

## ARTICLES

# Large-scale patterns of signal evolution: an interspecific study of *Liolaemus* lizard headbob displays

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Although many factors have been shown to influence the evolution of species recognition signals in a wide variety of taxa, it is difficult to draw general conclusions because of fundamental differences in the morphologies and ecologies of the animals considered. In this study, two morphologically and ecologically similar lizard genera (*Sceloporus* and *Liolaemus*) are used to provide replicate examples of the evolution of a complex visual display. New data on the headbob displays of 16 *Liolaemus* species are presented. As in other taxa, phylogenetic analyses show that evolutionary changes in display structure have been rapid, leaving little, if any, phylogenetic information in the display structure. Evolutionary changes in display structure also do not appear to be closely associated with any major habitat characteristics. Despite this rapid evolution, *Liolaemus* lizards produce headbob displays that are remarkably simple in structure in comparison to those produced by *Sceloporus*, perhaps compensating for lower complexity by frequent use of other visual displays such as forelimb and tail waves.

Species recognition signals are some of the most complex and diverse forms of communication and have been shaped over long periods of evolutionary time by the combined action of natural, sexual and social selection. For example, the macroevolutionary history of some signals has been influenced by the preference and physiology of signal receivers (e.g. Wilczynski et al. 2001) whereas other signals may be more closely associated with the morphology of the display producer (e.g. Prum 1998; Castellano et al. 2000; Podos 2001; Randall 2001). Other signals have been shaped by the habitats in which they occur (e.g. Marchetti 1993; Endler & Basolo 1998; Leal & Fleishman 2002) or by the requirements imposed by their information content (e.g. Couldrige & Alexander 2002;

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Shaw & Parsons 2002). Interspecific variation in most complex signals is likely to be the result of complex evolutionary interactions among several of these forces. Because the above studies were conducted on animals that differ in virtually all aspects of their biology (birds, fish, frogs, lizards, insects, etc.), it is difficult to determine whether the forces influencing signal evolution differ because of initial differences in the ancestors of each group or because of differences in the selective regimes to which each set of species was subjected. In the current study, we use animals from two genera that are morphologically and ecologically similar but phylogenetically distinct to distinguish between patterns that are unique to a particular group of animals and those that might be general properties of the evolution of communicative signals.

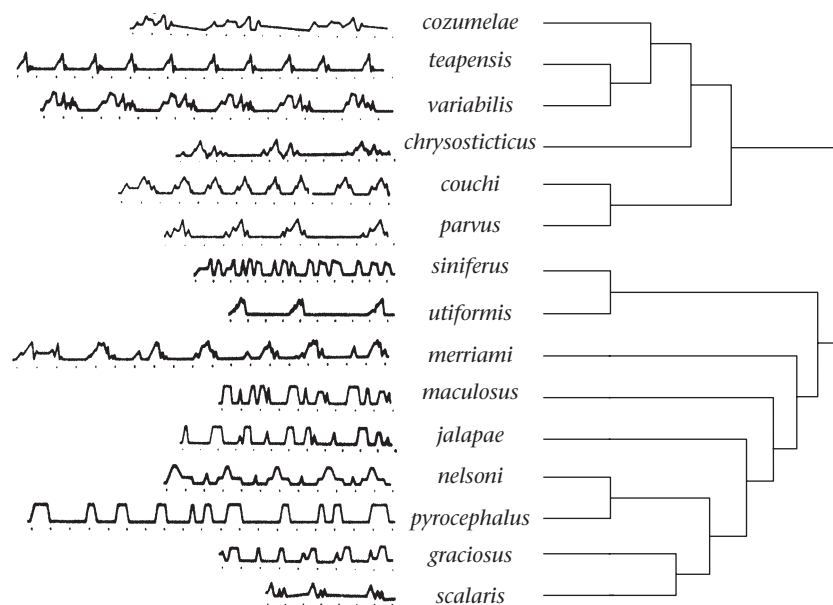
Specifically, herein, we present new interspecific data on the headbob displays of *Liolaemus* lizards, apply modern phylogenetic comparative methods to infer the evolutionary history of headbob displays in this group, and compare the result to what is already known about the evolution of headbob displays in *Sceloporus*. The lizard genera *Sceloporus* and *Liolaemus* are morphologically and

ecologically similar and have been considered a classic example of evolutionary convergence (e.g. Fuentes 1976). *Sceloporus* is a large genus of phrynosomatid lizards, consisting of approximately 90 species distributed throughout North and Central America (Sites et al. 1992; Wiens & Reeder 1997; Wiens et al. 1999; Leache & Reeder 2002). *Liolaemus* is a genus in the family Liolaemidae, with about 160 species distributed throughout South America (Schulte et al. 2000; Frost et al. 2001). Although Liolaemidae and Phrynosomatidae are both in the Iguania group, the two taxonomic families are quite large, such that *Sceloporus* and *Liolaemus* are not particularly closely related. However, *Sceloporus* and *Liolaemus* share many aspects of their morphology and ecology (e.g. Donoso-Barros 1966; Fuentes 1976; Carpenter 1978b; Stebbins 1985; Cei 1986, 1993; Schulte et al. 2000). Both genera are similar in general body form and range of body sizes. Both genera are also similar in being ecologically diverse. Although individual species may be more or less restricted in habitat, at the genus level, both *Liolaemus* and *Sceloporus* are generalists, occurring in a wide variety of habitats, including temperate and tropical montane regions, semiarid and arid habitats. Some species lay eggs whereas others give birth to live young. Most species of both genera are 'sit-and-wait' insectivores, usually found perching on top of rocks or trees (personal observation). The comparison thus offers an opportunity to examine what would have happened if the evolutionary process had been replicated with different organisms being subjected to similar selective regimes.

Communication in lizards of the Iguania group (including both *Sceloporus* and *Liolaemus*) is dominated by the use of stereotyped 'pushup' or 'headbob' displays (e.g. Carpenter & Ferguson 1977). Although lizards also

produce a variety of other visual, chemical and even acoustic signals, the headbob display can easily be distinguished as series of stereotyped up-and-down motions of the head and (sometimes) torso, sometimes accompanied by display-specific body postures such as back arches, dewlap extension and tail raises. These visual displays are used primarily in territorial defence and courtship and contain information about the individual identity, sex and social context of the displaying animal (e.g. Carpenter & Ferguson 1977; Martins 1991, 1993a; Decourcy & Jenssen 1994). Despite considerable within-species variation, most of the variation in headbob displays is seen across species, with most species producing a single, most common, display type. For example, although all *Sceloporus* headbob displays consist of long series of headbobs (e.g. Fig. 1; Martins 1993b), the actual form of the individual up-and-down motions can vary considerably, with some species producing complex jerky motions (e.g. *S. cozumelae*) and others producing temporally grouped sets of headbobs ('headbob bouts' sometimes described as 'doublets', 'triplets', etc.).

Lizard headbob displays seem to have been subjected to most of the same evolutionary pressures found in other types of communicative signals. Several researchers have suggested that body size and monocular vision have been important forces in creating interspecific signal diversity (Jenssen 1977; Carpenter 1978a; Ord & Blumstein 2002). Despite the apparent lack of female choice in many lizards (e.g. Tokarz 1995), evidence has also been found for the importance of receivers in the evolution of headbob display structure through intrasexual competition (Ord et al. 2001). The physical environment has also been potentially important, with more rapid high-amplitude motions evolving as attention-getting devices at the beginning of long-distance displays (e.g. Fleishman



**Figure 1.** Display action patterns or DAPgraphs of a few *Sceloporus* lizards, following Carpenter (1978a) and Martins (1993b); only a subset is included for illustration purposes. Each DAPgraph is a schematic depiction with the vertical motion of the lizard's head shown on the Y axis and time along the X axis (dots underneath each DAPgraph mark individual seconds). Phylogeny follows Wiens & Reeder (1997), based on a combination of mtDNA and morphological evidence.

1988). Arboreal lizards may be less likely to produce rapid, jerky motions (Carpenter 1978a; but see Martins 1993b) and more likely to produce colourful belly patches (Wiens 1999). Information content (i.e. display function), however, seems to have played the most important role. The use of headbob displays in species and individual recognition seems to be the main force underlying increased diversification and signal complexity in several groups (e.g. Jenssen 1977; Martins 1993b; Martins & Lamont 1998; Ord et al. 2001). There is also some evidence for structural constraints imposed by joint evolution of different aspects of a complex signal (Martins 1993b; Wiens 2000).

Herein, we use the similarities between *Sceloporus* and *Liolaemus* lizards to explore the generality of these factors across a common background of morphological and ecological constraints. We know a great deal about the communicative behaviour of *Sceloporus* lizards, primarily because of the lifetime of research conducted by Charles Carpenter, including detailed descriptions of the headbob displays of 42 species (summarized in Carpenter 1978a and reanalysed in Martins 1993b). In *Liolaemus*, previous studies showed that several species produce headbob displays (Halloy 1996; Trigosso-Venarino et al. 2002), but the detailed structure of these displays has not been documented. In the current study, we describe the headbob displays of 16 species of *Liolaemus* lizards, analysing them in a phylogenetic context and making comparisons with what is known about *Sceloporus* display evolution.

## METHODS

We collected data from 16 species of *Liolaemus* lizards (6 from the subgenus *Liolaemus*, 10 from the subgenus *Eulaemus*; Laurent 1985; Schulte et al. 2000; Figs 2, 3) during the 1998–1999 active season (October–March). *Liolaemus quilmes* and *L. ramirezae* were sampled from the precordilleran areas of the Tucumán province of Argentina, where they are found on rocky outcrops in semixerix type habitats. *Liolaemus scapularis* was found in landlocked dunes of the Salta and Catamarca provinces. *Liolaemus cuyanus*, *L. koslowskyi* and *L. robertmertensi* were studied in the sandy, partly desert areas of northern La Rioja and southern Catamarca provinces. *Liolaemus chacoensis* and *L. pseudoanomalus* were sampled in northern La Rioja province and *L. abaucan*, *L. laurenti* and *L. salinicola* were found in southern Catamarca province, all of the latter five species were also found in sandy semixerix habitats. We found *L. bibronii*, *L. elongatus* and *L. lobo* (Abdala 2003) on rocky outcrops and semidesert areas of the Argentinean Río Negro and Neuquén provinces, and we found *L. pictus* in the conifer woodlands of southern Neuquén and northern Río Negro provinces. *Liolaemus monticola* was studied in rocky areas in the precordilleran scrublands near Las Vizcachas, Chile (southeast of Santiago). We grouped the habitats in which we observed these species into four general types: 1: woodland; 2: scrublands with larger trees and shrubs; 3: open habitat with firm substrate and large rocks; 4: open habitat with sandy substrates, shrubs and grasses (Figs 2, 3).

We collected data on visual displays by videotaping focal animal samples of lizards in their natural habitats during hours of peak activity (usually between 0900–1200 and 1500–1800 hours). Focal animal sampling began when an active individual was spotted and continued for 30 min or until the animal disappeared from view. At the end of each focal animal sample, an attempt was made to capture the animal to determine its sex (especially in species without clear sexual dimorphism). Because we did not mark individual animals, we moved some distance away before searching for the next animal. In some cases, multiple individuals were observed interacting during a single focal sample, and were distinguished from each other based on their location in the videotape.

Videotapes were returned to the laboratory and carefully scored for visual displays. For simplicity, we focused on headbob displays defined herein as any series of stereotyped up-and-down motions of the head/trunk in which the animal did not raise its feet from the substrate during the display. Each individual up-and-down motion is termed a ‘headbob’. Multiple headbob displays produced in rapid succession (separated by less than 2 s, equivalent to Carpenter’s ‘doublets’ or ‘triplets’) were lumped into ‘headbob bouts’. In many species (but not all, see below), headbob bouts could also be combined into longer ‘headbob displays’ that were usually separated from each other by several minutes. Because in most species, headbob displays were usually separated from other displays by pauses of several minutes, we scored any two headbobs separated by locomotion (no matter how brief) as being part of different displays when we calculated overall species frequencies.

We recorded the detailed structure of the up-and-down motions (drawing DAPgraphs, sensu Carpenter & Grubitz 1961) and calculated frequencies of occurrence. We do not report data on ‘shudderbobs’ or ‘jiggles’ (up-and-down motions usually produced while moving from one spot to another, often associated with courtship) or any other form of head motions in our analyses, because they occurred infrequently in our sample. We did, however, calculate frequencies of occurrence of forelimb waves (sometimes lengthy series of circular motions of one or both forelimbs), tail waves (elaborate swinging of the tail from side to side and up over the torso and head) and tongue flicks (an index of general exploratory behaviour and/or activity level), for comparison. For these frequency calculations, we included only data from observation sessions lasting at least 5 min. Data on forelimb waves were analysed more thoroughly in Halloy & Castillo (2002).

We applied the phylogenetic generalized least squares (PGLS) approach proposed in Martins & Hansen (1997) to explore our data in a phylogenetic context. This method offers a flexible approach to phylogenetic analyses, allowing for (1) the estimation of ancestral states (see also Martins & Lamont 1998 for an example), (2) tests of the importance of phylogenetic effects, and (3) the estimation of correlations among traits. We performed all three types of analyses herein. The method was designed to be used with data having evolved under a broad range of microevolutionary scenarios, and performs reasonably

well in computer simulation tests (e.g. Martins et al. 2002). To apply PGLS, we began with two phylogenetic hypotheses. First, we apply the phylogeny developed by Schulte et al. (2000) based on mtDNA sequences (Figs 2, 3), placing *L. ramirezae* (not included in Schulte et al.'s analysis) as suggested by Lobo (2001)'s phylogenetic analysis of morphological traits. Schulte et al. (2000) provide the most recent phylogeny that includes almost all of the taxa in our study, and most of the nodes used in our own study were very highly supported (bootstrap values of at least 96%). Highlighting differences between Lobo (2001) and Schulte et al.'s (2000) phylogenetic hypotheses for the *chiliensis* group, we then conducted a second set of analyses using an alternate phylogeny, placing *L. chacoensis* as an outgroup to the *chiliensis* group and *L. elongatus* as a sister taxon of *L. pictus* rather than *L. monticola*. Other recent phylogenies for *Liolaemus* (e.g. Laurent 1985; Cei 1986, 1993; Etheridge 1995; Halloy et al. 1998) are identical to one or the other (or both) of our phylogenies in terms of the placement of our 16 taxa.

Application of a phylogenetic comparative method also requires making some assumptions about the type and amount of evolutionary change expected in each trait along each branch of the phylogeny (i.e. usually reported as branch lengths). Unfortunately, even when branch lengths were available as part of a published description of a phylogeny (branch lengths were not published with the above phylogenetic hypotheses), most phylogenetic methods required that they be converted from the usual units of time or mtDNA sequence divergence into the units of expected phenotypic divergence, a conversion process that depends on the heritabilities and selective regime of each character under consideration (Martins & Hansen 1996). We chose PGLS, in part, because it acknowledges this difficulty explicitly, offering a range of possible microevolutionary scenarios for each trait and a maximum likelihood estimator for choosing among them based on the interspecific data.

To apply PGLS, we began by arbitrarily setting each branch to the same length, as if equal amounts of character change were expected along each branch of the phylogeny. We then applied an exponential transformation to the branch lengths as suggested in Martins & Hansen (1997) for traits potentially subjected to selective constraints during their evolutionary history. In conducting our analyses, we used a single maximum likelihood estimator of the constraint parameter ( $\alpha$ ), shown by computer simulation (Martins et al. 2002) to perform reasonably well. When the  $\alpha$  constraint parameter is small, PGLS results are similar to those produced by Felsenstein's (1985) popular independent contrasts method. When  $\alpha$  is large, PGLS gives results comparable to not incorporating phylogeny at all. Results are reported as ranges to reflect that they are for analyses conducted using several possible PGLS  $\alpha$  values and for both phylogenetic hypotheses.

Specifically, we applied PGLS to estimate ancestral states of behavioural traits and to estimate evolutionary correlations between traits. We also applied Hansen's (1997) extension of PGLS to estimate the amount of variation in each trait explained by taxonomic clade. Although

originally designed to describe adaptation of a trait to the environment in which a species is found, Hansen's method can be used to estimate the importance of any single factor in explaining interspecific variation in a continuous trait. In this case, we used Hansen's method to determine the importance of the traditional division of *Liolaemus* into two major clades (the mostly Chilean subgenus *Liolaemus* and the mostly Argentinean subgenus *Eulaemus*) on interspecific variation in display frequency. The two clades are thought to have radiated on opposite sides of the Andes and show several major morphological differences, but note that although we refer to these clades throughout as 'Argentinean' and 'Chilean' subgenera, neither subgenus is restricted to one country and members of both subgenera occur in both Chile and Argentina. We used Hansen's method to estimate the average values for display traits in each clade (and the difference between the two clades), and also to estimate the total amount of variation explained by this taxonomic distinction. All phylogenetic statistics were calculated using COMPARE (Martins 2001).

## RESULTS

We recorded about 30 h of videotape of 16 *Liolaemus* species, including recordings of at least 103 animals producing a total of 345 headbob displays in 257 focal animal samples, varying in duration from 5 to 30 min. Most species produced headbob displays, forelimb waves, tail waves and tongue flicks, but did so at different rates (Table 1). Some species did not produce one or the other type of behaviour during our study. For example, no headbob displays, forelimb waves, tail waves, or tongue flicks were recorded for *L. abaucan* and *L. salinicola*, which were difficult to observe in the field, and were filmed for less than 5 min each. Five species were never observed producing forelimb waves, and we recorded tail waves from only eight species.

Headbob displays of *Liolaemus* are remarkably simple (Figs 2, 3) compared with those of *Sceloporus* (Fig. 1). Despite some variation in the structure of displays produced by different individuals of the same *Liolaemus* species, we were able to identify a single most common type of 'headbob bout' for most species. Although these bouts were sometimes combined into longer series of varying length, the single headbob bout was the most common display in every case (i.e. 'bout' = 'display' for these species). Only three species (*L. pictus*, *L. monticola* and *L. lobo*) produced multiple types of headbob bouts, either alone or in combination. Single displays that combined more than one type of headbob bout, however, were rare.

More interestingly, several of the 'species-typical' headbob displays were shared by different species. For example, one of the most common displays produced by five of the observed species (*pseudoanomalus*, *cuyan*, *lobo*, *monticola* and *pictus*) was a triplet (Figs 2, 3). The first up-and-down motion in *L. cuyan* often had slightly decreased amplitude, *L. pseudoanomalus* sometimes produced more than one triplet in a row, and the remaining species



**Table 1.** Mean ( $\pm$ SE) frequencies of headbobs and forelimb waves observed for 16 *Liolaemus* species\*

Species†	Headbobs		Forelimb waves	
	Number/h	Motions/unit	Number/h	Motions/unit
<b>Subgenus <i>Liolaemus</i> (mostly Chilean)</b>				
<i>bibronii</i> (2f, 20?; 5.6)	0.9 (0.59)	2.3 (0.47)	0.0 (0.00)	—
<i>elongatus</i> (1m, 23?; 2.8)	12.3 (4.22)	2.2 (0.36)	0.8 (0.46)	2.5 (0.87)
<i>monticola</i> (4m, 1f, 1j; 1.3)	29.1 (7.18)	1.5 (0.18)	19.9 (7.70)	1.0 (0.04)
<i>pictus</i> (6m, 7f, 22?; 4.5)	12.2 (2.31)	2.2 (0.25)	1.0 (0.53)	1.2 (0.25)
<i>ramirezae</i> (2?; 2.1)	5.3 (2.41)	0.3 (0.08)	0.0 (0.00)	0.0 (0.00)
<i>robertmertensi</i> (9m, 8f, 3?; 1.0)	104.3 (27.10)	2.6 (0.37)	0.0 (0.00)	1.1 (0.08)
<b>Subgenus <i>Eulaemus</i> (mostly Argentinean)</b>				
<i>abaucan</i> (3m, 2f; 0.1)	—	—	—	—
<i>chacoensis</i> (23m, 13f, 1?; 4.8)‡	44.0 (14.32)	2.1 (0.24)	2.6 (1.70)	1.8 (0.24)
<i>cuyanus</i> (4m, 4f; 0.4)	19.6 (9.75)	1.2 (0.25)	0.0 (0.00)	1.0 (—)
<i>loboi</i> (27m, 26f, 11?; 12.6)	3.3 (1.25)	2.4 (0.34)	0.2 (0.22)	1.0 (1.00)
<i>koslowskyi</i> (12m, 2f, 0?; 2.1)	24.9 (9.42)	1.8 (0.25)	3.6 (2.04)	1.3 (0.33)
<i>laurenti</i> (1m, 1f, 0?; 0.2)	57.7 (—)	1.0 (—)	0.0 (—)	—
<i>pseudoanomalus</i> (3m, 1f, 3?, 1nb; 0.3)	23.8 (23.79)	1.9 (0.28)	30.3 (6.84)	1.5 (0.29)
<i>quilmes</i> (16m, 14f, 3nb; 11.3)	9.3 (2.47)	2.8 (0.68)	3.4 (1.01)	1.6 (0.46)
<i>salinicola</i> (1nb, 1?; 0.1)	—	—	—	—
<i>scapularis</i> (3m, 1f, 6?, 6nb; 2.0)	5.7 (2.47)	1.6 (0.24)	1.2 (1.24)	5.0 (—)

\*Frequencies are given in displays per hour and were calculated separately for each focal observation session that lasted at least 5 min and then averaged for each species. Each display consisted of a series of motion units (individual motions of the head, forelimb, tongue or tail separated by less than 1 s). We thus also report the average number of motion units (one up-and-down headbob or one circular forelimb wave) per behavioural bout for each species, even if calculated from only one or two displays (i.e. display frequency may be rounded to 0.0). A dash is used when the behaviour was not observed or when very small sample sizes made it impossible to calculate standard errors.

†The numbers in parentheses following each species name refer to the number of males (m), females (f), juveniles (j), newborn (nb) and unknown (?) animals observed and the total time observed (in hours).

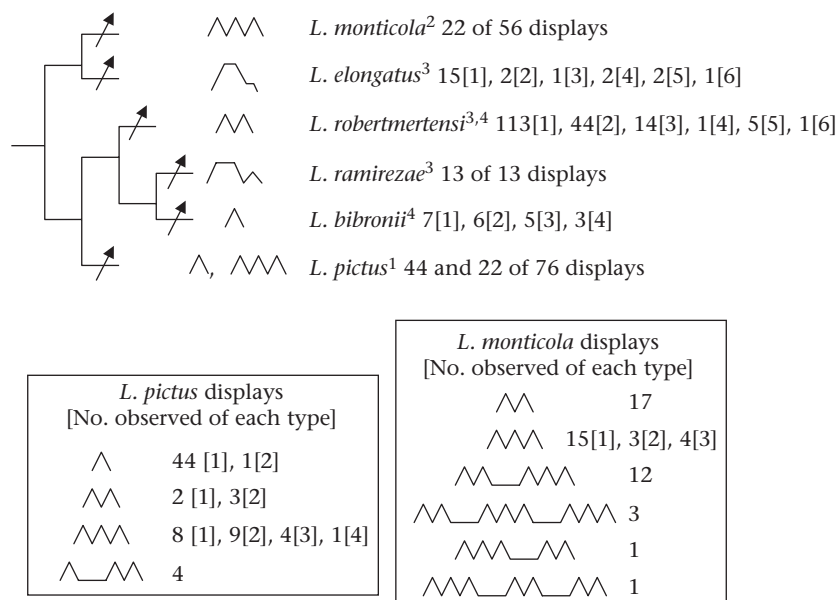
‡*L. chacoensis* is placed as a member of the subgenus *Eulaemus* by Schulte et al. (2000), but appears as a member of the subgenus *Liolaemus* in Lobo (2001).

produced other display types in addition to the single triplet. Moreover, although some species also produced different types of headbob displays (Figs 2, 3), at least two of the species (*L. pictus* and *L. loboi*) shared virtually their entire repertoires, differing only in the frequency with which different display types were produced. Three other species, *L. quilmes*, *L. robertmertensi* and *L. ramirezae*, shared the use of doublets, either alone or in series as their 'species-typical' displays. Although the first headbob in the *L. ramirezae* doublet is slightly longer in duration and higher in amplitude than the second, these and other differences between species were only distinguishable after careful frame-by-frame analysis of the videotape. *Liolaemus bibronii* produced one single headbob, as did *L. laurenti*, although the latter was longer in duration. *Liolaemus scapularis* made quadruplets, but this observation was based on only two displays. Only *L. koslowskyi*, *L. chacoensis* and *L. elongatus* produced headbob bouts that were obviously unique to each species (Figs 2, 3).

Phylogenetic history seems to have little effect on the number and types of headbobs used in species-typical *Liolaemus* displays (Figs 2, 3), with close relatives producing relatively different display types. For example, using Hansen's (1997) method, we found that the major division between the two subgenera (*Eulaemus* in Fig. 3 and *Liolaemus* in Fig. 2) at the root of the genus *Liolaemus* phylogeny explained less than 1% of the interspecific variation in the number of headbobs/display (difference in clade means  $\pm$  SE =  $0.0 \pm 0.38$ ). Towards the tips of the phylogeny, there were too few similarities between display

types to allow reconstruction of ancestral states of the display. In reconstructing evolutionary shifts in display measures (mean number of headbobs, tongue flicks, forelimb waves and tail waves per hour and per display), we found that virtually all major changes occurred very recently on the branches leading to extant species (near the tips of the phylogeny; e.g. Figs 2, 3).

Although several of the *Liolaemus* species in this study were found in sympatry, there was no obvious relationship between headbob display structure and the habitats in which the lizards were found (Figs 2, 3). For example, *L. loboi* and *L. bibronii*, which were often found under the same bushes, could be easily distinguished on the basis of their headbob displays. *Liolaemus robertmertensi* and *L. koslowskyi* also produced very different headbob displays, despite their occurrence in very similar habitats within only a few metres of each other. Although *L. cuyanus*, *L. loboi* and *L. pseudoanomalus* (which produced very similar triple headbob displays) tend to live in open scrubby desert, *monticola* lives in rocky areas, and *pictus* (which also produced the triple headbob display) is more likely to be found in forest. *Liolaemus loboi* is the only one of the five species that shows strong sexual dimorphism. *Liolaemus koslowskyi* and *L. quilmes*, which are so similar morphologically and ecologically that they were once thought to be a single species (Etheridge 1995), gave very different headbob displays. The similarity between *L. ramirezae* and *L. quilmes* headbob displays (produced in the same type of habitat) is the exception, rather than the rule, and even *L. ramirezae* and *L. quilmes*



**Figure 2.** Display action patterns or DAPgraphs for the *chiliensis* clade of *Liolaemus* lizards. Each DAPgraph is a schematic depiction with the vertical motion of the lizard's head shown on the Y axis and time along the X axis. All headbob bouts lasted less than 3 s. In many cases, the basic unit presented in the DAPgraph was repeated several times in a single display. In brackets, we report the number of observed displays in which the basic unit was repeated once ([1]), twice ([2]) or more times. Superscripts refer to the habitat in which each species was observed (see [Methods](#)): 1: woodland; 2: scrublands with larger trees and shrubs; 3: open habitat with firm substrate and large rocks; 4: open habitat with sandy substrates, shrubs and grasses. Arrows on the phylogeny mark branches along which major evolutionary changes were observed in the number of headbob displays per hour. Results for other behaviour patterns in [Tables 1 and 2](#) were identical. Major evolutionary changes were identified as differences between ancestral states (estimated using phylogenetic generalized least squares, PGLS, on data for species in [Figs 2, 3](#) simultaneously) larger than two standard errors in absolute magnitude. Phylogeny follows [Schulte et al. \(2000\)](#), based on mtDNA, with placement of *L. ramirezae* based on the morphological phylogeny of [Lobo \(2001\)](#).

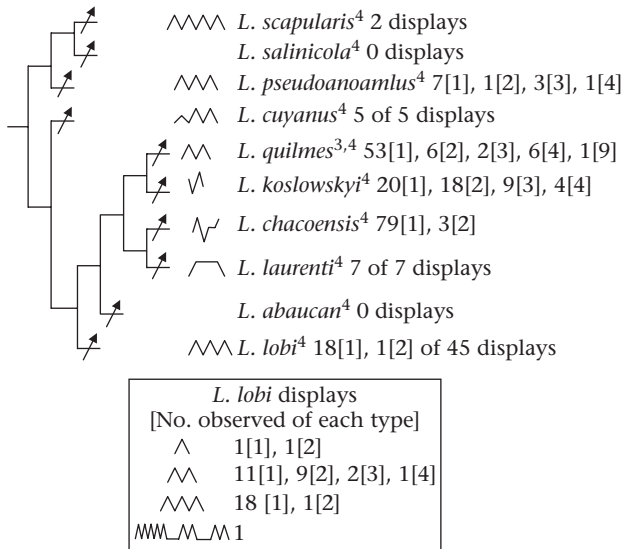
were quite easy to distinguish based on how they used their headbob displays (*L. quilmes* produced them continuously, see below).

In very general terms, *Liolaemus* headbob displays also seemed to be produced in the same contexts that have been described for most other lizard species (e.g. [Carpenter & Ferguson 1977](#)). Most of the observed headbob displays were preceded by locomotion as the animals moved from perch to perch along the boundaries of their territories, and were easily recognizable as 'broadcast' or 'signature' displays. Displays were also produced by both animals during aggressive interactions and during courtship. We found no evidence that headbob displays are used in appeasement contexts (e.g. [Martins & Lacy 2004](#)) or as antipredator mechanisms (e.g. [Leal 1999](#)), but our sample was not large enough to be conclusive on either point. Because we could not always determine the context clearly from the videotape, the above results were obtained from a combined analysis of all the headbob displays produced.

Still, we found that headbob displays were used frequently by lizards of most species, ranging up to 104 displays/h ([Table 1](#)), suggesting that these displays may be used differently from those of previously studied taxa (e.g. *Sceloporus*, see [Discussion](#)), perhaps in entirely new contexts. Species in the mostly Chilean subgenus *Liolaemus* produced an average of 19–21 headbob displays/h, whereas species in the primarily Argentinean subgenus

*Eulaemus* produced 10–11 headbob displays/h (standard error of the difference between clade means = 14.5 or 15.3, depending on the phylogeny). Although the absolute magnitude of the difference seems large, interspecific variation was also large, so that the difference between clades explained only 2.5% of the variation in headbob display frequency. In three species (*L. chacoensis*, *L. quilmes* and *L. robertmertensi*, not close phylogenetic relatives), headbob displays were produced continuously, interspersed by minor episodes of locomotion, changes in orientation or brief pauses (<5 s). Because these series sometimes continued for several minutes or even throughout the entire focal sample, our method of counting displays (separated from each other by bouts of locomotion) may have overestimated the true number of displays produced, particularly in the two species with the highest headbob display frequencies (*L. chacoensis* and *L. robertmertensi*). Using phylogenetic analyses, we found a strong positive evolutionary relationship between rate of headbob displays and rate of tongue flicking ( $r > 0.6$ – $0.7$ ,  $P < 0.05$ ). The PGLS method estimated a very large  $\alpha$  for this relationship, indicating that phylogeny had little effect on the results of statistical analyses.

Headbob displays did not seem to be closely associated with forelimb or tail waves. Using phylogenetic analyses, we found little if any evolutionary relationship between the rate of headbob displays and that of forelimb or tail waves ( $r < 0.2$  in all cases, NS). Forelimb waves were



**Figure 3.** Display action patterns or DAPgraphs for *Liolaemus* lizards in the subgenus *Eulaemus*. Each DAPgraph is a schematic depiction with the vertical motion of the lizard’s head shown on the Y axis and time along the X axis. All displays lasted less than 3 s. In many cases, the basic unit presented in the DAPgraph was repeated several times in a single display. In brackets, we report the number of observed displays in which the basic unit was repeated once ([1]), twice ([2]) or more times. Superscripts refer to the habitat in which each species was observed: 1: woodland; 2: scrublands with larger trees and shrubs; 3: open habitat with firm substrate and large rocks; 4: open habitat with sandy substrates, shrubs and grasses. Arrows on the phylogeny mark branches along which major evolutionary changes were observed in the number of headbob displays per hour. Results for other behaviour patterns in Tables 1 and 2 were identical. Major evolutionary changes were identified as differences between ancestral states (estimated using PGLS on data for species in Figs 2, 3 simultaneously) larger than two standard errors in absolute magnitude. Phylogeny follows Schulte et al. (2000), based on mtDNA.

observed frequently in many of the *Liolaemus* species (although not as frequently as the headbob displays; Table 1). Tail waves were observed in fewer taxa (only 7 of the 16 species), but also occurred at high frequency in these taxa (Table 2). Species that produced frequent tail waves, however, were also likely to produce frequent forelimb waves ( $r = 0.4–0.5$ ,  $P < 0.05$ ). Rate of tongue flicks (a general index of exploratory behaviour; Simon 1983; Labra et al. 2001) was slightly more closely related to rate of forelimb waves ( $r = 0.3–0.4$ , NS) than to rate of tail waves ( $r < 0.2$  in all cases, NS), but neither correlation was significantly greater than zero. Frequencies of these behaviour patterns were too small to warrant further phylogenetic exploration.

**DISCUSSION**

Despite marked morphological and other similarities between *Sceloporus* and *Liolaemus*, we found few commonalities in the details of how headbob displays have evolved in the two genera. *Liolaemus* headbob displays are remarkably simple in comparison to those of *Sceloporus*, despite the frequent use of dramatic display components such as forelimb and tail waves. As in other groups of lizards, evolutionary changes in the *Liolaemus* headbob display system have been both rapid and large, erasing any remnants of similarity due to shared ancestry and resulting in displays that are not obviously associated with any major, long-term habitat characteristics. Macroevolutionary patterns are consistent with the conclusion that the up-and-down motion of lizard headbob displays evolved primarily in response to diversifying selection for species recognition, with evolution of the structural details appearing to fluctuate stochastically (perhaps in response to fluctuating selective pressures) over long periods of evolutionary time.

**Table 2.** Mean ( $\pm$ SE) frequencies of tail waves and tongue flicks observed for 16 *Liolaemus* species\*

Species†	Tail waves		Tongue flicks	
	Number/h	Motions/unit	Number/h	Motions/unit
<b>Subgenus <i>Liolaemus</i> (mostly Chilean)</b>				
<i>bibronii</i> (2f, 20?; 5.6)	0.0 (0.00)	1.0 (NA)	0.7 (0.41)	1.0 (0.00)
<i>elongatus</i> (1m, 23?; 2.8)	0.0 (0.00)	5.0 (NA)	4.4 (2.25)	1.4 (0.35)
<i>monticola</i> (4m, 1f, 1j; 1.3)	7.2 (7.17)	1.1 (0.10)	6.4 (5.47)	1.7 (0.33)
<i>pictus</i> (6m, 7f, 22?; 4.5)	0.0 (0.00)	—	9.2 (1.84)	1.2 (0.25)
<i>ramirezae</i> (2?; 2.1)	0.0 (0.00)	0.0 (0.00)	2.4 (0.48)	0.1 (0.01)
<i>robertmertensi</i> (9m, 8f, 3?; 1.0)	0.0 (0.00)	1.0 (0.00)	14.3 (NA)	1.2 (0.17)
<b>Subgenus <i>Eulaemus</i> (mostly Argentinean)</b>				
<i>abaucaan</i> (3m, 2f; 0.1)	—	—	—	—
<i>chacoensis</i> (23m, 13f, 1?; 4.8)‡	3.1 (1.27)	1.0 (0.00)	6.2 (2.48)	2.2 (0.46)
<i>cuyanus</i> (4m, 4f; 0.4)	0.0 (0.00)	—	0.0 (0.00)	1.0 (—)
<i>loboi</i> (27m, 26f, 11?; 12.6)	0.8 (0.65)	0.7 (0.33)	1.2 (0.59)	0.9 (0.14)
<i>koslowskyi</i> (12m, 2f, 0?; 2.1)	0.0 (0.00)	1.0 (NA)	10.8 (5.50)	1.9 (0.27)
<i>laurenti</i> (1m, 1f, 0?; 0.2)	0.0 (—)	—	0.0 (—)	—
<i>pseudoanomalous</i> (3m, 1f, 3?, 1nb; 0.3)	0.0 (0.00)	—	8.8 (0.85)	2.0 (0.00)
<i>quillmes</i> (16m, 14f, 3nb; 11.3)	0.6 (0.31)	0.4 (—)	3.8 (1.30)	0.8 (0.29)
<i>salinicola</i> (1nb, 1?; 0.1)	—	—	—	—
<i>scapularis</i> (3m, 1f, 6?, 6nb; 2.0)	0.0 (0.00)	—	1.1 (0.84)	1.0 (0.00)

\*†‡Footnote designations are the same as those given in Table 1.

Despite the structural simplicity of *Liolaemus* headbob displays, phylogenetic analyses suggest that they have been evolving quickly and often through evolutionary time. Phylogenetic relationships among species explain trivial amounts of the variation in the variables measured, including headbob display structure and frequency of use. Estimates of ancestral states showed that virtually all major phenotypic changes occurred on branches leading to extant species, with similarities among species in display structure being due to recent changes, rather than to retained similarities from a common ancestral display. This is similar to what has been found for *Cyclura* iguana headbob displays (Martins & Lamont 1998), and consistent with the patterns found earlier for headbob displays of *Sceloporus* (Carpenter 1978a; Martins 1993b) and anoles (Jenssen 1977). In our study, phylogenetic distances among the observed taxa were quite large (we collected data from only one in 10 *Liolaemus* species), and greater phylogenetic signal may be observed at finer scales of phylogenetic resolution, for example between recently diverged species. But fast evolutionary change may also be expected for behaviour patterns, such as communicative signals, which are subject to considerable levels of both natural and sexual selection (e.g. DeQueiroz & Wimberger 1983). Rapid change might also be expected for traits with few constraints imposed by genetic correlations with other traits. Other studies measuring the magnitude of genetic relationships between communicative signal traits and other characters are needed to explore this possibility further.

More surprising was our finding that several *Liolaemus* species produced very similar headbob displays, making it difficult to conclude that the displays are 'species typical' because species could not be distinguished simply on the basis of headbob display structure. In other species (e.g. several anoles, Jenssen 1977), we might argue that headbob displays are not 'species typical' because each species produces more than one stereotyped display form. In *Liolaemus*, however, we found that not only were several display types within each species shared, but also that the entire suite of displays was sometimes completely shared among species. Species that shared headbob displays were not close phylogenetic relatives (Figs 2, 3), nor did they share the same ecological habitat, as might be expected if differences were the result of selection imposed by the physical environment in which the species live. This is similar to the pattern found for the chemical composition of *Liolaemus* preloacal pore secretions, which is also thought to serve a function in communication and recognition (Escobar et al. 2001; Labra et al. 2002). Further studies are needed to determine whether character displacement among sympatric species imposed by the need to recognize species could be responsible for the observed diversification in headbob display structure. Further elaboration of what it means for a display to be 'species typical' may also be warranted.

The similarity among the headbob displays of different *Liolaemus* species may be due more to a common structural simplicity (and therefore more limited options) than to similarity of ancestry or selective regime. *Sceloporus*

produced long, complex series of up-and-down motions with substantial variation between species (Fig. 1), whereas most *Liolaemus* in this study produced simpler, shorter headbob displays that differed across taxa only in subtle ways (Figs 2, 3). The single headbob bouts characteristic of *Liolaemus* displays are relatively simple, lacking the complex (jerky) up-and-down motions and the repetition of stereotyped components characteristic of many *Sceloporus* displays. With such short displays, it may not be surprising that several *Liolaemus* share the same 'species-typical' display. Moreover, only one species (*L. monticola*) regularly combined different types of headbob bouts into single displays, something that is relatively common for *Sceloporus* (Fig. 1; Carpenter 1978a).

It seems unlikely that *Liolaemus* produce simpler headbob displays because they have not yet had enough time to evolve more complex forms. Although we sampled only about 10% of the species in the genus, our sample of *Liolaemus* was widely scattered geographically and phylogenetically and presumably representative of the genus as a whole. If anything, we might conclude that *Liolaemus* has been diversifying for longer than *Sceloporus* simply because *Liolaemus* is a larger genus, and unless speciation rates have been very different for the two genera, *Liolaemus* would require a longer evolutionary period to reach this larger size. The relative simplicity of *Liolaemus* headbob displays also does not seem to be the result of greater constraints imposed by predators or morphology on the production of large visual motions. Most *Liolaemus* species observed in this study supplemented their headbob displays with other highly conspicuous and elaborate visual displays, including forelimb and tail waves (Halloy & Castillo 2002). Although tail waves occur occasionally in *Sceloporus* (E. Martins, personal observation) and *Urosaurus* (D. Hews, personal communication), they have yet to be described. *Liolaemus* seem to have increased complexity of visual displays, instead, by adding novel components (e.g. forelimb and tail waves), perhaps thereby supplementing the relative simplicity of their headbob displays.

Although the display contexts we observed in this study were superficially similar to those observed for *Sceloporus*, some *Liolaemus* also produced headbob displays at much higher rates, ranging up to an impressive 104 displays/h. *Sceloporus* display rates have been reported to be between 5 and 20 displays/h (Martins 1993a; Martins et al. 1998; Sheldahl & Martins 2000). In part, the increased display rate for *Liolaemus* was due to a difference in how the display was used. Instead of producing headbob displays only when reaching a new perch at a territory boundary or when engaged in social interactions, *L. chacoensis*, *L. quilmes* and *L. robertmertensi* produced individual headbob displays every few seconds, interspersing them with brief bouts of locomotion or changes in orientation (superficially similar to the 'nodding run' described for one population of *S. graciosus*; Martins et al. 1998). Considering only *Liolaemus* species that used headbob displays in much the same ways as described for other species, *Liolaemus* display rates were still somewhat higher than those reported for *Sceloporus*. In contrast, display rates of *Liolaemus* were lower than those reported for male



*Anolis carolinensis* during aggressive conspecific encounters (168 displays/h; Jenssen et al. 2000), reflecting the fact that displays described in the current study were collected during focal animal samples in which relatively few aggressive encounters occurred. Nevertheless, it seems possible that display rates of *Liolaemus* are more elevated than those of *Sceloporus* because *Liolaemus* species have evolved novel uses of headbob displays in other, unknown contexts or because they engage in more aggressive encounters than do *Sceloporus* species. Further research of territorial behaviour (e.g. Halloy & Robles 2002) is needed to determine exactly what these contexts might be and why display frequency is high in this group.

Other studies have shown a possible relation between the use of visual and chemical cues in lizards (e.g. Duvall et al. 1987; Alberts et al. 1994; Hews & Benard 2001; Labra et al. 2001), and it is possible that increased communicative complexity in *Liolaemus* has been attained by modifying the use of chemical signals. Both *Sceloporus* and *Liolaemus* lizards use chemical secretions exuded through femoral and preloacal pores (respectively), which are thought to be used in territorial defence and recognition contexts similar to that in which headbob displays are observed (Alberts 1989, 1991; Labra & Niemeyer 1999). Lizards in the mostly Chilean subgenus *Liolaemus* have fewer preloacal pores (Cei 1986, 1993) and might thus show less chemical communication than do members of the mostly Argentinean subgenus *Eulaemus*. If there were a trade-off between the use of visual and chemical signals (as suggested by Hews & Benard 2001 for *Sceloporus virgatus*), we might expect lizards in the mostly Chilean subgenus *Liolaemus* to show more visual behaviour than those in the mostly Argentinean subgenus *Eulaemus*. In our study, we found that although species in the subgenus *Eulaemus* tended to headbob less often than did members of the subgenus *Liolaemus*, variation between species within the mostly Chilean subgenus *Liolaemus* was also considerable and the difference between clades was not statistically significant. We found only a positive evolutionary relationship between the number of headbob displays produced and the frequency of tongue flicking, arguing that some species (particularly in the Chilean subgenus *Liolaemus*) have evolved to become more active than others. Further studies are needed to explore the possibility of current and historical interactions between signals in visual and chemical sensory modalities.

In other groups of lizards, headbob displays are generally complex in structure, suggesting that their evolution is the result of selective pressures for diversification and increased signal complexity for species recognition (e.g. Jenssen 1977; Carpenter 1978a; Martins 1993b; Martins & Lamont 1998; Ord et al. 2001). The specific form of this complexity, however, differs considerably across taxonomic groups. *Sceloporus* have evolved jerky but stereotyped variants of the basic up-and-down motion (Carpenter 1978a; Martins 1993b) whereas anoles have evolved complex use of colour and motion in their dewlap extensions (e.g. Jenssen 1977). Caribbean rock iguanas (*Cyclura*) have evolved a rolling back-and-forth motion to complement the basic up-and-down motion

(Martins & Lamont 1998). The results presented herein for *Liolaemus* suggest that despite rapid evolutionary change, there is little evidence for the evolution of complexity in the up-and-down motion of the headbob display. Instead, this genus may attain increased communicative complexity through the use of other dramatic visual signals such as forelimb and tail waves.

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