Visual display variations in neotropical lizards, *Liolaemus quilmes* (Iguania: Liolaemidae): relation to sex and season

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Visual displays in lizards are used to convey information related to species, sex, reproductive state, context and even individuality. Two displays that have been reported are headbobs, up and down movements of the head, and forelimb waves, circular movements of the forelegs, the former display generally being more conspicuous and frequent than the latter. Here I investigated these two displays in an iguanian neotropical species, *Liolaemus quilmes*, from northwestern Argentina. One-hundred-and-fifteen males and females were filmed over six years, in their habitat, during their daily activities. Headbob and forelimb display rates were compared between males and females and between the reproductive and post-reproductive seasons. In addition, the relation between headbob display rates and home range size was explored. As reported for many iguanian lizards, males made significantly more headbob displays than females in both the reproductive and post-reproductive seasons. They also performed more forelimb waves than females in both seasons. Finally, no correlation was found between headbob display rates and home range sizes in any of the two seasons, suggesting that although headbob displays have been associated with territorial defence it does not seem to be associated with the size of the defended area.

Key words: forelimb waves, headbobs, *Liolaemus quilmes*, neotropical lizards, visual displays

Visual displays are characteristic of many lizard species and may be part of elaborate species-specific communication systems (Carpenter, 1978; Fox et al., 2003). One of these displays is the headbob (consisting of stereotyped up and down movements of the head, Carpenter & Ferguson, 1977; Halloy, 1996; Martins et al., 2004). They may contain information related to territorial defence, courtship, sex, social context and even individual identity (e.g., Carpenter & Ferguson 1977; Martins 1991, 1993). Another important visual display is the forelimb wave display (circular movements of one or two of the forelegs). It has been reported in several *Liolaemus* species (Halloy & Castillo, 2006) and agamid species (e.g., Carpenter et al., 1970; Brattstrom, 1971; Gibbons, 1979; Ord et al., 2002) among others. Its function may vary between an overt challenge, to conflict, to an appeasement signal (Halloy & Castillo, 2006, and references therein). Other displays that may be observed but were not included in the present study are occasional lateral movements of the tail and mouth gapings. Here I investigate headbob and forelimb wave displays in a neotropical lizard species, *Liolaemus quilmes*, Liolaemidae, from northwestern Argentina. The objectives of this study were (i) to identify the presence of both displays in male and female *L. quilmes*, and (ii) to compare display rates in males and females during the reproductive and post-reproductive seasons. I expected males to perform more headbob displays than females as reported in many iguanian species (e.g., Carpenter & Ferguson, 1977; Martins, 1991), and that male display rates would be higher during the reproductive season because of the association of display and courtship behaviour or agonistic encounters between males (e.g., Carpenter & Ferguson, 1977; Carpenter, 1978; Halloy, 1996; Fox et al., 2003; Martins et al., 2004). It is not clear what results might be expected in forelimb wave displays since it is not as common as the headbob display, and its function is still being discussed (Halloy & Castillo, 2006). The final objective (iii), is to determine if a relationship between headbob display rates and home range sizes exists. Headbob displays are associated with territorial defence (e.g., Carpenter & Ferguson, 1977; Halloy, 1996; Martins et al., 2004). Therefore, I expected a positive relationship between headbob display rate and home range size.

The *Liolaemus* genus (Liolaemidae) belongs to an iguanian group of lizards from South America (Frost et al., 2001), ranging from Peru and Bolivia in the north to Tierra del Fuego in southern Argentina (Cei, 1986; Etheridge & De Queiroz, 1988). *Liolaemus quilmes* belongs to the *darwinii* complex (Etheridge, 1993) and is found in northwestern Argentina, between altitudes of 1600 m and approximately 3000 m, in arid to semi-arid regions of the phytogeographic province of the Monte (Cei, 1993; Etheridge, 1993) and the Prepuna (Halloy et al., 1998; for phytogeographic provinces, see Cabrera & Willink, 1980). *Liolaemus quilmes* is active during the austral spring and summer. It is a diurnal, oviparous (Ramirez Pinilla, 1992), insectivorous lizard (Halloy et al., 2006), with marked sexual dichromatism, males being more colourful than females (Etheridge, 1993). The activity period includes the reproductive season (October to December), and the post-reproductive season (January to March; Ramirez Pinilla, 1992). The study site was located at Los Cardones (26°40'1.5" S, 65°49'5.1" W, datum: WGS84; 2725 m), in the Tucumán province, Argentina, well within the distribution of the species (Etheridge, 1993). It is characterized by firm substrate, scattered large rocks, low shrubs, and tall cacti.

Sixty-one males and 54 females were filmed with a Sony Hi8 video camera (CCD-TR600), within their home ranges, in spring and summer, from October to March, between 1999 and 2005. The lizards were filmed when active, generally on sunny to partially cloudy days, between 1000 and 1700 hours. They were filmed in their natural surroundings from a distance of 4 to 5 metres. The lizards were habituated to the presence of an observer

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Table 1. Average headbob and forelimb wave display rates (X)±one standard error (SE) of male and female *Liolaemus quilmes*, filmed a minimum of 15 minutes each. *n*=number of lizards filmed during the reproductive and post-reproductive seasons, from October to March, between 1999 and 2005. See text for further details.

	Reproductive seasons		Post-reproductive seasons	
HEADBOBS	*n*	X±SE	*n*	X±SE
males	38	102.1±12.1	23	65.0±17.4
females	25	36.8±8.7	29	6.5±3.3
FORELIMB WAVES				
males	38	45.1±4.7	23	34.4±6.7
females	25	18.0 ± 3.3	29	24.3 ± 5.1

due to regular censuses performed three times a day, four to five days a month, which required walking slowly throughout the study area (e.g., Halloy & Robles, 2002, 2003; Robles & Halloy, 2009, 2010). Between these censuses, I searched and filmed any lizard that was active for a minimum of 15 minutes or until lost to the camera, after which I would search another lizard and start filming once again. I knew the identification of the lizards and their home ranges from previous and current studies on this species. The lizards had been marked with a unique combination of two coloured beads attached at the base of the tail with a surgical steel monofilament strand (Fischer & Muth, 1989; Halloy & Robles, 2002) and their home ranges had been calculated using the minimum convex polygon method based on a minimum of 9 sightings (CALHOME, Home Range Analysis Program, MS-DOS, Version 1.0, 1994; e.g., Halloy & Robles, 2002; Robles & Halloy, 2009, 2010).

A total of 59.78 hours were obtained, divided into 27.33 h for males and 11.06 h for females in springs (October to December, corresponding to the reproductive season, Ramirez Pinilla, 1992) and 9.41 h for males and 11.98 h for females in summers (January to March, corresponding to the post-reproductive season, Ramirez Pinilla, 1992). These close to 60 hours of filming included only the video-samples for which I had a minimum of 15 minutes per lizard. Lizards filmed less than 15 minutes were not used in the data analysis.

Videos were analyzed in the laboratory, recording all occurrences of headbob and forelimb wave displays for each individual. Male and female headbob and forelimb display rates (based on the number of headbobs or forelimb wave displays, per individual per hour) were compared using the Kruskal-Wallis analysis of variance (InfoStat, free version 2008) to test for differences between sexes and seasons. The Spearman rank-order correlation test was used to examine the relationship between headbob display rates and home range sizes (Siegel & Castellan, 1988).

Both headbob and forelimb wave displays were performed by male and female *L. quilmes* during the reproductive and post-reproductive seasons. When comparing headbob display rates, with respect to sex and season, the result was very significant ($H=47.40$; $p<0.0001$, $df=3$, Table 1). Males displayed significantly more than females in both seasons. They also displayed significantly more during the reproductive than during the post-reproductive season. Females also performed significantly more headbobs during the reproductive than during the post-reproductive season.

When comparing forelimb wave display rates, with respect to sex and season, the result was also very significant ($H=19.58$; $p<0.0002$, $df=3$, Table 1). Males also performed significantly more forelimb wave displays than females during both seasons but males or females were not significantly different when comparing seasons.

Table 2. Average home range areas (m^2) and average headbob display rates (HB) ± one standard error (X±SE) per reproductive and post-reproductive seasons, based on individuals filmed a minimum of 15 minutes each, having areas with a minimum of 9 sightings (Halloy & Robles, 2002; Robles & Halloy, 2009, 2010). *n*=number of lizards filmed during the reproductive and post-reproductive seasons, from October to March, between 1999 and 2005. r_s=Spearman rank-order correlation coefficient (Siegel & Castellan, 1988). NS: not significant.

AREAS & HEADBOBS (REPRODUCTIVE SEASONS)					
	n	Areas (X±SE)	HB (X±SE)	r_s	*p*
males	19	107.3±18.9	120.6±15.1	0.16	NS
females	4	10.7±3.9	25.2±21.0	-0.60	NS
AREAS & HEADBOBS (POST-REPRODUCTIVE SEASONS)					
	n	Areas (X±SE)	HB (X±SE)	r_s	*p*
males	6	94.6±21.5	62.1±17.4	- 0.09	NS
females	7	20.1±5.0	2.2±1.1	0.15	NS

Finally, no correlation was found between headbob display rates and home range sizes, in males and females, during the reproductive or the post-reproductive season (Table 2).

Overall, male *L. quilmes* performed significantly more headbob displays than females regardless of season. This has been reported in many other iguanian species (e.g., Carpenter & Ferguson, 1977; Martins, 1991). Headbobs typically occur during courtship or during agonistic encounters between males (e.g., Carpenter & Ferguson, 1977; Carpenter, 1978; Halloy, 1996; Fox et al., 2003; Martins et al., 2004). Thus, I expected male *L. quilmes* to perform more headbobs than females and that they would perform this display more often during the reproductive than during the post-reproductive season (courtship and territory defence occurring largely during the reproductive season, e.g., Carpenter & Ferguson, 1977; Carpenter, 1978; Halloy, 1996; Fox et al., 2003; Martins et al., 2004).

With respect to forelimb wave displays, males performed more forelimb waves than females during both seasons. If this display is related to signalling conflict and/or appeasement (Halloy & Castillo, 2006, and references therein), forelimb wave displays should occur at higher rates in males than females considering male-male agonistic encounters and the need to approach and possibly appease females. When comparing males or females, with respect to seasons, there were no significant differences.

Finally, no correlation was found between headbob display rates and home range size. This suggests that although headbob displays are associated to territorial defence (e.g., Carpenter & Ferguson 1977; Martins 1991, 1993), headbob display rate may not be related to the size of the territory.

Acknowledgements: I thank the numerous field assistants who have accompanied me to the field site throughout the years, Recursos Naturales y Suelos of the Tucumán province for permission to work in the field (permits 394-98, 95-2000, and 539-RN), and PIP-CONICET (4966/97; 2668/01), CIUNT, National University of Tucumán (G218) and Fundación Miguel Lillo, Tucumán, for financial support.

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Accepted: 22 June 2012