SALAMANDRA **60**(3): 168–182
15 August 2024 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

Acoustic, visual, and chemical social behaviours of the Chilean Marked Gecko (*Garthia gaudichaudii*)

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Manuscript received: 17 August 2023
Accepted: 12 June 2024 by Oliver Hawlitschek

Abstract. Geckos stand out among lizards for communicating by means of visual, chemical, and acoustic modalities. Although these lizards are known for using these three modalities, the number of studies using them as subjects is restricted, especially those focused on the Chilean endemic genus *Garthia*. Here, we quantify the social behaviour of *G. gaudichaudii*, with special focus on the acoustic component. We also examine behaviours linked to the use of visual and chemoreceptive signals, and how these relate to acoustic signals, shedding light on the potential use of multichannel communication in this species. We examined social interactions of these lizards during encounters between pairs of non-breeding adult individuals of same or different sex. We found that both sexes emit single chirp calls of low intensity and at a low rate. Females calls preceded the approach of an interacting individual (male or female), while a single male called exclusively while ramming a female. We suggest an intimidatory functional role for these calls. Geckos also performed different visual displays, among which aggressive vertical tail-waving is followed by aggressive single chirp calls. Both sexes performed tongue-flicks, mainly to the air or to a conspecific, suggesting that vomerolfaction of volatile and non-volatile chemicals is important for chemical communication in this species. Some males performed courtship behaviours, but no copulation was recorded. Females rejected males performing tail-waving displays and made escape attempts, likely because experiments involved non-breeding subjects. Our study demonstrated that female and male *G. gaudichaudii* use acoustic signals coupled to various visual and chemoreceptive behaviours during social interactions.

Key words**.** Reptilia, Squamata, aggressive interactions, lizards, multisensory communication, single chirp call, tail-waving, tongue-flick.

Introduction

Animals communicate by means of signals of one or different sensory modalities, including acoustic, visual, and chemical channels (Bradbury & Vehrencamp 2011, Stevens 2013). Most lizards (Squamata), rely on visual and chemical modalities to communicate during social interactions, such as mate searching, courtship and territory defense (Pianka & Vitt 2003, Pough et al. 2015), and the use of one or more of these sensory modalities relates to phylogeny (Pianka & Vitt 2003, Font 2010). For example, lizards of the group Iguania use primarily visual signals, and to a lesser extent chemical signals, while an opposite trend prevails among lizards of the Anguimorpha, Lacertoidea and Scincoidea clades (Schwenk 1995, Pianka & Vitt 2003, Pough et al. 2015; but see Whiting et al. 2003 and Labra 2008 for exceptions). Furthermore, nocturnal geckos (Infraorder Gekkota), stand out among lizards for using acoustic signals in addition to chemical and visual modalities (Bauer 2013, Bels & Russell 2019).

Geckos among Squamata are known for an extensive use of acoustic communication (Russell & Bauer 2020). Most nocturnal species produce frequency-modulated calls during social interactions, expelling air from the lungs through a cartilaginous larynx endowed with true vocal cords (Moore et al. 1991, Russell et al. 2000, Rohtla et al. 2019), producing different call types depending on the social context and the species (Frankenberg &

Werner 1992). Males and females can emit multiple chirp calls arranged into regular temporal patterns and characterized by broadband spectra that are used during territory defense and attraction of potential mates (Marcellini 1974, Frankenberg 1982a, Phongkangsananan et al. 2014). Males, females, and juveniles can also produce single chirp calls of short duration in aggressive encounters (Marcellini 1974, 1977, Frankenberg 1982a, b, Briggs 2012, Phongkangsananan et al. 2014). These calls can be emitted when geckos are bitten, pushed, or licked by other individuals. While these acoustic signals have been suggested to intimidate conspecifics (Marcellini 1977), their functional role has not been evaluated (Marcellini 1974, Phongkangsananan et al. 2014).

Vocalizations of geckos can be preceded or accompanied by different visual and chemoreceptive behaviours (Marcellini 1977, Regalado 2003a, b, Jono 2016), composing multimodal signals that integrate two or more sensory modalities (Partan & Marler 1999, 2005). Various visual displays, such as body postures, arched back or tail-waving can precede or accompany call production during courtship or aggressive encounters (Greenberg 1943, Marcellini 1977, Frankenberg 1982b, Regalado 2003b, Suchomelová et al. 2015). Some of these visual signals can be perceived even under low light intensity, as nocturnal geckos have a sensitive nocturnal colour vision (Roth & Kelber 2004) and a remarkable sensitivity for perception of movement (Frankenberg 1981).

Vocalizations can be emitted after scent marking and/or individual chemical recognition during social interactions (Regalado 2003b). These secretions are perceived mainly by two interrelated chemosensory systems, the olfactory and the vomeronasal circuits (Dial & Schwenk 1996, Halpern & Martínez-Marcos 2003, Filoramo & Schwenk 2009). The olfactory system is highly sensitive in geckos, allowing these animals to perceive volatile chemicals (Schwenk 1993, Dial & Schwenk 1996). Meanwhile, the vomeronasal system detects volatile and non-volatile chemicals (Halpern 1992, Schwenk 1995). Vomerolfaction is mediated by tongue-flicks, a characteristic behaviour of lizards that allows capturing chemicals from the environment and carry these components to the vomeronasal organ (Filoramo & Schwenk 2009, Martín & López 2014). For example, many geckos capture skin-derived particles by tongue-flicks for species and sexual recognition (Mason & Gutzke 1990, Szabo & Ringler 2023), which in turn may trigger call production (Regalado 2003b).

The Chilean Marked Gecko, *Garthia gaudichaudii* (Duméril & Bibron, 1836) (Fig. 1), is a nocturnal lizard whose social repertoire remains virtually unknown, with just anecdotal published reports on the use of visual and acoustic signals (Codoceo 1957). Visual interactions have been reported to occur during inter-male encounters in captivity: when two males meet, they observe each other while slightly raising their body and making tail-waving displays, until one of them escapes swiftly (Codoceo 1957). In addition, acoustic signals 'reminiscent of crickets' have been reported in captivity (Donoso-Barros & Vanzolini 1965), suggesting that this species also communicates acoustically in social encounters (Reyes-Olivares & Labra 2017).

Therefore, we aimed this study at describing the social behavioural repertoire of *G. gaudichaudii*, with special emphasis on the analysis of acoustic signals. Specifically, (1) we recorded and analysed acoustic signals emitted by these lizards during social interactions with same or different sex conspecifics, (2) described the occurrence, mean duration, and relative duration, of non-acoustic behaviours, (3) evaluated the interaction between calls and non-acoustic behaviours, (4) examined the potential functional

Figure 1. Adult individual of the Chilean marked gecko (*Garthia gaudichaudii*) observed in the wild. Photographer: Vicente Valdés.

role of displays exhibited during social interactions, and (5) determined whether the displays vary according to the type of interaction (i.e. intra- or inter-sexual). We tackled these objectives recording the behaviour of wild subjects during paired encounters with other subjects of the same or different sex in captivity.

Material and methods

Study model

Garthia gaudichaudii (Fig. 1), is a small gecko (mean snout–vent length, SVL = 31.8 ± 1.9 mm, n = 25; Reyes-Olivares & Campos-Cifuentes 2019), that inhabits semiarid coastal environments in central-northern Chile (Demangel 2016). This species can be found actively at night under boulder exfoliations (Marquet et al. 1990), or among algae in the supralittoral zone, preying on small fly larvae (Codoceo 1957). During the day, this gecko hides under boulder exfoliations, stones, or vegetation (Codoceo 1957), where individuals are usually found isolated. However, we have recorded some cases in which two or three individuals of different ages and sexes were found grouped in close proximity (C. Reyes-Olivares unpubl. data).

Study site and subjects

Geckos were collected at El Panul (30°00' S, 71°23' W; 110 m a.s.l.), Coquimbo Region, Chile, a coastal locality dominated by steppe scrub. We searched for individuals during the day under boulder exfoliations and collected exemplars larger than 30 mm SVL (i.e., mature individuals, Marquet et al. 1990), excluding gravid females. Gravid females were detected by direct visual observation of the eggs through their translucent ventral skin (Codoceo 1957). In total, we collected 35 individuals during two field trips conducted out of the mating season of the species, which likely occurs from July to November (Donoso-Barros 1966, Marquet et al. 1990). In February 2017, we captured 13 individuals (six males and seven females, mean SVL = 31.3 ± 0.7 mm, hereafter 'Group A'), and in February 2018, we captured 22 individuals (11 males and 11 females, mean SVL = 31.9 ± 0.4 mm, hereafter 'Group B'). No statistically significant differences occurred in SVL between populations, sexes or for the interaction of these factors (ANOVA: $p > 0.05$ for all comparisons). The sex of the individuals was verified by eversion of male hemipenis (Harlow 1996). Location of captures was georeferenced for each gecko, and each subject was released back to their exact collecting site weeks after conducting the behavioural observations in captivity.

Geckos were housed individually in plastic boxes (20 × 15 × 15 cm), with absorbent paper as substrate, a cardboard shelter, and a pot containing water. Water was provided ad libitum and geckos were fed three times per week with flour beetle larvae (*Tribolium* sp.), dusted with calcium and vitamin D3 (Exo Terra Calcium + D3 Powder Supplement). Individuals from Group A were kept in a vivarium located 1 km from the collecting site, where animals were exposed to the natural daily changes in humidity (70–90%) and temperature (12–26 °C) of the locality (www.weather-avenue.com). Individuals of Group B were transported to the Laboratory of Neuroethology, Universidad de Chile, located in Santiago, approximately 400 km south of the study site, and placed in an indoor vivarium with continuous ventilation and conditions mimicking those recorded in the study site during normal summer days (humidity and temperatures ranging between 70–90% and 12–26 °C, respectively, and a 14:10 L:D photoperiod cycle). In the laboratory, we exposed animals to halogen lights (100 W) to regulate ambient temperature and photoperiod. We maintained humidity using sprinklers and buckets of water placed inside the vivarium. Upon arrival of these subjects, we reversed progressively the photoperiod during the subsequent six days, until lights went off at 09:00 h and on at 19:00 h. Individuals of both groups were left undisturbed for a week before any trials, to allow habituation to captivity. At the end of the experiments, the photoperiod was progressively restored during a week before releasing back all the animals at their original capture site.

Experimental design

We conducted intra-sexual (same sex) and inter-sexual (between sex) encounters of pairs of adults to record their behavioural repertoire. We carried out nine encounters with individuals of Group A: 5 male–female (M–F), 2 male–male (M–M), and 2 female–female (F–F). These trials were performed during the evening (21:00–02:00 h) in a conditioned room. With Group B, 20 encounters were conducted: 10 M–F, 5 M–M, and 5 F–F. Experiments with this group were conducted in the laboratory between 1000–1800 h, under a light/dark reversed cycle. All individuals were used only once in each of the two types of encounter trials, except for a male from Group A which was subjected to two M–F encounters. The order of the two types of trials was randomized and the time between trials was the same (at least 2 days) for all individuals.

All trials were held in a neutral experimental box (30 × 15 × 20 cm) with black acrylic walls, except for the top and front panels, which were made of clear acrylic (Jono & Inui 2012). This box was divided into two equal-sized compartments by a removable black acrylic partition. For each trial, each gecko was initially located in one compartment, and left undisturbed for 5 min before starting the trial. Thereafter, we removed the partition to allow the focal animal to interact with the stimulus subject. We recorded all interactions in darkness, with the use of two infrared lamps (150 W) hanging 60 cm above the experimental box. Since temperature can affect the locomotor and behavioural performance of geckos (e.g., Ringenwald et al. 2021), we maintained the temperature of the experimental box within a range measured in the field during the nocturnal activity of *G. gaudichaudii* (24–26 °C; Marquet et al. 1990) using sprinklers and buckets of water.

An omnidirectional microphone (Sennheiser MKE 2, K6 power supply), was suspended at the centre of the top of the box to register the vocalizations emitted. These were recorded with a Tascam DR-100 recorder at a sample rate of 44.1 kHz. Before placing individuals in the arena, we recorded a pure tone of 93.8 dB sound pressure level (SPL) (root-mean-square, RMS, fast time weighting, linear frequency weighting), emitted by a sound calibrator (Brüel & Kjaer 4231) to calculate the amplitude of calls produced by geckos (see data analysis). We videorecorded social interactions during 60 min with a digital camcorder (Panasonic HDC-TM20, Panasonic, Kadoma, Japan), placed in front of the transparent lateral wall of the box. At the end of each trial, we returned each experimental subject to its maintenance cage and kept it undisturbed for at least two days before exposing them to a new trial. Between consecutive trials, we rinsed the experimental box with ethanol 95% to remove any scents from the geckos that may affect the behaviour of the next focal individual.

Acoustic display

Sound recordings (WAV files, 16 bits) were band-pass filtered at 200 Hz to reduce the presence of low-frequency noise, and then analysed using the package 'seewave' (Sueur et al. 2008) in R (version 3.5.1, R Core Team 2018). Call features were measured in the temporal and frequency domains; we recorded call duration (s) from oscillograms, and the spectral variables from spectrograms using a fast short-term Fourier transform (Hanning window, window length = 256 points, 85% overlap). Spectral measurements, were: 1 – fundamental frequency (Hz), 2 – dominant frequency (Hz), 3 – frequency at first quartile (FQ_{25}; Hz), 4 – frequency at third quartile (FQ_{75}; Hz), 5 – interfrequency range (IQR; frequency range between FQ_{25} and FQ_{75}; kHz), and 6 – spectral complexity (Hz), estimated from the spectral flatness measure or Wiener entropy, an index of energy distribution of the frequency spectrum (pure tone ~ 0; noisy ~ 1; Sueur et al. 2008, Sueur 2018, Baeckens et al. 2019). Additionally, we measured the RMS amplitude of the vocalizations and the pure tone emitted by the calibrator to calculate the absolute amplitude of the biological signals. We quantified call amplitude as:

$$\text{Call amplitude (dB SPL)} = 93.8 \text{ (dB SPL)} - 20 \log_{10} \text{(pure tone RMS amplitude / call RMS amplitude)}$$

In this formula, 93.8 dB SPL RMS is the known amplitude of the calibrator pure tone. To perform these calibrations, the pure tone and vocalizations were recorded with the same microphone (Senhneiser MKE 2) and using the same recording level of the digital recorder (Tascam DR-100). Averages of all these acoustic variables were calculated to characterize the vocalizations of the individuals.

Non-acoustic displays

We quantified behaviours of geckos from videotapes by using the software BORIS (Friard & Gamba 2016). Because individuals of Group B were used only once in each trial, descriptions of behaviours and patterns of social interactions were made only from the videotapes of this group to prevent pseudoreplication.

Based on pilot experiments with *G. gaudichaudii* and following Rivera Rodríguez et al. (2011), we categorized all behaviours in four major categories (Table 1): submissive (n = 4), aggressive (n = 6), exploratory (n = 2), and neutral (n = 2). During submissive behaviours geckos avoided contact with the other individual. Aggressive behaviours were displayed by an individual attempting to initiate contact or exert dominance over another subject. Exploratory behaviours were involved in the potential sampling of chemical cues in the environment, e.g., tongue-flick. Finally, neutral behaviours were those not directed towards the other animal. We coded the occurrence, the relative duration, and the absolute duration of each non-acoustic behaviour recorded. For those that had a short duration (< 1 s, i.e., jump, tongue-flick, and head-turn), only occurrence was recorded. To assess the effect of sex and type of encounter on four types of behaviours (i.e., submissive, aggressive, exploratory, and neutral) as a group or individually, we performed Wilcoxon Signed Rank and Mann-Whitney U tests for intra- and inter-sexual comparisons, respectively (Regalado 2003b), because data were not normally distributed.

To explore the interactions between calls and non-acoustic behaviours we evaluated the occurrence of behaviours performed by a sender just before it emitted a call, by means of a sequential analysis (Regalado 2003b). In addition, the potential role of calls was evaluated examining the occurrence of the behaviours performed by the receiver immediately after the call was produced (modified from Regalado 2003b). The potential role of the most frequently observed non-acoustic behaviours directed at another individual, i.e., tongue-flick to conspecific, vertical tail movements, approach, and raised-tail displays, was examined by counting the times that individuals responded with a specific behaviour during the 10 s after the deployment of each of these behaviours (modified from Regalado 2003a, b). For tongue-flick, the behaviour performed by the same subject after this chemical exploratory behaviour was recorded, while for the other three visual displays, the behaviours exhibited by the opponent were recorded.

Results

Acoustic displays

During the experimental social interactions, *G. gaudichaudii* emitted single chirp calls that were relatively infrequent (Fig. 2; Supplementary audio 1). Of 35 individuals included in the experiments, only five (14.3%) vocalized (4 females and 1 male), producing a total of seven calls. Females vocalized during intra- and inter-sexual encounters (Table 2),

Table 1. Description of non-acoustic behaviours recorded during social interactions in *G. gaudichaudii*. These behaviours are presented in alphabetical order within four categories (submissive, aggressive, exploratory, and neutral; Rivera Rodríguez et al. 2011). Three behaviours having brief durations: jump, tongue-flick, and head-turn, were measured as number of occurrences and the rest as the total time (s) that individuals exhibited the behaviour.

Behaviour	Description	References
Submissive		
Escape attempt (s)	Sudden runs forward and attempts to escape from the test box, rubbing the tip of the snout against the walls of the enclosure. Attempts to climb the walls or 'dig' in the floor (Supplementary videos 1 and 5)	Hoare & Labra (2013), Webb et al. (2010)
Jump	Fast jump by a startled individual	This study
Reverse (s)	Individual moves backwards slowly (Supplementary video 2)	Downes & Shine (1998)
Raised-tail (s)	The tail remains elevated vertically, at an angle < 90° relative to the floor (Supplementary video 3)	Regalado (2003b), Rivera Rodríguez et al. (2011)
Aggressive		
Approach (s)	Movement forward while staring at the other animal. Some of these movements are accompanied by tail displays (i.e., raised tail or tail-waving) or body raised (see below) and also by strong ramming against the other individual (Supplementary video 3)	Regalado (2003a, b)
Arched back (s)	Back arched up and tail tip resting on substrate (Supplementary video 4)	Regalado (2003b)
Bite (s)	Mouth grabbing the skin of the opponent (Supplementary video 4)	Regalado (2003a, b)
Body raised (s)	Four-leg extension with no arched back and tail tip resting on substrate (Supplementary video 5)	Regalado (2003b)
Mount (s)	Individual climbs on top of the interacting individual	Wissmann et al. (2005)
Tail-waving (s)	Three types of tail-waving displays were detected: 1) Horizontal: tail is undulated laterally slightly separated from the substrate. (Supplementary video 6) 2) Vertical: tail is elevated and undulated (Supplementary video 5) 3) Tip: fast lateral movements of just the tip of the tail	Regalado (2003b), Martínez-Cotrina et al. (2014), Suchomelová et al. (2015)
Exploratory		
Tongue-flick	Fast single tongue extrusion lasting less than 1 s directed to different targets: 1 – air, 2 – substrate, 3 – conspecific's body, 4 – self-licking of the cloaca and 5 – self-licking of an eye (Supplementary video 7)	Regalado (2003a, b), Rivera Rodríguez et al. (2011), Hoare & Labra (2013)
Head-turn	Head motion in an angle of 45–90° relative to the longitudinal axis of the body	Thompson et al. (2008), Rivera Rodríguez et al. (2011)
Neutral		
Movements (s)	Walking and position changes other than listed above	Hoare & Labra (2013)
Rest (s)	The animal remains motionless but can perform tongue-flick or head-turn	Regalado (2003a, b), This study

whenever the opponent (male or female) approached to a distance of ~ 5 cm, and the male vocalized while ramming against the interacting female.

All vocalizations recorded were single-chirp calls (Marcellini 1977), which were short and high-pitched sounds with wide broadband spectra and harmonics embedded in a noisy structure (Fig. 2). Table 3 includes means for temporal and spectral variables of these calls. Acoustic characteristics of calls were similar between the male and females in inter-sexual contexts, with the exception that male's signals had slightly lower IQR and higher fundamental and dominant frequencies, FQ_{25} and amplitude than those of females (Table 3). Only one female vocalized in an intra-sexual context, and some characteristics of its call, such as fundamental and dominant frequencies, FQ_{75}, FQ_{25} and IQR, exceeded the maximum value recorded for females in inter-sexual contexts (Table 3).

Non-acoustic displays

The visual and chemoreceptive behaviours exhibited by the geckos during inter- and intra-sexual encounters were similar in general (Table 4). In inter-sexual contexts, individuals of both sexes displayed most of the behaviours listed, with the exception of tongue-flicks to the cloaca (Table 4). However, only males displayed bite, body raised, mount and horizontal tail-waving during inter-sexual interactions (Table 4). Likewise, only one male hit twice the female's rostrum with the tail while performing horizontal tail-waving. During intra-sexual interactions, individuals of both sexes also performed most of the behaviours listed, with the exception of bite, body raised, mount and tip tail-waving. In addition, only males performed tongue-flicks directed to the cloaca, but only females performed arched back and horizontal tail-waving (Table 4).

Table 2. Number of single chirp calls emitted by individuals of *G. gaudichaudii* in social encounters between individuals of the same (intra-sexual encounters) and different (inter-sexual encounters) sex. Each encounter had a total duration of 60 min. F = female; M = male; N = total number of individuals tested.

Group	Social encounter	Sex	N	Number of individuals that vocalized	Number of calls emitted
A	Inter-sexual	F	5	2	2
		M	5	–	–
	Intra-sexual	F	4	1	1
		M	4	–	–
B	Inter-sexual	F	10	1	1
		M	10	1	3
	Intra-sexual	F	10	–	–
		M	10	–	–

Exhibition of submissive, aggressive, and exploratory behaviours did not vary between the sexes or type of encounters (Table 4). In contrast, display of neutral behaviours (i.e., movements plus resting) were more frequent during intra- than in inter-sexual interactions within each sex and more frequent in intra-sexual interactions between females than between males ($Z > 2.00$, $p < 0.05$ for all comparisons; Table 4).

Comparisons for specific behaviours revealed significant differences between sexes and type of encounter. The aggressive behaviour of tail-waving, was performed more often by both sexes during inter- than intra-sexual encounters ($Z > 2.00$, $p < 0.05$ for all comparisons; Table 4). The vertical tail-waving sub-type was performed more frequently by females during inter- than in intra-sexual interactions ($T = 5.00$, $p < 0.05$; Table 4). In contrast, the exploratory behaviours of tongue-flick to substrate and head-turn were exhibited more often by females during intra- than inter-sexual encounters ($T = 5.50$, $p < 0.05$), and more frequently by females than males during intra-sexual encounters ($Z = 2.12$, $p < 0.05$) (Table 4). In addition, males performed tongue-flicks to a conspecific more frequently during inter- than during intra-sexual encounters ($T = 2.00$, $p < 0.05$; Table 4). Furthermore, among neutral behaviours, males performed more movements during intra- than during inter-sexual encounters ($T = 5.00$, $p < 0.05$), and females displayed rest more often than males in intra-sexual encounters ($Z = 2.34$, $p < 0.05$) (Table 4).

The analysis of relative duration of behaviours showed that during interactions, animals spent the largest proportion of time resting, followed by attempts to escape and movements (Fig. 3). As such, neutral behaviours (movements and rest) occupied a relatively high proportion of experimental time (Fig. 3). The proportion of time that females spent resting and males performing movements was longer in intra- than inter-sexual contexts ($T = 1.00$, $p < 0.01$, for both comparisons; Fig. 3). Approach, raised-tail, and vertical tail-waving lasted similarly during the different types of interactions, but females spent longer intervals in escape attempts in inter- than intra-sexual encounters ($T = 2.00$, $p < 0.01$; Fig. 3).

The absolute duration of specific non-acoustic behaviours was in most cases similar between sexes and encounter types, with the exception of resting ($T = 1.00$, $p < 0.05$),

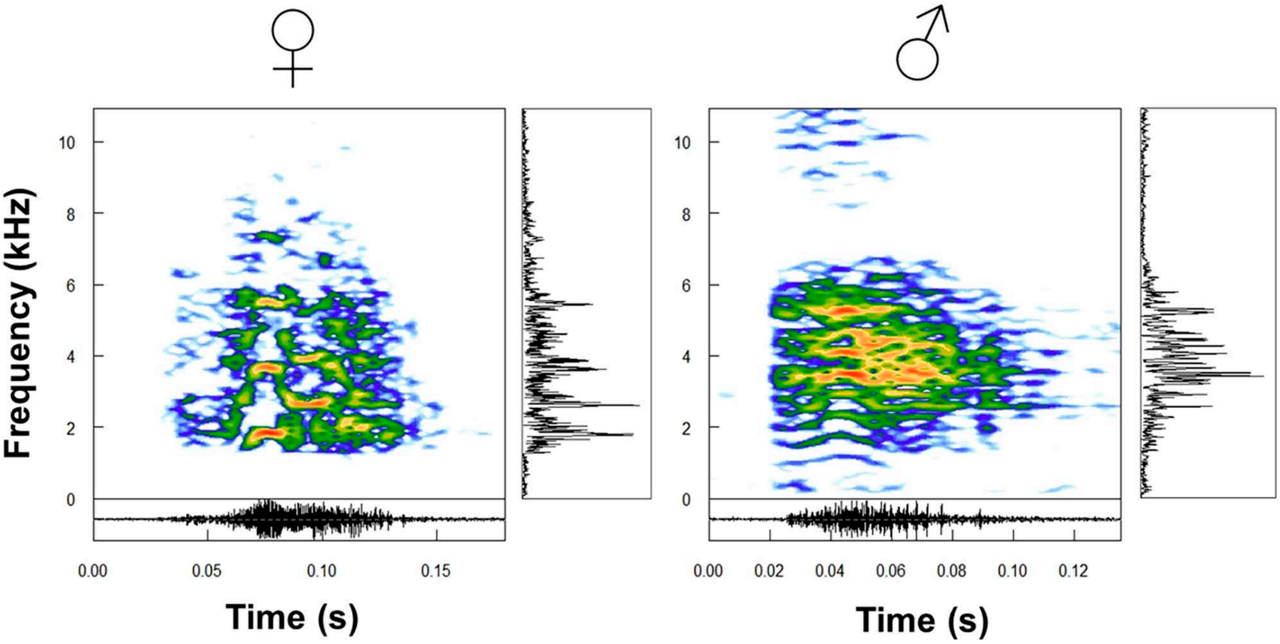

Figure 2. Spectrogram (left), oscillogram (bottom) and power spectrum (right) (Hanning window, window length = 256 points, 85% overlap) of single chirp calls of a representative female (SVL = 35.7 mm) and male (SVL = 34.0 mm) of *G. gaudichaudii*.

Table 3. Descriptive statistics (mean ± SE, range) for eight variables measured in the single chirp calls of *G. gaudichaudii*. Statistics are shown for the calls of all individuals (N = 5; SVL = 32.0 ± 0.8 SE mm), for females (N = 4; SVL= 31.5 ± 0.8 SE mm), and for the single male (SVL = 34.0 mm), in inter- and intra-sexual contexts. Each female vocalized only once (three in inter-sexual contexts and one in an intra-sexual context) while the male vocalized three times (in the same inter-sexual interaction). C = total number of calls emitted. FQ$_{25}$: First quartile frequency; FQ$_{75}$: Third quartile frequency; IQR: Inter frequency range.

	All calls (C = 7)	Calls females inter-sexual (C = 3)	Calls female intra-sexual (C = 1)	Calls male inter-sexual (C = 3)	Calls male intra-sexual (C = 0)
Duration (s)	0.06±0.01 (0.04–0.08)	0.06±0.01 (0.04–0.08)	0.07	0.04±0.01 (0.03–0.06)	–
Fundamental frequency (kHz)	3.21±0.79 (1.49–5.91)	2.05±0.29 (1.49–2.46)	5.91	4.01±0.92 (2.47–5.65)	–
Dominant frequency (kHz)	5.45±0.41 (4.29–6.72)	4.88±0.31 (4.29–5.36)	5.88	6.72±0.51 (5.71–7.36)	–
FQ$_{25}$ (kHz)	4.96±0.24 (4.48–5.56)	4.56±0.04 (4.48–4.61)	5.56	5.54±0.43 (5.10–6.41)	–
FQ$_{75}$ (kHz)	10.3±0.37 (9.76–11.7)	10.1±0.20 (9.76–10.4)	11.7	9.67±0.11 (9.47–9.83)	–
IQR (kHz)	5.38±0.35 (4.12–6.15)	5.54±0.16 (5.28–5.54)	6.15	4.12±0.43 (3.29–4.72)	–
Spectral complexity	0.59±0.02 (0.53–0.65)	0.58±0.03 (0.53–0.65)	0.63	0.55±0.04 (0.47–0.62)	–
Amplitude (dB SPL RMS)	55.3±4.23 (45.6–65.3)	54.9±5.64 (45.6–65.0)	47.1	65.3±1.73 (63.4–68.7)	–

Table 4. Mean occurrence (± SE) of behaviours exhibited by males (M) and females (F) of *G. gaudichaudii* in intra- and inter-sexual encounters. Each individual was submitted to 10 intra- and inter-sexual interactions. Behaviours are presented grouped into four categories: submissive, aggressive, exploratory and neutral behaviours (in bold). The mean total of each category, as well as the values for each behaviour are listed. Dashes indicate behaviours not displayed. Symbols: *, # and $ indicate comparisons of behaviours between encounter types (M–F, M–M, M–F and F–F) for which significant differences occurred (Wilcoxon Signed Rank and Mann-Whitney U tests for intra- and inter-sexual comparisons, respectively; p = 0.05). For descriptions of the recorded behaviours see Table 1.

	Male		Female	
Behaviours	M–F	M–M	F–M	F–F
Submissive	**33.3 ± 6.1**	**33.4 ± 3.9**	**38.6 ± 5.3**	**42.3 ± 3.9**
Escape attempt	29.1 ± 5.4	30.2 ± 3.2	35.4 ± 4.7	39.8 ± 3.6
Jump	2.30 ± 0.9	0.70 ± 0.4	1.20 ± 0.4	1.10 ± 0.3
Reverse	0.50 ± 0.2	0.20 ± 0.1	0.50 ± 0.3	0.40 ± 0.2
Raised-tail	1.40 ± 0.5	2.30 ± 1.4	1.50 ± 0.7	1.00 ± 0.3
Aggressive	**14.7 ± 4.1**	**11.1 ± 1.2**	**11.5 ± 1.9**	**19.5 ± 5.1**
Approach	9.50 ± 2.8	9.70 ± 1.3	7.90 ± 1.5	17.9 ± 5.2
Arched back	1.10 ± 1.1	–	0.40 ± 0.2	0.10 ± 0.1
Bite	0.20 ± 0.2	–	–	–
Body raised	0.10 ± 0.1	–	–	–
Mount	0.10 ± 0.1	–	–	–
Tail-waving	3.80 ± 0.9*	1.30 ± 0.5*	3.20 ± 0.8#	1.50 ± 0.7#
Horizontal	0.30 ± 0.2	–	–	0.10 ± 0.1
Vertical	3.40 ± 0.9	1.30 ± 0.5	3.10 ± 0.8#	1.40 ± 0.7#
Tip	0.10 ± 0.1	–	0.10 ± 0.1	–
Exploratory	**35.4 ± 5.0**	**49.3 ± 6.9**	**44.1 ± 8.9**	**64.9 ± 7.0**
Tongue-flick	21.7 ± 3.5	27.8 ± 5.9	30.8 ± 7.8	33.0 ± 6.1
air	17.3 ± 3.4	22.0 ± 5.5	26.1 ± 7.0	26.0 ± 5.7
conspecific	1.80 ± 0.7*	0.40 ± 0.2*	1.00 ± 0.4	0.50 ± 0.3
cloaca	–	0.20 ± 0.2	–	–
eye	0.80 ± 0.6	1.60 ± 0.7	1.00 ± 0.5	1.30 ± 1.3
substrate	1.80 ± 0.6	3.60 ± 0.8	2.70 ± 0.7#	5.20 ± 0.7#
Head-turn	25.2 ± 3.1	50.2 ± 11$	31.7 ± 5.6#	63.4 ± 11#,$
Neutral	**80.0 ± 9.9***	**111 ± 6.9*,$**	**93.7 ± 11#**	**165 ±20#,$**
Movements	26.1 ± 3.6*	39.0 ± 3.4*	34.0 ± 5.2	55.8 ± 8.1
Rest	53.9 ± 7.1	72.2 ± 3.8$	59.7 ± 6.6	109 ± 13$

movement (T = 5.00, $p < 0.05$), and escape attempts (T = 3.00, $p < 0.05$), all of which were significantly longer in females during inter- than intra-sexual encounters (Table 5). Males displayed significantly longer movements in intra-sexual contexts (Z = -2.90, $p < 0.01$), and longer tail-waving during inter-sexual trials than females (T = 7.00, $p < 0.05$; Table 5).

Relationships between call emission and non-acoustic displays

The emission of single chirp calls was typically preceded by submissive or aggressive behaviours by female senders, such as escape attempts or vertical tail-waving, respectively (Fig. 4a), and by submissive, aggressive or neutral behaviours by male sender (Fig. 4c). For female senders, call emission was followed by submissive behaviours such as escape attempts and jumps (Fig. 4a), and for males, it was followed by submissive jump and aggressive approach (Fig. 4c). Before being exposed to calls, female receivers displayed different aggressive behaviours, such as approach, body raised or vertical tail-waving (Fig. 4b), while male receivers displayed neutral rest (i.e., they stood motionless) or submissive escape attempt (Fig. 4d). After the calls, receivers of both sexes remained resting and exhibited submissive escape attempts (Figs 4b, d).

Effects of most frequent non-acoustic behaviours

The analysis of the effects of the four specific behaviours that triggered responses showed that individuals responded differently depending on sex and type of interaction

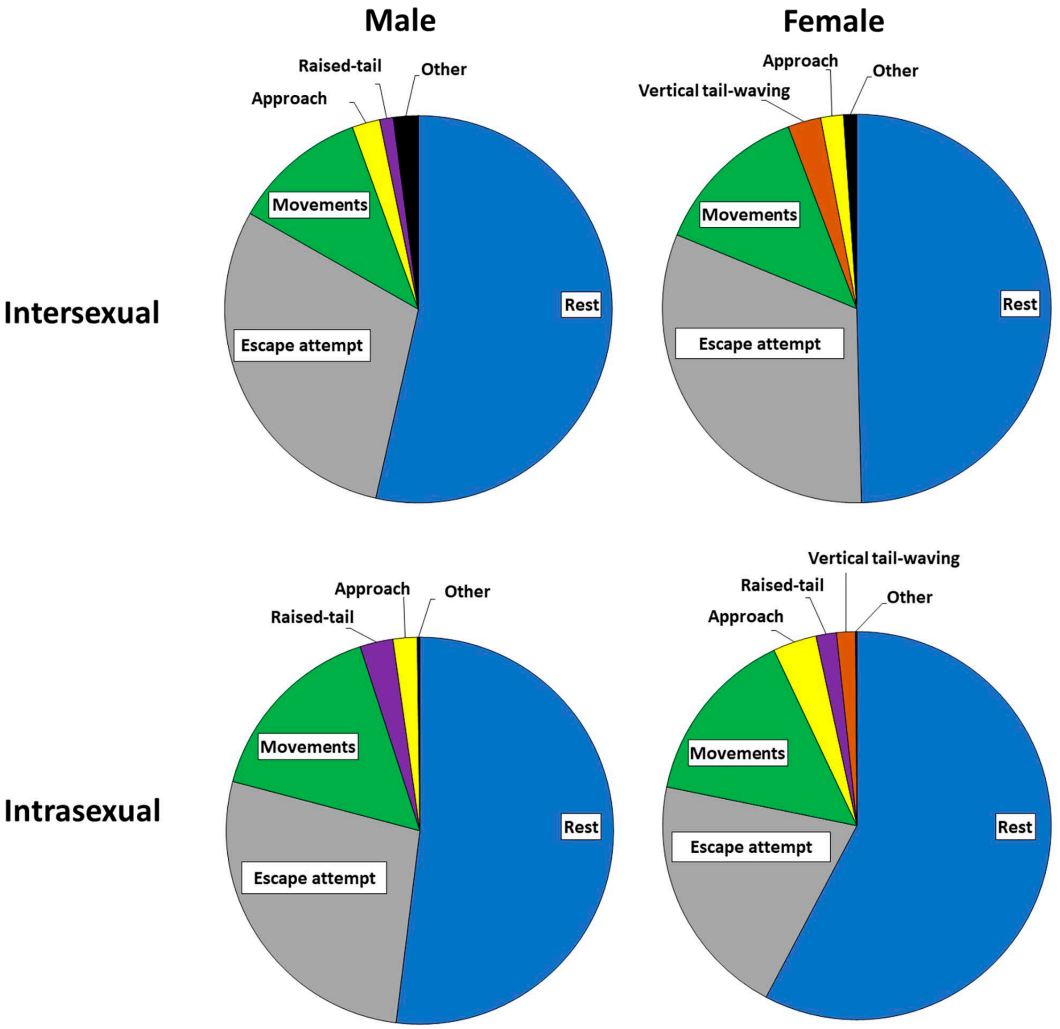

Figure 3. Relative duration of non-acoustic specific behaviours performed by males (left) and females (right) of *G. gaudichaudii* in inter- (top) and intra-sexual (bottom) contexts. Slices represent the average proportions of time during which each behaviour was performed. Behaviours with a proportion < 1% were grouped as 'other' (see Table 4). See Table 1 for descriptions of behaviours. Three behaviours having brief durations: jump, tongue-flick, and head-turn are not included in the graphs.

Table 5. Mean durations (± SE) of specific behaviours displayed by males (M) and females (F) of *G. gaudichaudii* in social encounters. Each sex was submitted to 10 intra- and inter-sexual interactions. Behaviours are presented grouped into categories: submissive, aggressive and neutral behaviours. Behaviours measured as events (i.e., exploratory behaviours, tongue-flick and head-turn, and jump) are not listed. Dashes indicate behaviours not exhibited. Symbols *, # and $ indicate comparisons between encounters for which significant differences occurred. For descriptions of the recorded behaviours see Table 1.

	Male		Female	
Behaviours	M-F	M-M	F-M	F-F
Submissive				
Escape attempt	56.5 ± 8.0	41.2 ± 3.4	42.6 ± 2.5#	32.4 ± 4.2#
Reverse	2.00 ± 1.3	0.50 ± 0.3	1.10 ± 0.7	1.10 ± 0.6
Raised-tail	18.8 ± 8.0	9.60 ± 6.2	9.50 ± 4.5	58.1 ± 42
Aggressive				
Approach	9.23 ± 1.3	9.12 ± 1.3	10.3 ± 2.1	9.43 ± 1.3
Arched back	2.60 ± 2.6	–	5.50 ± 3.0	2.80 ± 2.8
Bite	4.80 ± 4.8	–	–	–
Body raised	1.40 ± 1.4	–	–	–
Mount	0.41 ± 0.41	–	–	–
Tail-waving	8.50 ± 1.7*	3.42 ± 1.0*	17.7 ± 8.7	13.9 ± 8.2
Horizontal	0.59 ± 0.4	–	–	0.14 ± 0.1
Vertical	7.70 ± 1.7	3.40 ± 1.0	17.3 ± 8.7	13.8 ± 8.2
Tip	0.30 ± 0.3	–	0.40 ± 0.4	–
Neutral				
Movements	15.7 ± 1.3	15.5 ± 1.4$	14.2 ± 1.7#	10.0 ± 0.8#,$
Rest	48.7 ± 12	26.9 ± 2.1	36.2 ± 6.7#	23.5 ± 4.4#

(Fig. 5). Both sexes had a broader behavioural repertoire during inter- than during intra-sexual interactions. Males displayed 11 and 5 different behaviours during inter- and intra-sexual encounters, respectively (Figs 5A, C), and females displayed 11 and 8 behaviours, respectively (Fig. 5B, D). Both sexes had similar repertoire size (11 behaviours) during inter-sexual encounters (Figs 5A, B), but females had a broader repertoire during intra-sexual encounters than males (8 versus 5 behaviours, Figs 5C, D).

After geckos tongue-flicked a conspecific of the opposite sex, males displayed submissive (escape attempts) or exploratory (tongue-flicks to the air) behaviours (Fig. 5A), but females responded with a larger repertoire that included also aggressive behaviours (Fig. 5B). During intrasexual encounters, in contrast, males after tongue-flicking another male only exhibited submissive behaviour (escape attempt, Fig. 5C), while females only exhibited aggressive behaviour (vertical tail-waving, Fig. 5D).

Geckos responded with a broad range of submissive, aggressive, and exploratory behaviours to the vertical tail-waving, approach, and raised-tail visual behaviours, across all encounter types (Figs 5A–D). The only exceptions were the lack of exploratory responses to vertical tail-waving and raised tail in M–M encounters. Overall, the most observed responses to vertical tail-waving, approach, and raised-tail were the submissive behaviour of escape attempts and the aggressive behaviours of vertical tail-waving and approach (Figs 5A–D).

General social interactions pattern

Figure 6 shows the most frequent behavioural sequence observed in intra- and inter-sexual encounters examined in males and females. The sequence began with both individuals in rest and performing head-turns, until one of them displayed tail-waving and/or tongue-flick to the air (Fig. 6). Subsequently, the active or 'dominant' individual approached to the inactive or 'submissive' individual, which in turn remained motionless, until one or both escaped quickly (Fig. 6). Initially, this sequence was performed by one individual and then by the other, and occasionally both individuals did it simultaneously. In two M–F encounters, this sequence was repeated > 5 times by the males after they tongue-flicked the female's skin. In one of these cases, a male bit the female on the base of the tail and neck, and then tried to mount her, until she fled.

Discussion

Behavioural displays in social contexts were virtually unknown in *G. gaudichaudii*. The only available information indicated that individuals performed tail-waving displays during male–male interactions (Codoceo 1957). Here, we showed for the first time that this species emits single chirp calls during social encounters. Additionally, male and female geckos displayed a diversity of visual and chemosensory behaviours during intra- and inter-sexual encounters that parallel previous findings in other nocturnal geckos (Greenberg 1943, Marcellini 1974, 1977, Frankenberg 1982a, b, Leuck et al. 1990, Regalado 2003b, Phongkangsananan et al. 2014, Suchomelová et al. 2015).

Acoustic displays

Similar to findings in *Hemidactylus garnotii* Duméril & Bibron, 1836, the vocal repertoire of *G. gaudichaudii* during social encounters consisted in one-note squeaks (Fig. 2; Frankenberg 1982b). However, this finding contrasted with what has been described for most nocturnal geckos, which exhibit broader call repertoires in social contexts (Frankenberg & Werner 1992, Rohtla et al. 2019). Many species emit single, double or multiple chirps calls in sexual interactions during courtship and copulation (Marcellini 1974, Regalado 2003b, Hibbitts et al. 2007, Jono & Inui 2012, Phongkangsananan et al. 2014, Jono 2016). The relatively reduced vocal repertoire shown by *G. gaudichaudii* recorded during our study may relate to experiments were conducted outside the reproductive season of this species. We currently know that in this species oviposture occurs between October and December (spring–summer of the southern hemisphere), and eggs hatch in February and March (end of the summer) (Donoso-Barros 1996, Reyes-Olivares et al. 2021).

Rather, characteristics of single chirp calls of *G. gaudichaudii* are comparable with those reported for other nocturnal geckos in aggressive contexts (Table 6): these calls are typically produced by both sexes during aggressive encounters, and have a short duration and low amplitude (Table 6). However, we also found an intriguing contrast, as the dominant frequency (range: ~ 4.0–7.0 kHz) of *G. gaudichaudii* calls seems higher than those reported for most other species (Table 6). This difference is likely related to the small relative size of this gecko, as the frequency of calls emitted by lizards is inversely related to body size (Labra et al. 2013, Baeckens et al. 2019).

The emission rate exhibited by *G. gaudichaudii* seems lower than that reported for other geckos. For instance, males, females and juveniles of *Gegyra dubia* (Macleay, 1877) and *H. turcicus* (Linnaeus, 1758) emit more single chirp calls during social encounters than any other call type (e.g., multiple chirp calls; Frankenberg 1982a, Phongkangsananan et al. 2014). Potentially, these differences in emission rate relate to interspecific dissimilarities in the levels of territoriality and/or antagonism in social interactions, and these vocalizations seem more frequent in highly territorial species (Marcellini 1977, Phongkangsananan et al. 2014).

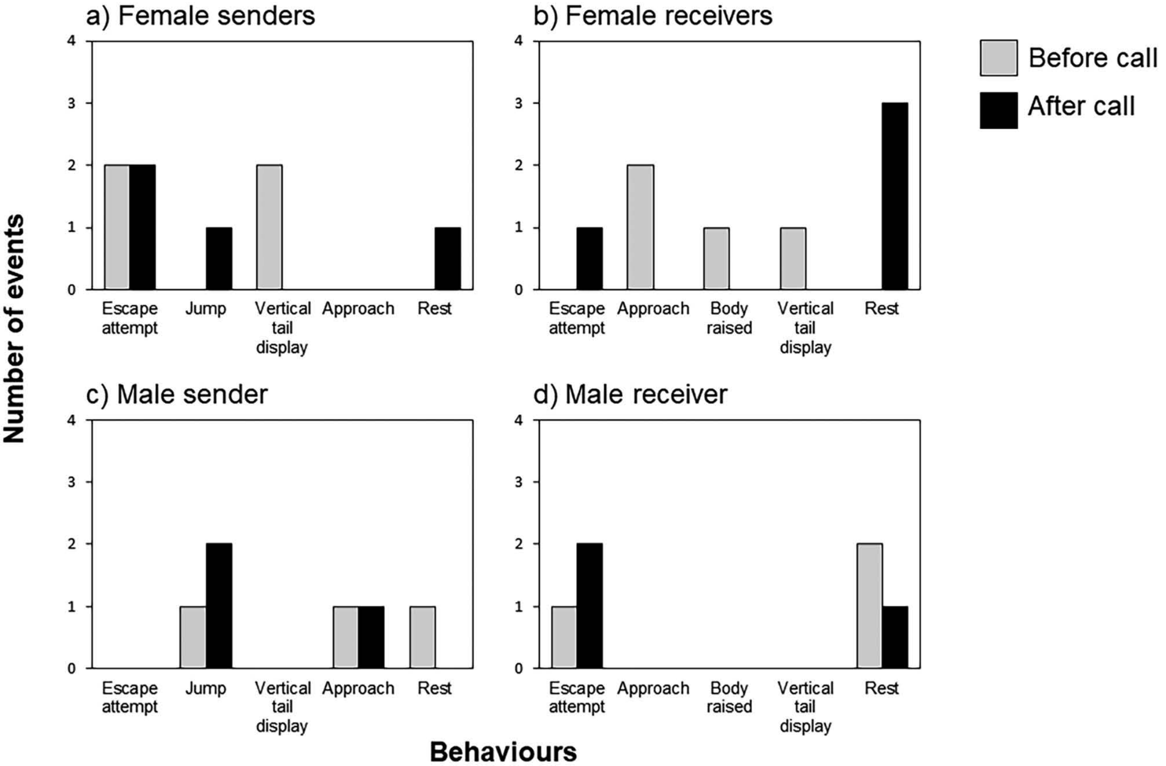

Figure 4. Occurrence of behaviour displayed by sender and receiver females (a–b), and sender and receiver male (c–d), before (grey bars) and after (black bars) single chirp calls uttered by the senders. Behaviours correspond to those displayed by four females and one male. Submissive behaviours: Escape attempt and jump; Aggressive behaviours: Approach, body raised and vertical tail-waving; Neutral behaviour: Rest.

The analysis of behaviours displayed by *G. gaudichaudii* before and after call emissions suggests that calls reduce aggressive behaviours but increase submissive behaviours in receivers and emitters of both sexes (Fig. 4). Most individuals emitted these calls as a 'final intimidation' signal during interactions in which both individuals performed aggressive behaviours, including vertical tail-waving, approach or body raised. During our essays, both individuals performed less aggressive behaviours and more submissive behaviours after relative to the pre-call period, mainly escape attempts (Fig. 4), as observed in other nocturnal geckos (Marcellini 1977, Frankenberg 1982a, Regalado 2003a, Rivera Rodríguez et al. 2011, Briggs 2012). However, attributing a specific functional role for the calls of *G. gaudichaudii* needs caution, as single chirp calls present a large plasticity in geckos (Frankenberg 1975, 1982a), and in our study in particular these vocalizations were emitted by a restricted number of individuals. Ideally, data from additional individuals should be incorporated for a more robust assessment of the potential function of these calls.

Non-acoustic displays

Garthia gaudichaudii displayed a more diverse repertoire of visual behaviours than previously described (Codoceo 1957), comprising different types of tail displays (Table 1). Males and females mainly performed vertical tail-waving before approaching an opponent and responded to this same signal mainly with submissive escape attempts, or aggressive approach or tail-waving, in intra- and inter-sexual interactions (Fig. 5). Likely, this vertical tail-waving would allow individuals to warn conspecifics and establish dominance relationships previous to physical contact (Rivera Rodríguez et al. 2011), especially for females rejecting a male.

Vertical tail-wavings were performed in some cases before single-chirp calls (Fig. 4). Similar associations of visual and acoustic displays have been observed in other nocturnal geckos (Briggs 2012), a tactic that may function to startle opponents (Marcellini 1977). The warning function of this visual signal could be increased by associating it with a single chirp call when an opponent is approaching aggressively (Marcellini 1977, Briggs 2012). How-

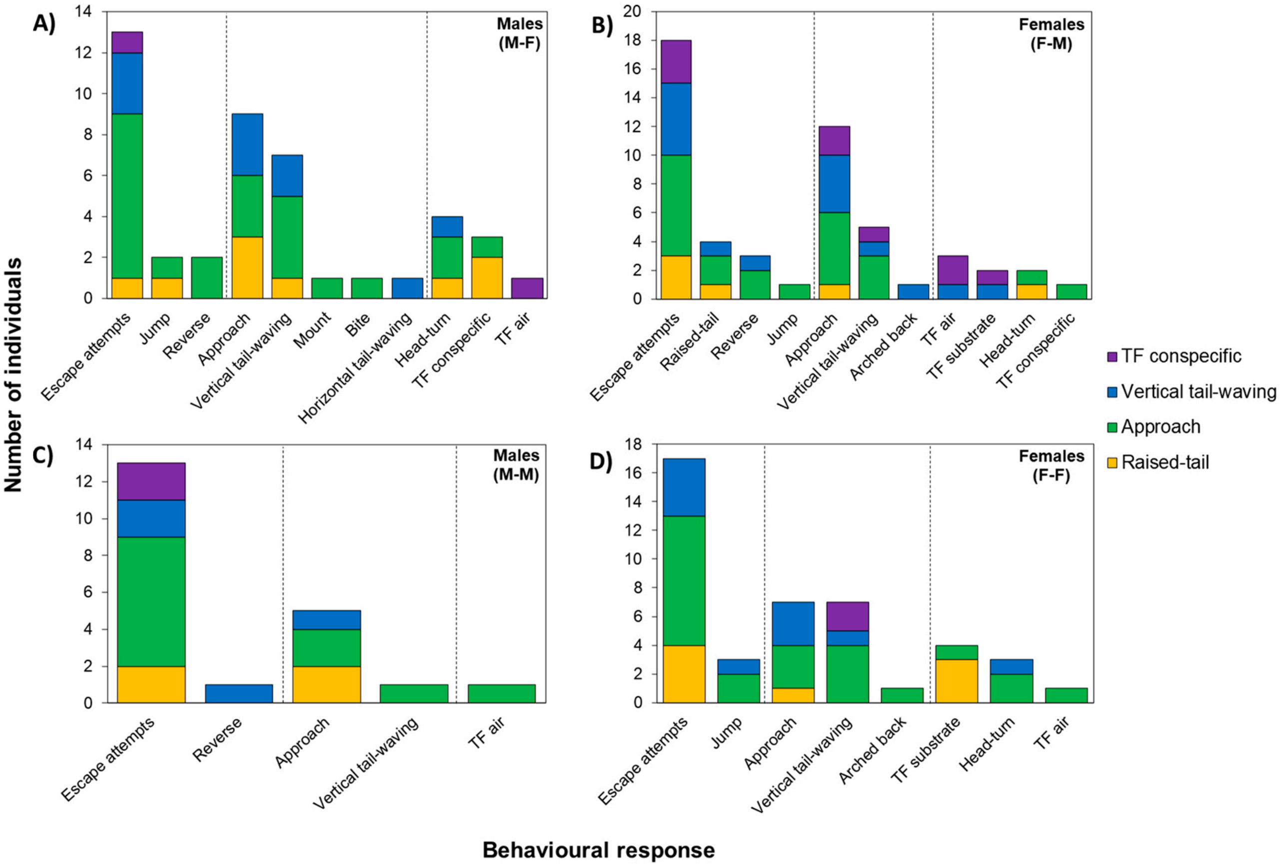

Figure 5. Number of individuals of *G. gaudichaudii* (y-axis) that responded at least once with a specific behaviour (x-axis) when tongue-flicking (TF) the opponent, or when exposed to three opponent's behaviours: vertical tail-waving, approach, or raised-tail, in inter- (A, B) and intra-sexual (C, D) interactions. Only the response to these four behaviours was evaluated because they are the most frequently observed during direct social interactions (see Fig. 3). Submissive, aggressive, and exploratory behaviours exhibited in response to the four opponent displays are separated, from left to right in each graph, by vertical dotted lines.

Table 6. Characteristics of the single chirp calls reported in nocturnal geckos (including this study). Dashes indicate information lacking for a specific topic.

Gecko species	Emitters	Context of emission	Call duration (s)	Dominant frequency (kHz)	Qualitative spectral structure	Qualitative sound level	Reference
Garthia gaudichaudii	Males Females	Aggressive interactions	0.06	5.45	Noisy and harmonics	Variable, can be heard from up to about 5 m	This study
Coleonix sp.	–	Aggressive male-male interactions; related to biting	–	–	–	–	Greenberg (1943)
Gehyra dubia	Males Females	Aggressive physical encounters	0.003	1.7 (males); 2.3 (females)	–	–	Tremul (2003), Phongkangsananan et al. (2014)
Hemidactylus frenatus	Males Females Juveniles	Aggressive interactions; related to biting	< 0.05	~ 2.0	Harmonic	Variable, can be heard from a few to 10 m	Marcellini (1974)
Hemidactylus garnotii	-	Aggressive close encounters	0.008–0.07	1.3–6.0	No frequency modulations	Loud squeak	Frankenberg (1982b)
Hemidactylus turcicus	Males Females Juveniles	Aggressive interactions; related to biting or female licked by males	< 0.05	0.3–5.0	Noisy and harmonics	Variable, can be heard from a few to 10 m	Marcellini (1977), Frankenberg (1982a), Briggs (2012)

ever, we cannot rule out that vertical tail-waving and single chirp calls have another type of function depending on context. For instance, these stimuli may be used as pursuit-deterrent signals to potential predators in other geckos in addition to a role in social communication (Marcellini 1977, Bohórquez Alonso et al. 2010).

Horizontal tail-wavings represented agonistic behaviours, as these movements could result in hitting an opponent. Females have been recorded to perform horizontal tail displays in order to reject an approaching male in other species (Regalado 2003b, Wissmann et al. 2005). Tip tail-waving seem to signal inter-sexual communication in *G. gaudichaudii*, as they were observed only during male–female interactions (Tables 4 and 5). Raised-tail in *G. gaudichaudii* may be a submissive behaviour, as males responded with behaviours leading to direct contact, such as approximation and exploratory behaviours, when females performed raised-tail behaviour (Fig. 5A; Marcum et al. 2008). Alternatively, raised-tail could be considered aggressive since females and males escaped from individuals that displayed this behaviour (Fig. 5; Rivera Rodrígues et al. 2011).

The most conspicuous chemoreceptive behaviour of *G. gaudichaudii* was tongue-flicking, which was mainly directed to the air (Table 4), and may be involved in individual and sexual recognition, as suggested for gekkonid lizards (Regalado 2003a, b, Bauer 2013). The observation that most tongue-flicks were directed to the air suggests that chemical perception of volatile compounds may be relevant for *G. gaudichaudii* during short- or long-distance social interactions (López & Martín 2009, Baeckens 2019, Campos et al. 2020). The chemoassessment of a conspecific without physical contact may reduce the likelihood of possible aggressive encounters between interacting geckos (Regalado 2003b, Marcum et al. 2008). Potentially, olfaction may also be relevant to detect volatile compounds, considering that geckos use more this chemoreceptive mechanism than vomerolfaction (Schwenk 1993, Dial & Schwenk 1996).

Tongue-flicks directed to conspecifics seem to have an important role in sexual recognition, as both sexes responded differently after tongue-flicking a conspecific during intra- and inter-sexual contexts (Fig. 5). Females displayed a relatively diverse behavioural repertoire after tongue-flicking a male, including exploratory tongue-flick to the air or substrate, submissive displays with escape attempts, and aggressive approach or vertical tail-waving (Fig. 5B; Regalado 2003a, b, Marcum et al. 2008, Rivera Rodríguez et al. 2011). In contrast, whenever males tongue-flicked a female, these only escaped or performed tongue-flicks to the air (Fig. 5A; Rivera Rodríguez et al. 2011, Martinez-Cotrina et al. 2014). In addition, during intra-sexual encounters, males performed escape attempts and females vertical tail-waving (Fig. 5C, D).

The behavioural differences observed between sexes during intra- and inter-sexual contexts suggest that chemoreception of skin-derived semiochemicals is important for individual recognition in this species, as suggested for other geckos (Mason & Gutzke 1990, Szabo & Ringler 2023). Given that *G. gaudichaudii* does not exhibit visual sexual dimorphism (Donoso-Barros & Vanzolini 1965), visual signals alone would not allow geckos to identify the gender of an individual and skin compounds may play a role during individual and sexual recognition (Mason & Gutzke 1990, Brillet 1993). Further observations on inter-sexual interactions during the breeding season would allow a more precise evaluation of the role of chemosensory behaviours on sexual recognition.

During intra-sexual interactions, additionally, females were more aggressive than males, a finding that parallels observations in the genus *Sphaerodactylus* Wagler, 1830 (Wissmann et al. 2005) and in *Gonatodes daudini* Powell & Henderson, 2005 (Rivera Rodríguez et al. 2011). Males of *G. gaudichaudii* did not show aggressive behaviours such as arched back or bites, but generally ignore each other, avoiding direct contact. This observation contrasted with male–male interactions reported in other nocturnal geckos (e.g., *H. mabouia* (Moreau De Jonnès, 1818), Regalado 2003b; genus *Teratoscincus* Strauch, 1863, Suchomelová et al. 2015), which are mostly territorial and defend resources such as food or shelters (Bauer 2013). Nevertheless, species that are not strictly territorial can fight for access to a resource (Bauer 2013). Further observations are needed to evaluate accurately the territoriality of male and female *G. gaudichaudii*.

Comparisons between behaviours exhibited during inter- and intra-sexual encounters show that tail-waving has higher occurrence during inter-sexual relative to intra-sexual interactions in males and females. In addition, vertical tail-waving and tongue-flick to conspecifics have higher occurrence during inter-sexual relative to intra-sexual interactions in females and males, respectively. Furthermore, the duration of tail-waving is longer during inter-sexual relative to intra-sexual interactions in males whereas in females the duration of escape attempts, movements and rest are longer during inter-sexual relative to intra-sexual interactions. These results contribute to identify the behaviours outlined as sexual recognition displays and/or potential courtship components.

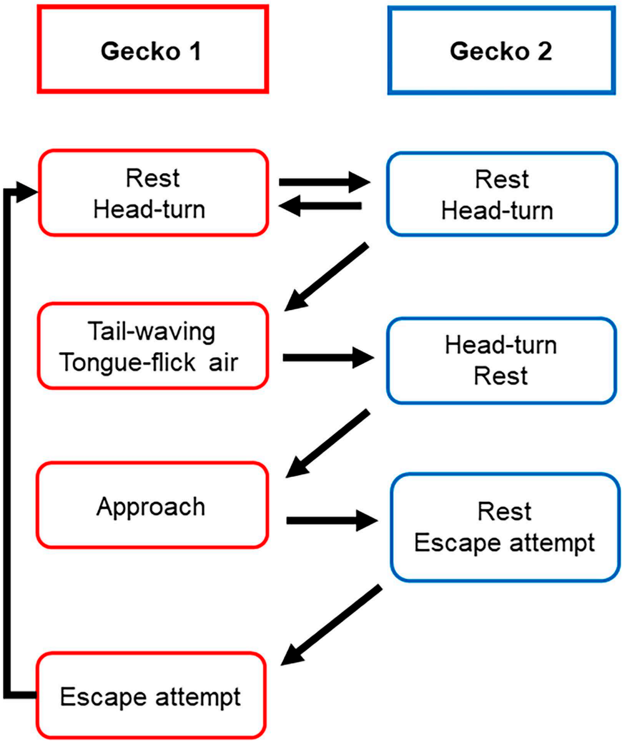

Figure 6. Typical behavioural sequence during an encounter of two individuals of *G. gaudichaudii* in intra- and inter-sexual interactions. This sequence was usually performed first by one individual (i.e., 'dominant', red) and subsequently by the other (i.e., 'submissive', blue), and in some cases displays by both individuals occurred simultaneously. The arrows indicate the direction of the behavioural sequence.

Social interaction patterns

Garthia gaudichaudii exhibits a general pattern of social interactions defined by a tandem sequence of behaviours interspersed between the interactants, and a relatively more diverse behavioural repertoire during inter- than in intra-sexual encounters compared with other geckos species (Regalado 2003a, b, Wissmann et al. 2005, Marcum et el. 2008). Our observations, however, bear similarities with some of these same studies (Wissmann et al. 2005, Marcum et el. 2008), since only some males performed mating behaviours (body raised, bite or mount) and interacting females rejected the males by displaying tail-waving, escape attempts or emitting single chirp calls (Frankenberg 1975, 1982a, Regalado 2003b).

Overall, our study reported first-time quantitative data on the behavioural displays of *G. gaudichaudii* during social contexts, revealing that this species uses acoustic, visual, and chemical modalities during communication. Specifically, we recorded single chirp calls during social interactions, which may be emitted in association with vertical tail-waving. It is necessary to evaluate their functional role considering a more representative number of individuals. In addition, many visual displays represent submissive or aggressive signals, and tongue-flicks seem important during chemical exploratory behaviour in social interactions.

Acknowledgements

The study was authorized by the Servicio Agrícola y Ganadero (Resolución Exenta no. 9059/2018) and the Comité Institucional de Cuidado y Uso de Animales (CICUA) of the Universidad de Chile. We thank Conny Reyes-Olivares, Inger Rain-Garrido, Germán Reyes, Hilda Palacios and Roberto Reyes for their invaluable help in carrying out this study. Finally, our thanks to Luis Ebensperger, Rigoberto Solis, Claudio Veloso, Rodrigo Vásquez and two anonymous reviewers for their valuable comments on an early version of this manuscript. CR-O thanks the fellowship CONICYT-PCHA Doctorado Nacional/2015 21150353 and the Postdoctoral Fondecyt fund N°3230799.

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Supplementary data

The following data are available online:

Supplementary audio 1. Single chirp call of *Garthia gaudichaudii.*

Supplementary video 1. Escape attempt behaviour.

Supplementary video 2. Reverse behaviour.

Supplementary video 3. Approach and raised-tail behaviours.

Supplementary video 4. Arched back and bite behaviours.

Supplementary video 5. Vertical tail-waving, body raised and escape attempt behaviours.

Supplementary video 6. Horizontal tail-waving behaviour.

Supplementary video 7. Tongue-flick behaviour.