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Arm-wave display in a *Liolaemus* lizard

Natalin S. Vicente

Instituto de Herpetología, Unidad Ejecutora Lillo (UEL), Fundación Miguel Lillo, CONICET. San Miguel de Tucumán, Tucumán, Argentina.

Lizards show a great variety of visual displays. Among them, arm-waving is a behaviour that has received little attention and its role is still controversial. Here, I analyse the arm-waves of *Liolaemus pacha* lizards in their natural habitat with the aim of determining their function. Arm-waving was performed by both sexes, usually with the ventral body surface in contact with the ground. Furthermore, it was more frequent when alone, and during female-male interactions. The results of this study are suggestive but not conclusive regarding the possible function of this behaviour.

Keywords: communication; predator-prey interaction; reptiles; social signal; submissive; visual display

Identifying the role and the information-content of a signal can be challenging. In lizards, while some signals like dewlap displays (Nicholson et al., 2007; Driessens et al., 2015; Ingram et al., 2016), headbob displays (Macedonia et al., 2013; Ossip-Klein et al., 2013; Ossip-Drahos et al., 2018; Vicente, 2018) and colour patterns (Bastiaans et al., 2013; Klomp et al., 2016; 2017; Pérez i de Lanuza et al., 2014; Pérez i de Lanuza & Font, 2016) have been the focus of many studies, other behaviours have received less attention. This is the case of arm-waving, also known as foot-shakes or circumduction (sensu Carpenter & Ferguson 1977).

Arm-waves consist of the movement of both front arms (singly or alternately), which are raised and rotated in a circular or undulating motion (Carpenter & Ferguson, 1977). Arm-waving is shown in a variety of contexts and could, therefore, have different functions. For instance, some arm-waves are social signals, functioning as aggressive or submissive signals (Van Dyk & Evans, 2008; Woo & Rieucau, 2012). During male-male interactions, agamid lizards perform fast-waves combined with headbobs that are interpreted as signals of dominance status or aggression (Brattstrom, 1971; Van Dyk & Evans, 2008). However, when arm-waves are displayed at slow speed they function as appeasement or submissive signals (e.g. Woo & Rieucau, 2013). Arm-waves can also have a pursuit-deterrent function (Cooper et al., 2004; Cooper, 2010; Font et al., 2012). Pursuit-deterrent signals can inform the predator that it has been detected, or that the signaller would be difficult or costly to capture (Hasson, 1991; Caro, 2005; Cooper, 2010). Finally, alternative functions have been proposed including removing a foot from contact with a hot substrate, maintaining individual distance, or inducing predators to move, revealing their location (Schall, 1974, Magnusson, 1996; Cooper et al., 2004).

Arm-waving has been described in lizards of the families Agamidae (e.g. Brattstrom, 1971; Ord et al., 2002; Van Dyk & Evans, 2008), Lacertidae (e.g. Font et al., 2012), Teidae (e.g. Baird et al., 2003; Cooper et al., 2004), Dactyloidae (Jenssen, 1979), Iguanidae (Distel & Veazey, 1982), Phrynosomatidae (Carpenter, 1967) and, Liolaemidae (Halloy & Castillo, 2006). Specifically, for the genus *Liolaemus*, two types of arm-waves, depending on the type of movement, have been described: one-arm forelimb displays and two-arm forelimb displays (Halloy & Castillo, 2006). *Liolaemus* two-arm wave displays are performed with the body in contact with the substrate, and consist of the lizard lifting both arms simultaneously and/or alternatively, similar to the butterfly and crawl stroke in swimmers (Fig. 1). However, their function is still unknown (Halloy & Castillo, 2006). In one-arm forelimb displays, the lizard lifts one arm up and down; these displays have been interpreted to have a role in territorial signalling. In the present study, I analyse 52 two-arm-wave displays of *Liolaemus pacha* with the aim of determining their function.

I made eight field trips, three during 2012 (October to December), three in 2013 (October to December), and two in November 2014 and 2015 to Los Cardones, located 20 km East from Amaicha del Valle, Department of Tafi del Valle, Province of Tucuman, Argentina (26°40´1.5´´S, 65°49´5.1´´W). The site is located at 2725 m above sea level on the western slope of Sierras Calchaquíes. The field trips lasted two to five days, and I made observations from 10:00 h until 16:00 h, a period adequate for observing social interactions in this species (Vicente, unpublished data). I walked along the study area (approximately 1 ha) in a fixed direction, approaching lizards at a slow speed (i.e. slow walking). I videotaped adult lizards at an average distance of 4 m, to minimise interference, using a digital camcorder (Sony Handycam HDR-Cx290). I used a focal animal sampling rule (Martin & Bateson 2007) such that each focal lizard was recorded during 15 min or until it went out of sight. As lizards were not captured and marked, and to avoid

Correspondence: Natalin Vicente (natalinvic@gmail.com)

Figure 1. Photograms extracted from a video recording of a displaying *L. pacha* lizard performing an arm-waving display. Numbers shown correspond to the respective frame.

recording the same individual twice, I started sampling each day from different points through the area and walking in different directions. Individuals with natural marks were recorded only once.

I analysed videotapes from 350 individuals (total of 13 h and 41m) and identified sequences in which the lizards performed arm-waves. The sequences of interest were cut from the original video, using .avi or .m2ts format videos (full-HD) with a resolution of 25 frames/second. I used the software TRACKER (Brown, 2009) for frame by frame analysis. In total, videotapes were obtained of 10 one-arm and 42 two-arm-wave displays. I recorded the sex and context (alone, male-male, and male-female interactions; for a detailed description of social contexts see Vicente, 2018). In this study, the context alone corresponds to those arm-waves displayed by lizards apparently alone, which might include arm-waves directed to an undetected receiver. Additionally, I classified the posture of the displaying lizard according to a scale ranging from zero to three (Fig. 2).

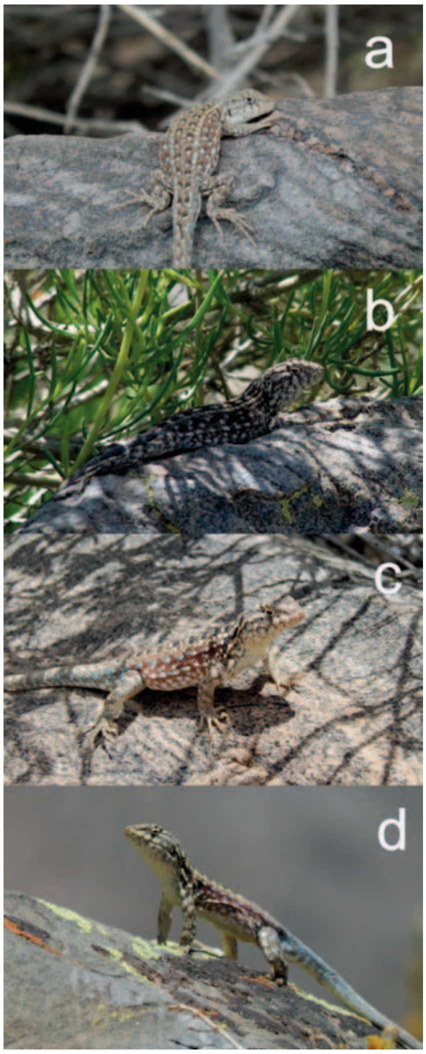

Figure 2. Examples of the four postures (0-3) described for *L. pacha*. The posture 0 is characterised by the complete ventral surface in contact with the substrate including throat and head **(a)**. Posture 1 involved the head and throat contactless with the substrate **(b)**. Posture 2 is characterised by the belly partially in contact with the substrate and the arms partially extended **(c)**. Posture 3 is determined when the belly is fully exposed and the arms fully extended **(d)**.

Table 1. GLM Analysis of arm-waves duration. Parameter estimates (PE ± SE), and *p*-value of explanatory variables (sex and context) describes variation in arm-wave duration. Estimate values represent the difference between sexes and contexts, with respect to the reference values (females and alone), when corresponding.

Response Variable	Explanatory variables	PE ± SE	*p*
Arm-wave duration	Intercept	3.62 ± 0.09	< 0.001
	Sex (males)	0.02 ± 0.11	> 0.05
	Context (female-male)	0.09 ± 0.11	> 0.05
	Context (male-male)	-0.01 ± 0.17	> 0.05

Table 2. Counts of arm-waves among contexts according to the following variables: laterality, orientation to the observer, quantity of arms used, posture, association with movement, and presence of headbobs.

		Alone	Male-Female interaction	Male-Male interaction	N total
Laterality	Left arm	5	9	3	17
	Right arm	21	12	2	35
Orienta-tion to the observer	Orientated	15	9	3	27
	Non-orientated	11	12	2	25
Quantity of arms	One arm	6	4	0	10
	Two arms	20	17	5	42
Posture	Zero	16	11	2	29
	One	6	7	1	14
	Two	4	3	2	9
	Three	0	0	0	0
Movement	Stationary	13	11	3	27
	Movement	13	10	2	25
Headbobs displayed	With	7	11	4	22
	Without	19	10	1	30

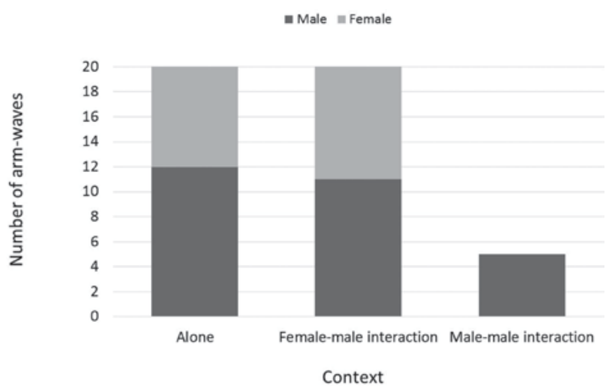

Figure 3. Bar plot showing the number of arm-waves performed by male and female *L. pacha* among the three contexts considered: alone, female-male interaction, male-male interaction.

I estimated the percentage of occurrence of arm-waving and the coefficient of variation (CV) for the arm-wave duration, considering that a CV of less than 30 % is stereotyped (Lehner, 1998). Then, for each arm-wave display I measured: a) arm-wave duration (seconds), b) lateralisation, determined as the type of arm that initiated the behavior (left or right hand), c) orientation to the observer, whether the arm that initiated the display was the one closer to the observer (oriented or non-oriented), d) movement, if lizards moved from one position to another before or after the arm-wave (movement or stationary), e) quantity of arms used, if lizards displayed with one or both arms (one or two), f) posture (0-3) and, g) presence of headbobs (presence or absence).

I evaluated the effect of sex and social context on the duration of arm-waving with a Generalized Linear Model (GLM), with duration as a response variable, and sex and social context as explanatory variables. The model was fitted using a negative binomial distribution because duration was transformed as a discrete variable and it also showed overdispersion (Logan, 2010). The differences in the frequency of lateralisation, orientation, movement, quantity of arms used, posture, and concurrence of headbobs between sexes and among contexts were estimated using Chi-square tests. I used $p \leq 0.05$ as the cut-off for statistical differences. All values are shown as mean ± SE.

Arm-waves in *L. pacha* are not a common behaviour; only 14.8 % of lizards showed this display (lizards videotaped = 350; arm-waves = 52). Duration of arm-waves was not stereotyped (37.09 ± 1.79 ds, CV = 34.7 %), and it was not influenced by sex (GLM, $p > 0.05$, Table 1; $n = 24$, 36.13 ± 2.23 ds; males $n = 28$, 37.93 ± 2.75 ds) or context (GLM, $p > 0.05$; alone context: $n = 26$, 35.23 ± 2.08 ds; female-male interaction: $n = 21$, 39.24 ± 3.58 ds; male-male interaction: $n = 5$, 36.13 ± 2.50 ds). Arm-waving was statistically more frequent in the alone context ($n = 26$) and female-male interaction ($n = 21$) than in male-male interactions ($n = 5$; Chi-square test, 13.79, df = 2, $p = 0.001$). Arm-waving frequency was not statistically different between males ($n = 28$) and females ($n = 24$; Chi-square test, 0.31, df = 1, $p > 0.05$; Fig. 3).

Arm-waves were performed and initiated more often with the right hand ($n = 35$, Chi-square test, 6.23, df = 1, $p = 0.01$) than with the left hand ($n = 17$; see Table 2 for differences among contexts). Lizard arm-waves oriented to an observer ($n = 25$) were performed at the same frequency as non-oriented displays ($n = 27$, Chi-square test, 0.08, df = 1, $p > 0.05$). Arm-waves associated with movement ($n = 25$) were performed at the same frequency as stationary ones ($n = 27$, Chi-square test, 0.08, df = 1, $p > 0.05$). Most arm-waves were displayed with both arms ($n = 42$, Chi-square Test, 19.69, df = 1, $p < 0.001$), and in a few occasions with one arm ($n = 10$). Posture 0 is the one adopted more often for performing arm-waves ($n = 29$, Chi-square Test, 12.81, df = 2, $p = 0.002$), while posture 1 ($n = 14$) and 2 ($n = 9$) were used less. No lizard used posture 3. Arm-waving was more often displayed without ($n = 32$) than with headbobs ($n = 20$, Chi-square test, 2.77, df = 1, $p > 0.05$).

The results of this study are suggestive but not conclusive regarding the potential functions of arm-waving. Arm-waving was displayed equally by both sexes and it was most frequently displayed in the contexts of alone and female-male interaction. Arm-waves could function as submissive signals. Most of the arm-waves were displayed with the ventral surface completely in contact with the substrate, head down, and in two cases with eyes closed, which can be considered as a submissive posture (Carpenter & Ferguson, 1977; Labra et al., 2007; Hamilton et al., 2013). Finally, arm-wave display orientation to the observer, which can be related to a pursuit-deterrent function (e.g. Hasson, 1991; Font et al., 2012), was not significant. Moreover, when *L. pacha* lizards were approached by an observer simulating a predator, arm-waves were not elicited (Salido & Vicente, 2019).

In conclusion, arm-waves in *L. pacha* are displayed by both sexes and their function is still unknown. Arm-waving could function as a social signal, as a submissive signal, or as a pursuit-deterrent signal. In either case, further studies are strongly needed including juveniles, and also, assessing possible differences in size and reproductive status between signaller and receiver, in order to investigate when arm-waving is elicited.

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