



Lizard calls convey honest information on body size and bite performance: a role in predator deterrence?

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Abstract

When encountering predators, prey animals often signal their ability to fight or flee to discourage the predator from an attack or pursuit. A key requirement for evolutionary stability of these predator-deterrent signals is that they convey honest information on the prey's fighting or fleeing performance. In this study, we investigate the enigmatic 'distress call' of the lacertid lizard *Psammodromus algirus*, and test whether it conveys reliable information on an individual's body size, and bite and sprint performance. Our acoustic analyses revealed a complex spectral structure in the vocalization of *P. algirus*, showing a wide frequency bandwidth, multiple harmonics, and a marked frequency modulation. This spectral design may allow such calls to be perceived by multiple potential predators, as it was assessed by a literature search comparing the call frequency range with the hearing ranges of *P. algirus*' top predators. In addition, we found considerable inter-individual variation in the call design of lizards ('call signatures'), which was linked with inter-individual variation in body size and maximum bite force, but not with sprint speed (a proxy of escape performance). As a whole, our study supports the hypothesis that the vocalizations of *P. algirus* lizards have the potential to serve as honest calls to deter predators. Further research on the behavioural response of predators towards lizard calls is essential in order to unravel the true predator deterrence potential of these calls.

Significance statement

When eye-to-eye with a predator, prey animals may signal their ability to fight or flee to convince the predator not to attack or pursue them. Reptiles typically use visual displays to deter predators, but fascinatingly, *Psammodromus algirus* lizards have been observed to vocalize when encountered by predators. Here, we explored the acoustic properties of these calls and examined whether they convey honest information on a lizard's fighting and fleeing performance. Our recordings indicate that the acoustic profile of the calls fall within the hearing sensitivity of the lizard's top predators. Moreover, our experiments show a significant link between the acoustic profile of lizard calls and lizard fighting ability, but not with fleeing ability. Together, our results imply that these lizard calls have predator deterrence potential. Additionally, this study provides the first evidence of honest acoustic signalling of performance in a reptile.

Keywords Bioacoustics · Bite force · Honest signalling · *Psammodromus algirus* · Sprint speed · Vocalizations

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Introduction

Animals use signals from a variety of sensory modalities during interactions with con- and heterospecifics that can mediate territory defence, female receptivity, mate assessment, kin recognition, and predator deterrence, among many others (Espmark et al. 2000; Greenfield 2002; Rogers and Kaplan 2002; Bradbury and Vehrencamp 2011). In predator-prey interactions, prey animals often send out transient visual, chemical, or acoustic signals to evoke startle responses in predators in order to increase the probability of their escape. Some species display deimatic and bluffing behaviour, while others signal their unpalatability or ability to fight or flee, strategies that are advantageous to the prey if it prevents attacks (Berglund et al. 1996; Maynard-Smith and Harper 2003; Searcy and Nowicki 2005). If these signals are honest, ceasing the attack is also beneficial for predators because they then avoid the potential energetic cost of pursuit, risk of injury, and the waste of time that could be spent more profitably (Woodland et al. 1980; Vega-Redondo and Hasson 1993; Bergstrom and Lachmann 2001). Signal honesty is, therefore, a key requirement for evolutionary stability of signals directed to the predator with the function of deterring its attack or pursuit (Hasson 1991; Vega-Redondo and Hasson 1993; Caro 1995; Cooper 2010).

Signals of predator deterrence have been documented in mammals (e.g. FitzGibbon and Fanshawe 1988), birds (e.g. Cresswell 1994), amphibians (e.g. Gosavi et al. 2014), fish (e.g. Godin and Davis 1995), and reptiles (Blair 1968; Greene 1988; Martins 1996; Swaisgood et al. 1999). In lizards, various visual predator-deterrent displays have been described, such as tail curling and tail waving (Dial 1986; Cooper 2001, 2007, 2010, 2011; Telemeco et al. 2011; York and Baird 2016), full-tongue displays (Badiane et al. 2018), frill erections (Shine 1990), foot shakes (Font et al. 2012), and dewlap extensions (Leal and Rodríguez-Robles 1995, 1997a, b; Leal 1999). Still, only a few studies on predator-deterrent behaviour in lizards have tested the honesty of these visual signals (e.g. Vanhooydonck et al. 2005a, b; Lailvaux and Irschick 2007; Lailvaux et al. 2012; Driessens et al. 2015). More strikingly, however, is the lack of studies on the honesty of vocalizations in lizards (Labra et al. 2013, 2016), although this is most likely because research on the bioacoustics of lizards is de facto scarce (Reyes-Olivares and Labra 2017). Those studies that did investigate lizard vocalizations have predominantly focused on the social calls of geckos (e.g. Marcellini 1978; Hibbitts et al. 2007; Jono and Inui 2012), probably because all other lizard groups are largely considered ‘voiceless’ (Pianka and Vitt 2003; Bradbury and Vehrencamp 2011), as they do not possess the unique laryngeal specialization

for vocalization and well-developed auditory sensitivity of geckos (Eatock et al. 1981; Manley 1990; Russel et al. 2000; Manley and Kraus 2010). However, several non-gekkonid lizards have been documented to emit sounds occasionally (often described as ‘short squeaks’; Böhme et al. 1985) when under threat (Johnson 1976; Crowley and Pietruszka 1983; Labra et al. 2007) or in contact with a predator (Milton and Jenssen 1979; Bowker 1980; Ouboter 1990). Although based on merely anecdotal evidence, these vocalizations are generally deciphered as ‘distress’ or ‘warning’ calls that would startle or frighten predators to deter (Milton and Jenssen 1979; Böhme et al. 1985; Carothers et al. 2001; Labra et al. 2013). Notwithstanding, as in other animal groups, lizard vocalizations might equally well serve to alarm conspecifics of impending danger (Sherman 1977) or to attract additional predators that disrupt the predator event (Högestedt 1983). Vocalizations may also play a role during intraspecific interactions or can even be vestigial and non-functional (Hibbitts et al. 2007; Colafrancesco and Gridi-Papp 2016).

In a scenario where lizard calls operate as anti-predator vocalizations, calls are expected to carry honest information about the lizard’s ability to fight off or escape predators in order to achieve evolutionary stability (Zahavi 1975; Dawkins and Guilford 1991; Viljugrein 1997; Bergstrom and Lachmann 2001). To the best of our knowledge, no study to date has examined the relationship between the acoustic design of reptilian vocalizations and whole-animal performance traits relevant in predator-prey interactions. To fill this hiatus, we examined the vocalizations of the lacertid lizard *Psammotriton algirus* and assessed whether they convey honest information on individual performance features that are of potential relevance to fight off (defend against) or escape from a predator attack. Vocalizations of this lizard species have been documented in free-ranging animals (e.g. when lifting up stones, sheltering lizards sometimes vocalize when exposed), in individuals kept in enclosures, and when handled (Mertens 1946; Böhme et al. 1985; JM pers. obs.). In this study, we measured ecological relevant morphological and performance traits, which are likely related to lizards’ ability to fight off and escape from predators, i.e. body size, bite force, and sprint speed. Hypothesizing that the vocalization of *P. algirus* acts as an honest call (with predator-deterrent potential) informing about individual features, we expect inter-individual variation in key acoustic variables of the vocalizations to correlate with body size, bite force, or sprint speed. Lastly, we explored and discussed the hearing range of *P. algirus* and its top predators in relation to the design of *P. algirus*’ vocalizations in order to assess the theoretical goal audience of these vocalizations.



Fig. 1 Photograph of the study species, *Psammodromus algirus*. Picture taken by Roberto García-Roa

Material and methods

Study species

The Algerian *Psammodromus* (*Psammodromus algirus*) is a ground-dwelling lacertid lizard (adult snout-vent length (SVL), 59–79 mm; this study) that inhabits northwest Africa, the Iberian Peninsula, and Mediterranean France (Böhme 1981; Díaz et al. 2017), and is usually found near bushes and shrubs (Arnold 1987; Díaz and Carrascal 1991). In the past, the vocalization of *P. algirus* (Fig. 1) has been labelled as a ‘short squeak’ (Böhme 1981) with a duration ranging between 220 and 750 ms and a frequency band ranging between 2 and 16 kHz (Böhme et al. 1985). Although the exact function of their vocalizations is still unclear, it has been suggested to operate as a ‘distress call’ that might signal honest information on alertness and ability to fight off or escape predators (Böhme et al. 1985).

In April 2016, at the onset of the reproductive season (Salvador et al. 1995), we caught 21 adult *P. algirus* lizards in a deciduous oak forest near Cercedilla (40° 44' N, 04° 02' W), central Spain. To eliminate any potential effect of intersexual variation on morphology, performance, and call features, and to increase statistical power, only male lizards were included in this study. Individuals were captured by hand or noose, transported in cloth bags to a nearby field station (‘El Ventorrillo’, Navacerrada), and housed indoors in individual plastic enclosures (0.8 × 0.5 m) containing a coconut fibre substratum and plywood for shelter. Within the enclosures, lizards had access to drinking water at all times and were fed thrice a week (*Tenebrio molitor* larvae and *Acheta domesticus* dusted with multivitamin powder). After completion of the experiments, lizards were returned in good health at the exact site of capture.

Morphology

At the field station, we recorded for each lizard the following: body mass, body size (SVL), head length, head width, and head height (following Herrel et al. 1999, 2001). Head length was measured from the posterior extremity of the parietal scale to the tip of the snout. Head width was the largest distance measured between the temporal scales, and head height was the maximum distance measured between the base of the mandible and the parietal surface. All length variables were

measured using digital callipers (CD-20PP, Mitutoyo Corporation, Japan, precision = 0.01 mm). Body mass was measured with a microbalance (Adventurer, Ohaus Corp., precision = 0.01 g).

Performance

We measured the performance of each individual lizard by quantifying its maximum sprint speed and maximum bite force. Prior to each performance test, animals were placed in individual cloth bags and kept for 1 h in an incubator set at 32 °C (as in, e.g. Vanhooydonck and Van Damme 2003). This procedure ensured that all measures were taken near the physiologically preferred and optimal body temperature of the species (Bauwens et al. 1995; Castilla et al. 1999). Tests for sprint speed and bite force were executed on alternate days, with 1 day of ‘rest’ in-between. All measurements were obtained during the lizards’ peak activity hours (10:00 h–16:00 h).

We measured sprint speed by chasing the lizard as fast as possible along a horizontal racetrack (2 m), equipped with a cork substrate, which provides excellent traction. Photocells, positioned at 25-cm intervals along the track, registered the passing of the lizards to a computer, which calculated the sprint speed over each interval. Every individual was tested three times with at least 1 h between trials. The fastest velocity attained over any 25 cm was retained as an estimate of an individual’s maximum sprint capacity.

Following standard protocols, bite force was measured in vivo using an isometric force transducer (type 9203, range ± 500 N; Kistler, Switzerland) mounted on a custom-built holder and connected to a charge amplifier (type 5058 A, Kistler) (for a more detailed description of the protocol and experimental setup, see Herrel et al. 1999; Vanhooydonck et al. 2005a, b; Anderson et al. 2008). Lizards readily and repeatedly bit onto the two metal plates positioned at the free end of the holder. The bite force of every individual was measured five consecutive times, and the highest bite force was considered as an estimate of the maximal bite capacity (Anderson et al. 2008).

Acoustics

We recorded vocalizations of 19 individuals with the microphone of a sound meter level (model 2238, Brüel and Kjær; Nærum, Denmark) fitted with a 5-m extension cable and 10-

cm-high tripod and positioned at 0.5 m in front of the lizards. The output of the microphone was fed into a digital recorder (Marantz PMD660; Kawasaki, Japan) by the audio line input and sampled at 48 kHz and 16-bit depth. The recording tests lasted 2–4 min per individual and were conducted in indoor settings to standardize recording conditions and to prevent environmental noise interference. Special care was taken to keep constant recording settings among trials, including recorder gain, and distance and orientation of individuals relative to the microphone. Since spontaneous vocalizations are infrequent and unexpectedly emitted by lizards in captivity (only 7 individuals emitted calls spontaneously), vocalizations were evoked following the same procedure as for recording distress calls in other animal taxa, such as anurans (Leary 2001; Walkowiak 2007). Focal lizards were removed from their enclosure, held at a constant distance from the microphone, and clasped behind their forelimbs while applying soft pressure on the thorax. This procedure resulted in 2–11 calls per individual. Blinded methods were used to minimize observed bias, in the sense that the investigators collecting data on acoustics (DL, RG-R) were unaware of how well the lizards performed during the sprint and bite trials (SB). Similar to the preparations of the performance trials, animals were placed in individual cloth bags and kept for 1 h in an incubator set at 32 °C prior to recordings.

Acoustic variables of all recorded vocalizations were analyzed with the R package Seewave (Sueur et al. 2008). The description of these variables is detailed in Table S1. For the analysis, the position of each selected vocalizations was annotated using Audacity 2.0.0 software (SourceForge or University Carnegie Mellon, PA, USA). Recorded calls with amplitudes below 3-dB signal-to-noise ratio were considered too low and were excluded from further analysis. All selected recordings were standardized by removing low-frequency noise using a high-pass filter set at 1 kHz with an adjusted version of the R function ‘fir’ (Sueur et al. 2008). Temporal measurements were calculated on oscillograms, while spectral measurements were calculated on spectrograms computed through a fast short-term Fourier transformation (Hanning window, window length of 512 points, and overlapping of 75%; temporal resolution, 10.7 ms; spectral resolution, 93.7 Hz). Next, individual average values were calculated for each acoustic variable in order to characterize the vocalizations of each lizard. To assess the relationship between call structure, morphology, and performance, and for the sake of simplicity, we only used those acoustic variables with a hypothesized biological relevant function (i.e. call duration, call amplitude, fundamental frequency, dominant frequency, and spectral complexity; Morton 1977; August and Anderson 1987). Spectral complexity was calculated using the function ‘sfm’ in R and corresponds to an index of the number of frequency bands within the call. This measure is based on the spectral flatness or Wiener entropy that computes the ratio

between the geometric mean and the arithmetic mean of the frequency binds of the frequency spectrum of the call (Sueur 2018). For the seven individuals that emitted spontaneous calls, we tested for differences between average values of acoustic variables in their spontaneous and evoked calls. Repeated measures ANOVAs confirmed no statistical difference between the two types of vocalization for any of these acoustic variables ($F_{1,6} < 0.99$, $P > 0.100$; in all cases), validating the use of both spontaneous and evoked calls in further analyses.

Statistics

To assess the effect of morphology and performance (i.e. body size, bite force, and sprint speed) on the duration, amplitude, fundamental frequency, dominant frequency, and spectral complexity of lizard vocalizations, we used multiple linear regression analyses. Since absolute bite force in *P. algirus* is heavily affected by size (Herrel et al. 2004; this study), we used size-adjusted values for bite force (hereafter referred to as ‘relative bite force’) in the regression analyses, i.e. the residual values calculated from a regression analysis of bite force as response variable and SVL as predictor variable (as, e.g. Herrel et al. 2001, 2006). Sprint speed was not corrected for SVL since there was no significant relationship between the two variables ($R^2 = 0.014$, $F_{1,20} = 0.24$, $P = 0.633$). Prior to the analyses, all variables (except sprint speed) were \log_{10} -transformed to meet the assumptions of normality (Shapiro-Wilk’s test with $W \geq 0.95$) and homoscedascity, and to avoid influential cases.

We checked several diagnostics of model validity and stability (Cook’s distance, DFFits, leverage and variance inflation factors, distribution of residuals, residuals plotted against fitted values), and none of these indicated obvious influential cases or deviations from the assumptions of normality and homogeneity of residuals (Quinn and Keough 2002). To test the significance of the predictors as a whole, we compared the fit of the full model with that of the null model comprising only the intercept (Forstmeier and Schielzeth 2011). We ran the analysis using the function ‘lm’ of the statistics package R (version 3.2.1; R Core Team 2015). Model diagnostics were calculated using the functions ‘VIF’ (R package fmsb; Fox and Weisberg 2011), ‘dffits’, and ‘cooks.distance’.

In addition, we determined whether the vocalizations of individual lizards are distinct from those of conspecifics and contain individual ‘signatures’. Thus, we performed a multivariate analysis of variance (MANOVA) to establish whether calls from different individuals were significantly dissimilar, and a stepwise (weighted) discriminant function analysis (Fisher’s coefficients) to predict group membership for each vocalization. The latter test ultimately resulted in a percentage documenting the average correct assignment to individuals. The outcome of a preliminary MANOVA and discriminant

analysis validated the use of averages for the acoustic variables in the inter-individual comparisons. Analyses were conducted in SPSS v. 22.0 (Chicago, IL, USA).

Data availability The data collected during the current study are available from the corresponding author on reasonable request.

Results

Call design

The vocalizations emitted by male individuals of *P. algirus* were high-pitched squeaks, with a complex and variable broadband spectral structure, showing multiple harmonics (1–14) and a marked frequency modulation (Fig. 2; Table S2). A total of 118 evoked calls from 19 lizards were analyzed, with a mean of 7 calls per individual. Recorded vocalizations had an average duration of 0.431 s (range = 0.051–2.152 s), a fundamental frequency of 5.8 kHz (range = 1.3–16.0 kHz), and a dominant frequency of 12.2 kHz (range = 1.9–20.1 kHz). According to the spectrograms, some of the calls might have carried ultrasonic components (above 20 kHz) that were not captured due to restrictions of the recording equipment. Amplitude modulation was characterized by a wide variation, with a rise duration ranging from 43 to 96% of the duration of the calls and a mean of 74%.

Both the MANOVA and the discriminant analysis provided evidence for individual acoustic signatures in *P. algirus* males. The MANOVA showed significant differences among individuals (Wilks' $\lambda = 0.259$, $F_{4,96} = 461.38$, $P < 0.001$), and the discriminant analysis revealed that 89.0% of the calls were correctly assigned to individual lizards.

Linking morphology and performance with call design

On average, male *P. algirus* lizards in our study had a snout-to-vent length of 69.39 mm and showed a maximum sprint speed of 251.21 cm/s, and a maximum bite force of 9.69 N (Table S3). As in most lizards (Herrel and O'Reilly 2006), head width (not head length or head height) best explained variation in maximum bite force (multiple regression; $R^2 = 0.859$, $F_{1,20} = 97.86$, $P < 0.001$). Moreover, fast sprinters were not bigger in size ($R^2 = 0.014$, $F_{1,20} = 0.24$, $P = 0.633$) nor bit significantly harder than slow sprinters ($R^2 = 0.065$, $F_{1,20} = 0.72$, $P = 0.868$).

Acoustic variables of the vocalizations emitted by focal lizards were found to be associated with lizard morphology and performance (Fig. 3). Overall, as shown by multiple regression models, the predictors significantly influenced dominant frequency (R^2 -adjust = 0.330, $F_{1,15} = 3.96$, $P = 0.029$) and call amplitude (R^2 -adjust = 0.290, $F_{1,15} = 3.45$, $P = 0.044$). The predictors merely tended to affect spectral complexity (R^2 -adjust = 0.391, $F_{1,15} = 3.18$, $P = 0.053$), but did not influence call duration ($F_{1,15} = 0.123$, $P = 0.945$). Specifically, body size affected both dominant frequency (estimate \pm SE = -7.77 ± 2.61 , $t_{15} = -2.977$, $P = 0.009$; Fig. 3a) and spectral complexity (estimate \pm SE = -6.12 ± 2.68 , $t_{15} = -2.281$, $P = 0.037$; Fig. 3b), with larger lizards producing lower pitched and less complex calls in comparison with smaller lizards. These spectral variables were not significantly related to bite force (for dominant frequency: estimate \pm SE = -6.03 ± 7.96 , $t_{15} = -0.758$, $P = 0.460$; for spectral complexity: estimate \pm SE = -14.69 ± 8.18 , $t_{15} = -1.796$, $P = 0.092$) or sprint speed (for dominant frequency: estimate \pm SE = 0.46 ± 0.26 , $t_{15} = 1.789$, $P = 0.094$; for spectral complexity: estimate \pm SE = 0.09 ± 0.26 , $t_{15} = 0.326$, $P = 0.748$). Furthermore, call amplitude increased with relative bite force and was selected as best predictor in the model (estimate \pm SE = 3.83 ± 1.40 ,

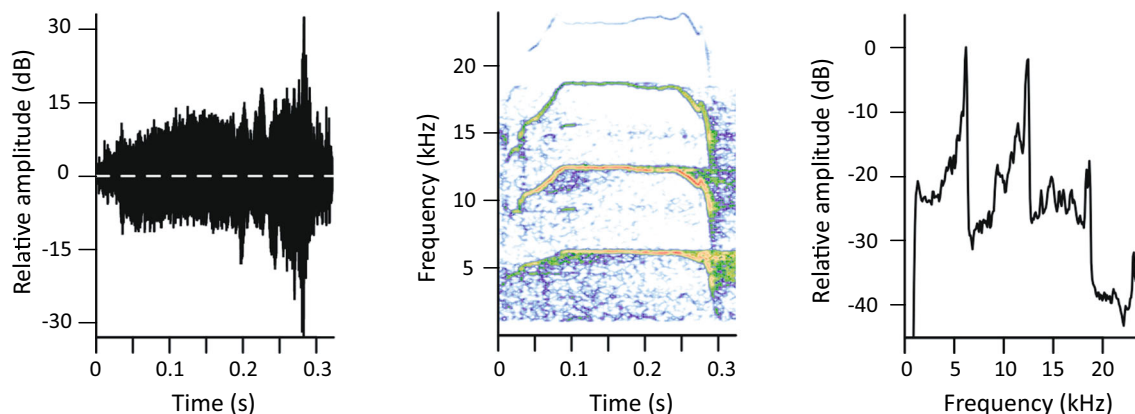


Fig. 2 Oscillogram (left), sound spectrogram (middle), and power spectrum (right; Hanning window, 512 points of window length, and 75% overlap) of the vocalizations of a representative *P. algirus* lizard.

Recordings were filtered with a high-pass filter set at 1 kHz and peak-normalized

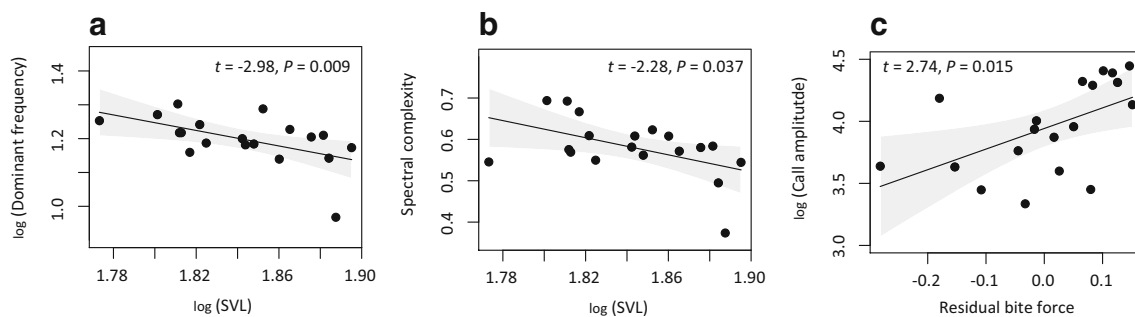


Fig. 3 Scatter plots with regression lines showing the relationship between acoustic variables of the vocalization of *P. algirus* and body size and relative bite force: **a** dominant frequency and snout-vent length

(SVL), **b** spectral complexity and SVL, and **c** call amplitude and relative bite force. The shaded areas represent 95% confidence intervals

$t_{15} = 2.740$, $P = 0.015$), indicating that lizards with a relatively high bite force emit louder vocalizations than lizards with a relatively soft bite (Fig. 3c). No association was observed with body size (estimate \pm SE = 0.05 ± 0.03 , $t_{15} = 1.682$, $P = 0.113$) or sprint speed (estimate \pm SE = -0.001 ± 0.003 , $t_{15} = -0.117$, $P = 0.908$). Conversely, none of the predictors influenced call duration ($F_{1,15} = 0.123$, $P = 0.944$) nor fundamental frequency ($F_{1,15} = 0.184$, $P = 0.905$).

Discussion

This study presents the first detailed quantitative description of the acoustic properties of vocalizations by males of the lacertid lizard *P. algirus* and provides evidence for individual specificity or ‘call signatures’. Moreover, our results revealed a link between inter-individual variation in acoustic variables (call amplitude, dominant frequency, spectral complexity) of these vocalizations and inter-individual variation in morphology (i.e. body size) and performance (i.e. relative bite force, but not sprint speed). Thus, the call of *P. algirus* broadcasts reliable information on traits that could be useful to fight off predators. As such, these findings support the hypothesis that the vocalizations of *P. algirus* lizards might have the potential to serve as honest distress calls to deter predators.

Proximate explanations

Based on our recordings, we can describe the vocalizations emitted by *P. algirus* males as a harsh, broadband, high-pitched (average 12.19 kHz; range = 1.9–20.1 kHz), and short sound (average 0.43 s; range 0.05–2.2 s), similar to those of closely related lizards, such as *P. hispanicus* (1.5–16 kHz; 0.7–0.9 s), *Gallotia atlantica* (1–7 kHz; 0.1–0.8 s), *Gallotia galloti* (0.5–13 kHz; 0.02–1.8 s), and *Gallotia stehlini* (0–12 kHz; 0.25–0.9 s) (Böhme et al. 1985). While our comprehensive acoustic analysis revealed a more complex spectral structure than previously documented for *P. algirus* (Böhme et al. 1985), its vocalizations are, nevertheless, far less

elaborate than those of geckos, a lizard group which is known to rely strongly on acoustic signalling for intraspecific communication (Colafrancesco and Gridi-Papp 2016).

Our analyses also show considerable within-species variation in call design, with each individual having a unique call signature, defined by only a few acoustic variables. Individual-specific vocalizations are relatively common in a range of mammal species (e.g. Janik et al. 2006), birds (e.g. Lengagne et al. 2001), and amphibians (e.g. Gambale et al. 2014; Hubáček et al. 2019), but are less so in reptiles (e.g. Vergne et al. 2007; Ferrara et al. 2014). This is not unexpected, since the majority of reptiles are considered ‘voiceless’ (Pianka and Vitt 2003; Bradbury and Vehrencamp 2011), and as such, less studied than other more vocal animals. Yet, the surprising complexity and individual character of the calls of *P. algirus* demonstrate that the field of bioacoustics in reptiles deserves more attention.

Most excitingly, we found that the vocalizations emitted by *P. algirus* broadcast individual information on body size and bite performance. First, we observed that large-sized lizards produce lower and less complex frequency calls than small-sized lizards. The finding of an inverse relationship between dominant frequency of a sound and the size of the animal producing such a sound is not new; it has been documented for a variety of vertebrate groups, both on an inter- and intra-specific level (Ryan and Brenowitz 1985; Fitch and Hauser 1995; Martin et al. 2017). The origin of this frequency-size relationship is purely mechanistic and can be explained by the basic laws of acoustic allometry (Morton 1977). In vertebrates, acoustic signals are strongly influenced by the size of the individual components of the sound production structures (e.g. lungs, larynx, vocal tract). For example, in mammals and birds, the primary determinant of sound frequency is the size of the vocal cords, which is also known to scale with overall body size (Fitch and Hauser 1995; Fletcher 2004). Hence, the larger the animal, the lower the sound frequency it can produce, making (the frequency of) the call a reliable indicator of a vocalizer’s size (Fitch and Hauser 1995). Compared with the extensive body of knowledge on mammalian, avian, and

anuran vocalizations (e.g. Morton 1977; Ryan and Brenowitz 1985; Martin et al. 2017), records on the frequency-size relationship in lizards are, however, limited. Still, they are not inexistent. For instance, a negative correlation between these variables has also been observed in the liolaemid *Liolaemus chiliensis* (Labra et al. 2013) and the gecko *Ptenopus garrulus* (Hibbitts et al. 2007). These findings, together with our findings on the lacertid *P. algirus*, corroborate the generality of the relationship between dominant frequency and body size in lizards, and by extension, the reliability of sounds as an honest signal of animal size.

Aside from such an association with spectral properties, we also established that lizards with a higher (relative) bite force (for their size) emit louder calls than those with a lower bite force. The proximate mechanism that explains the link between the structure of an animal's call and its bite performance is, however, less clear-cut. In vertebrates, call amplitude is predominantly determined by the degree of subglottal pressure and vocal fold adduction, which are controlled by the respiratory and laryngeal muscles, respectively (Gans and Maderson 1973; Stein 1973; Elemans et al. 2015). Individuals with more massive respiratory and laryngeal muscles are able to produce louder vocalizations than those with less developed muscles (Colafrancesco and Gridi-Papp 2016). Although the vocal muscle architecture is anatomically independent from the jaw muscles (that are responsible for an animal's bite), it is not unlikely that individuals with well-developed respiratory/laryngeal muscles are those in overall good condition, hence, those that carry well-developed muscles across their whole cranial system.

Another explanation of why *P. algirus* lizards with a high bite force vocalize loudly might be due to the relationship between bite force and head size, and with the mouth operating as a 'megaphone'. In lizards, head size is a key predictor of bite force (Herrel and O'Reilly 2006; Anderson et al. 2008; this study), and lizards with a large head are able to open their mouths more widely than those with a small head (measured as the gape distance between the upper and lower jaw tips). It is plausible that the mouth opening, while vocalizing, acts as a sound amplifier with gape distance determining the degree of amplification. This is true in blackbirds (*Turdus merula*), where an increase in beak-opening angle causes an increase in call intensity; beak-opening angle operates here as a volume control (Larsen and Dabelsteen 1990). Consequently, one could assume that lizards with a strong bite (due to their large head), also have a large gape, and therefore can amplify their calls more strongly than those with a softer bite (due to their smaller head). Obviously, more detailed morphological research is essential to (dis)prove such hypothesis and to disentangle the precise mechanics behind the relationship between bite performance and call amplitude.

Ultimate explanations

For decades, the vocalizations emitted by non-gekkonid lizards, including *P. algirus*, have been interpreted as distress calls that would startle or frighten predators to deter (Wever 1978; Böhme et al. 1985; Hoare and Labra 2013). Yet, evidence to support this hypothesis is entirely lacking. To fill this gap in our understanding, it is useful to first question the requirements for a vocalization to qualify as a potential predator-deterrent signal.

Following Caro (1995), a predator-deterrent signal can be defined as a signal emitted by a prey animal towards a predator indicating that it has detected the predator, and which may cause the predator to give up its approach towards the prey as a result of this information alone. As such, a first requirement of a predator-deterrent signal is that it should be tuned to the sensitivity of the sensory system of the predator, so predators are capable to perceive the emitted signal. This means that the call of *P. algirus* should be intense enough at particular frequencies within the predator's hearing range. In the Mediterranean forests of the Iberian Peninsula, *P. algirus* lizards are preyed upon by a number of predators that rely on visual and acoustic cues to hunt, such as raptorial birds (e.g. *Tyto alba*, *Falco* sp.), shrikes (*Lanius excubitor*), weasels (*Mustela nivalis*), and foxes (*Vulpes vulpes*) (Martín and López 1990; Salvador 2015). Comparing the frequency bandwidth of the call of *P. algirus* with the hearing ranges of the lizards' key predatory species suggests that all predators are theoretically able to perceive calls of *P. algirus* (Fig. 4). While predatory birds are only able to perceive the relatively low-frequency components of lizard calls, mammals are, in theory, capable to hear most of the frequencies emitted in these vocalizations, including the highest recorded frequencies exceeding 12 kHz. Snakes, another important lizard predator (e.g. *Malpolon monspessulanus* and *Rhinechis scalaris*; Díaz-Paniagua 1976; Pleguezuelos 1989), are equipped with a poorly developed hearing apparatus (Wever 1978), and therefore, unable to perceive airborne sounds. Behavioural assays using playback experiments are, nonetheless, essential to test whether potential predators are truly able to hear the calls of *P. algirus*.

The most spectral components of the calls emitted by *P. algirus* lizards seem, thus, to be tuned to the hearing sensitivity of a number of mammalian and bird predators. Consequently, these calls can have the ability to inform predators that they have been seen (perception advertisement; Ruxton et al. 2004), a deterring tactic effective with ambush or stalking predators that need to come near the prey without being detected in order to be successful (Broom and Ruxton 2012). Yet, the situation in *P. algirus* lizards is slightly different, since they are primarily preyed upon by active predators (Salvador 2015). In addition, lizards in our study showed substantial among-individual variation in intrinsic quality, such as

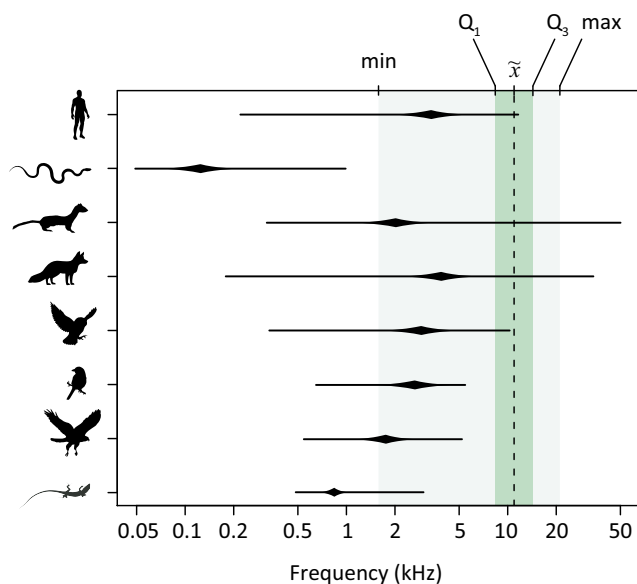


Fig. 4 Who can hear the vocalizations of the lizard *Psammotriton algirus*? Illustration of the hearing sensitivity of the main predatory species of *P. algirus*; those of humans and *P. algirus* are also included for comparison. The figure shows the frequency sensitivity range per species (black lines) for which the species is able to hear sounds up to 28 dB (i.e. the maximum recorded amplitude of the *P. algirus* call). The position of line thickening indicates a species' optimal frequency sensitivity. The light green-coloured area visualizes the frequency range (min–max) of the *P. algirus* call; the dark green area represents the call frequency range of the middle 50% (interquartile range); the vertical dotted line shows the average call frequency recorded. Data on frequency sensitivity were gathered from literature. From top to bottom: humans (Jackson 2012), snakes (*Elaphe obsoleta*; Wever 1978), weasel (*Mustela nivalis*; Malkemper et al. 2015), red fox (*Vulpes vulpes*; Malkemper et al. 2015), barn owl (*Tyto alba*; Dooling 2002), Passeriformes (Dooling et al. 2000), Falconiformes (*Falco sparverius*; Dooling 2002), *P. algirus* (Wever 1978)

sprint speed and bite force, and by extension, the ability to flee and fight (Huyghe et al. 2005; Zamora-Camacho et al. 2014). In such a scenario, theoretical models suggest that it would be highly advantageous for (especially, high-quality) individuals to signal their quality to predators (Vega-Redondo and Hasson 2003). And indeed, our findings revealed that *P. algirus* calls (i.e. frequency and amplitude) convey honest information on a lizard's size and maximum bite performance. There was no evidence for a significant relationship between inter-individual variation in call design and variation in sprint speed. In lizards, both body size and bite performance are well-recognized indicators of an individual's quality as they are key predictors in determining intraspecific combat outcome (Tokarz 1985; Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006; Hardy and Briffa 2013). Consequently, this result implies that while vocalizations of *P. algirus* provide no information on their capacity to flee, they are reliable indicators of their capacity to fight. By extension, one might assume that individuals with a high fighting ability are also able to better fight off or defend themselves

from a predator attack than those with a low fighting ability. Although challenging, further research is necessary to assess whether a lizard's fighting ability against conspecifics translates to the capability to defend itself in a predator-prey context.

While predator deterrence is one potential hypothesis on the function of *P. algirus* vocalizations, lizard calls might equally well function in a context of intraspecific communication, as agonistic calls in male-male competition, or sexual signals for mate choice. Similar to the predator-prey system, signals used for intraspecific communication are expected to be tuned to the sensitivity of the sensory system of the conspecific receiver. According to Wever (1978), *P. algirus* lizards have an excellent hearing sensitivity in the low-frequency range, with prominent peaks at 700 Hz and 1000 Hz. The acuity of their hearing, however, falls off rapidly after 3000 Hz (Wever 1978). Interestingly, from the 118 calls recorded in this study, only 2 of the calls had a dominant frequency of less than 3 kHz. This would imply that the vast majority of the calls produced by *P. algirus* males are too high-pitched to be heard by members of their own species. If true, this finding strongly discards the hypothesis that *P. algirus* vocalization might function for intraspecific communication. Again, playback experiments are necessary to validate this assumption. Lastly, we cannot rule out that the call of *P. algirus* might be non-functional, and that our observed link between call design and animal performance is merely a by-product of the anatomical architecture of the lizard's vocal system.

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Authors' contributions SB, DL, and RG-R conceived and designed the study; SB and DL conducted statistical analyses; SB prepared figures, and drafted and revised the manuscript; all authors aided in collecting data and interpreting the results; all authors contributed to editing the final paper.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. After completion of the experiments, animals were returned in good health at the exact site of capture. The study was performed under license (permit number: 10/056780.9/16) from the Environmental Agency of Madrid Government ('Consejería de Medio Ambiente de la Comunidad de Madrid', Spain), and in accordance with the national animal welfare standards and protocols supervised by the Bioethical Committee of the Spanish Research Council (CSIC).

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