Herpetological Journal

Male headbob display structure in a neotropical lizard, *Liolaemus pacha* (Iguania: Liolaemidae): relation to social context

Natalin Vicente[1,2] & Monique Halloy[2]

[1]CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

[2]Instituto de Herpetología, Fundación Miguel Lillo, Tucumán, Argentina

Visual communication is important in many lizard species. One conspicuous visual signal is the headbob display, which consists of a stereotyped up and down movement of the head and/or torso. We analysed male headbob displays in the neotropical lizard, *Liolaemus pacha*, in its natural environment. Our objectives were to describe and analyse the structure and form of these headbob displays and to relate these to two social contexts: male without an apparent receiver (MA context) and male responding to another male (MM context). We measured duration of each headbob bout, its maximum amplitude, duration of intervals, number of headbob bouts and presence or absence of three modifiers (gular inflation, back arching and lateral compression). We found two types of triple headbob displays, corresponding to what has been previously reported as the challenge headbob and the broadcast headbob display. Duration and maximum amplitude were significantly greater in headbob displays in the MM context compared to the MA context. We did not observe modifiers when a male was in the MA context but there was at least one modifier present in the MM context.

Key words: headbob display, *Liolaemus pacha*, neotropical lizards, visual displays

Visual signalling is an important form of communication in many lizards, involving changes in colour and/or posture, as well as movements of the head, limbs or tail. In many species, the use of headbob displays is common and conspicuous. Headbob displays consist of stereotyped up-and-down movements of the head and/or torso (Carpenter & Ferguson, 1977). They are used in different contexts such as territorial defence, agonistic interactions and courtship (Stamps & Barlow, 1973; Carpenter & Ferguson, 1977; Martins, 1991, 1993a; Decourcy & Jenssen, 1994; Martins et al., 2004). In addition, headbob displays may provide information related to species, sex, or individual recognition (Carpenter, 1962; Hunsaker, 1962; Jenssen, 1971; Stamps & Barlow, 1973; Rothblum & Jenssen, 1978; Martins, 1991). Traditionally, headbob displays have been classified into three types:

i) "broadcast or assertion displays", which appear to be a declaration of the lizard´s presence to any other lizard in the immediate area, also occurring in absence of an audience; ii) "challenge displays", usually performed by dominant males towards other males in an agonistic context; and iii) "courtship display", produced by males to females during reproductive activity (Carpenter, 1961a, b; 1962; 1967, Carpenter & Ferguson, 1977). However, Decourcy & Jenssen (1994) stated that choosing a display label that reflects a perceived function or causation could be problematic since other functions for a display can be uncovered, and several labels could be assigned to the same display or several displays may go undifferentiated being assigned the same label. During what has been referred to challenge displays, the use of static modifiers (Jenssen, 1979) may be common. These modifiers change the appearance of the displayer and are used during encounters between males. They include inflation of the gular region, back arching and lateral compression.

Most studies on visual display communication have been conducted on *Anolis* (Jenssen 1971, 1977; Jenssen et al., 2012) and *Sceloporus* (Carpenter, 1978; Martins 1993a, b; Rothblum & Jenssen, 1978). The genus *Liolaemus* (Iguania: Liolaemidae) comprises 257 described species to date (Frost et al., 2001; Abdala & Quinteros, 2014), and offers further potential for research in visual communication (Martins et al., 2004; Halloy & Castillo, 2006; Labra et al., 2007). The genus is distributed from the Peruvian Andes to Tierra del Fuego, displaying wide variation in habitat preferences, reproductive strategies and feeding habits; little is however known about visual displays and functions (Halloy, 1996, Martins et al., 2004; Labra et al., 2007; Halloy, 2012; Halloy et al., 2013). Here, we analyse male headbob display structure in the recently redescribed *Liolaemus pacha* (Juárez Heredia et al., 2013), previously known as *L. quilmes* (Etheridge, 1993), in its natural environment. Our objectives were to describe and analyse the structure and form of its headbob displays and to compare these in relation to two social contexts in which they were given, a male in the presence of another male (MM) and a male without an apparent audience (MA).

Correspondence: Natalin Vicente (natalinvic@gmail.com)

Liolaemus pacha (Juárez Heredia et al., 2013) is a diurnal, insectivorous, and oviparous lizard (Ramirez Pinilla, 1992; Halloy et al., 2006). It shows marked sexual dichromatism, with males being more colourful than females (Juárez Heredia et al., 2013). According to Ramirez Pinilla (1992), the reproductive season occurs during the austral spring (October to December) followed by a post-reproductive season during the austral summer (January to March). The study site is located at 'Los Cardones' (26°40"1.5' S, 65°49"5.1' W, datum: WGS84; 2725 m), Tucumán province, Argentina, and it is characterised by the presence of tall cacti, low shrubs and a firm rocky substrate.

We define a lizard headbob display as a succession of ups and downs of the head, separated from subsequent displays by at least two seconds. The headbob display corresponds to what has been called a "display-action-pattern" or DAP sensu Carpenter & Grubitz (1961). Thirty-nine adult males were filmed with a digital camcorder (Sony DVD-DCR 508), in their natural environment, during October and November 2012. However, only 14 males were used in the analysis, considering those that were filmed from lateral view to obtain good quality videos. Eighteen headbob displays and three hours and thirty minutes of video recordings were obtained of which we analysed 63 headbob bouts. Active lizards were filmed between 1000 and 1700 hours, during sunny or partially cloudy days. We conducted focal observations for 15 minutes or until the lizard moved out of sight. The observer was located at approximately four metres from the focal subject to minimise interference. The observer never sampled the same area twice in order to avoid filming the same lizard multiple times. We recorded the use of static modifiers such as gular inflation, back arching and lateral compression, and the social context.

The social context was given by the presence or absence of other male lizards of the same species near the displayer. We considered two contexts: when the observer could see a second male responding to the displayer (MM context) and when the observer could not see any other male in the proximity of the displaying animal (within a 5 m radius, MA context).

Headbob displays were analysed using the software Tracker (Brown, 2009) which has a video resolution of 30 frames per second. Graphs were obtained (DAP graphs) marking the position of the snout, frame by frame, through time. Techniques used to estimate amplitude vary considerably (e.g., Stamps & Barlow, 1973; Jenssen, 1975; Rothblum & Jenssen, 1978; Macedonia & Clark, 2003; Brandt & Allen, 2004; Labra et al., 2007). We estimated the absolute amplitude using the tool "calibration stick" in the Tracker program. This tool estimated the ratio of the real head height in millimetres to the image distance in pixels between two points (Brown, 2009) independently of the distance between recordings. Because individual measurements of head height were lacking, we used the average height for adult males presented in the description of this species (Juárez Heredia et al., 2013, 8.3 mm, SD=0.8 mm). The amplitude of each headbob bout was measured taking the initial position of the snout as the point of reference.

The following variables were measured: i) duration of each headbob bout within a headbob display, ii) maximum amplitude of each headbob bout within a headbob display, iii) duration of the intervals or pauses between headbob bouts, iv) number of headbob bouts per headbob display, and; v) presence or absence of three modifiers: gular inflation, back arching and lateral compression.

To compare maximum amplitude and duration of headbob bouts and intervals between contexts we performed generalised linear mixed-effects models (GLMMs), for normal and gamma distribution when appropriate (Pinheiro & Bates, 2000; Crawley, 2007) using the software R v. 3.0.1 (R Core Team, 2013). We tested for the assumptions of normality and homogeneity of variance using Shapiro-Wilk´s and Fligner-Killeen´s tests, respectively. For duration and maximum amplitude of headbob bouts and duration of intervals, we used the nlme package (Pinheiro et al., 2013), and included the duration of headbob bouts, maximum amplitude of headbob bouts and duration of intervals as response variables. In all cases the social context was a fixed effect, and individual and headbob displays were random effects. Fixed effects influenced the mean of the response variable and random effects influenced only the variance of the response variable (Crawley, 2007). To compare the number of headbob bouts per headbob display between

Table 1. Parameter estimates±standard error (PE±SE) and *t* values from linear mixed-effects models reporting variation in duration of headbob bouts (sec), maximum amplitude of headbob bouts (mm) and duration of intervals (sec), for males of *Liolaemus pacha* without an apparent audience (MA) and in male-male (MM) contexts. Significant *p* values are shown in *italic*.

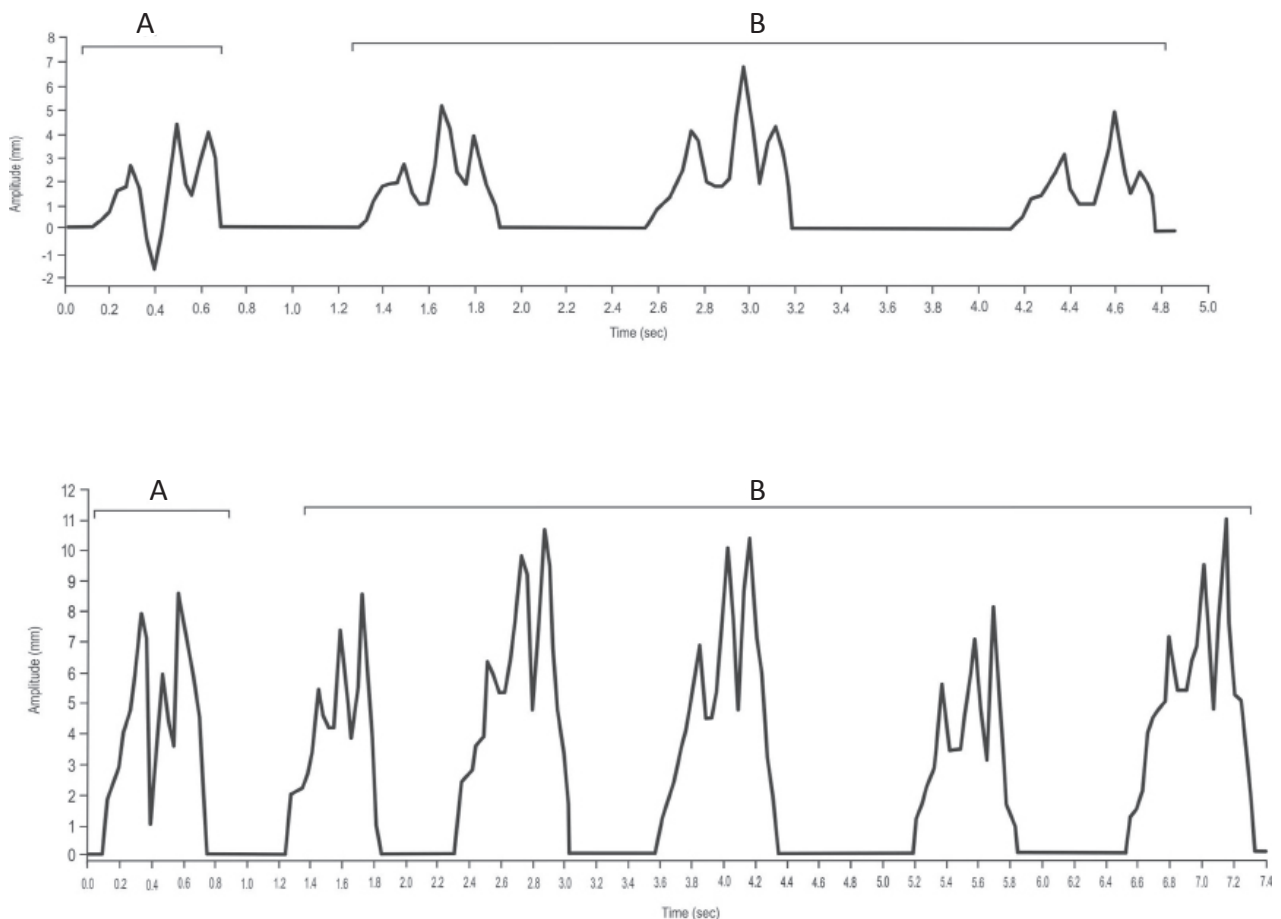| Response variable	Explanatory variable	PE±SE	*t*	*p*
Duration	MM context	0.59±0.02	29.85	*0.0014*
n=63	MA context	0.46±0.05	-4.11	
Amplitude	MM context	8.19±0.67	12.14	*0.0027*
n=63	MA context	4.76±1.58	-3.77	
Interval	MM context	1.54±0.11	12.95	0.63
n=46	MA context	1.22±0.28	-1.85	

Fig. 1. Graphic representations of the two typical headbob displays in male *Liolaemus pacha*: above, when no apparent audience could be detected; below, when another male was present (more details in the text).

contexts, we estimated averages per individual. Because they did not satisfy the assumptions of normality and homogeneity of variance, a Mann-Whitney test was conducted (Siegel & Castellan, 1988). For each headbob display, frequencies of modifiers were counted. In all cases, our alpha level was $p \leq 0.05$.

Previously, *L. pacha* was reported to perform headbob displays that included double headbob bouts (Halloy, 1996; Martins et al., 2004). However, using motion analysis software and video-recording technology we found that male headbob displays in this species included triple headbob bouts (Fig. 1). Within a headbob display we distinguished two types of headbob bouts: Type A, the head is raised up and down quickly, followed by two high amplitude up and down movements of the head, in quick succession, forming a triplet; and Type B, the head is slowly raised, followed by a pause of less than 1 second, continuing with two high amplitude headbobs (Fig. 1). In most cases (94%, 17 headbob displays), a headbob display started with a type A headbob bout, followed by one or more of type B headbob bouts.

From the 18 headbob displays (14 males), 10 occurred in the MA context and 8 in the MM context. The duration of headbob bouts were significantly greater in the MM context, lasting 0.59±0.02 sec, compared to 0.46±0.05 sec in the MA context (p=0.001, Table 1). Considering maximum amplitude, we found that in the MM context, the snout rose significantly higher (on average 8.19±0.67 mm), than in the MA context (on average 4.76 (±1.58 mm) (p=0.003, Table 1). The duration of intervals was

longer in the MM context (1.54±0.11 sec) compared to the MA context (1.22±0.28 sec). However, these were not significantly different (p>0.05, Table 1).

Taking the number of headbob bouts per headbob display into account, we observed more headbob bouts per headbob display in the MM than in the MA context (Mann-Whitney, W=43, p=0.012, $n1$=7, $n2$=7). On average, a headbob display in the MA context included almost three headbob bouts versus almost five when the context was MM.

Static modifiers were not used in the MA context. However when a male was in the presence of another male (MM context), at least one modifier was used in all of the headbob displays (100%). Gular inflation occurred in 86% of cases, followed by back arching (57%) and lateral compression (29%).

The *L. pacha* headbob display is similar in general form to that described for other species of *Liolaemus* (*L. pseudoanomalus*, *L. cuyanus*, *L. loboi*, *L. monticola*, *L. pictus*: Martins et al., 2004; *L. lemniscatus*: Labra et al., 2007). In the study of Martins et al. (2004), although a good approximation of typical headbob displays in several species of *Liolaemus* is shown, their structure was not quantified. In Labra et al. (2007), however, the male headbob structure of *L. lemniscatus* was quantified in a male-male context in experimental conditions. As in *L. pacha*, the species performed triple headbob bouts, although specific parameters are difficult to compare since different methods of measurement were used.

51

We found that the pattern of headbob displays in *L. pacha* (headbob bout type A at the beginning of the display followed by one or more headbob bouts type B) remain similar regardless of social context. Headbob bout Type A is characterised by a sharp drop which marks the beginning of the display, possibly to attract the attention of potential recipients of the display. In some lizards of the genus *Anolis*, wide variation in the introductory part of a display precedes the species-specific headbob (Jenssen, 1971; Stamps & Barlow, 1973; Fleishman, 1992). Because the detailed headbob display structure of females still needs to be studied, we cannot make such generalisations for *L. pacha*.

Despite rather stereotyped displays observed we can distinguish two general types of headbob displays occurring in a different context (MA or MM). The headbob display given in the MM context was characterised by longer durations and higher amplitudes of headbob bouts, a greater number of headbob bouts per headbob display, and the presence of static modifiers. The headbob display given in the MA context was characterised by shorter durations and lower amplitudes of headbob bouts, fewer headbob bouts per headbob display, and the absence of static modifiers. These two contexts corresponded to what has traditionally been referred to "challenge" and "broadcast" headbob display, respectively (Carpenter, 1961a, b; 1962; 1967; Martins 1993a). Modifiers were not used in any of the MA contexts whereas at least one of these was present in any of the MM contexts. Modifiers made the display more complex, changing the appearance of the displayer and possibly the information that was being conveyed. Considering the three modifiers separately, inflation of the gular region was most common, followed by the arched back and finally the lateral compression. These may occur separately, but they usually followed this sequence.

REFERENCES

Abdala, C.S. & Quinteros, A.S. (2014). Los últimos 30 años de la familia de lagartijas más diversa de Argentina. Actualización taxonómica y sistemática de Liolaemidae. *Cuadernos de Herpetología* 28 (2), 55–82.

Brandt, Y. & Allen, J.R. (2004). Persistence of individually distinctive display patterns in fatigued side-blotched lizards (*Uta stansburiana*). *Behavioral Ecology and Sociobiology* 55, 257–265.

Brown, D. (2009). Computer program TRACKER video analysis and modeling tool. Version 4.81. Available from: <http://www.cabrillo.edu/~dbrown/tracker/>.

Carpenter, C.C. (1961a). Patterns of social behavior in the desert Iguana, *Dipsosaurus dorsalis. Copeia* 4, 396–405.

Carpenter, C.C. (1961b). Patterns of social behavior of Merriam´s Canyon lizards (*Sceloporus merriami* - Iguanidae). *The Southwestern Naturalist* 6, 138–148.

Carpenter, C.C. (1962). Patterns of behavior in two Oklahoma lizards. *The American Midland Naturalist* 67, 132–151.

Carpenter, C.C. (1967). Aggression and social structure in Iguanid lizards. In *Lizard Ecology*: *a symposium*, 87–105. Milstead, W.W. (ed.). Columbia, Missouri: University of Missouri Press.

Carpenter, C.C. (1978). A comparative display behavior in the genus *Sceloporus* (Iguanidae). *Milwaukee Public Museum Contributions in Biology and Geology* 18, 1–71.

Carpenter, C.C. & Grubitz, G. III. (1961). Time-Motion Study of a Lizard. *Ecology* 42, 199–200.

Carpenter, C.C. & Ferguson, G.W. (1977). Variation and evolution of stereotyped behavior in reptiles. In *Biology of the Reptilia: Ecology and Behaviour A,* 335–554. Gans, C. & Tinkle, D.W. (eds.). New York: Academic Press.

Crawley, M.J. (2007). *The R book*. England: John Wiley & Sons Ltd.

Decourcy, K.R. & Jenssen, T.A. (1994). Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Animal Behaviour* 47, 251–262.

Etheridge, R. (1993). Lizards of the *Liolaemus darwinii* complex (Squamata: Iguania: Tropiduridae) in Northern Argentina. *Bolletino Museo Regionale di Scienze Naturali*, Torino, 11, 137–199.

Fleishman, L.J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of Anoline lizards and other vertebrates. *The American Naturalist* 139, S36–S61.

Frost, D.R., Etheridge, R., Janies, D. & Titus, T.A. (2001). Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). *American Museum of Natural History, Novitates* 3343, 1–38.

Halloy, M. (1996). Behavioral patterns in *Liolaemus quilmes* (Tropiduridae), a South American lizard. *Bulletin of the Maryland Herpetological Society* 32, 43–57.

Halloy, M. (2012). Visual display variations in neotropical lizards, *Liolaemus quilmes* (Iguania: Liolaemidae): relation to sex and season. *Herpetological Journal* 22, 265–268.

Halloy, M. & Castillo, M. (2006). Forelimb wave displays in lizard species of the genus *Liolaemus* (Iguania: Liolaemidae). *Herpetological Natural History* 9, 127–133.

Halloy, M., Robles, C. & Cuezzo, F. (2006). Diet in two syntopic neotropical lizard species of *Liolaemus* (Liolaemidae): interspecific and intersexual differences. *Revista Española de Herpetología* 20, 47–56.

Halloy, M., Robles, C., Salica, M.J., Semhan, R., Juárez Heredia, V. et al. (2013). Estudios de comportamiento y ecología de lagartijas de los géneros *Liolaemus* y *Phymaturus* (Iguania: Liolaemini). *Cuadernos de Herpetología* 27, 15–26.

Hunsaker, D. III. (1962). Ethological isolating mechanisms in the *Sceloporus torquatus* group of lizards. *Evolution* 16, 62–74.

Jenssen, T.A. (1971). Display analysis of *Anolis nebulosus* (Sauria, Iguanidae). *Copeia* 1971, 197–209.

Jenssen, T.A. (1975). Display repertoire of a male of *Phenacosaurus heterodermus* (Sauria: Iguanidae). *Herpetologica* 31, 48–55.

Jenssen, T.A. (1977). Evolution of anoline lizard display behavior.

American Zoologist 17, 203–215.

Jenssen, T.A. (1979). Display modifiers of *Anolis opalinus* (Lacertilia: Iguanidae). *Herpetologica* 35, 21–30.

Jenssen, T.A., Garrett, S. & Sydor, W.J. (2012). Complex signal usage by advertising male green anoles (*Anolis carolinensis*): A test of assumptions. *Herpetologica* 68, 345–357

Juárez Heredia, V., Robles, C. & Halloy, M. (2013). A new species of *Liolaemus* from the *darwinii* group (Iguania: Liolaemidae) Tucumán province, Argentina. *Zootaxa* 3681, 524–538.

Labra, A., Carazo, P., Desfilis, E. & Font, E. (2007). Agonistic interactions in a *Liolaemus* lizard: structure of head bobs displays. *Herpetologica* 63, 11–18.

Macedonia, J.M. & Clark, D.L. (2003). Headbob Display structure in the naturalized *Anolis* lizards of Bermuda: sex, context, and population effects. *Journal of Herpetology* 37, 266–276.

Martins, E.P. (1991). Individual and sex differences in the use of push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Animal Behaviour* 41, 403–416.

Martins, E.P. (1993a). Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Animal Behaviour* 45, 25–36.

Martins, E.P. (1993b). A comparative study of the evolution of *Sceloporus* push-up displays. *The American Naturalist* 142, 994–1018.

Martins, E.P., Labra, A., Halloy, M. & Thompson, J.T. (2004). Large-scale patterns of signal evolution: an interspecific study of *Liolaemus* lizard headbob displays. *Animal Behaviour* 68, 453–653.

Pinheiro, J.C. & Bates, D.M. (2000). *Statistics and Computing. Mixed-Effects Models in S and S-Plus*. New York, Springer-Verlag.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & the R Development Core Team. (2013). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-113.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org/>.

Ramirez Pinilla, M.P. (1992). Ciclos reproductivos y de cuerpos grasos en dos poblaciones de *Liolaemus darwinii* (Reptilia: Sauria: Tropiduridae). *Acta Zoologica Lilloana* 42, 41–49.

Rothblum, L. & Jenssen, T.A. (1978). Display repertoire analysis of *Sceloporus undulatus hyacinthinus* (Sauria : Iguanidae) from south-western Virginia. *Animal Behaviour* 26, 130–137.

Siegel, S. & Castellan, N.J. Jr. (1988). *Nonparametric Statistics for the Behavioral Sciences*, 2nd ed. New York: McGraw-Hill.

Stamps, J.A. & Barlow, G.W. (1973). Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). *Behaviour* 47, 67–94.