0.11)	0.26 (0.21–326)

inant frequency values (Table 4). This inverse relationship between body size and advertisement call frequency was previously documented by Rothla Jr. et al. (2019), mainly in Diplodactylidae and Gekkonidae. Although further testing is needed, our findings support extending this acoustic allometry pattern to the four Phyllodactylidae species examined in this study.

Past studies have found that advertisement calls exhibit lower dominant frequency than distress calls in Gekkota (Frankenberg 1975, Brown 1984, Rothla Jr. et al. 2019), which likely reflects the intraspecific communication function of advertisement calls (Chen et al. 2016, Rothla Jr. et al. 2019). Still, we lacked sufficient data to perform statistical comparisons between advertisement and distress call notes within the same note type. In our current dataset, mean dominant frequency measurements had considerable variation. We also noticed that mean dominant frequencies of advertisement and distress notes overlap in range for several of the species and note types (Fig. 5).

We detected ultrasonic components (>20000 Hz) in the distress calls of *P. clinatus*, *P. kofordi,* and *P. microphyllus*. Brown (1984) suggested that such high-frequency elements in gecko distress calls may serve interspecific functions, potentially reaching ultrasound levels. This supports the hypothesis that ultrasonic components could deter non-gekkotan predators like mammals or birds (Weber & Werner 1977, Werner et al. 1978, Rothla Jr. et al. 2019). In our study area, we noticed the presence of the Sechuran Fox (*Lycalopex sechurae*) and the Burrowing Owl (*Athene cunicularia*), two vertebrates previously reported as predators of *Phyllodactylus* lizards (Huey 1969, Costa-Dos Santos et al. 2021, Pulido et al. 2021). Although acoustic data exist for both predator species (Birdseye 1956, Martin 1973), their auditory sensitivity ranges remain unknown. This represents a key gap to be addressed to fully understand the selective pressures shaping this trait. We therefore suggest that future studies should include ultrasonic recording and playback experiments involving both predators and prey to test whether ultrasonic distress calls in *Phyllodactylus* have a predation-adaptive function.

While our current data do not clarify the context or function of these vocalisations, this study establishes acoustic analyses as a new approach for studying *Phyllodactylus* geckos. This shift in perspective opens up new research opportunities that could significantly improve our understanding of this group. We recommend that future studies on *Phyllodactylus* acoustics focus on expanding the dataset to describe their vocal repertoire fully, exploring variation in calls between species, examining the purpose of distress and advertisement calls, and investigating whether vocalisation patterns are related to phylogenetic inheritance among leaf-toed geckos. We see this study as an initial step in documenting the vocal repertoires of these geckos, and it should not be considered a complete record of their calls. These acoustic methods have the potential to enhance ecological knowledge, as well as our understanding of taxonomy and evolutionary relationships within this group.

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Appendix I

Reviewed specimens

Species	Voucher	Type series specimen	Collection locality	Department	Country
Phyllodactylus clinatus	MVZ 82227	Yes	Punta Aguja, Illescas, Bayovar	Piura	Peru
Phyllodactylus clinatus	CORBIDI 26256	No	Quebrada Nunura, Illescas, Bayovar	Piura	Peru
Phyllodactylus clinatus	CORBIDI 26265	No	Quebrada Nunura, Illescas, Bayovar	Piura	Peru
Phyllodactylus clinatus	CORBIDI 26268	No	Quebrada Nunura, Illescas, Bayovar	Piura	Peru
Phyllodactylus clinatus	CORBIDI 26273	No	Quebrada Nunura, Illescas, Bayovar	Piura	Peru
Phyllodactylus kofordi	TCWC 27912	Yes	Cerro de la Vieja, Motupe	Lambayeque	Peru
Phyllodactylus kofordi	MUPRG-0181	No	Cerro de la Vieja, Motupe	Lambayeque	Peru
Phyllodactylus kofordi	MUPRG-0182	No	Cerro de la Vieja, Motupe	Lambayeque	Peru
Phyllodactylus magister	MCZ-R 17974	Yes	Chinchipe Valley, Jaen	Cajamarca	Peru
Phyllodactylus magister	CORBIDI 5696	No	Perico, Jaen	Cajamarca	Peru
Phyllodactylus magister	CORBIDI 5697	No	Perico, Jaen	Cajamarca	Peru
Phyllodactylus magister	CORBIDI 5698	No	Perico, Jaen	Cajamarca	Peru
Phyllodactylus magister	CORBIDI 5699	No	Perico, Jaen	Cajamarca	Peru
Phyllodactylus microphyllus	ANSP 11364	Yes	Jequetepeque Valley, Pacasmayo	La Libertad	Peru
Phyllodactylus microphyllus	CORBIDI 27582	No	Zaña Valley, Lagunas	Lambayeque	Peru
Phyllodactylus microphyllus	CORBIDI 27583	No	Zaña Valley, Lagunas	Lambayeque	Peru
Phyllodactylus microphyllus	CORBIDI 27584	No	Zaña Valley, Lagunas	Lambayeque	Peru
Phyllodactylus pachamama	CORBIDI 5700	Yes	Balsas, Chachapoyas	Amazonas	Peru
Phyllodactylus pachamama	CORBIDI 7710	Yes	Balsas, Chachapoyas	Amazonas	Peru
Phyllodactylus pachamama	ZFMK 91724	Yes	Balsas, Chachapoyas	Amazonas	Peru
Phyllodactylus pachamama	ZFMK 91728	Yes	Balsas, Chachapoyas	Amazonas	Peru
Phyllodactylus sentosus	TCWC 27913	Yes	Lima City, Lima	Lima	Peru
Phyllodactylus sentosus	CORBIDI 17601	No	Ica River, San Fernando National Reserve, Santiago	Ica	Peru
Phyllodactylus sentosus	CORBIDI 17604	No	Ica River, Reserva Nacional San Fernando, Santiago	Ica	Peru
Phyllodactylus sentosus	CORBIDI 17606	No	Ica River, Reserva Nacional San Fernando, Santiago	Ica	Peru
Phyllodactylus sentosus	CORBIDI 17613	No	Ica River, Reserva Nacional San Fernando, Santiago	Ica	Peru
Phyllodactylus reissi	QCAZR 14181	No	Surroundings of Bosque Protector Cerro Blanco	Guayas	Ecuador
Phyllodactylus reissi	QCAZR 14182	No	Botanical Garden of Bosque Protector Cerro Colorado	Guayas	Ecuador
Phyllodactylus reissi	ZMB 4567	Yes	Guayaquil	Guayas	Ecuador
Phyllodactylus reissi	ZMB 3734A	Yes	Guayaquil	Guayas	Ecuador
Phyllodactylus reissi	ZMB 3734B	Yes	Guayaquil	Guayas	Ecuador
Phyllodactylus reissi	ZMB 3734C	Yes	Guayaquil	Guayas	Ecuador
Phyllodactylus reissi	ZMB 3734D	Yes	Guayaquil	Guayas	Ecuador
Phyllodactylus reissi	ZMB 4567_1	Yes	Guayaquil	Guayas	Ecuador