

Headbob displays signal sex, social context and species identity in a *Liolaemus* lizard

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Abstract. Animal communication has a key role in animals and identifying the signals' function is crucial. Most lizards communicate with each other through visual signals with headbob displays, which are up-and-down movements of the head or the anterior part of the body. In the present work, I described and analysed the headbob displays of *Liolaemus pacha* lizards in their natural habitat. Specifically, the objectives were to describe the form of headbobs, to analyse their structure and to compare between sexes and social contexts. Adult lizards were video-recorded, registering the sex and the social context, classified as broadcast, same-sex and female-male interactions. The form and structure of sequences and headbobs were obtained. To evaluate the effect of sex and social context on the structure of headbob sequences and on headbob bouts, generalized linear mixed models were made. Intersexual differences were found in headbob display frequency and in the structure of headbob sequences. Lizards in same-sex context made sequences with more bouts, shorter intervals, headbob bouts of longer duration and higher amplitude than broadcast and female-male context. Presence of concurring behaviour such as lateral compression, gular expansion, and back arching occurred simultaneously with headbobs in same-sex context. *Liolaemus pacha* made four different headbob bout forms, and males were characterised by using bouts A and B, whereas females used bouts D more frequent. Sex and social context influenced only the structure of bouts A and B. The results showed that bouts A and B might be multi-component signals and non-redundant.

Keywords: behaviour, communication, multicomponent, non-redundancy, visual signal.

Introduction

Animal communication has a key role in animals, mediating processes such as mate search, reproduction, species isolation, and also, determining spatial patterns and dispersion. Thus, signals keep individuals informed and interconnected. Identifying the signals' function and the information conveyed by them could be challenging. For instance, a single signal might have multiple functions and one function might be performed by multiple signals (Pérez i de Lanuza et al., 2014; Stuart-Fox and Goode, 2014; Martín and López, 2015; Pruett et al., 2016). Thus, as a first step, we might search the link between signal form and function, in order to evaluate future questions such as their adaptive value, the influence of the environment on signals, whether they are under sexual selection,

how physiology could influence their production, among others.

From reptiles, lizard's behaviour is the most studied and known, because of their almost worldwide distribution and their diurnal habits. Also, lizards may offer the opportunity to study the whole array of signals performed in the laboratory, but more interesting, under natural conditions. Most lizards communicate with each other through visual signals, involving coloration patterns, temporal displays, and posturing. However, one of the most conspicuous signals is the headbob display, a sequentially stereotyped up-and-down movement of the head or the anterior part of the body (i.e., push-up displays, Carpenter and Ferguson, 1977). Headbob displays can be produced simultaneously with other behaviours, such as gular extension, back arching and, lateral compression, that change the appearance of the signaller (Carpenter and Ferguson, 1977) and may function as amplifiers (e.g., Brandt, 2003). Headbobs are innate (Carpenter, 1967) and species-specific, meaning that each species is identified by a characteristic

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headbob pattern (i.e., signature headbob; Carpenter and Ferguson, 1977).

Headbob displays are performed mainly by males, displaying after moving from perch to perch, in presence of other male or when court females (Martins, 1993). Headbobs are stereotyped, which means that they present a defined structure of sequential behavioural units. However, they can show some degree of variation in the duration and/or amplitude of their units among sexes and individuals (Rothblum and Jenssen, 1978; Martins, 1991), social contexts (Martins, 1993; Decourcy and Jenssen, 1994) and populations (Martins et al., 1998; Macedonia and Clark, 2003; Macedonia et al., 2015). Therefore, headbob displays would inform identity, sex, and a social function.

Liolaemus lizards (Liolaemidae) is the second genus most diverse of lizards (Uetz et al., 2016) and they conform an excellent object study to investigate visual and chemical signals from an ecological and evolutionary perspective. Specifically, *L. pacha* lizards are known to perform headbob displays during aggressive encounters and courtship (Halloy, 1996) and also, males display more frequently than females (Halloy, 2012). Previously, Vicente and Halloy (2015) have found that males showed two types of headbobs and the structure (amplitude and duration) varied between the male-male and male-alone context. In this work, I presented a complete analysis of *Liolaemus pacha* headbob displays in their natural habitat, including females and the male-female context. More specifically, the objectives were to describe the form of headbobs displays, to analyse their structure and to compare between sexes and social contexts.

Materials and methods

Study species

Liolaemus pacha is a small, diurnal and terrestrial lizard. Males are bigger and colourful than females, showing a pattern of yellow, reddish and blue spots, whereas females are brownish and cryptic (Juárez Heredia et al., 2013). It is

an insectivorous lizard (Halloy et al., 2006), but occasionally their diet can include vegetal parts (Vicente and Halloy, 2014). It is an oviparous species and matings occur at the end of October and in the beginning of November (i.e. reproductive season; Ramírez Pinilla, 1992). Males emerge in September, whereas females emerge at the end of October (Halloy and Robles, 2003). During the reproductive season, males establish their territory (Halloy and Robles, 2002), patrolling their surroundings and using headbob displays to signal other rival males. This is reflected in the high frequencies of head-bobbing behaviour during reproductive season (Halloy, 2012). *Liolaemus pacha* is found in the area of Los Cardones, located 20 km East from Amaicha del Valle, Department of Tafi del Valle, Province of Tucuman (26°40'1.5" S, 65°49'5.1" W). The site is located at 2725 m on the western slope of Sierras Calchaquíes.

Field trips

I made eight field trips, three during 2012 (October to December), three during 2013 (October to December) and two in November 2014 and 2015. Field trips lasted two to five days, starting from 10:00 h until 16:00 h, being these hours the ideal for social interactions (pers. obs.). Adult lizards were actively sought, walking by the area (approximately 1 ha) in the same direction. Sampling started each day from different points to avoid filming twice the same individual. Adult lizards were video-recorded with a digital camcorder (Sony Handycam HDR-Cx290), following the animal focal technique (Martin and Bateson, 2007), during 15 minutes or until the individual was lost to sight. The sex and social context were also registered.

Social context

Social context was classified as the following way: same-sex interaction, female-male interaction, and broadcast. The same-sex context was determined by the presence of a same-sex conspecific in a range of 5 m. Typically, same-sex context occurs in face of territorial intrusion of another rival male because female aggression is rare or less mentioned (Carpenter, 1982; Halloy, 1996). In this context, individuals displayed more frequently, using elevated perches and maintaining an erected posture. In addition, other behaviours such as gular expansion, lateral compression and, back arching of the trunk can be displayed simultaneously (fig. 1A-B; Vicente and Halloy, 2015). The female-male context was determined by the presence of a conspecific of the opposite sex in a range of 5 m, including displays directed by females to males and viceversa. In the proximity to a female, male approaches displaying headbobs, with his head lowered and their legs flexed (fig. 1C-F; Halloy, 1996). Then, male contacts female pushing with his snout her cloaca or licking the area (fig. 1E). If female remains passive, the male takes a neck-bite and mount her, approaching his cloaca to the female's (Carpenter, 1978). Female rejection posture is characterized by the body inflated, legs stretched and a tail raised, usually directed to

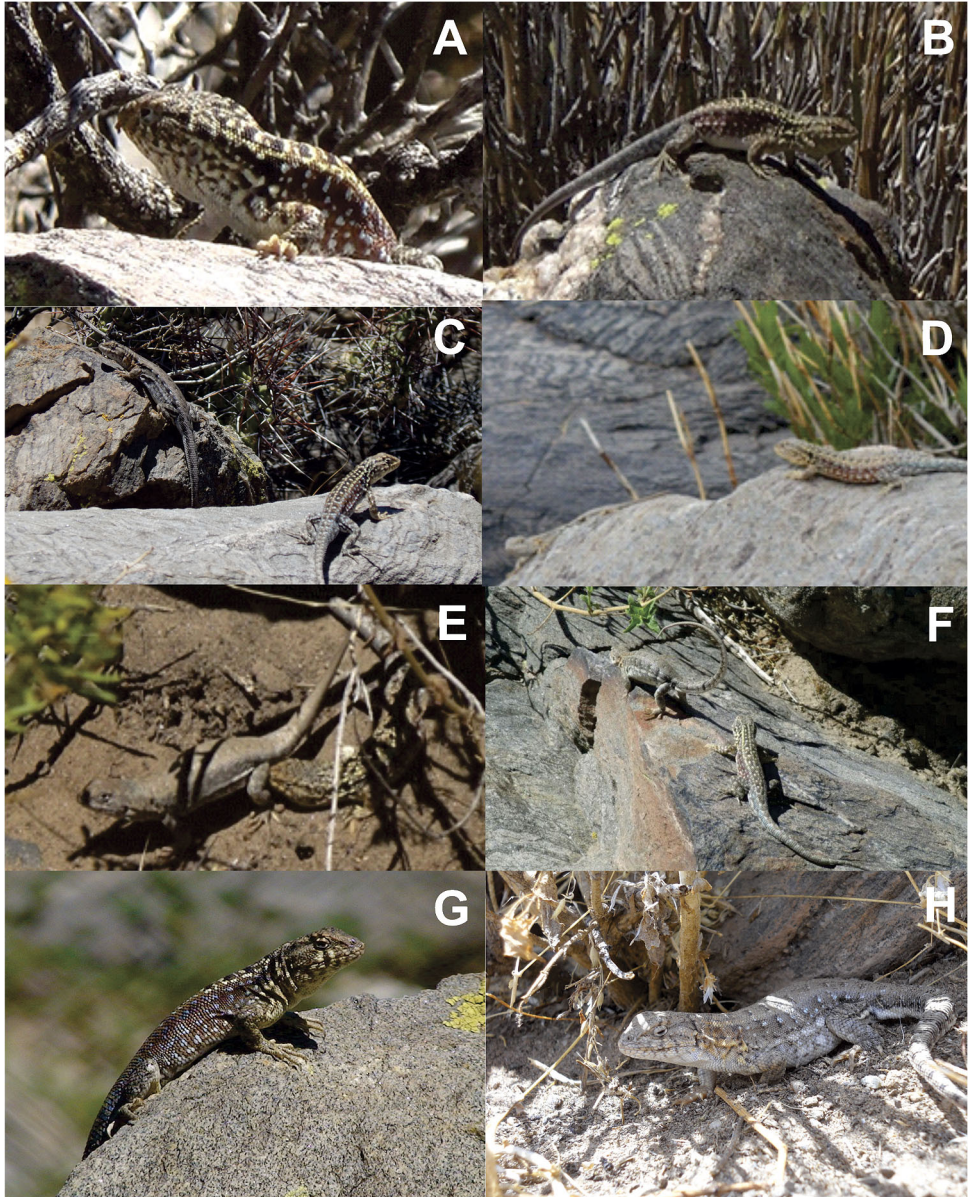


Figure 1. Same-sex context: video captures showing different males which in presence of other males, performed headbob displays with back arching, lateral compression, and gular expansion (A-B). Female-male context: a male approaches a female by displaying headbobs, with a low posture (C and D). When the male is near to the female, he can press with his snout the female cloacal area (E). If female rejects him, she raises in her four limbs fully stretched, inflates her body, raises her tail and moves away hopping from the side (F). Broadcast context: Headbob displays can be produced in absence of conspecifics, with a resting posture, characterized by hind limbs flexed and forelimbs going from stretched to flexed. Male (G) and female (H) *L. pacha*.

the male (pers. obs). After that, she moves away giving short hopping to side (i.e., sidle-hopping; fig. 1F; Carpenter and Ferguson, 1977). Broadcast context was determined by the apparent absence of conspecific in a range of 5 m. In this social context, lizards displayed from a resting posture, with their hind limbs flexed and their forelimbs flexed

or stretched. Lizards usually perform few low-amplitude headbobs and other concurring behaviour are rare or absent (*sensu* Carpenter, 1961a; Vicente and Halloy, 2015). Headbobs were performed after moving from a perch to another (fig. 1G-H; *assertion display*; Carpenter, 1961b; *broadcast display*; Martins, 1993).

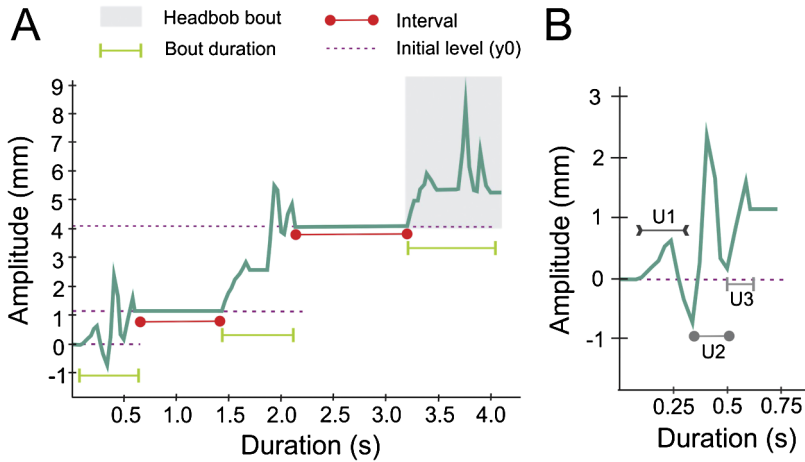


Figure 2. Analysis of headbob display structure. A) Headbob sequences, showing the initial level (y_0) for each headbob bout, the intervals, and bout duration. From each sequence, the mean interval, the mean headbob bout duration and the number of bouts per sequence were obtained. B) Headbob bout, indicating the units that comprise: U1, U2, U3. From each bout, the amplitude and duration of each unit were also measured.

Video analysis

I analysed video-recordings in detail registering the moments where lizards performed headbobs. The headbob sequences of good quality with the focal individual placed sideways or in front of the camcorder were used for the analysis of the structure. The sequences of interest were cut from the original video, using .mov or .m2ts format (full-HD) format videos with a resolution of 30 frames/second.

The display-action-pattern can be obtained plotting the vertical motion of the head through time (i.e., DAP-graph; Carpenter and Grubitz III, 1961). I used the software TRACKER (Brown, 2009) for headbob analysis. To obtain the headbob pattern, I marked frame by frame the position of the snout, obtaining this way a graph of the vertical movement of the snout of the lizard (y-axis) over time (x-axis; Supplementary figure S1). I located the initial point (y_0) at the beginning of each headbob bout, by changing the axis (figs S1 and 2A). Because individuals were filmed neither at the same distance nor lizards were captured, I calibrated the videos with the calibration stick tool, using the average height of the head from the description of the species (i.e., mean \pm SD: males = 8.31 ± 0.8 mm; females = 7.06 ± 0.8 mm; Juárez Heredia et al., 2013). Calibration stick estimates the proportion between any real distance and the same distance in the image in pixels (Brown, 2009).

Terminology

In this study, a headbob is considered as the up-and-down movement of the head or anterior part of the trunk (fig. 2A). Moreover, a headbob bout (also referred simply as a bout) is a stereotypical sequence of headbobs that follow each other within less than 2 seconds (fig. 2A). A bout is characterized by a defined form which is defined by the number of headbobs and the location of pauses between them, obtaining as a result different types of bouts. The amplitude and duration

of units (i.e., headbobs and pauses) that composed a bout defined the structure (fig. 2B). Finally, a sequence is a succession of bouts that occur within less than 30 s (fig. 2A).

Measures

Initially, I estimated the percentage of occurrence of headbob sequences, calculated as the number of individuals who made headbob sequences on the total number of individuals. The analysis of the headbob display structure was divided into two parts. First, I analysed the sequences, estimating the next variables (fig. 2A): 1) mean bout duration (s), as an average of the duration of all headbobs bouts comprising the sequence; 2) number of bouts per sequence; 3) presence or absence of concurring behaviours, such as gular expansion, back arching and, lateral compression, and; 4) mean interval (s), as an average of the duration of intervals. Second, I analysed the structure of each bout, calculating the amplitude (mm) and duration (s) of each unit (U1, U2, and U3, when appropriate; fig. 2B). For each bout the initial level was zero, changing the axis for each headbob (figs S1 and 2B).

Statistical analyses

To evaluate the effect of sex and social context on the structure of sequences and bouts, I made generalized linear mixed models (GLMM; Zuur et al., 2009). For sequences, mean bout duration, the presence of concurring behaviours and, mean interval were considered as response variables. For bouts, the amplitude and duration of each unit (headbob) were response variables. In every model, sex and social context were considered as fixed effects and individual as a random effect. Models with quantitative discrete variables were fitted using a poisson or a negative binomial distribution when showed over-dispersion and, those

with quantitative continuous variables were fitted following a gamma distribution because they did not comply with the normality assumption (Zuur et al., 2009). I estimated a full model for each response variable (Response variable ~ Sex + Context + Sex: Context + (1|individual)) and I performed model selection using backward single term deletions ($P \leq 0.05$) followed by model comparisons via likelihood ratio tests (Zuur et al., 2009). I also calculated 95% confidence interval limits (CL) of parameter estimates.

I compared frequencies of individuals in each headbob bout between sexes and among contexts with G-Test. All analyses were carried out using the software R (R Core Team, 2016), considering the differences significant when $P \leq 0.05$. All values are reported as mean \pm SE. I estimated the coefficient of variation (CV) for all headbob bouts units and following Barlow's (1968) criterion, those with CVs less than 35% were considered stereotyped.

Results

I observed 295 individuals, 145 males (Mean duration: 08 m 52 s; Total duration: 47 h 14 m), and 150 females (Mean duration: 09 m 48 s; Total duration: 48 h 02 m). The headbob occurrence in the natural habitat, was significantly higher in males (G Test, $G = 10.93$; $P < 0.001$; $n = 112$; 77.3%) than in females ($n = 67$; 44.7%). From those 179 individuals, 124 were used for the analysis of headbob bout structure ($n \sigma = 77$, $n \text{♀} = 47$) because they complied with the video requirements (See Materials and Methods, video analysis for more detail).

Headbob sequences

Variation in mean headbob bout duration in a sequence was influenced by sex and social context (table 1; fig. 3), after the sex:context interaction were removed from the model ($P = 0.74$). Males register longer bouts than females (0.51 ± 0.03 s). In the same-sex context, mean bout duration was significantly higher (0.66 ± 0.02 s) than female-male (0.56 ± 0.02 ; Tukey's post hoc: $z = 2.65$, $P = 0.02$) or broadcast context (0.54 ± 0.02 ; Tukey's post hoc: $z = 3.28$, $P = 0.003$); in contrast, there was not significant differences between the latter two contexts (Tukey's post hoc: $z = 0.22$, $P = 0.97$).

The number of bouts per sequence was significantly influenced by context (table 1). Males included more bouts per sequence (3.26 ± 0.15) than females (2.16 ± 0.19 ; fig. 3); however these differences did not quite achieve significance ($P = 0.09$). In the same-sex context, the number of bouts included in a sequence were significantly higher (4.60 ± 0.27) than in a female-male context (3.33 ± 0.20 ; Tukey's post hoc: $z = 3.70$, $P < 0.001$) or broadcast context (1.91 ± 0.12 ; Tukey's post hoc: $z = 8.66$, $P < 0.0001$). Moreover, differences between courtship and broadcast sequences were

Table 1. Analyses of headbob sequences. Parameter estimates (PE \pm SE), 95% confidence interval limits (CL) for explanatory variables (sex and/or context) describing variation in mean bout duration, the number of bouts per sequence, the presence of concurring behaviours (gular inflation, lateral compression and, back arching) and, mean interval. Estimates represent the difference between sexes and contexts, with respect to the reference values (females and same-sex context), when correspond.

Response variable	Explanatory variables	PE \pm SE	CL Inf.	CL Sup.	<i>P</i>
Mean bout duration	Intercept	-0.61 \pm 0.08	-0.76	-0.45	<0.001
	Sex (males)	0.19 \pm 0.08	0.03	0.35	0.018
	Context (female-male)	-0.18 \pm 0.07	-0.31	-0.05	0.008
	Context (broadcast)	-0.19 \pm 0.06	-0.31	-0.08	0.001
Number of bouts per sequence	Intercept	1.54 \pm 0.07	1.39	1.68	<0.001
	Context (female-male)	-0.35 \pm 0.09	-0.54	-0.16	<0.001
	Context (broadcast)	-0.89 \pm 0.10	-1.10	-0.69	<0.001
Presence of concurring behaviours	Intercept	0.32 \pm 0.87	-1.88	3.10	0.71
	Context (female-male)	-5.41 \pm 2.24	-11.42	-2.60	0.02
	Context (broadcast)	-6.16 \pm 2.19	-12.16	-3.32	0.005
Mean interval	Intercept	-0.50 \pm 0.09	-0.68	-0.32	<0.001
	Sex (males)	0.31 \pm 0.08	0.17	0.46	<0.001
	Context (female-male)	0.34 \pm 0.08	0.18	0.50	<0.001
	Context (broadcast)	0.26 \pm 0.08	0.11	0.41	<0.001

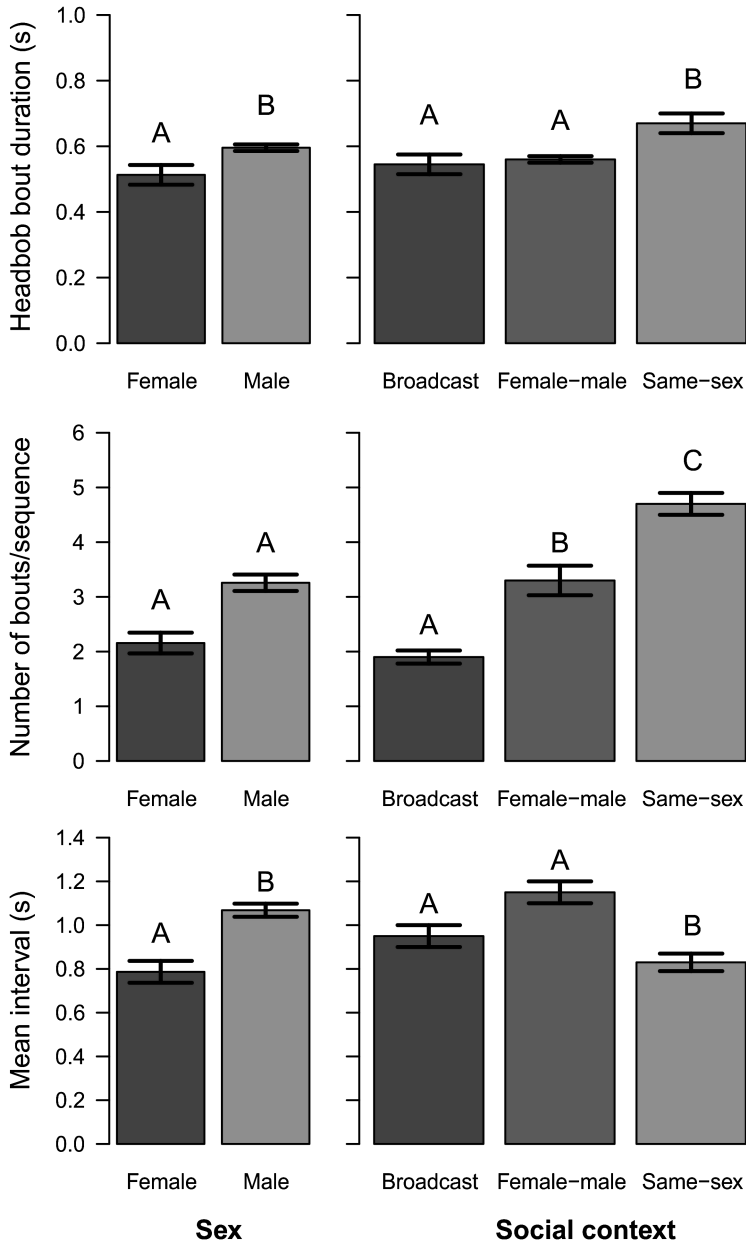


Figure 3. Effect of sex and social context in mean headbob bout duration, the number of bouts per sequence, and mean interval, showing standard errors. Means with the same letter are not significantly different ($P > 0.05$).

also significant (Tukey's post hoc: $z = 5.77$, $P < 0.0001$; fig. 3).

The presence of concurring behaviors was determined significantly by social context only (table 1). In presence of a same-sex conspecific, gular expansion, lateral compression and, back arching were more frequent than in female-male

context (Tukey's post hoc: $z = 2.42$, $P = 0.04$) or broadcast context (Tukey's post hoc: $z = -2.81$, $P = 0.01$); however, there were no differences between the latter two contexts (Tukey's post hoc: $z = 0.58$, $P = 0.83$). More than a half (74%) of the headbobs displayed in same-sex interactions included these concur-

ring behaviours, whereas they were rare during female-male interactions (4%) and broadcast context (3%).

Mean interval was influenced by sex and social context (table 1). Males performed sequences with larger intervals (1.07 ± 0.03 s) than females (0.79 ± 0.05 s; fig. 3). Same-sex context generated sequences with shorter intervals (0.83 ± 0.04 s) than female-male context (1.15 ± 0.05 s; Tukey's post hoc: $z = -4.21$, $P < 0.001$) and broadcast context (0.95 ± 0.05 s; Tukey's post hoc: $z = -3.35$, $P = 0.002$); in contrast, there was not significant differences between broadcast and female-male context (Tukey's post hoc: $z = -0.75$, $P = 0.47$; fig. 3).

Form of headbobs

I registered four headbob bouts (see Terminology in Methods section for more detail). While headbob bouts A and B are composed of three units, bout C is composed of two units and bout D by one unit (fig. 4).

Headbob bout A was the most frequently observed, being registered in the 38.8% of total bouts ($n = 45$; $\sigma^3 = 37$, n bouts = 169; $\sigma^3 = 8$, n bouts = 15). The bout A is characterized by a U1 of lower amplitude and longer duration (1.81 ± 0.10 mm, 0.22 ± 0.007 s) than U2 and U3, which contrarily have high amplitude and short duration (U2: 3.92 ± 0.22 mm, 0.15 ± 0.002 s; U3: 3.41 ± 0.19 mm, $0.16 \pm$

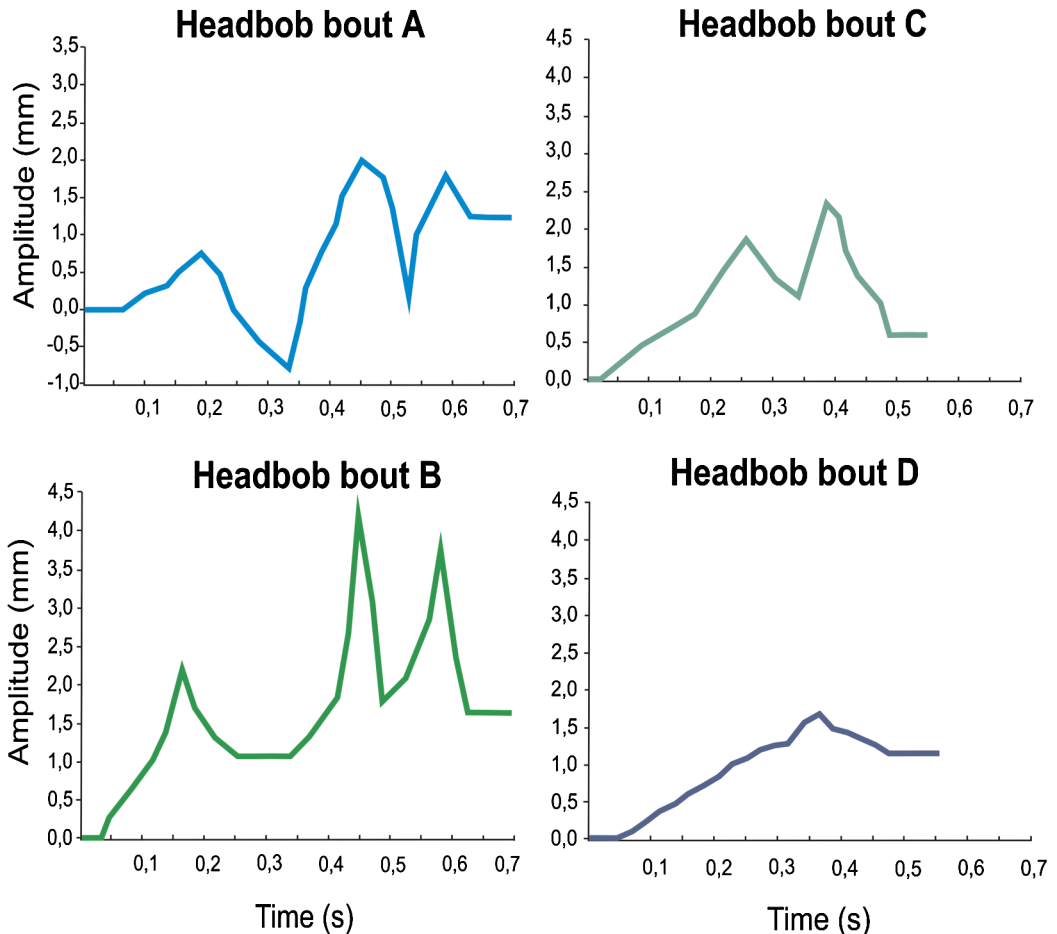


Figure 4. *Liolaemus pacha* headbob bouts forms: type A (top left), type B (bottom left), type C (top right) and type D (bottom left).

0.003 s; fig. 4). In some bouts, U1 is considerably sharper because the snout ends below the initial level (i.e., below zero, fig. 4). Duration of U2 y U3 showed a CV of 25%, this way was considered stereotyped. The mean duration of bout A was 0.54 ± 0.01 s.

Headbob bout B was also frequently displayed, being observed in the 37.4% of total bouts ($n = 39$, $\sigma = 33$, n bouts = 143; $\varphi = 6$, n bouts = 16). The form of bout B is similar than bout A, but presenting a characteristic short pause (0.10 ± 0.005 s) between U1 and U2 (fig. 4). The amplitude of U1 (2.42 ± 0.12 mm) was smaller than U2 and U3 (U2: 4.80 ± 0.19 mm, U3: 4.03 ± 0.20 mm). Duration of all units showed CV smaller than 35%, being stereotyped (U1: 0.23 ± 0.007 s, U2: 0.16 ± 0.004 s, U3: 0.17 ± 0.004 s). The mean duration of headbob bout B was 0.67 ± 0.01 s.

On the other side, headbob bout C was recorded in 8.2% of total bouts ($n = 15$; $\sigma = 6$, n bouts = 7; $\varphi = 9$, n bouts = 34), being the rarest to observe. Its form was determined by two units, with a small-amplitude and long-duration U1 (1.16 ± 0.13 mm, 0.17 ± 0.009 s), whereas U2 has a short duration and a high amplitude (1.63 ± 0.14 mm, 0.20 ± 0.011 s; fig. 4). The mean duration of headbob bout C was 0.37 ± 0.02 s. Duration of U1 and U2 showed some degree of stereotypy (35% and 36%, respectively).

Finally, headbob bout D was registered in 15% of bouts ($n = 27$; $\sigma = 1$, n bouts = 1; $\varphi = 26$, n bouts = 65). Headbob bout D is formed by one unit (2.38 ± 0.24 mm, 0.48 ± 0.04 s; fig. 4), which was not stereotyped (i.e., CV > 35%).

Effect of sex and context on headbobs bouts

The differences in bout use between sexes was significant (G Test, $G = 65.84$, $P < 0.001$). All bouts differed in their frequency among each other except for bouts A and B (A-B: $P > 0.05$, A-C: $P < 0.004$, A-D: $P < 0.001$; B-C: $P < 0.004$, B-D: $P < 0.001$, C-D: $P = 0.005$). Males perform mostly bouts A (G test, $G = 18.8$, $P < 0.001$) and B (G Test, $G = 18.8$, $P < 0.001$). Whereas, females were

characterised by the use of bouts D (G test, $G = 27.1$, $P < 0.001$). The number of lizards using bouts C did not showed differences (G test, $G = 0.27$, $P > 0.05$).

Contrarily, the differences in bout use among contexts was not significant (G Test, $G = 12.4$, $P > 0.05$). Males did not differ in the number of bouts used among contexts (G Test; Bout A: $G = 1.02$, $P > 0.05$, B = 15, SS = 10, FM = 12; Bout B: $G = 2.19$, $P > 0.05$, B = 15, SS = 8, FM = 12; Bout C: $G = 5.55$, $P > 0.05$, B = 2, SS = 4, FM = 0; Bout D: $G = 2.2$, $P > 0.05$, B = 0, SS = 0, FM = 1). Only the number of females displaying A and D bouts was significantly influenced by context, displaying these bouts more during broadcast (G Test; Bout A: $G = 8.6$, $P = 0.01$, B = 6, SS = 0, FM = 2; Bout B: $G = 0.001$, $P > 0.05$, B = 2, SS = 2, FM = 2; Bout C: $G = 2.4$, $P > 0.05$, B = 4, SS = 1, FM = 4; Bout D: $G = 20.5$, $P < 0.001$, B = 19, SS = 1, FM = 6).

With respect to structure of bouts A, sex affected significantly amplitude and duration of U2 (table 2). Males showed a higher amplitude and longer duration of U2 than females (table 3). Social context influenced significantly the amplitude of U1, U2, and U3 (table 2). Amplitude of U1, U2 and, U3 in same-sex context were higher than broadcast and female-male context (table 4; Tukey's post hoc: U1, SS-B, $z = -3.45$, $P = 0.002$; SS-FM, $z = -3.33$, $P = 0.003$; B-FM, $z = 0.42$, $P > 0.05$; U2, SS-B, $z = -2.94$, $P = 0.009$; SS-FM, $z = -2.86$, $P = 0.01$; B-FM, $z = 0.28$, $P > 0.05$; U3, SS-B, $z = -2.18$, $P > 0.05$; SS-FM, $z = -2.59$, $P = 0.03$; B-FM, $z = -0.73$, $P > 0.05$). Duration of U1, U2 and U3 were stereotyped in the three contexts, except for U1 duration in same-sex context (table 4). Duration of U1 seems to be influenced by social context (table 2); however, multiple comparisons did not quite achieve significant differences among social contexts.

Regarding the structure of bouts B, only sex influenced amplitude of U2 (table 2), with males showing significantly higher amplitudes in U2

Table 2. Analyses of headbob bouts A and B. Parameter estimates (PE \pm SE), and *P*-value of explanatory variables (sex and context), describing variation in amplitude and duration of units of headbob bouts A and B. Estimate values represent the difference between sexes and contexts, with respect to the reference values (females and same-sex context), when correspond.

Response variable	Explanatory variables	Headbob A		Headbob B	
		PE \pm SE	<i>P</i>	PE \pm SE	<i>P</i>
Amplitude					
U1	Intercept	0.49 \pm 0.10	<0.001	0.54 \pm 0.13	<0.001
	Context (broadcast)	0.35 \pm 0.10	<0.001	0.43 \pm 0.09	<0.001
	Context (female-male)	0.31 \pm 0.09	<0.001	0.27 \pm 0.05	<0.001
U2	Intercept	0.37 \pm 0.08	<0.001	0.34 \pm 0.06	<0.001
	Context (broadcast)	0.13 \pm 0.05	0.003	0.19 \pm 0.04	<0.001
	Context (female-male)	0.12 \pm 0.04	0.004	0.09 \pm 0.02	<0.001
	Sex (males)	-0.15 \pm 0.08	0.046	-0.15 \pm 0.06	0.01
U3	Intercept	0.29 \pm 0.06	<0.001	0.33 \pm 0.06	<0.001
	Context (broadcast)	0.14 \pm 0.06	0.03	0.19 \pm 0.05	<0.001
	Context (female-male)	0.18 \pm 0.07	0.01	0.14 \pm 0.03	<0.001
Duration					
U1	Intercept	4.62 \pm 0.36	<0.001	4.91 \pm 0.41	<0.001
	Context (broadcast)	0.72 \pm 0.34	0.035	0.89 \pm 0.39	0.02
	Context (female-male)	0.45 \pm 0.39	0.25	0.54 \pm 0.27	0.045
U2	Intercept	10.53 \pm 0.71	<0.001	6.45 \pm 0.47	<0.001
	Context (broadcast)			1.10 \pm 0.40	0.006
	Context (female-male)			1.33 \pm 0.35	<0.001
	Sex (males)	-3.58 \pm 0.78	<0.001		

Table 3. Amplitude (mm) and duration (s) of the headbob bout types of male and female *L. pacha*, showing *n*, mean values \pm SE and, CV% of each unit. Bold values of each unit are significantly different between sexes (*P* \leq 0.05).

Bout	Sex	<i>n</i>	Unit	Amplitude		Duration	
				Mean \pm SE	CV	Mean \pm SE	CV
A	♂	37	U1	1.81 \pm 0.11	74%	0.23 \pm 0.008	45%
			U2	4.07 \pm 0.23	73%	0.16 \pm 0.007	23%
			U3	3.55 \pm 0.20	39%	0.16 \pm 0.003	28%
	♀	8	U1	1.35 \pm 0.32	88%	0.19 \pm 0.01	29%
			U2	2.07 \pm 0.42	78%	0.10 \pm 0.02	27%
			U3	1.72 \pm 0.47	56%	0.14 \pm 0.010	28%
B	♂	33	U1	2.51 \pm 0.12	81%	0.23 \pm 0.006	32%
			U2	5.09 \pm 0.20	47%	0.17 \pm 0.004	30%
			U3	4.17 \pm 0.22	62%	0.18 \pm 0.004	31%
	♀	6	U1	1.84 \pm 0.28	44%	0.22 \pm 0.02	38%
			U2	2.68 \pm 0.30	45%	0.12 \pm 0.008	26%
			U3	2.93 \pm 0.37	50%	0.17 \pm 0.01	31%
C	♂	6	U1	2.01 \pm 0.58	70%	0.18 \pm 0.03	38%
			U2	2.68 \pm 0.56	51%	0.21 \pm 0.04	41%
	♀	9	U1	1.01 \pm 0.10	59%	0.17 \pm 0.01	36%
			U2	1.43 \pm 0.11	45%	0.19 \pm 0.01	37%
D	♂	1	U1	6.05 \pm 0.00	–	0.50 \pm 0.00	–
	♀	27	U1	2.38 \pm 0.24	81%	0.48 \pm 0.04	66%

Table 4. Amplitude (mm) and duration (s) of the headbob bout types among different social contexts, showing *n*, mean values \pm SE and, CV% of each unit. Bold values of each unit are significantly different between contexts ($P \leq 0.05$).

Bout	Context	<i>n</i>	Unit	Amplitude		Duration	
				Mean \pm SE	CV	Mean \pm SE	CV
A	Broadcast	21	U1	1.53 \pm 0.13	60%	0.19 \pm 0.007	26%
			U2	3.00 \pm 0.22	54%	0.15 \pm 0.006	31%
			U3	3.09 \pm 0.26	61%	0.17 \pm 0.007	31%
	Female-male	14	U1	1.42 \pm 0.08	57%	0.23 \pm 0.007	30%
			U2	3.15 \pm 0.16	50%	0.16 \pm 0.003	23%
			U3	2.73 \pm 0.19	69%	0.16 \pm 0.007	20%
	Same-sex	10	U1	3.18 \pm 0.33	63%	0.26 \pm 0.03	70%
			U2	7.18 \pm 0.75	63%	0.15 \pm 0.005	30%
			U3	5.59 \pm 0.59	64%	0.17 \pm 0.003	24%
B	Broadcast	17	U1	1.70 \pm 0.14	60%	0.19 \pm 0.008	27%
			U2	3.02 \pm 0.25	54%	0.14 \pm 0.007	27%
			U3	3.04 \pm 0.28	61%	0.15 \pm 0.01	39%
	Female-male	12	U1	2.01 \pm 0.13	49%	0.24 \pm 0.009	27%
			U2	4.48 \pm 0.25	41%	0.16 \pm 0.005	22%
			U3	3.27 \pm 0.26	59%	0.16 \pm 0.005	24%
	Same-sex	10	U1	3.17 \pm 0.21	54%	0.25 \pm 0.01	35%
			U2	6.08 \pm 0.31	41%	0.18 \pm 0.007	35%
			U3	5.19 \pm 0.34	55%	0.20 \pm 0.005	22%
C	Broadcast	6	U1	1.13 \pm 0.17	96%	0.15 \pm 0.01	45%
			U2	1.46 \pm 0.19	83%	0.17 \pm 0.007	25%
	Female-male	8	U1	1.18 \pm 0.15	64%	0.18 \pm 0.01	32%
			U2	1.67 \pm 0.16	46%	0.20 \pm 0.02	40%
	Same-sex	1	U1	0.81 \pm 0.00	–	0.17 \pm 0.00	–
			U2	2.06 \pm 0.00	–	0.20 \pm 0.00	–
D	Broadcast	19	U1	2.24 \pm 0.28	79%	0.49 \pm 0.05	67%
	Female-male	7	U1	2.64 \pm 0.44	82%	0.46 \pm 0.06	63%
	Same-sex	1	U1	6.05 \pm 0.00	–	0.50 \pm 0.00	–

than females (table 3). U1, U2, and U3 amplitudes were affected by social context, registering the same-sex context the highest amplitudes (table 4; Tukey's post hoc: U1, SS-B, $z = -4.83$, $P < 0.001$; SS-FM, $z = -5.73$, $P < 0.001$; B-FM, $z = 1.88$, $P > 0.05$; U2, SS-B, $z = -0.18$, $P < 0.001$; SS-FM, $z = -4.84$, $P < 0.001$; B-FM, $z = 2.56$, $P = 0.02$; U3, SS-B, $z = -3.83$, $P = 0.0004$; SS-FM, $z = -4.42$, $P < 0.001$; B-FM, $z = 1.07$, $P > 0.05$). U1 duration would be influenced by context (table 2); however, I did not find differences between the contexts. Duration of U2 was also influenced by context (table 2) with same-sex context showing the longest U2 duration (table 4; Tukey's post hoc: SS-B, $z = -2.76$, $P = 0.01$; SS-FM, $z = -3.77$, $P < 0.001$;

B-FM, $z = -0.56$, $P > 0.05$). U3 duration was not affected either by sex or context (table 2). Duration of U1, U2 and U3 were stereotyped in the three contexts, except for U3 duration in broadcast context (table 4).

Neither the sex nor social context influenced the structure of bouts C and D ($P > 0.05$; table 4; Supplementary table S1).

Discussion

Few studies have evaluated sexual differences of the structure and frequency of visual displays, possibly due to the fact that females of most species of lizards make fewer displays than males and they are more difficult to observe (Carpenter and Ferguson, 1977). As expected,

the results showed sexual differences in the frequency of headbob displays and in the type of headbob bouts used. Males head-bobbed more frequently than females, and also, they differ in the type of bout they used. Males displayed significantly more often bouts A and B, whereas females performed usually bouts D. Higher frequencies of headbob displays were also found in this species (Halloy, 2012) and in other lizards species as well (e.g., Martins, 1991; Radder et al., 2006). In the same way, sexual differences were also reflected in the structure of sequences; accordingly, males made sequences involving more headbobs bouts with longer duration and intervals than females. Also, these intersexual differences were in the structure of bouts types A and B, mainly in the amplitude and duration of some of its units. These results provide the first evidence that headbob structure for *L. pacha* presents clearly a sexual variation. In other lizard species, there have been found sexual differences in the structure of their headbob displays. For instance, female *Anolis extremus* and *A. grahami* produced significantly more units per display than males (Macedonia and Clark, 2003); whereas Jenssen et al. (2000) found sexual differences in total duration of display type B of *A. carolinensis*. The differential use of headbob might reflect the different forces acting on each sex. On one hand, male *L. pacha* are territorial and home range size is related positively to the number of females they include (Robles and Halloy, 2009, 2010). Thus, I hypothesised that males may experience higher intrasexual selection in an attempt to increase their territories, which also influence the access to females. In contrast, females did not overlap with each other, thus they might be under minimal intrasexual selection, as was also suggested for *A. carolinensis* (Jenssen et al., 2000). Therefore, male *L. pacha* would play the most active role in signalling to other males as well as to females.

Social context had a strong influence on visual displays of *L. pacha*. It has been found that in same-sex and female-male contexts, lizards

performed significantly more headbobs compared to broadcast context. In same-sex context, the sequences were characterized by including a high number of headbob bouts, larger and longer bouts and, short intervals. Another important factor was the co-occurrence of behaviours such as lateral compression, back arching, and gular expansion, which were exclusive of same-sex context; thus, suggesting that the information they make available, could only be relevant to other male receivers. This finding agreed with previous studies, where these behaviours were suggested to make more complex the visual display (Ord et al., 2001); in addition, they may function as size indexes and as honest indicators of fighting abilities (Brandt, 2003; Husak, 2004; Osborne et al., 2013). A study performed in *Uta stansburiana* determined that the threat posture of lizards can act as a quality handicap, advertising the endurance capacity of displaying lizards (Brandt, 2003). In the same way, rates of lateral displays in *Crotaphytus collaris* are a conventional signal of motivation to attack (Husak, 2004). Headbobs displayed in same-sex interactions would allow a preliminary assessment by rivals, reducing the associated costs with aggressive encounters, such as injuries, energy expenditure and exposure to predators (Dawkins and Krebs, 1978; Van Dyk and Evans, 2008; Briffa, 2014). Thus, I hypothesised that *L. pacha* visual displays performed in male-male interactions, which consist in headbobs, lateral compressions, back arching and, gular expansion, might constitute a multicomponent signal. During agonistic encounters, these complex signals may facilitate rival assessment, increase the accuracy of assessment and the amount of information, and, improve signaller detection (Partan and Marler, 2005; Candolin, 2003). Further study in standardized experimental conditions of the association between agonistic behaviour and each visual signal, would help to understand the variation and the information that carry the signals.

At the other extreme, broadcast and female-male context were characterized by a short duration and low amplitude headbob bouts, and short intervals. These contexts were only different in the number of bouts per sequence which was higher in female-male interactions than in broadcast context. Those similarities suggest that both contexts may have the same function and headbobs produced in broadcast context would also mediate intersexual signalling (e.g., Decourcy and Jenssen, 1994; Baird, 2013). I suggest that headbobs given during the absence of an audience may actually signal to the opposite sex over long distances. Whereas headbobs performed in the close proximity of the opposite sex, which characterised female-male context, may trigger courtship when the probability of mating is high. Similarly, a study made in *Crotaphytus collaris* found that high display frequencies given in broadcast context were related with courtship frequencies, suggesting that broadcast displays play a prominent role in the advertisement to females (Baird, 2013). Therefore, future studies may consider more factors such as locomotion, posturing, number of females in the male's home range, among others, in order to evaluate whether both contexts are different.

Previously, *Liolaemus pacha* had been considered as a lizard performing double headbob bouts (Halloy, 1996). However, using more modern techniques which allowed to analyse and quantify in detail the structure of headbob displays, I found that *L. pacha* made four different forms of headbob bouts, categorized as type A and B (triple; see Vicente and Halloy, 2015), C (double) and D (simple). Martins et al. (2004) described the headbob bouts for other *Liolaemus* and noted that several species share a common pattern, for example, *L. pseudoanomalus*, *L. cuyanus*, *L. loboii*, *L. monticola* and *L. pictus* made also triple headbob bouts; however, bout structure was not quantified. Probably, whether a more accurate measurement technique is used, bouts might differentiate to each other and new patterns might

be obtained. The headbob bout of *Liolaemus lemniscatus* roughly resembles *L. pacha* bout, which consists in a low amplitude headbob, a short pause and two high amplitude headbobs (Labra et al., 2007). However, comparison of structure parameters must be made carefully because they were experimentally measured only for male-male interactions. It is hypothesised that congeneric species tend to differ in signal parameters used for intraspecific communication hence, facilitating species recognition (e.g. Ord and Stamps, 2009; Macedonia et al., 2013). *Liolaemus ramirezae*, which is sympatric with *L. pacha*, shows a different bout pattern (Vicente and Halloy, 2016a), which may facilitate species recognition at a distance and may minimize costly identification errors. Further studies about the form and structure of headbob bouts of sister taxa of *L. pacha* are needed, using objective measurement techniques as they will allow generating genus comparisons and predictions in an ecological and evolutionary framework.

The analysis of the headbob bouts of *L. pacha* showed that amplitude of headbob bouts A and B were highly variable. This variation could be partly explained by the significant effect of sex and/or social context had on amplitude and duration of the different units of these bouts. Similar results were found in males of *L. lemniscatus* in which all components of the amplitude showed great variability (Labra et al., 2007). In opposite way, duration of most units of bouts A and B were stereotyped, with just a few exceptions (e.g. U1 duration of bout A in males and in same-sex context and, U3 duration of bout B). The stereotypy found in duration might indicate that the temporal pattern of headbob bouts could signal the species identity. Similar results have been described by Rothblum and Jenssen (1978) for *Sceloporus undulatus hyacinthinus* (Phrynosomatidae) in which the headbob display type B showed a high degree of stereotypy between individuals from the same population, suggesting that would signal the species. The results should clearly explain the hypothesis that the different

units of bouts A and B might sequentially combine forming a multicomponent visual signal in which each unit might have non-redundant informational content (Hebets and Papaj, 2005; Partan and Marler, 2005). Headbob bouts A and B might signal sex, social context and possibly species identity, offering the advantage of transferring more information per unit of time. The role of each unit should be further evaluated in controlled experiments.

The structure of headbobs bouts C and D were not influenced by either the sex or the social context and also, their structure showed great variability, except for the duration of some units which reveals stereotypy. Bouts C could be individual variations of bouts A and B, based on the low number registered. However, for bouts D, the results of this study are not conclusive to assign them a function. Moreover, bouts D were mostly performed by females during broadcast and female-male contexts. So, I suggest three possible hypotheses which need to be tested in future studies. The first one is that headbob bouts might show signs of ontogenetic variation. Considering that there have been observed in the field juvenile *L. pacha* performing only bouts D and none of the other types of bouts (NSV pers. obs.), it is possible that bouts D could be a precursor of the adult bout form, obtained by the addition of units (e.g. Roggenbuck and Jenssen, 1986; Lovern and Jenssen, 2003). As a second hypothesis, I suggest that bouts D might be functioning as a submissive or appeasement signal, indicating nonaggressive intentions by juveniles and females, and inhibiting the likelihood to being attacked, especially for males (e.g. Ligon, 2014; Van Dyk and Evans, 2008). Finally, headbob bouts D displayed in broadcast context may function as a pursuit-deterrent signal (e.g. Leal and Rodríguez-Robles, 1997) indicating to a predator that they are aware of the predator's presence and can escape if attacked (e.g. Leal and Rodríguez-Robles, 1997; Font et al., 2012).

The results of this study highlight the complexity that can be found in lizard's visual signals. The striking similarities shared by *Liolaemus* and *Sceloporus* in the use and the structure of headbobs suggest that they could be examples of convergent evolution and, they might have been subjected to the same evolutionary pressures (Martins et al., 2004). Headbob displays might be the result of complex interactions among several forces, such as the environment, the signal content (i.e. the information being conveyed by the signal), the receiver sensory system, and natural and sexual selection (e.g. Fleishman, 1988; Ord et al., 2001; Ossip-Klein et al., 2013; Ossip-Drahos et al., 2016; Pruett et al., 2016). *Liolaemus* lizards also used chemical cues for intra- and interspecific communication (Labra, 2011; Vicente and Halloy, 2016b, 2017; García-Roa et al., 2016, 2017) and some species exhibit striking colour patterns. This way, using multimodal signals, some species may respond flexibly by turning on and off different signal components in different social and physical contexts (e.g. Hews et al., 2011; Martins et al., 2015). A recent study has found that *Liolaemus* showed an evolutionary trade-off between visual and chemical signals, where species with a reduced number of precloacal pores performed a high number of visual displays (Ruiz Monachesi, comm. pers.). However, species like *L. pacha* did not show this inhibition, instead, a dominance of chemical modality was found (Vicente and Halloy, 2017). Therefore, additional studies that investigate how selection acts on visual and chemical signals of *Liolaemus*, as well as how they interact, are highly encouraged, because they will enable a fuller understanding of the evolution of signal diversity.

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