Herpetologica, 63(1), 2007, 11–18

AGONISTIC INTERACTIONS IN A *LIOLAEMUS* LIZARD: STRUCTURE OF HEAD BOB DISPLAYS

Antonieta Labra[1,3,4], Pau Carazo[2], Ester Desfilis[2], and Enrique Font[2]

[1]*Programa de Fisiología y Biofísica, Instituto de Ciencias Biomedicas, Facultad de Medicina, Universidad de Chile, Chile*
[2]*Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia, España.*

Abstract: Males from different iguanian lizard species engage in frequent visual signaling during agonistic interactions, mainly by displaying head bobs. We conducted a detailed study of the structure of head bob displays mediating male agonistic interactions in *Liolaemus lemniscatus* lizards. We staged pair-wise encounters where one male, the intruder, was placed in the terrarium of a conspecific male, the resident. During these interactions, males exhibited only one type of head bob display made up of three distinct units: a low amplitude bob (unit 1), a brief pause (unit 2), and two consecutive high-amplitude bobs (unit 3). Head bob displays occurred singly or as a part of a bout, with a mean number of head bob displays per bout of two. Total head bob display duration was stereotyped. The highest inter-individual variation (duration and amplitude) was recorded for unit 3, suggesting that this unit may provide information about the individual identity of the sender. Winners of interactions performed more head bob displays than losers, and these were composed of units of longer duration and higher amplitude than head bob displays exhibited by losers. Although preliminary, our results suggest that, in *L. lemniscatus*, head bob displays may facilitate opponent assessment by conveying information about individual fighting ability, motivation, or dominance status.

Key words: Agonistic interactions; Head bobs; *Liolaemus*; Opponent assessment; Tongue flicks

Visual signals are used in many different social contexts, including territory advertisement, courtship, and intrasexual interactions (Bradbury and Vehrencamp, 1998). One of the most characteristic visual displays used by iguanian lizards is the head bob, which consists of discrete, sequentially predictable up-and-down motions of the head or the anterior part of the lizard's body (see Carpenter, 1978; Hunsaker, 1962). Head bob displays convey information about individual identity (e.g., Brandt, 2003; Carpenter, 1978; Crews, 1975; Jenssen, 1977; Martins, 1993), age (Lovern and Jenssen, 2003), sex (Jenssen et al., 2000; Macedonia and Clark, 2003), and the social context of the displaying animal (e.g., Bloch and Irschick, 2006; DeCourcy and Jenssen, 1994; Ferguson, 1971; Jenssen et al., 2000; Orrell and Jenssen, 2003). Moreover, different studies suggest that head bob displays exhibited during agonistic encounters are honest signals that provide reliable information about the sender. Hence, the rate of head bobbing is positively related to endurance capacity (Leal, 1999; Perry et al., 2004), and more head bobs are displayed by larger (Tokarz, 1985), territorial (Watt and Joss, 2003), or dominant individuals (Baird and Sloan, 2003; Perry et al., 2004; Pratt et al., 1992). In addition, individuals can enhance the information conveyed by head bobs by using behavioral modifiers (Harper, 2006; Jenssen, 1979), such as dewlap extension, body compression, leg extension, tail waving, and arm-waving (see Martins et al., 2004; Ord et al., 2002).

Despite a substantial literature devoted to the study of head bob displays, our understanding of the structure and function of these signals has two major biases. First, most available studies have been descriptive in scope, reporting just temporal patterning and unit composition of head bobs and/or the rate at which they are produced (e.g., Ord and Evans, 2003). However, other aspects of head bob structure, such as the absolute amplitude of head bob units, have been relatively neglected (but see Brandt and Allen, 2003; Jenssen et al., 2000). Second, most studies have been conducted with species of the genera *Anolis* (Polychrotidae) and *Sceloporus* (Phrynosomatidae) (Carpenter, 1978; Jenssen, 1977; Martins, 1993). In contrast, *Liolaemus* (Liolaemidae) lizards, the second most diverse iguanid genus, with over 160

---

[3] Present Address: Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, Oslo, N-0316. Norway.

[4] Correspondence: e-mail, antonieta.labra@bio.uio.no

species distributed in South America (Cei et al., 2003; Harmon et al., 2003), have received very little attention. *Liolaemus* lizards exhibit a variety of visual displays, including head bobs and forelimb displays, but very little is known about their structure and function (Halloy, 1996; Halloy and Castillo, 2002; Labra and Niemeyer, 2004; Martins et al., 2004; Trigosso-Venario et al., 2002). Our aim is to provide a detailed description of the structure of head bob displays exhibited during agonistic male-male interactions by *Liolaemus lemniscatus*, a species that relies heavily on visual signals to communicate (Fox and Shipman, 2003).

Materials and Methods

Study Species, Collection and Husbandry

Liolaemus lemniscatus is a saxicolous, insectivorous (Núñez et al., 1989), and oviparous species (Donoso-Barros, 1966). Its biology and social behavior have been poorly studied despite it being very abundant in central Chile (Jaksic and Núñez, 1979). It is a territorial and aggressive species, in which male home ranges do not overlap more than 20%, while female home ranges overlap less than 6% (Fox and Shipman, 2003). During intrasexual agonistic interactions, both in natural and laboratory conditions, *L. lemniscatus* frequently exhibit aggressive behaviors such as fights, chases, bites, tail waving and head bobs (Fox and Shipman, 2003). Moreover, the detection of chemical signals from a conspecific is enough to trigger some of these displays, including head bobs (Labra and Niemeyer, 2004).

Sixteen *L. lemniscatus* adult males of similar size (snout–vent length, SVL, $\bar{x}$ ± SEM = 49.3 ± 0.5 mm; mass = 3.3 ± 0.1 g) were collected in the Mediterranean scrublands of Codegua, south of Rancagua (Chile), during the 2002 austral spring. Lizards were transported to the laboratory (Universidad de Valencia, Spain) and were kept in a temperature-controlled room in glass terraria (40 × 20 × 30 cm). The enclosures had a substrate of 1–2 cm of fine gravel, a shelter, and a 40-w incandescent bulb suspended ca. 20 cm above the floor of the terrarium as a source of heat and light, with a 14L:10D photoperiod, mimicking the mid-summer conditions of *L. lemniscatus'* natural habitat. Lizards had constant access to water (provided in avian water dispensers) and were fed 2–3 mealworms (*Tenebrio molitor* larvae) dusted with multivitamin powder (Nekton-MSA) three times weekly. Experimental subjects had at least one month to acclimate before testing, and interactions were conducted within five months of their arrival to the laboratory during their normal activity season (i.e., September–April).

Staged Encounters

We staged pair-wise encounters (n = 8) between residents (i.e., terrarium owners) and intruders (i.e., lizards introduced into the terrarium of another lizard). Males were paired randomly, and the mean size and mass differences between members of pairs was 1.86 ± 0.59 mm (range 0–4 mm) and 0.33 ± 0.1 g (range 0–0.8 g), respectively. To avoid pseudoreplication, each male participated in only one interaction. Just before the beginning of a trial, we removed the shelter and the water dispenser from the resident's terrarium, and added a second 40-w incandescent bulb to provide enough illumination for videotaping. Temperatures inside the experimental terraria oscillated between 34 and 37 C, which is in the range of the selected body temperature of *L. lemniscatus* (Labra and Bozinovic, 2002). Meanwhile, the intruder was removed from his terrarium and placed in a cloth bag. Encounters began by placing the intruder into the resident's terrarium and lasted 15 min. As in previous studies, winners and losers of contests could be easily established based on their behavior (e.g., Perry et al., 2004). Losers exhibited conspicuous submissive behaviors such as dorsoventral flattening, eye closing, and tail waving (for descriptions of behaviors see Carpenter and Ferguson, 1977). Therefore, we decided to perform separate analyses for losers and winners.

Data Acquisition

We recorded the number of head bob displays performed by both lizards during contests using a portable computer equipped with JWatcher 0.9 event-recorder software

(Blumstein et al., 2000). We also recorded the number of tongue flicks, an index of chemical exploratory behavior (e.g., Burghardt, 1970; Mason, 1992), because chemical signals are used by *L. lemniscatus* in different social contexts (Labra and Niemeyer, 2004). Additionally, we videotaped both resident and intruder head bob displays *ad libitum* (sensu Lehner, 1996) using a color video camera (Panasonic WV-F-15H5) mounted on a tripod and a portable VCR (Panasonic AG-7450) in an attempt to obtain as many display sequences as possible for each contestant. Videotapes were played back and display-action-pattern (DAP) graphs were plotted using standard procedures (Jenssen, 1971). Briefly, displays were projected field by field against a ruled paper using a VCR deck (Panasonic AG-7330) which allowed a temporal resolution of 50 fields per second (0.02 s increments).

Variation in the amplitude of display units is a potentially important feature of the visual display (Brandt and Allen, 2003). However, because direct measurements of absolute vertical displacement may be biased by variation in the distance between the camera and the subject, we proceeded as follows to obtain amplitude values of the head bob units. We measured the distance from the center of the nostril to the center of the eye on the same side of the head (hereafter NED = nostril eye distance) in all individuals. We also measured the NED of the projected image of the displaying lizard in a completely lateral view (pNED), which, along with the actual NED of each lizard, allowed us to transform relative vertical displacement values to absolute values [absolute value (mm) = measured value (mm) × NED/pNED].

Data Analyses

Bout length.—Males of *L. lemniscatus* exhibited only one type of head bob display in these interactions, which occurred singly or as a part of a bout. We used 886 head bob displays performed by 14 males to calculate the minimum interval separating successive bouts — the bout criterion interval (BCI) — by conducting a standard log-survivorship analysis. Because two lizards failed to produce head bobs, they were discarded from the analysis. We plotted the cumulative frequency of gap lengths (on a logarithmic scale) against gap length (on a linear scale) and determined the BCI as the break point of the line (Lehner, 1996). Head bob displays separated by intervals shorter than this interval were considered as belonging to the same bout.

DAP graph analyses.—Data were obtained from 178 head bob displays. Each lizard contributed 5–35 head bob displays. Three of the 14 lizards contributed less than five head bob displays (an arbitrarily set criterion) and were discarded from the analysis. We divided DAP graphs into discrete units and measured duration and amplitude of each unit. Because accurate pNED measurements (see *Data Acquisition*) were not always possible, we only obtained absolute amplitude data for eight lizards.

Statistical analyses.—Descriptive statistics [i.e., mean ($\bar{x}$), standard error of the mean (SEM), and coefficient of variation (CV for small sample size, Sokal and Rohlf, 1995)] were calculated for all measured variables. Each individual contributed a single mean value. Coefficients of variation were judged unreliable when $\bar{x} < 0.1$. Following Barlow's (1968) criterion, head bob units with CVs less than 35% were considered stereotyped. Total variation in head bob display variables was partitioned into intra- and inter-individual variation (i.e., adjusted r^2) using an adjusted estimate of the proportion of variation due to inter-individual differences for small samples (Font and Kramer, 1989).

We used Wilcoxon signed-ranks test to analyze differences between opponents (i.e., winners vs. losers) in the number of head bob displays and tongue flicks, and Spearman rank correlation to test for a correlation between number of head bob displays and tongue flicks. Statistical analyses were conducted using SPSS 12.05 software and significance for rejection of the null hypothesis was set at 0.05. Tests were corrected for experiment-wise error rate using the sequential Bonferroni correction (Holm, 1979). Although uncorrected values are given, tests reported as significant remained so after applying the Bonferroni correction. All reported probabilities are two-tailed.

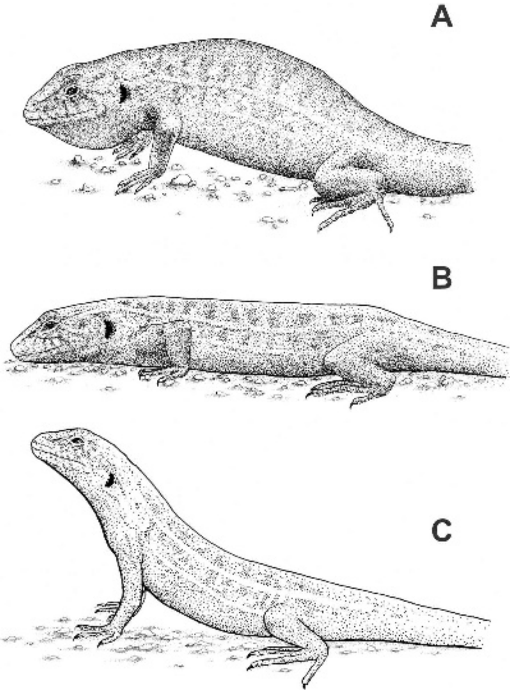

FIG. 1.—Postures observed during male-male agonistic interactions of *Liolaemus lemniscatus*. A. Throat extension, back arching, and trunk compression. B. Dorsoventral flattening. C. Two-leg raised-body posture.

RESULTS

Male-Male Interactions

Agonistic interactions usually were preceded by a period of variable duration (0.5–4 min) during which both lizards remained motionless. Action typically started with one lizard head bobbing steadily and exhibiting throat extension, lateral trunk compression (Fig. 1A) and occasionally, back arching (for descriptions of behavioral units see Carpenter and Ferguson, 1977). The other lizard would respond by engaging in similar aggressive behavior, and both lizards would then approach each other until they were at close range (ca. 5–7 cm), exhibiting simultaneous lateral presentation with their heads oriented in the same (face-to-face) or in opposite (face-off) direction. During highly aggressive interactions, lizards gaped and/or assumed a four-leg raised body posture, which was often followed by circling. Mutual lateral presentation was always followed by one lizard charging and biting the other, which would roll over, disengage, and flee. Mutual charging and biting was only observed in one encounter. Bites did not draw blood or cause any observable injury.

Escalated interactions continued until one of the contestants assumed a flattened posture by dorsally depressing the body and pressing it against the substrate (Fig. 1B). This posture frequently was accompanied by eye closing and, occasionally, by tail waving. Following these submissive behaviors, dominant individuals assumed a distinctive two-leg raised body posture by extending the forelegs, often resulting in the lizard standing on the tips of its forefingers (Fig. 1C). This posture, commonly displayed in the absence of other aggressive modifiers (e.g., throat extension and trunk compression), was adopted early by some dominant individuals in encounters where the other contestant did not engage in full-blown aggressive behavior (i.e., four-leg raised posture, throat extension, trunk compression), and was accompanied by frequent head bobbing. Head bob displays exhibited during aggressive behavior typically were accompanied by extension and flexion of the forelegs, particularly during the four-leg raised posture. However, these foreleg movements were barely discernible when lizards displayed while assuming the flattened or the two-leg raised posture.

There was a significant correlation between the numbers of tongue flicks and head bob displays performed by each individual lizard ($r_s = 0.681$, $n = 14$, $P = 0.007$), and winners made more head bob displays ($T = 27$, $n = 7$, $P = 0.032$) and tongue flicks ($T = 28$, $n = 7$, $P = 0.016$) than losers did. Winners made 102.28 ± 18.58 head bob displays and 54.57 ± 10.50 tongue flicks, while losers made 29 ± 10.08 head bob displays and 9 ± 3.05 tongue flicks. Intruders won four out of seven combats.

Display Structure, Stereotypy, and Sources of Display Unit Variance

Males of *L. lemniscatus* exhibited only one type of head bob display during agonistic encounters (Fig. 2). From the log-survivorship analysis, we obtained a bout criterion interval of two seconds. According to this criterion, 75% of head bob displays occurred

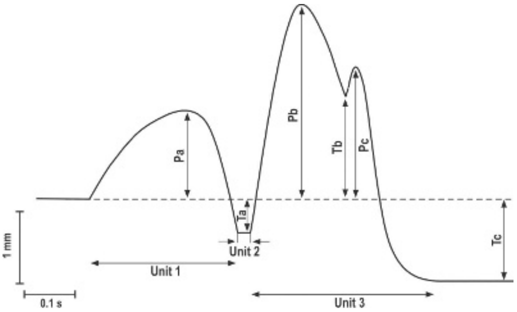

FIG. 2.—Schematic representation of a head bob display of *Liolaemus lemniscatus*, exhibited in male-male agonistic interactions. P=peak, T=trough.

in bouts of between two and 13 head bob displays, and the most frequent bout consisted of two head bob displays. The mean number of head bob displays per bout was 1.9 ± 0.16.

The typical head bob display exhibited by males is shown in Fig. 2. It consists of a low amplitude bob (unit 1), a brief pause (unit 2), and two consecutive high-amplitude bobs (unit 3). Total head bob display duration was highly stereotyped and most of its variance can be attributed to intra-individual variation (see adjusted r^2, Table 1). Unit duration also was stereotyped for units 1 and 3, but not for unit 2. On the other hand, while inter-individual variability contributed little to variance in the duration of units 1 and 2, it accounted for nearly 50% of the variance observed for the duration of unit 3 (Table 1). None of the amplitude variables were stereotyped (CV > 35%), although troughs tended to show more variability than peaks (Table 2). Inter-individual variability accounted for most of the observed variance in the amplitude of peak b, trough b, and peak c (Table 2), all of which are components of unit 3.

Descriptive statistics indicated quantitative differences in the head bob displays of winners and losers (Tables 1 and 2). Results suggest that winners exhibited head bob displays with longer duration, especially in units 1 and 3 (Table 1), and with higher amplitude of peak a, than losers (Table 2). The CV values of amplitude variables of unit 3 components (i.e., peak b, trough b and peak c) also were higher in losers than in winners.

DISCUSSION

Behaviors exhibited by male *L. lemniscatus* during agonistic interactions were similar to those previously described for other lizard taxa, including throat extension, trunk compression, and head bobs (e.g., Carpenter, 1978). Head bob displays of *L. lemniscatus* are structurally simpler and of shorter duration than those of most *Anolis* and *Sceloporus* lizards (Carpenter, 1978; Jenssen, 1978; Lovern and Jenssen, 2003) and roughly resemble those of the congeneric *L. monticola*, *L. pseudoanomalus*, *L. loboi* (Martins et al., 2004) and *L. quilmes* (Halloy, 1996). Evidence collected in different taxa indicates that congeneric species living in sympatry tend to differ in the signal patterns used for intraspecific communication (Butlin and Ritchie, 1994). Therefore, it is puzzling that the head bob pattern exhibited by *L. lemnis-*

TABLE 1.—Duration (mean ± SEM, in s) of the units comprising the head bob displays of *Liolaemus lemniscatus*, with their associated coefficient of variation (CV); r^2_{adj} corresponds to inter-individual variation. For description of display units see Fig. 2. % Dur: percent of duration, the duration of each unit as a percentage of the total duration of the display (Orrell and Jenssen, 2003). Statistics are given separately for winners and losers.

	Unit	Mean ± SEM	CV	% Dur	r^2_{adj}
Winners (n = 6)	1	0.38 ± 0.02	12.83	51.31	
	2	0.03 ± 0.01	93.89	3.88	
	3	0.34 ± 0.01	9.14	44.81	
	Sum	0.75 ± 0.03	10.08	—	
Losers (n = 5)	1	0.31 ± 0.01	10.23	48.62	
	2	0.04 ± 0.01	93.65	5.50	
	3	0.29 ± 0.02	17.93	45.88	
	Sum	0.64 ± 0.02	8.44	—	
Total (n = 11)	1	0.35 ± 0.02	15.86	50.19	0.19
	2	0.03 ± 0.01	87.78	4.55	0.28
	3	0.32 ± 0.01	14.18	45.26	0.49
	Sum	0.70 ± 0.03	12.21	—	0.16

Table 2.—Amplitude (mean ± SEM, in mm) of peaks (P) and troughs (T) measured in the head bob displays of eight male *Liolaemus lemniscatus*, with their associated coefficient of variation (CV); r^2_{adj} corresponds to inter-individual variation. For description of display variables see Fig. 2. Coefficients of variation (CV) were not calculated when means < 0.1. Statistics are given separately for winner and losers.

	Variable	Mean ± SEM	CV	r^2_{adj}
Winners ($n = 4$)	Pa	1.57 ± 0.23	30.74	
	Ta	0.10 ± 0.12	—	
	Pb	3.05 ± 0.52	36.16	
	Tb	1.60 ± 0.46	60.78	
	Pc	1.88 ± 0.32	35.97	
	Tc	0.12 ± 0.18	—	
Losers ($n = 4$)	Pa	0.86 ± 0.15	37.45	
	Ta	−0.03 ± 0.13	—	
	Pb	2.32 ± 0.99	90.72	
	Tb	1.54 ± 0.69	95.24	
	Pc	1.76 ± 0.81	97.37	
	Tc	−0.18 ± 0.15	—	
Total ($n = 8$)	Pa	1.21 ± 0.19	44.55	0.28
	Ta	0.04 ± 0.09	—	0.12
	Pb	2.68 ± 0.54	58.18	0.63
	Tb	1.57 ± 0.38	71.27	0.63
	Pc	1.82 ± 0.40	64.40	0.62
	Tc	−0.03 ± 0.12	—	0.07

catus is so similar to that described for *L. monticola*, a species that is sympatric and syntopic with *L. lemniscatus* over most of its geographic range (Donoso-Barros, 1966). However, our results must be interpreted with caution as we cannot rule out that further studies using larger sample sizes or more naturalistic testing conditions might reveal the existence of other types of head bob displays (DeCourcy and Jenssen, 1994; Orrell and Jenssen, 2003). Studies with *Anolis* lizards have reported increased variability in the introductory part of head bob displays, which may function to alert receivers to the rest of the display (i.e., alerting components; Fleishman, 1992; Jenssen, 1971). However, *L. lemniscatus* showed the highest inter-individual variation in duration and amplitude in the last unit (unit 3). This result suggests the hypothesis that unit 3 acts as an individual signature allowing individual recognition (Macedonia and Clark, 2001; Martins, 1991).

Tongue flicking is involved in the collection of chemical stimuli for Squamata (e.g., Mason, 1992), including *Liolaemus* (e.g., Labra and Niemeyer, 2004). In our study, males of *L. lemniscatus* exhibited this behavior during intrasexual interactions, as has been previously reported for this species (Fox and Shipman, 2003) and for *Gallotia galloti* lizards (e.g., Molina-Borja et al., 1998). In *L. lemniscatus*, as in *G. galloti*, winners performed more tongue flicks than losers. Interestingly, our results also showed a positive relationship between the rate of head bob displays and the rate of chemical exploration (i.e., tongue flicks), as has been reported previously for other lizard species (Molina-Borja et al., 1998; Ord et al., 2002). This relationship also has been reported at the interspecific level: Martins et al. (2004) analyzed displays performed by lizards of different *Liolaemus* species in their natural habitat and found that those exhibiting high head bob display rates also exhibited high tongue flick rates. The significance of this relationship between head bob display rate and tongue flick rate remains unclear at both the intra- and interspecific levels. This result is a clear indication that future research should focus on the interactions between different sensory modalities during communication (e.g., Partan and Marler, 1999).

Finally, our results revealed differences in the head bob displays of *L. lemniscatus* males according to whether they won or lost a contest. Winners exhibited significantly higher head bob display rates, and descriptive statistics suggest that their displays were composed of units that were longer in duration and higher in amplitude than those exhibited by losers. Although our results must be considered preliminary, they suggest that head bob displays may convey information regarding competitive ability or motivation to fight in this species (e.g., Husak, 2004). Beyond mere head bob pattern, structural characteristics of head bob displays (i.e., amplitude and duration of their units) may code functionally important information. Many questions remain open, such as whether the amplitude and duration of head bob displays are fixed individually or vary throughout agonistic encounters.

Acknowledgments.—We thank the Chilean Servicio Agrícola y Ganadero (SAG) for reptile capture and export permits (No 3842/2002) and J. Bosch for animal transportation. A.L. thanks the Generalitat Valenciana for a fellowship (CTESIN 2002/17) and the International Foundation of Science (Sweden) for grant 2933-1/2. This research was supported in part by a grant from the Spanish Ministerio de Educación y Ciencia to E.F. (CGL2006-03843/BOS). P.C. was supported by a research grant (FPU) from the Spanish Ministerio de Educación y Ciencia.

Literature Cited

Baird, T. A., and C. L. Sloan. 2003. Interpopulation variation in the social organization of female collared lizards, *Crotaphytus collaris*. Ethology 109:879–894.

Barlow, G. W. 1968. Ethological units of behavior, Pp. 217–232. *In* D. Ingle (Ed.), The Central Nervous System and Fish Behavior. The University of Chicago Press, Chicago, Illinois, U.S.A.

Bloch, N., and D. J. Irschick. 2006. An analysis of interpopulation divergence in visual display behavior of the green anole lizard (*Anolis carolinensis*). Ethology 112:370–378.

Blumstein, D. T., C. S. Evans, and J. C. Daniel. 2000. JWatcher 0.9 event-recorder. Available at http://www.eb.ucla.edu/Blumstein/danpubs.html.

Bradbury, J. W., and S. L. Vehrencamp. 1998. Principles of Animal Communication. Sinauer Associates, Sunderland, Mass.achusetts, U.S.A.

Brandt, Y. 2003. Lizard threat display handicaps endurance. Proceedings of the Royal Society of London B 270:1061–1068.

Brandt, Y., and J. R. Allen. 2003. Persistence of individually distinctive display patterns in fatigued side-blotched lizards (*Uta stansburiana*). Behavioral Ecology and Sociobiology 55:257–265.

Burghardt, G. M. 1970. Chemical perception in reptiles, Pp. 241–308. *In* J. W. Johnston, D. G. Moulton, and A. Turk (Eds.), Advances in Chemoreception, Vol. 1: Communication by Chemical Signals. Appleton-Century-Crofts, New York, New York, U.S.A.

Butlin, R. K., and M. G. Ritchie. 1994. Behaviour and speciation. Pp. 43–79. *In* P. J. B. Slater and T. R. Halliday (Eds.), Behaviour and Evolution. Cambridge University Press, Cambridge, U.K.

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., and G. W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles, Pp. 335–554. *In* C. Ganz and D. W. Tinkle (Eds.), Biology of the Reptilia: Ecology and Behaviour A. Academic Press, New York, New York, U.S.A.

Cei, J. M., F. Videla, and L. Vicente. 2003. From oviparity to viviparity: a preliminary note on the morphometric differentiation between oviparous and viviparous species assigned to the genus *Liolaemus* (Reptilia, Squamata, *Liolaemidae*). Journal of Zoology, Systematic and Evolutionary Research 41:152–156.

Crews, D. 1975. Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. Herpetologica 31:37–47.

DeCourcy, K. R., and T. A. Jenssen. 1994. Structure and use of male headbobs signals by the lizard *Anolis carolinensis*. Animal Behaviour 47:251–62.

Donoso-Barros, R. 1966. Reptiles de Chile. Universidad de Chile, Santiago, Chile.

Ferguson, G. W. 1971. Variation and evolution of the push-up displays of the side-blotched lizard genus *Uta* (Iguanidae). Systematic Zoology 20:79–101.

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. American Naturalist 139:S36–S61.

Font, E., and M. Kramer. 1989. A multivariate clustering approach to display repertoire analysis: headbobbing in *Anolis equestris*. Amphibia-Reptilia 10:331–344.

Fox, S. F., and P. A. Shipman. 2003. Social behavior at high and low elevations: environmental release and phylogenetic effects in *Liolaemus*, Pp. 310–355. *In* S. F. Fox, J. K. McCoy, and T. A. Baird (Eds.), Lizard Social Behavior. John Hopkins University Press, New York, New York, U.S.A.

Halloy, M. 1996. Behavioral patterns in *Liolaemus quilmes* (Tropiduridae), a South American lizard. Bulletin of Maryland Herpetological Society 32:54–57.

Halloy, M., and M. Castillo. 2002. Forelimb wave displays in lizards species of *Liolaemus* (Iguania: Liolaemidae). Herpetological Natural Hististory 9:127–133.

Harmon, L. J., J. A. Schulte, II., A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. Science 301:961–964.

Harper, D. G. C. 2006. Maynard Smith: Amplifying the reasons for signal reliability. Journal of Theoretical Biology 239:203–209.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

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

Husak, J. F. 2004. Signal use by collared lizard, *Crotaphytus collaris*: the effects of familiarity and threat. Behavioral Ecology and Sociobiology 55:602–607.

JAKSIC, F. M., AND H. NÚÑEZ. 1979. Escaping behavior and morphological correlates in two *Liolaemus* species of central Chile (Lacertilia: Iguanidae). Oecologia 42:119–122.

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

JENSSEN, T. A. 1977. Evolution of anoline lizard display behavior. American Zoologist 17:203–215.

JENSSEN, T. A. 1978. Display diversity in anoline lizards and problems in interpretation, Pp. 269–285. *In* N. Greenberg and D. Maclean (Eds.), Behavior and Neuroetology of Lizards. National Institute of Mental Health, Washington, D.C., U.S.A.

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

JENSSEN, T. A., K. S. ORRELL, AND M. B. LOVERN. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. Copeia 2000:140–149.

LABRA, A., AND F. BOZINOVIC. 2002. Interplay between pregnancy and physiological thermoregulation in *Liolaemus* lizards. Écoscience 9:421–426.

LABRA, A., AND H. M. NIEMEYER. 2004. Variability in the assessment of snake predation risk by *Liolaemus* lizards. Ethology 110:649–662.

LEAL, M. 1999. Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. Animal Behaviour 58:521–526.

LEHNER, P. N. 1996. Handbook of Ethological Methods. Cambridge University Press, Cambridge, U.K.

LOVERN, M. B., AND T. A. JENSSEN. 2003. Form emergence and fixation of head bobbing displays in the green anole lizard (*Anolis carolinensis*): a reptilian model of signal ontogeny. Journal of Comparative Psychology 117: 133–141.

MACEDONIA, J. M., AND D. L. CLARK. 2001. Headbob display analysis of the Grand Cayman anole, *Anolis conspersus*. Journal of Herpetology 35:300–310.

MACEDONIA, J. M., AND D. L. CLARK. 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 the push-up display by the sagebrush lizard, *Sceloporus graciosus*. Animal Behaviour 41:403–416.

MARTINS, E. P. 1993. A comparative study of the evolution of *Sceloporus* push-up displays. American Naturalist 142:994–1018.

MARTINS, M. P., A. LABRA, M. HALLOY, AND J. T. THOMPSON. 2004. Repeated large scale patterns of signal evolution: an interspecific study of *Liolaemus* lizards headbob displays. Animal Behaviour 68:453–463.

MASON, R. T. 1992. Reptilian pheromones, Pp. 114–228. *In* C. Gans and D. Crews (Eds.), Hormones, Brain and Behavior. Biology of Reptilia. The University Chicago Press, Chicago, Illinois, U.S.A.

MOLINA-BORJA, M., M. PADRON-FUMERO, AND T. ALFONSO-MARTIN. 1998. Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). Ethology 104:314–322.

NÚÑEZ, H., P. A. MARQUET, R. G. MEDEL, AND F. M. JAKSIC. 1989. Niche relationships between two sympatric *Liolaemus* lizards in a fluctuating environment: the "lean" versus "feast" scenario. Journal of Herpetology 23:22–28.

ORD, T. J., AND C. S. EVANS. 2003. Display rate and opponent assessment in the jacky dragon (*Amphibolurus muricatus*): an experimental analysis. Behaviour 140:1495–1508.

ORD, T. J., R. A. PETERS, C. S. EVANS, AND A. J. TAYLOR. 2002. Digital video playback and visual communication in lizards. Animal Behaviour 63:879–890.

ORRELL, K. S., AND T. A. JENSSEN. 2003. Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. Behaviour 140:603–634.

PARTAN, S., AND P. MARLER. 1999. Behavior: communication goes multimodal. Science 283:1272–1273.

PERRY, G., K. LEVERING, I. GIRARD, AND T. J. GARLAND. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. Animal Behaviour 67:37–47.

PRATT, N. C., A. C. ALBERTS, K. G. FULTON-MEDLER, AND J. A. PHILLIPS. 1992. Behavioral, physiological, and morphological components of dominance and mate attraction in male green iguana. Zoological Biology 11:153–163.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry—The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, New York, New York, U.S.A.

TOKARZ, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Animal Behaviour 33:746–753.

TRIGOSSO-VENARIO, R., A. LABRA, AND H. N. NIEMEYER. 2002. Interactions between males of the lizard *Liolaemus tenuis:* roles of familiarity and memory. Ethology 108:1057–1064.

WATT, M. J., AND J. M. P. JOSS. 2003. Structure and function of visual displays produced by male jacky dragons, *Amphibolorus muricatus*, during social interactions. Brain, Behavior and Evolution 61:172–183.

Accepted: 11 December 2006
Associated Editor: Troy A. Baird