



Complex distress calls sound frightening: the case of the weeping lizard

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Individuals of many species utter distress calls when are attacked or trapped by a predator. These vocalizations can help them to escape but may also help conspecifics to reduce their predation risk, by inducing antipredator behaviours. Calls can encode information that modulates these antipredator responses, and the 'nonlinearity and fear hypothesis' proposes that complex nonlinear calls may trigger more fearful responses, because they encode higher levels of stress. We tested this hypothesis with the weeping lizard, *Liolaemus chiliensis*, which utters distress calls with and without nonlinear phenomena (complex and simple calls, respectively), and conspecifics respond to simple calls with antipredator behaviours. Here, we evaluated whether this species discriminates between these two types of calls, predicting higher levels of fear with complex calls. We also tested whether lizards experience less fear if calls are perceived in a safe environment, such as one full of their own scents ('home'). Our playback experiments showed that complex calls scared the lizards more than simple calls, triggering a reduction in activity, and prolonging attempts to escape. Lizards in their own-scented environments took longer to restore their activity after hearing complex than simple calls, suggesting that this combination of stimuli was more alarming. We postulate that the predation event was unexpected at 'home', which together with the nonlinearity of the call made a more frightening event for the lizards.

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Distress calls are uttered by infants of many species when they experience situations of discomfort (e.g. isolation, hunger or capture), and trigger the attention of their caregivers (Lingle, Wyman, Kotrba, Teichroeb, & Romanow, 2012). Such calls are, however, also uttered by noninfant individuals of many species (e.g. Carter, Schoeppler, Manthey, Knörnschild, & Denzinger, 2015) when they are cornered, attacked or seized by a predator (for more detailed explanations of distress calls: Caro, 2005; Klump & Shalter, 1984; Magrath, Haff, Fallow, & Radford, 2015). In the predator–prey context, distress calls have been reported in all the tetrapod taxa: birds and mammals (Caro, 2005), reptiles (Labra, Silva, Norambuena, Velásquez, & Penna, 2013; Vergne, Pritz, & Mathevon, 2009) and amphibians (Forti, Zornosa-Torres, Márquez, & Toledo, 2018; Franzen & Glaw, 1999). This widespread occurrence of distress calls across tetrapods underscores their relevance for the prey. Calls are also important for

conspecifics' survival, owing to the behavioural changes that calls may trigger in predators and/or the conspecifics (Caro, 2005; Conover, 1994; Högstedt, 1983). Distress calls may, for example, startle the attacker, which may release the captured prey (Neudorf & Sealy, 2002). Alternatively, calls can attract secondary predators that attempt to trap the primary predator, which escapes to reduce its own predation risk (Högstedt, 1983; Schuett & Gillingham, 1990). In addition, calls can serve as a cry for help, attracting conspecifics to approach and mob the predator (Russ, Racey, & Jones, 1998), which may then release the caught prey. Nevertheless, conspecifics may approach just to learn about the predator and the predatory event (Carter et al., 2015). Finally, conspecifics can reduce their own predation risk after hearing distress calls by displaying antipredator behaviours such as immobility (Hoare & Labra, 2013; Vergne, Aubin, Taylor, & Mathevon, 2011) or escape (Conover & Perito, 1981).

Exposure to conspecific distress calls may induce hormonal changes characteristic of stressful states (Mariappan et al., 2013, 2016), which may elicit antipredator responses. The strength of these behavioural responses is, however, modulated by the information conveyed by calls. For example, individuals of the cockatiel,

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Nymphicus hollandicus, show stronger responses when calls are from familiar than from unfamiliar individuals (Liévin-Bazin et al., 2018). Therefore, if animals are able to respond in agreement with the urgency or the information encoded by the vocalizations, distress calls with nonlinear phenomena such as deterministic chaos or subharmonics (Fitch, Neubauer, & Herzel, 2002) might trigger more fearful responses. Studies on alarm calls, uttered by prey in the presence of a predator that warn conspecifics about predation risk (Caro, 2005; Magrath et al., 2015), have led to the 'nonlinearity and fear hypothesis'. This postulates that calls with nonlinear phenomena induce stronger fearful responses in conspecifics, because these phenomena encode a state of arousal and/or fear (Blumstein & Récapet, 2009), as they tend to be uttered in more stressful situations (e.g. Manser, 2001; Schneider & Anderson, 2011; but see Blumstein & Chi, 2012). The nonlinear phenomena are consequences of a desynchronization of the vocal cords resulting from stress, and calls with these phenomena are considered complex, as their description involves nonlinear equations (i.e. include squared, cubed or higher-order terms; see Fitch et al., 2002). Some findings such as those from the social meerkat, *Suricata suricatta*, support the 'nonlinearity and fear hypothesis': individuals respond to complex alarm calls not only with antipredator behaviour (e.g. escape), but also by reducing their foraging activity (Townsend & Manser, 2011).

Adults of different taxa utter distress calls with nonlinear phenomena (Amaya, Zufiaurre, Areta, & Abba, 2019; Carter et al., 2015; Labra et al., 2013; Lingle et al., 2012), but their effects upon conspecifics in a predator–prey context, as in the case of the alarm calls (e.g. Blesdoe & Blumstein, 2014; Townsend & Manser, 2011), have not been tested.

The weeping lizard, *Liolaemus chiliensis*, utters a diversity of distress calls (Labra et al., 2013). Conspecifics respond with prolonged inactivity to the most common call, which has a downward frequency-modulated pattern without nonlinear phenomena, compared to white noise (Hoare & Labra, 2013; Labra, Reyes-Olivares, & Weymann, 2016). In nature, adults can be found relatively close to each other (< 3m; Labra & Reyes-Olivares, n.d.), which would allow individuals to benefit by eavesdropping on distress calls independently of the sociability of this species, the extent of which is unknown. Based on the 'nonlinearity and fear hypothesis', complex and simple distress calls (with and without nonlinear phenomena, respectively) should encode information on the level of fear. Here, we hypothesized that if the weeping lizard decodes this information, individuals will respond to complex distress calls with stronger antipredator responses (e.g. longer periods of immobility), than they would do with the simple distress calls.

The behavioural responses of different *Liolaemus* species are modulated by scents (e.g. Labra, 2008). This has also been shown for the weeping lizard (Labra & Hoare, 2015; Valdecantos & Labra, 2017). In this species, Hoare and Labra (2013) tested the hypothesis that simple distress calls heard in a conspecific-scented environment might be perceived as indicating a higher predation risk than in an environment without scents, because conspecific scents indicate proximity of the trapped lizard, and thus of the predator. The authors found that the acoustic information was only partially modulated by the conspecific scents, since any acoustic stimuli heard in the conspecific-scented environment triggered more stressful responses (e.g. escape attempts) than in an unscented environment. Potentially, more relevant scents, such as an individual's own scent, may be more important in modulating the response to distress calls. An own-scented environment, such as a retreat site or 'home' (e.g. Aguilar, Labra, & Niemeier, 2009), may represent a safe place (e.g. Richardson, Siegel, & Campbell, 1988). Under this scenario, we hypothesized that even if complex calls are

scarier than simple calls, they would be less scary when they are encountered at 'home'.

METHODS

We captured by noosing 24 adults of *L. chiliensis* (15 nonpregnant females, nine males; mean snout–vent length \pm SE: 78.38 ± 1.39 mm), at Isla de Maipo ($33^{\circ}45'S$, $70^{\circ}54'W$), Chile, during October 2014, mid-spring. At the laboratory, we weighed the lizards and kept them in an indoor vivarium with a photoperiod of 13:11 h light:dark, and temperatures between $33^{\circ}C$ and $12^{\circ}C$, mimicking field conditions. We housed lizards individually in plastic enclosures (44.5×32 cm and 25 cm high) that had a front window (10×5 cm) covered with plastic mesh, which improves animal welfare (e.g. providing extra climbing surface, ventilation and light). Enclosures had a 3 cm deep sand layer on the floor and were furnished with a perch (a wooden stick), a pot for water, and an inverted tile used as a refuge and basking place. The hermetic lids of the enclosures were also partially replaced by a plastic mesh. Lizards had water ad libitum, and we fed them three times per week with mealworms, *Tenebrio molitor*, dusted with reptile vitamins (sera Reptimineral C). We maintained lizards undisturbed in their enclosures for 1 week before starting the experiment. This allowed lizards to get used to the experimental conditions, and to release enough scents, because we used the enclosures as the substrate-borne scents.

Experiment

Lizards were exposed individually, and only once, to four treatments using a counterbalanced design (for details see Hoare & Labra, 2013). Treatments were the combination of stimuli from two sensory modalities, chemical (scents) and acoustic (distress calls). For the scents, we used enclosures previously occupied by a lizard (e.g. Aguilar et al., 2009), which were from the focal lizard (own

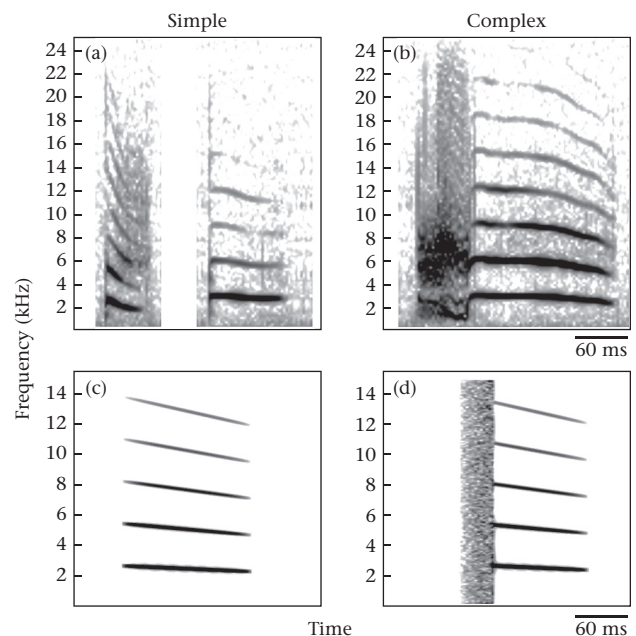


Figure 1. Spectrograms of (a, b) natural and (c, d) synthetic distress calls of *Liolaemus chiliensis*. (a) Two simple calls uttered by females. The snout–vent length of the female on the left-hand side was 83.7 mm and that of the one on the right-hand side was 90 mm. (b) Complex call with deterministic chaos uttered by a male 84.5 mm long. (c) Simple and (d) complex calls with white noise as a surrogate of deterministic chaos.

scents) or a conspecific of similar size, but of different sex, as the focal lizard (conspecific scents). Because females laid eggs during the period when we collected lizards (Troncoso-Palacios & Labra, 2017), we were confident that the mating season had passed so that there would be no effects of reproduction on the behaviour.

We used a complex and a simple distress call as acoustic stimuli. Because calls differ in their characteristics (e.g. duration, dominant frequency, frequency-modulated pattern; Fig. 1a), we built a synthetic distress call (see Hoare & Labra, 2013), using Adobe Audition 3. We first made a simple call with a downward frequency-modulated pattern, the most frequently registered in the studied and other populations (Labra et al., n.d.; Labra et al., 2013). The synthetic call had the mean temporal and spectral characteristics of 47 calls with a downward frequency-modulated pattern, produced by 13 adults from the studied population. To elicit calls, we gently grasped a lizard with the hand and touched its snout slightly with a finger for 2 min (for details of the used protocol see Labra et al., 2013). The simple distress call had five harmonics built from the frequencies measured at the beginning and end of each harmonic. When down modulated, the fundamental frequency was 2.7 to 2.4 kHz and the envelope had its maximum amplitude at 75 ms. Preliminary analyses showed that complex calls were on average longer than the simple calls (see also Labra et al., 2013), and therefore we built the synthetic call using the maximal duration recorded for a simple call (Fig. 1c).

Deterministic chaos was the most common nonlinear phenomenon in our sample. This generally occurred at the beginning of the calls, having a mean duration of 0.045 ms (Fig. 1b). We replaced the first 0.045 ms of the simple call by white noise (Fig. 1d), as a substitute for the deterministic chaos (e.g. Blumstein & Récapet, 2009). In this way, both call types had the same duration, avoiding an effect of call duration on the lizard's response (Blumstein, Richardson, Cooley, Winternitz, & Daniel, 2008). During the call recordings we positioned a sound level meter 15 cm from the lizard

to measure the call intensities. Based on the data we obtained, distress calls were set to 51 dB RMS SPL, measured at the centre of the experimental enclosure. We reproduced the stimuli using a Behringer loudspeaker placed on the floor, 15 cm in front of the window of the experimental enclosure. We connected the loudspeaker to an NAD Electronics 3020i amplifier, and this to an iPod Nano to reproduce the stimuli.

Before a trial, we removed the lizards to be used and all the elements of the treatment enclosure (e.g. refuge), except the sand. The focal lizard was held in a cloth bag for 10 min to reduce stress related to handling (Labra, 2011), while the scent donor individual, when relevant, remained in its bag until the end of the trial. We placed the bag with the focal lizard on the top of the enclosure allowing the individual to move freely into it. Once the lizard was free in the enclosure, we removed the bag and covered the enclosure with a sheet of glass (37 x 30 cm) instead of the plastic lid. After the trial, we cleaned the glass with ethanol (96%) to remove any chemical traces of the focal lizard to avoid affecting the behaviour of the next lizard. Because variations in body temperature may affect behaviour, we kept the experimental area at 35 °C. In addition, at the end of the trial, we measured the cloacal temperature of the focal lizard, and if this was not close to the selected mean body temperature of the species ($\sim 35 \pm 2^\circ\text{C}$; Labra, Pienaar, & Hansen, 2009), the trial was discarded and repeated another day. We returned the focal lizard (and the scent donor, when relevant) to its furnished enclosure, and allowed an intertrial resting period of 3 or more days.

We placed the experimental enclosure 60 cm below a Panasonic HDC-TM20 camcorder to record the lizard's behaviour. The filming began when the individual made its first tongue flick (Fig. 2). Experiments had three stages: (1) prestimulus, the first 4 min after the start of the trial, (2) stimulus, the phase when we played back the acoustic stimulus, which lasted 2.64 s, and (3) poststimulus, the last 4 min after stimulus. The acoustic stimulus consisted of three

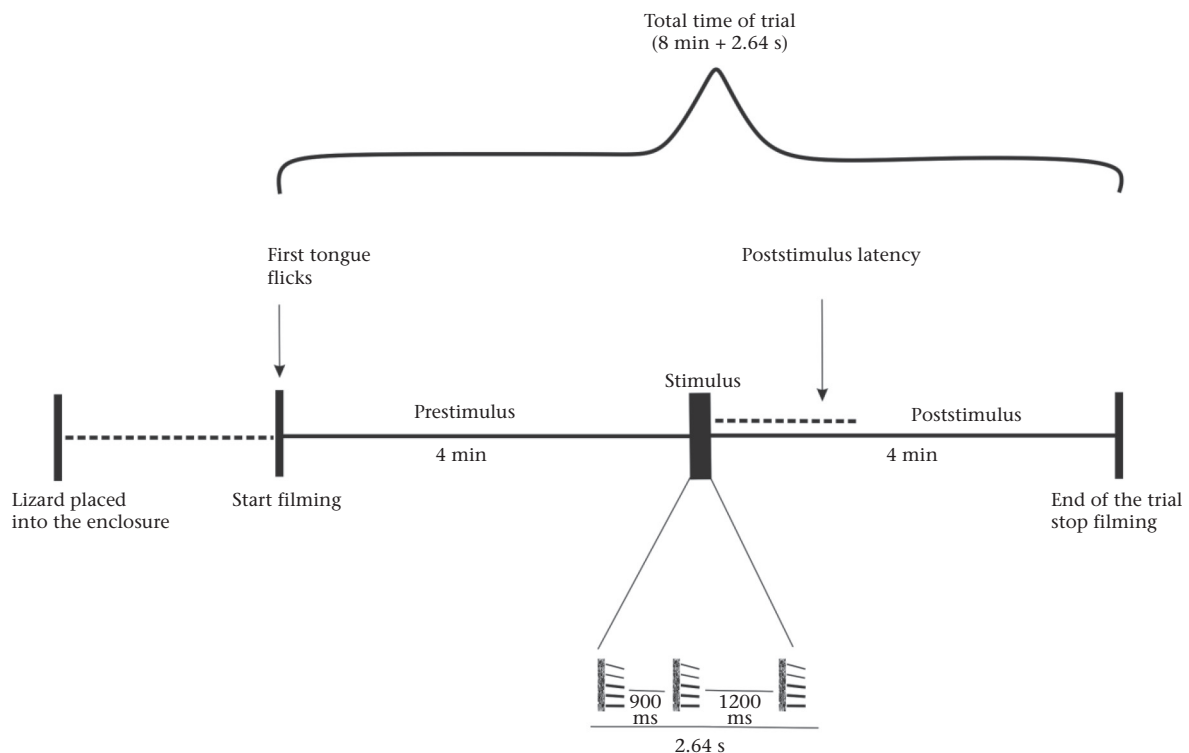


Figure 2. Schematic representation of the experimental design, showing the different stages of a trial. Vertical bars represent the different events during a trial. Dashed lines represent variable recording time, while solid lines represent fixed recording time during pre- and poststimulus. Below the stimulus event there is an example of a complex call, with the three calls and the silence intervals.

Table 1
Behaviour recorded from videotapes for *L. chiliensis*

Variable	Description	Source
Time in motion (s)	Total time that a lizard moves and changes its position, excluding the time escaping and the chemical exploration. A reduction in motion may decrease predation risk	Labra (2006), Labra and Hoare (2015)
Time escaping (s)	Total time that a lizard attempts to escape, i.e. runs, rubs its snout, makes fast movements of its forelimbs on the enclosure walls or digs a hole	Font and Desfilis (2002)
Chemical exploration (tongue flicks)	Number of times that a lizard protrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate or wall or is waved in the air. This is an index of chemical exploration	Font and Desfilis (2002), Labra (2006)
Time spent in the front half of the enclosure (s)	We virtually divided the treatment enclosure in half, recording the time that a lizard stays in the front, near the sound source. A reduction in use of the front half after the stimulus suggests avoidance of a scary area	Labra et al. (2016)
Poststimulus latency (s)	Time elapsed between the end of the stimulus and the restarting of any activity (i.e. chemical exploration, movement, attempt to escape). Longer latency may indicate more fear	Hoare and Labra (2013)

identical sounds (simple or complex calls) of 180 ms separated by two silent periods (Fig. 2). From the videotapes, we recorded four variables during the pre- and poststimulus stages (Table 1): time in motion, time escaping, chemical exploration and time spent in the front half of the enclosure. We measured poststimulus latency during the last stage (poststimulus) of the trial (Fig. 2, Table 1). The short duration of the stimulus presentation stage precluded us from recording behaviour during this phase.

Ethical Note

This study was authorized by the Chilean Agricultural and Livestock Service (SAG; Resolution No. 2374) and by the Scientific Ethics Committee of Facultad de Medicina, Universidad de Chile. During the period when lizards remained in the laboratory, we avoided stressful situations (e.g. minimizing human presence and noises). Lizards received food with vitamins to prevent deficiency due to the laboratory diet or problems caused by the lack of sun. We kept lizards for the shortest period possible in the laboratory, and at the end of the experiment we reweighed them, verifying that they maintained or increased their weight. After checking that lizards were healthy, we returned them to their georeferenced collecting points.

Statistical Analysis

We determined the behavioural changes triggered by the distress calls by calculating the pre- to poststimulus difference (i.e. post-stimulus values minus pre-stimulus values; see Hoare & Labra, 2013) of the four variables recorded in both stages (Table 1). The effect of scents (own versus conspecific), distress call

(simple versus complex), sex of the focal lizard (female versus male) and their interactions upon the four behavioural changes and the poststimulus latency were analysed with a general linear model using a partially nested design of three-way repeated measures. Sex was the between-subject variable and scents and distress calls were the within-subject variables (repeated measurements). After these analyses, we applied Fisher LSD post hoc tests. We log transformed the poststimulus latency to ensure the normality of residuals. The residuals of all variables appeared homoscedastic and normally distributed in all analyses.

RESULTS

Distress calls affected the changes in time in motion and time escaping (Table 2): complex calls triggered a reduction in time in motion (Fig. 3a), but an increase in the time escaping (Fig. 3b). The interaction between distress calls and scents affected the change in chemical exploration (Table 2). However, this was only marginally significant (post hoc test: $P=0.059$): lizards in the conspecific-scented environment tended to reduce their chemical exploration more in response to the complex than to the simple call (Fig. 3c). The interaction between distress calls and the sex of the focal lizards induced a change in the time that they spent in the front half of the enclosure (closer to the stimulus source; Table 2): after the complex calls, males spent less time in the front part of the enclosure, while females did not change the use of this area (Fig. 3d). The type of scents modulated the poststimulus latency (Table 2): lizards took longer to restore their activity when they were with their own scents than with conspecific scents (Fig. 4a). This latency was also affected by the interaction between calls and scents (Table 2): for lizards exposed to complex calls latency was

Table 2
Results of the general linear model with a partially nested design of three-way repeated measures

	Δ Time in motion	Δ Time escaping	Δ Chemical exploration	Δ Time spent in the front	Poststimulus latency
Call	4.35(0.049)	5.57(0.003)	0.81(0.380)	1.65(0.212)	0.02(0.879)
Scent	1.39(0.252)	0.06(0.808)	0.15(0.750)	0.38(0.542)	19.43(<0.001)
Sex	0.60(0.446)	0.50(0.484)	0.24(0.627)	0.02(0.884)	0.67(0.421)
Call * Scent	0.68(0.419)	0.92(0.347)	4.46(0.046)	2.49(0.129)	15.01(<0.001)
Call * Sex	1.02(0.324)	1.76(0.198)	1.43(0.245)	6.35(0.019)	0.07(0.801)
Scent * Sex	0.68(0.419)	2.51(0.128)	0.44(0.515)	4.08 (0.056)	0.55(0.467)
Call * Scent * Sex	0.09(0.769)	0.00(0.965)	0.40(0.533)	0.128(0.724)	0.05(0.822)

Analyses tested the effect of the distress call (simple versus complex, without versus with nonlinear phenomena, respectively), scents (own versus conspecific), sex of the focal lizard (male versus female) and their interactions upon the behavioural changes (Δ =poststimulus minus prestimulus values) of four variables (time in motion, time escaping, chemical exploration and time spent in the front) and the poststimulus latency (i.e. after the stimuli or calls). Poststimulus latency was log transformed. Values shown are the F statistics (P value in parentheses). The degrees of freedom of the tests were 1, 22. Statistically significant tests are shown in bold.

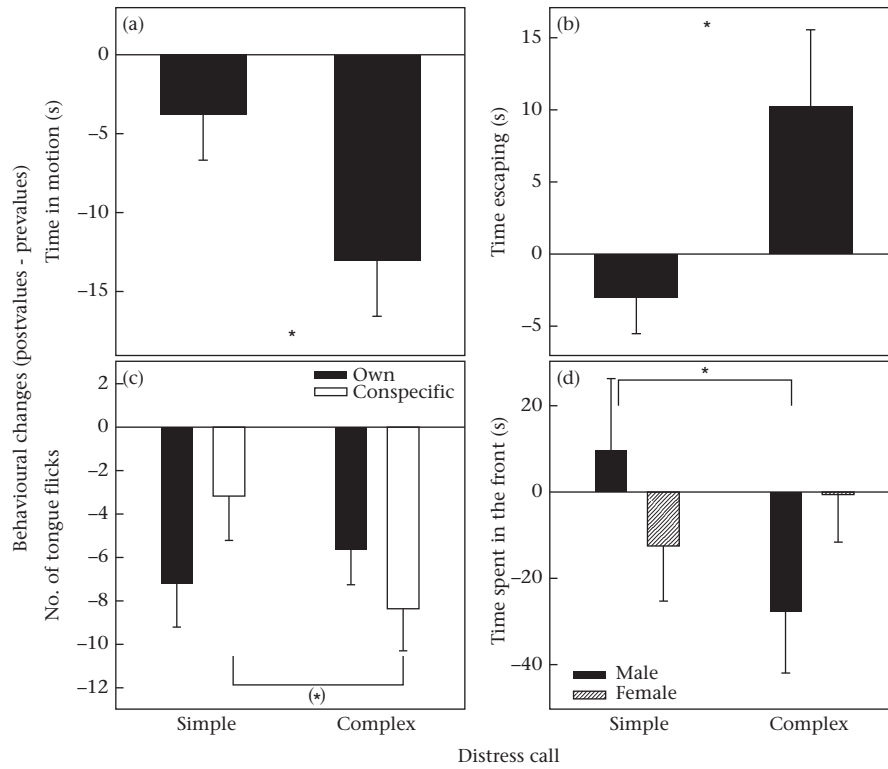


Figure 3. Mean behavioural changes (\pm SE) of four variables recorded in *Liolaemus chiliensis* individuals when they were confronted with two acoustic stimuli, with (complex) and without (simple) nonlinear phenomena. We used white noise as a surrogate of deterministic chaos. The horizontal line (zero) indicates the point where there is no change between the pre- and poststimulus periods. Negative values indicate that after the stimulus, the behaviour decreased in relation to the prestimulus condition. (a) Time in motion. (b) Time escaping. (c) Chemical exploration of the individual's own and a conspecific scent. (d) Time spent in the front half of the enclosure for males and females. * $P < 0.05$; (*) $P = 0.059$.

longest when they were in the own-scented environment and shortest in the conspecific-scented environment (Fig. 4b).

DISCUSSION

The simple distress calls of the weeping lizard act as a warning signal for conspecifics (Hoare & Labra, 2013; Labra et al., 2016), and here we found that this species discriminated between simple and complex distress calls, showing more fearful responses to complex than to simple calls. These results support the 'nonlinearity and fear

hypothesis', as the nonlinearity present in the complex calls, specifically deterministic chaos in this study, elicited fearful behavioural responses (see Blumstein & Récapet, 2009). The scents available where the lizards heard the calls also modulated their antipredator responses: in the own-scented environment, complex distress calls triggered a longer recovery period before resuming activity.

We built the complex call using white noise as a surrogate for deterministic chaos, which seems appropriate considering that highly acoustic animals, such as birds, do not discriminate white

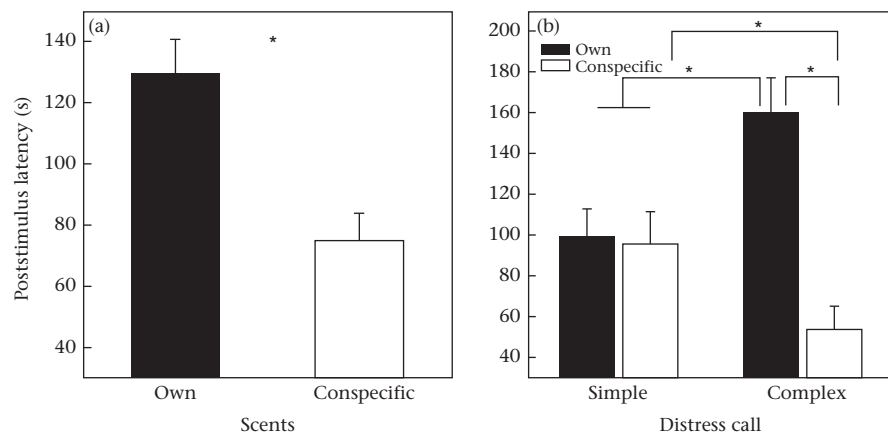


Figure 4. Mean untransformed poststimulus latency (\pm SE) exhibited by *Liolaemus chiliensis* after the acoustic stimuli (a) in two scented environments: own (scents from the focal individual) and conspecific. (b) The interaction between the scents (own versus conspecific) and the two distress calls (simple versus complex, without versus with nonlinear phenomena, respectively). * $P < 0.05$.

noise from deterministic chaos (Blumstein, Whitaker, Kennen, & Bryant, 2017). These results validate previous use of white noise as a substitute for a nonlinear phenomenon of vocal signals (e.g. Blesdoe & Blumstein, 2014; Blumstein & Récapet, 2009), and also ensure that it was acceptable to use white noise to test the response of the weeping lizard to complex distress calls with deterministic chaos. We also discard the possibility that the artificial white noise would induce a more fearful response due to being a novel stimulus, because previous studies showed that lizards respond less to white noise than to simple calls (Hoare & Labra, 2013; Labra et al., 2016). Thus, we are confident that white noise by itself was not eliciting fear and lizards were responding to the message encoded in distress calls.

The presence of nonlinearity in the weeping lizard distress calls triggered a more fearful response, as was observed in meerkats after exposure to complex alarm calls (Townsend & Manser, 2011). Under our experimental conditions, the weeping lizard exhibited similar strategies as the lizard *Anolis cristatellus* confronted with a predator: immobility as the main response and then, secondarily, escape (Leal & Rodríguez-Robles, 1997). The reduction in activity may increase the probability of the focal lizard remaining undetected by a predator that has trapped the screaming conspecific. In fact, immobility is a common antipredator response of different prey taxa (e.g. Magellan, 2019), because various predators detect prey by their movements (e.g. Nishiumi & Mori, 2015; Shine & Sun, 2003). In addition, the increased escape time after complex calls also suggests more fear; individuals of the frog *Pelophylax nigromaculatus* made more escape attempts under more stressful conditions, such as a higher predation risk (Nishiumi & Mori, 2015).

Chemical exploratory behaviour (tongue flicks) was modulated by the interaction between distress calls and scents, but there was only a tendency to reduce exploration when the lizards heard complex calls in the conspecific-scented environment. In contrast, the change in the use of the front half of the enclosure was significantly modulated by the complex calls in interaction with the sex of the focal lizard: males, but not females, reduced the time spent in the front where the predation risk information came from. Therefore, males seem to perceive the complex distress calls as a more threatening stimulus than females. Sexual variation in antipredator behaviour has also been reported in the closely related *Liolaemus nitidus* (Troncoso-Palacios & Labra, 2012), but its causes are unclear. We need information on the species' social behaviour to understand these sex differences.

The poststimulus latency to activity has been informative in determining whether the weeping lizard discriminates between acoustic stimuli, and a longer latency has been interpreted as a more fearful response (Hoare & Labra, 2013; Labra et al., 2016). We found that lizards took longer to restart their activity when they were in their own-scented environment than when with conspecific scents, and, in contrast to our prediction, this was significantly more evident when lizards heard the complex distress calls. We postulate that this more fearful response may be because lizards were isolated in their enclosures, with total control of their own environment, and therefore not expecting a predatory threat. The surprising appearance of a threat together with complex distress calls would elicit a more fearful response. If we only considered the effect of scents, then it would be possible to postulate that lizards remained immobile for longer in the own-scented environment than with conspecific scents, because they felt safer. However, we reject this hypothesis because the poststimulus latency was longer with the complex calls and the evidence from the other variables indicated that these calls were scarier than simple calls. On the other hand, in the conspecific-scented environment the best antipredator strategy seems to be to search for an escape route as soon as this could be done safely, as reflected in the shorter latency to

activity recorded in this environment. The fact that the duration of the poststimulus latency was modulated by the interaction between chemical and acoustic information suggests that at least some behavioural responses of the weeping lizard are mediated by multimodal communication (Partan & Marler, 1999).

In summary, in agreement with the 'nonlinearity and fear hypothesis', the complex distress calls of the weeping lizard, specifically with deterministic chaos (i.e. white noise), are scarier than simple calls. The chemical environment modulates the duration of the immobility after the acoustic stimuli, as lizards showed longer immobility when they were exposed to complex calls in an environment with their own scents, suggesting that this combination of signals made lizards more fearful. These results constitute the first evidence that a vocal lizard species responds to its own distress calls with nonlinear phenomena. The only similar evidence come from the nonvocal lizard *Emoia cyanura*, which showed discrimination among sounds with different nonlinear phenomena (Yan, Pinto, Vartany, & Blumstein, 2019). Our study species, however, has distress calls with different types of nonlinear phenomena (e.g. subharmonics, frequency jumps; Labra et al., 2013), and it remains unclear whether individuals would have responded similarly to calls with nonlinearities other than deterministic chaos. For other species, findings indicate that not all nonlinear phenomena have the same effects and, moreover, that species differ in the nonlinearities that trigger the highest response (see Yan et al., 2019).

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