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Ecology and signal evolution in lizards

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Current models of signal evolution explain diversity by invoking a variety of social, perceptual and environmental factors. Social systems and spacing patterns determine the active space of signals and their function. Receiver sensory systems and habitat characteristics interact to constrain signal design. These factors are traditionally implicated in promoting directional evolutionary change, leading to increases or decreases in signal complexity. We examine macro-evolutionary trends in signal design, as reflected by display modifier repertoire size, for 124 species of iguanian lizards to identify the importance of ecological factors in display evolution. Possessing a small home range, being arboreal and feeding on moving prey are all correlated with the evolution of large repertoires. However, living in closed habitats is associated with increased evolutionary change in repertoire size, producing greater signal diversity. Ecological factors can thus act either directionally or to promote evolutionary lability. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **77**, 127–148.

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INTRODUCTION

A major challenge faced by any attempt to formulate a general theory of signal evolution is the sheer diversity of structure (Dawkins, 1993). It is widely recognized that this variation reflects the action of a range of selective pressures and constraints, so the essential first step is to compile a comprehensive list of evolutionary forces. Current theoretical models incorporate a variety of social (Andersson, 1994; Blumstein & Armitage, 1997; Ord, Blumstein & Evans, 2001), perceptual (Endler, 1987, 1992; Fleishman, 1988a,b; Ryan & Rand, 1993) and environmental factors (Morton, 1975; Hansen, 1979; Wiley & Richards, 1982; Ryan & Brenowitz, 1985; Endler, 1987, 1992; Fleishman, 1988b; Ryan, Cocroft & Wilczynski, 1990; Marchetti, 1993). Social systems and spacing patterns influence the distance over which a signal must function. Receiver sensory systems constrain the structure of signals to those that are perceivable (Endler, 1992; Ryan & Rand, 1993), while habitat structure determines signal degradation (Morton, 1975; Marten & Marler, 1977; Marten, Quine & Marler, 1977; Wiley & Richards, 1978, 1982; Hansen, 1979; Daniel & Blumstein, 1998).

Lizards of the agamid and iguanid families typically possess a complex display repertoire, which is used in both male–male contests over territories (Carpenter, 1978; Trivers, 1976) and male–female courtship interactions (Jenssen, 1970a). These visual signals are composed of discrete, and sequentially predictable, movements centred on a head-nod and/or push-up display. Signal complexity varies across species and can be quantified by the number of modifiers used (Jenssen, 1977, 1978; Ord *et al*., 2001). Modifiers may be either static (e.g. dewlap extensions, crest raising, body compression/inflation, back arching, body

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raising/tilting and changes in body colouration) or dynamic (e.g. tail-wagging and arm-waving). In a previous study (Ord *et al*., 2001), we reported that differences in modifier repertoire size between species are partially explained by differences in male–male competitive intensity and suggested that more complex signals have evolved to improve opponent assessment. In the present study, we report a complementary analysis of the way in which ecological factors have influenced this aspect of signal evolution.

There are at least two possible consequences of natural selection: directional responses generate increases or decreases in the mean value of a trait, while disruptive or diversifying responses promote greater variance. As part of an investigation into the evolution of visual signals in lizards, we examine the pattern of selective response to four ecological factors that are likely to have influenced signal structure: habitat structure, home range size, arboreality and diet.

HABITAT STRUCTURE

Signals transmitted for any distance inevitably degrade before they reach potential receivers (Dusenbery, 1992; Bradbury & Vehrencamp, 1998). Transmission efficiency is determined by an interaction between signal properties and the physical structure of the environment. Signals designed for long range communication should thus be subjected to minimal or predictable degradation (e.g. ranging in birds: McGregor & Krebs, 1984; Morton, 1986; Naguib & Wiley, 2001; and primates: Whitehead, 1987). Studies of acoustic communication have shown that transmission range in bird song is maximized by tailoring calls to the acoustic environment in which they are typically given (Morton, 1975; Marten & Marler, 1977; Marten *et al*., 1977; Wiley & Richards, 1982). Similarly, the poor visibility characteristics of some habitats has selected for the evolution of conspicuous visual signals (Endler, 1987, 1992; Fleishman, 1992; Marchetti, 1993; Losos & Chu, 1998). The evolution of communication systems in response to properties of the signalling environment can hence generate and maintain differences in signal design when animals occur in different habitat types.

Habitat choice might influence the complexity of visual signals in at least two ways. In denser habitats, light levels are lower and obstructions potentially reduce signal active space (i.e. the distance over which signals are likely to remain effective). This latter factor will limit the maximum distance over which visual signals can be exchanged. However, as the distance between a signaller and receiver diminishes, the constraint of degradation is relaxed and more complex signals can emerge (Endler, 1992). Lizards in closed habitats may only become aware of conspecifics at close range (Stamps, 1983), and display interactions may consequently be restricted to those conducted over short distances (Jenssen, 1978). This is one mechanism by which closed habitats might enable selection for complex repertoires.

In addition, reductions in ambient light level should interact with properties of the lizard visual system to dictate the maximum rate of display movements. Experimental studies of electroretinographic response in three species of anoles demonstrate that critical flicker fusion frequency, which influences the ability to detect fast-moving objects, declines as the intensity of ambient light falling on a visual stimulus is reduced (Fleishman, Marshall & Hertz, 1995). It follows that the same rapid movements that effectively stimulate the visual system of an opponent in bright sunlight would be ineffective in shade. This sensory constraint should select for slower display movements in closed habi-tats (Fleishman *et al*., 1995). If signal structure is unchanged, then the maximum rate of information transmission will be reduced and aggressive interactions involving opponent assessment will become more costly because of the extra time required. Alternatively, animals could add display modifiers to compensate for the constraint on movement rate and enhance information transfer. This latter scenario also predicts that complex signals will evolve with closed habitat preference.

HOME RANGE SIZE

Species patrolling smaller home ranges will engage in bouts of territorial defence over shorter distances. In lizards, the intensity and vigour of signal exchanges typically escalates as conspecific distances decrease (Hover & Jenssen, 1976; Scott, 1984; Losos, 1985a; Decourcy & Jenssen, 1994). If opponents are evenly matched in size and condition, signal exchanges may degrade into physical combat (Stamps & Krishnan, 1994), which may also be facilitated by the proximity of participants (Scott, 1984). The increased injury risk under such conditions potentially favours large display repertoires for more efficient and accurate opponent assessment (Jenssen, 1978; Ord *et al*., 2001). We therefore test whether species possessing small home ranges are also more likely to evolve complex signals.

ARBOREALITY

Martins (1993b) examined the evolution of push-up displays in a subset of lizards and found that 'jerky' displays tended to be lost in arboreal species, perhaps because of the physical difficulty of performing signal movements in such environments. However, arboreal habitats could facilitate the evolution of complex signals or elaborate display repertoires as a secondary consequence of the enhanced locomotor flexibility that they require (Moermond, 1979). For example, Losos (1990a) suggested that display rate may coevolve with rapid movements such as running and jumping. Similarly, the ability to negotiate complex habitats is related to visual acuity (Jenssen & Swenson, 1974). Since animal signals are designed to exploit the sensory properties of receivers (Guilford & Dawkins, 1991, 1993; Bradbury & Vehrencamp, 1998), species living in complex habitats may be pre-adapted to evolve complex signals. Thus, we assess the relationship between arboreal locomotion and signal structure.

DIET

Most lizards are insectivores, but one subfamily of iguanids is predominantly herbivorous (the iguaninae). Males in this group are typically less aggressive than insectivores (Stamps, 1983). This relationship implies that species feeding on moving prey might have evolved more complex visual signals to mediate aggressive interactions. We therefore investigate whether a diet of typically fast-moving and/or small prey is associated with the evolution of complex signals.

MATERIAL AND METHODS

Published data on modifier repertoire size, habitat preference, home range size, arboreality and diet were compiled from a total of 141 sources for a variety of agamid and iguanid lizard species (see Appendix).

We began by collating together any papers describing display behaviour (total of 215 sources). Studies that did not report display structure in sufficient detail were then excluded. Species ecology was well documented in many of the remaining studies, but additional sources focusing primarily on ecological factors were used to supplement this material when necessary. The final set of sources was used to construct a data set covering 124 species.

DATA CATEGORIZATION

One inherent problem in comparing communicative systems across a diverse range of species is obtaining an appropriate and reliable index of signal variation that can be standardized. Visual displays in agamid and iguanid lizards almost invariably include the stereotyped head and body movements commonly termed 'head-nod' or 'push-up' displays. Subtle variation does exist within these displays (e.g. differences in display rate, speed, amplitude, etc.) and there are several species for which this variation has been quantified (e.g. Martins, 1993b; Martins & Lamont, 1998). However, we found that this information could not be incorporated into our display complexity index because of methodological differences among published accounts. In addition, these core displays (head-nod and/or push-up) may vary within a species. For example, some anoline lizards are reported to have up to five different core display types, each varying in structure and social context (Hover & Jenssen, 1976; Jenssen & Rothblum, 1977). It was hence impractical to obtain a single value for each species based upon core display characteristics.

We focused instead on 'display modifiers', which are postures or movements that accompany and elaborate core displays (Jenssen, 1977). Modifier use varies across species and accounts for a considerable proportion of signal diversity. In addition, information on modifier repertoire size could be readily collated from the literature, using standard criteria. This allowed us to include a large, and taxonomically diverse, range of species in our analyses.

Modifiers scored included: back arching, arm waving, body compression/inflation, body raising, body tilting, eye 'orbing', changes in body colouration, lip smacking, crest raising, tail displays, throat displays (dewlap extensions, gorging of the throat, etc.), and tongue protrusions. To be conservative, and to acknowledge the presence/absence of core displays, four species (see Appendix) that were reported not to possess a core display were scored as having a repertoire size of 0, irrespective of the presence of any modifiers (two species were observed to possess a throat display, while others had a tail display).

Some modifiers are unique to species or species groups. However, our aim was to quantify repertoire size to obtain an index of signal complexity across species. For this reason, we did not compare individual modifiers to assess more subtle differences or similarities in structure with those of other species.

In iguanian lizards, visual displays are typically performed by males. This tendency is reflected in the published literature, with many studies focusing primarily on male signal behaviour. While there are some descriptions of display structure for females and juveniles, repertoire size is invariably either equal to, or smaller than, that reported for males. In addition, although the presence of specific modifiers may be influenced by social context in some species, many are employed across all types of display interaction. Our goal was to obtain an estimate of maximum repertoire size for each species. We therefore used the number of modifiers accompanying male core displays.

We acknowledge the possibility that, in some cases, the original sources from which we obtained repertoire size information may have underestimated the number of modifiers used. This might result when only part of the display repertoire was observed and/or if the focus of the investigator(s) was on other aspects of behaviour. Such errors would have the affect of increasing apparent variation in repertoire size, but there is no reason to expect them to be systematically associated with the other factors of interest. The effect would hence be to reduce the likelihood of detecting significant relationships (see Benton, 1999; Nunn & Barton, 2001).

Habitat preference was classified as 'closed' or 'other'. 'Closed' habitats consisted of environments with large amounts of ground and/or canopy cover and were commonly referred to in the literature as rainforest, forest or closed woodland. 'Other' habitats were typically described as desert, plains, steppe, savannah, prairies, shrubland or open woodland. To be conservative, four species that were reported to occur in various habitats were scored as 'other' (see Appendix). Most data on display structure describe signals produced by males, so data on male home range size was favoured. However, in species that were reported to have no significant difference between the sexes, or when male data were not available, species values were used. When reported, maximum home range size was favoured, otherwise average values were used. All home range values were converted to m^2. Locomotion was categorized as either 'arboreal' or 'semi-arboreal/terrestrial' following author interpretations. Diet was categorized as 'moving prey' if a species was exclusively insectivorous or carnivorous. Omnivorous species were those with a diet that included vegetation, but that consisted predominately of moving prey. Species were considered to have a diet of 'non-moving prey' when they were reported to be exclusively herbivorous.

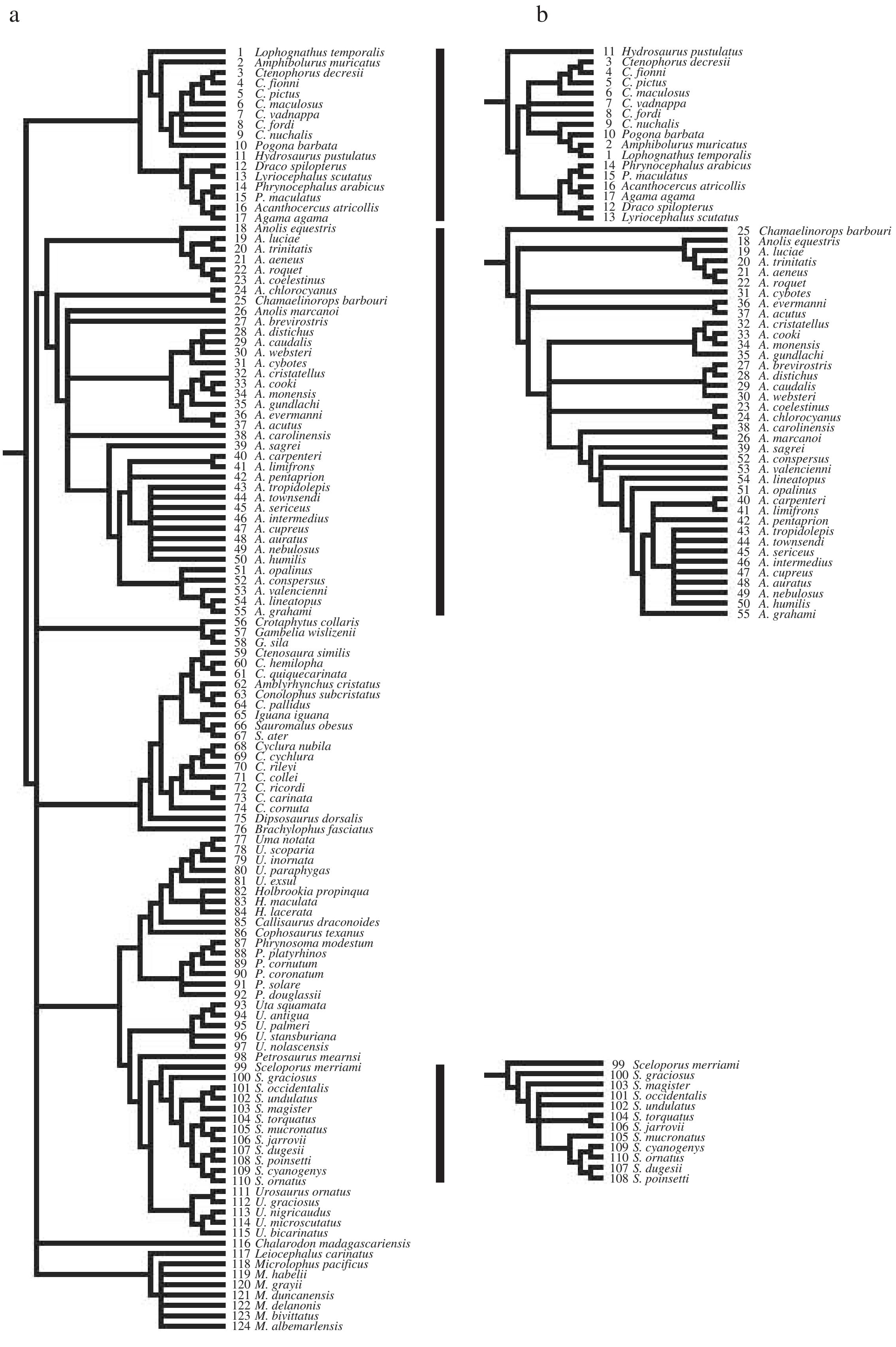
PHYLOGENY

No complete phylogeny of all the species of interest was available, so we compiled a composite tree from several sources. In some cases, several phylogenetic hypotheses were available. Phylogenies were 'ranked' with those based on combined data favoured over purely molecular data, which was, in turn, favoured over purely morphological data. If hypotheses were still equally ranked, we preferred trees based on parsimony methods of tree construction, then those with the fewest number of polytomies (where the precise phylogenetic relationship between species is unknown), and finally those more recent in publication. Species synonyms were checked using the 'EMBL Reptile Database' (http://www.embl-heidelberg.de/~uetz/livingreptiles.html).

Using these criteria, hypotheses ranked highest were used to construct tree 1 (Fig. 1a). Agamidae: genera positions follow Macey *et al*. (2000) with *Acanthocercus* positioned by Moody (1980). Species within the genus *Ctenophorus* are based on A. E. Greer (unpublished data) with *C. fordi* and *C. vadnappa,* which were unrepresented by Greer, positioned as polytomies. Iguanidae: subfamilies were positioned following the most resolved hypothesis of Schulte *et al*. (1998). The anoles and *Chamaelinorops* are based on Jackman *et al*. (1999) with additional species positioned as follows; *Anolis auratus, A. cupreus, A. nebulosus* (Stamps, Loso & Andrews, 1997); *A. caudalis, A. chlorocyanus, A. conspersus, A. cybotes, A. opalinus, A. websteri* (Burnell & Hedges, 1990); *A. cooki, A. evermanni, A. gundlachi, A. monensis* (Roughgarden & Pacala, 1989); *A. roquet, A. trinitatis* (Roughgarden & Pacala, 1989; Yang, Soule & Gorman, 1974); *A. carpenteri, A. intermedius, A. sericeus, A. townsendi, A. tropidolepis* (Echelle, Echelle & Fitch, 1971); *A. pentaprion* (Echelle *et al.*, 1971; Guyer & Savage, 1992). Crotaphytinae and genera level positions of Phrynosomatinae are based on Schulte *et al*. (1998) and Reeder & Wiens (1996). Species were positioned from several sources; *Phrynosoma* (Garland, 1994); *Sceloporus* (Wiens & Reeder, 1997) with *S. mucronatus* by Mindell, Sites & Graur (1989); *Uma* (Adest, 1977); *Urosaurus* (Reeder & Wiens, 1996) with *U. bicarinatus* by Mittleman (1942); *Uta* (Upton & Murphy, 1997). Iguaninae are based on Sites *et al*. (1996) and on Wiens & Hollingsworth (2000) combined morphological and molecular hypothesis, with additional *Cyclura* and *Ctenosaura* species by Martins & Lamont (1998) and De Queiroz, 1987), respectively. No hypotheses for *Holbrookia* or *Microlophus* were found; we positioned species within these genera as polytomies.

Most variation between phylogenetic hypotheses occurred for the anoles and *Sceloporus* genera. To recognize this, we generated a second tree (tree 2) using an alternative hypothesis for each of these two groups (Fig. 1b). Each hypothesis was deliberately selected to reflect the more extreme alternatives in topology. The anoles are based on Hedges & Burnell (1990) with additional species as follows; *Anolis limifrons* (Hass, Hedges & Maxson, 1993); *A. acutus, A. evermanni*

Figure 1. Species and phylogenetic hypotheses used to calculate independent contrasts and to reconstruct ancestor states for concentrated-changes tests. 'Polytomies', where the precise relationship between species is unknown, are left unresolved. (a) Topology of tree 1 illustrating the most preferred phylogenetic hypothesis and (b) alternative topologies for the agamids, anoles and *Sceloporus* used to construct tree 2. See text for methods.


a
1 Lophognathus temporalis
2 Amphibolurus muricatus
3 Ctenophorus decresii
4 C. fionni
5 C. pictus
6 C. maculosus
7 C. vadnappa
8 C. fordi
9 C. nuchalis
10 Pogona barbata
11 Hydrosaurus pustulatus
12 Draco spilopterus
13 Lyriocephalus scutatus
14 Phrynocephalus arabicus
15 P. maculatus
16 Acanthocercus atricollis
17 Agama agama
18 Anolis equestris
19 A. luciae
20 A. trinitatis
21 A. aeneus
22 A. roquet
23 A. coelestinus
24 A. chlorocyanus
25 Chamaelinorops barbouri
26 Anolis marcanoi
27 A. brevirostris
28 A. distichus
29 A. caudalis
30 A. websteri
31 A. cybotes
32 A. cristatellus
33 A. cooki
34 A. monensis
35 A. gundlachi
36 A. evermanni
37 A. acutus
38 A. carolinensis
39 A. sagrei
40 A. carpenteri
41 A. limifrons
42 A. pentaprion
43 A. tropidolepis
44 A. townsendi
45 A. sericeus
46 A. intermedius
47 A. cupreus
48 A. auratus
49 A. nebulosus
50 A. humilis
51 A. opalinus
52 A. conspersus
53 A. valencienni
54 A. lineatopus
55 A. grahami
56 Crotaphytus collaris
57 Gambelia wislizenii
58 G. sila
59 Ctenosaura similis
60 C. hemilopha
61 C. quiquecarinata
62 Amblyrhynchus cristatus
63 Conolophus subcristatus
64 C. pallidus
65 Iguana iguana
66 Sauromalus obesus
67 S. ater
68 Cyclura nubila
69 C. cychlura
70 C. rileyi
71 C. collei
72 C. ricordi
73 C. carinata
74 C. cornuta
75 Dipsosaurus dorsalis
76 Brachylophus fasciatus
77 Uma notata
78 U. scoparia
79 U. inornata
80 U. paraphygas
81 U. exsul
82 Holbrookia propinqua
83 H. maculata
84 H. lacerata
85 Callisaurus draconoides
86 Cophosaurus texanus
87 Phrynosoma modestum
88 P. platyrhinos
89 P. cornutum
90 P. coronatum
91 P. solare
92 P. douglassii
93 Uta squamata
94 U. antigua
95 U. palmeri
96 U. stansburiana
97 U. nolascensis
98 Petrosaurus mearnsi
99 Sceloporus merriami
100 S. graciosus
101 S. occidentalis
102 S. undulatus
103 S. magister
104 S. torquatus
105 S. mucronatus
106 S. jarrovii
107 S. dugesii
108 S. poinsetti
109 S. cyanogenys
110 S. ornatus
111 Urosaurus ornatus
112 U. graciosus
113 U. nigricaudus
114 U. microscutatus
115 U. bicarinatus
116 Chalarodon madagascariensis
117 Leiocephalus carinatus
118 Microlophus pacificus
119 M. habelii
120 M. grayii
121 M. duncanensis
122 M. delanonis
123 M. bivittatus
124 M. albemarlensis
b
11 Hydrosaurus pustulatus
3 Ctenophorus decresii
4 C. fionni
5 C. pictus
6 C. maculosus
7 C. vadnappa
8 C. fordi
9 C. nuchalis
10 Pogona barbata
2 Amphibolurus muricatus
1 Lophognathus temporalis
14 Phrynocephalus arabicus
15 P. maculatus
16 Acanthocercus atricollis
17 Agama agama
12 Draco spilopterus
13 Lyriocephalus scutatus
25 Chamaelinorops barbouri
18 Anolis equestris
19 A. luciae
20 A. trinitatis
21 A. aeneus
22 A. roquet
31 A. cybotes
36 A. evermanni
37 A. acutus
32 A. cristatellus
33 A. cooki
34 A. monensis
35 A. gundlachi
27 A. brevirostris
28 A. distichus
29 A. caudalis
30 A. websteri
23 A. coelestinus
24 A. chlorocyanus
38 A. carolinensis
26 A. marcanoi
39 A. sagrei
52 A. conspersus
53 A. valencienni
54 A. lineatopus
51 A. opalinus
40 A. carpenteri
41 A. limifrons
42 A. pentaprion
43 A. tropidolepis
44 A. townsendi
45 A. sericeus
46 A. intermedius
47 A. cupreus
48 A. auratus
49 A. nebulosus
50 A. humilis
55 A. grahami
99 Sceloporus merriami
100 S. graciosus
103 S. magister
101 S. occidentalis
102 S. undulatus
104 S. torquatus
106 S. jarrovii
105 S. mucronatus
109 S. cyanogenys
110 S. ornatus
107 S. dugesii
108 S. poinsetti

(Roughgarden & Pacala, 1989); *Chamaelinorops* (Guyer & Savage, 1992). Other species are positioned as in tree 1. *Sceloporus* are positioned using Reeder & Wiens (1996), with additional species also positioned as in tree 1. In addition to these, we also based Agamidae solely on A. E. Greer (unpublished data) with those species unrepresented by Greer positioned using Moody (1980).

TRAIT EVOLUTION AND CORRELATION

For the continuous variable of home range size, we first $\log_{10}$ transformed values (Turner, Jennrich & Weintraub, 1969; Christian & Waldschmidt, 1984) and then calculated standardized independent contrasts (Felsenstein, 1985) using the program CAIC v. 2.6.2 (http://evolve.bio.ic.ac.uk/evolve/software/caic/index.html; see also Purvis & Rambaut, 1995), which were then used in subsequent regression analyses. Independent contrasts are a common way to control for possible phylogenetic non-independence of species data (Harvey & Pagel, 1991). While the CAIC program can calculate contrasts from trees possessing polytomies, to be consistent with the phylogenetic hypothesis used in the concentrated-changes test (CCT; see below), we conducted analyses by randomly resolving polytomies using MacClade software v. 3.08a (Maddison & Maddison, 1992, 1999). Branch length data were available for only a few species pairs. We therefore set all branch lengths equal to include the maximum number of species in our analyses. We selected the 'Crunch' algorithm for contrast analyses. As required by this method (Purvis & Rambaut, 1995), regressions were forced through the origin.

Body size covaries with home range size (Turner *et al.*, 1969; Christian & Waldschmidt, 1984), so we used additional published data (see Appendix) and regressed contrasts for body size (maximum male snout–vent length) against contrasts for home range size. The residuals from this analysis were then used to control for possible body size effects in subsequent tests (Losos, 1990a).

To investigate patterns of trait evolution, we used the phylogenetic program MacClade v. 3.08a (Maddison & Maddison, 1999) to reconstruct ancestor states for each trait. To use Maddison's (1990) CCT, we first had to randomly resolve polytomies using MacClade. An additional requirement of the CCT is that all data should be dichotomous. We created frequency distribution plots of repertoire and home range size and then used the median value to split the data for each variable into two discrete states. Species with greater than the median number of display modifiers (4; range: 0–8) were scored as having large modifier repertoires, while those with less than or equal to this number were scored as having small modifier repertoires. Similarly, species with smaller than or equal to the median home range size (mass-free residual −0.13; range: −2.04–1.83) were considered to have small home ranges. All other traits were inherently dichotomous.

We reconstructed five alternative parsimony-based ancestor states and applied the CCT to each. We began by reconstructing ancestor states using Swofford & Maddison's (1987) linear parsimony MINSTATE & MAXSTATE and Maddison's (1991) squared-change parsimony algorithms; the last of these provides identical results to those obtained using generalized least squares and independent contrasts approaches (Martins & Hansen, 1997; Pagel, 1999). MINSTATE and MAXSTATE reconstructions reflect the smallest and largest sets of equally parsimonious values at each node, respectively. Squared-change parsimony minimizes the sum of the squared changes on branches and forces changes to spread out more evenly over the tree. These algorithms are designed for continuously distributed variables; traits that are naturally discrete were therefore reconstructed as if continuous. Areas were then defined manually using the 'fix state' option in MacClade. For continuous variables (i.e. modifier repertoire size and home range size) the median cut-off was used (see above). For discrete variables (i.e. habitat, arboreality and diet), branches with values less than 0.5 were defined as lacking the trait, while those greater than or equal to 0.5 were defined as possessing it.

Finally, we applied the ACCTRAN (which accelerates changes toward the root) and DELTRAN (which delays changes away from the root) linear parsimony algorithms (Swofford & Maddison, 1987). These models require that variables be discrete. Modifier repertoire size and home range size were thus dichotomously transformed prior to ancestor state reconstruction. All other traits were inherently dichotomous.

We used the CCT to examine two hypotheses. First, we examined directional changes in modifier repertoire size. We tested whether evolutionary gains in large repertoire size were more concentrated than expected by chance on branches that also possessed an ecological trait. A significant association would indicate that the trait preceded, or evolved simultaneously with, the evolution of signal complexity. Second, we investigated whether an ecological trait has led to increased variation in repertoire size. We analysed the probability that both gains *and* losses in large repertoire size were associated with an ecological trait: a significant association would reveal that high levels of evolutionary change in signal complexity were associated with the trait.

The CCT has low statistical power and is therefore likely to be conservative (Lorch & Eadie, 1999). Following Ortolani & Caro (1996) and suggestions by Lorch & Eadie (1999), we considered associations with $P < 0.05$ as highly significant, while P-values falling between 0.05 and 0.10 were considered to be marginally significant. Out of 124 different species for which modifier repertoire data were available (Fig. 1), only those species having complete data on the ecological trait of interest, were used in each analysis (range: 28–104 species). The large number of species being investigated prevented us from calculating an exact probability; we report P-values calculated using a simulation algorithm (Maddison & Maddison, 1992) with 10 000 replicates. This method has been shown to provide results consistent with those of exact P-value calculations (Maddison, 1990).

RESULTS

Large modifier repertoire size evolved between two and 19 times across the agamid and iguanid families and has subsequently been lost between one and 18 times, depending on ancestor reconstruction (MINSTATE, MAXSTATE, ACCTRAN, DELTRAN or squared-change parsimony), tree topology (tree 1 or 2; Fig. 1) and the number of species analysed.

We found no consistent relationship between evolutionary gains in large modifier repertoire size and a pre-existing preference for living in closed habitats. There was a marginally significant association using two sets of evolutionary assumptions (tree 2; Fig. 1, MAXSTATE and DELTRAN), but in most cases, closed habitat preference did not generate increases in repertoire size (Table 1; Fig. 2). However, when both gains and losses in large modifier repertoire size were analysed, there was a significant association between changes in repertoire complexity (regardless of direction) and closed habitat preference (Table 1). This suggests that, while living in closed habitats does not select for increased signal complexity, it does increase the probability of evolutionary change.

Small home range size also resulted in greater evolutionary change in modifier repertoire size in several trait resolutions (Table 1). However, both regression analyses (raw species data corrected for body size: d.f. = 27, $R = 0.33$, one-tailed $P = 0.043$; species data corrected for body size and phylogeny (tree 1): d.f. = 27, $R = 0.36$, one-tailed $P = 0.031$; species data corrected for body size and phylogeny (tree 2): d.f. = 27, $R = 0.28$, one-tailed $P = 0.075$) and most trait evolution analyses (Table 1; Fig. 3) revealed a strong tendency for modifier use to be negatively associated with home range size. Thus, the majority of available evidence supports the hypothesis that having a small home range is associated with increased signal complexity.

Finally, in most evolutionary scenarios, there was a tendency for gains in large modifier repertoire size to occur in regions of the phylogenetic tree reconstructed as being arboreal (Table 1; Fig. 4) or possessing a diet of moving prey (Table 1; Fig. 5). These relationships suggest that an arboreal lifestyle and foraging for moving prey may have enabled, or pre-adapted, species to evolve complex signals.

DISCUSSION

Current theories of signal evolution have identified a variety of selective forces that promote or reduce complexity in communicative systems (e.g. female mate choice decisions: Andersson, 1994; male–male competition: Ord *et al*., 2001; properties of the signalling environment: Endler, 1992; receiver sensory biases: Ryan & Rand, 1993; predation risk: Stoddard, 1999; and social complexity: Blumstein & Armitage, 1997). Our analyses of macro-evolutionary trends in lizard display modifier use suggest that ecological factors have also played a role in promoting signal diversity (Fig. 6). Specifically, habitat preference can promote evolutionary plasticity in signal repertoires, while possessing a small home range, arboreal locomotion and a diet of moving prey may facilitate (or be coupled with factors that facilitate) the evolution of complex signals.

SIGNAL DIVERSITY

The evolution of visual displays is clearly constrained by an interaction between properties of receiver sensory systems and those of the environment through which signals must be transmitted (Endler & McLellan, 1988; Endler, 1992; Fleishman, 1992). Many studies have identified directional influences of environmental factors on signal structure (Morton, 1975; Wiley & Richards, 1982; Endler, 1987, 1992; Ryan *et al*., 1990; Fleishman, 1992; Marchetti, 1993; Losos & Chu, 1998). In contrast, we have found that closed habitat choice is significantly associated with high levels of evolutionary lability, suggesting that closed habitats promote a wide range of adaptive solutions for signal design (Fig. 6). Few previous studies have suggested that the environment produces greater levels of signal diversity (although see Alexander, 1962).

At least two non-mutually exclusive hypotheses may explain the evolution of signal diversity in closed habitats. First, because of the conservative nature of the lizard visual system (Fleishman *et al*., 1995), there is a certain amount of evolutionary inertia in sensory processes. Thus, when distantly related species occur in similar habitats, variation in signal repertoires may

Table 1. The influence of four ecological factors on the evolution of large repertoire size in iguanian lizards

			Directional change				Variable change			
			Tree 1		Tree 2		Tree 1		Tree 2	
Trait	No. of species[a]	Reconstruction	No. of gains and losses[b]	*P*	No. of gains and losses[b]	*P*	No. of gains and losses[c]	*P*	No. of gains and losses[c]	*P*
Closed habitat	103	Linear parsimony								
		MINSTATE	G10 L8/G2	ns	G9 L8/G2	ns	G10 L8/G2 L4	0.004	G9 L8/G2 L3	0.020
		MAXSTATE	G5 L18/G1	ns	G6 L17/G3	0.098	G5 L18/G1 L5	0.023		
		ACCTRAN	G11 L5/G3	ns	G9 L6/G3	ns	G11 L5/G3 L3	0.013	G9 L6/G3 L4	0.002
		DELTRAN	G13 L3/G3	ns	G12 L3/G4	0.087	G13 L3/G3 L3	0.002		
		Squared-change parsimony	G13 L8/G3	ns	G10 L6/G2	ns	G13 L8/G3 L3	0.033	G10 L6/G2 L3	0.037
Small home range	28	Linear parsimony								
		MINSTATE	G6 L4/G5	0.061	G8 L1/G7	0.004				
		MAXSTATE	G2 L7/G1	ns	G6 L2/G5	0.050	G2 L7/G1 L3	ns		
		ACCTRAN	G5 L3/G4	ns	G3 L5/G2	ns	G5 L3/G4 L2	0.020	G3 L5/G2 L5	0.004
		DELTRAN	G7 L1/G6	0.011	G7 L1/G6	0.011				
		Squared-change parsimony	G5 L6/G4	0.052	G6 L6/G4	ns			G6 L6/G4 L4	0.049
Arboreality	104	Linear parsimony								
		MINSTATE	G14 L2/G4	ns	G11 L3/G5	0.042	G14 L2/G4 L1	0.065		
		MAXSTATE	G10 L6/G5	0.052	G9 L5/G4	ns			G9 L5/G4 L2	0.035
		ACCTRAN	G11 L6/G5	0.039	G10 L4/G5	0.068				
		DELTRAN	G15 L2/G5	0.112	G11 L3/G5	0.101				
		Squared-change parsimony	G13 L8/G4	ns	G9 L7/G3	ns	G13 L8/G4 L2	0.069	G9 L7/G3 L3	0.036
Moving prey diet	96	Linear parsimony								
		MINSTATE	G18 L2/G14	ns	G15 L2/G11	0.092	G18 L2/G14 L2	ns		
		MAXSTATE	G8 L12/G5	0.016	G10 L8/G7	0.061				
		ACCTRAN	G9 L10/G7	0.089	G11 L6/G8	0.107				
		DELTRAN	G19 L1/G15	0.028	G13 L4/G9	0.044				
		Squared-change parsimony	G12 L12/G9	0.105	G12 L9/G8	0.034				

The number of evolutionary gains and losses were calculated following alternative ancestor state reconstructions by parsimony using MacClade v. 3.08a (Maddison & Maddison, 1992, 1999). Directional evolutionary change (i.e. increases in large repertoire size) was investigated by determining the number of gains in large repertoire size occurring on branches of the tree also possessing the ecological trait, and whether this distribution could be attributed to chance alone, using Maddison's (1990) concentrated-changes test. Similarly, greater evolutionary variation in repertoire size was investigated by determining the number of both gains and losses in large repertoire size occurring on branches of the tree also possessing the ecological trait and whether this distribution was due to chance alone. Results are given for ancestor reconstructions produced by both tree 1 (Fig. 1a) and tree 2 (Fig. 1b). 'ns' = not significant.

[a] Total number of species with available data.

[b] Total number of gains (G) and losses (L) in large repertoire size against number of gains (G) in large repertoire size on branches also possessing the ecological trait.

[c] Total number of gains (G) and losses (L) in large repertoire size against number of gains (G) and losses (L) in large repertoire size on branches also possessing the ecological trait.

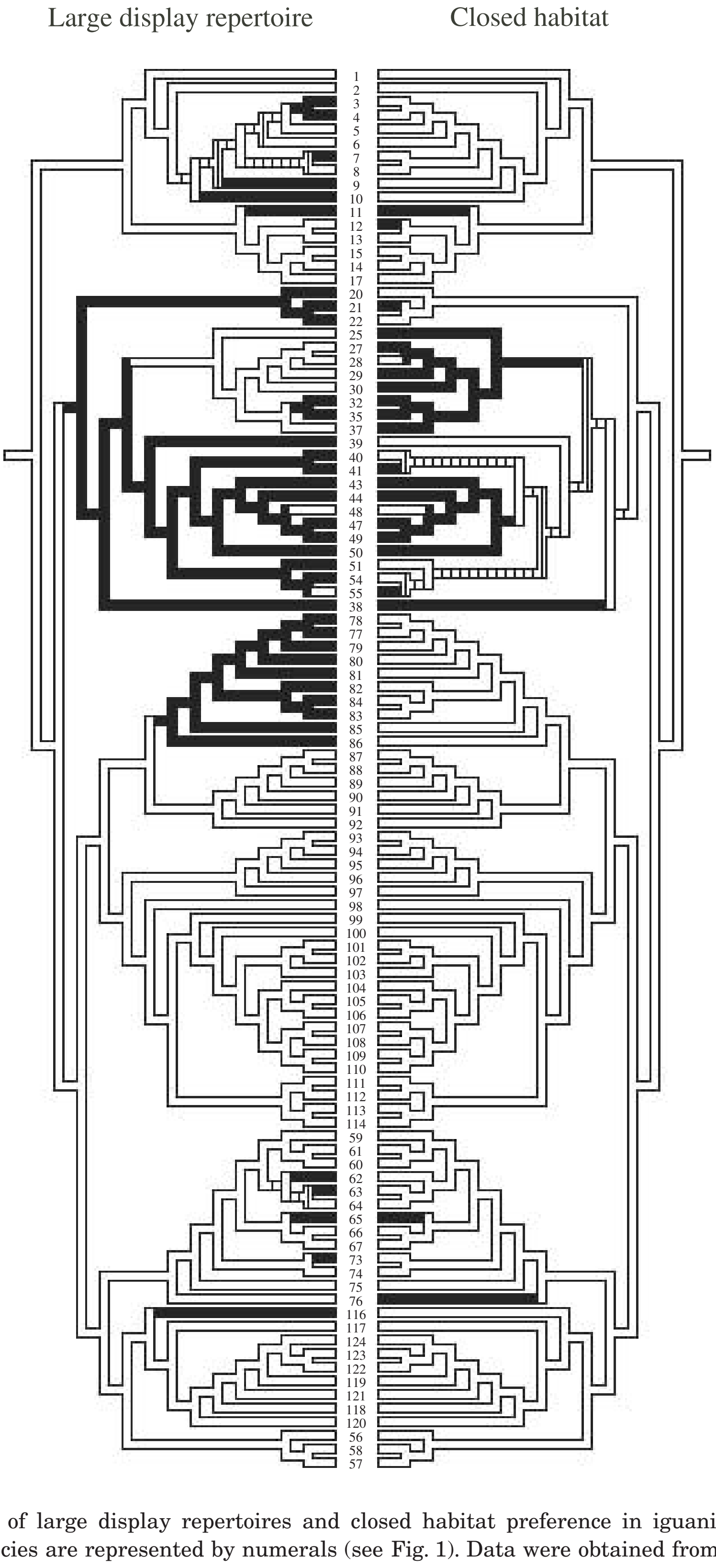


Figure 2. The evolution of large display repertoires and closed habitat preference in iguanian lizards reconstructed assuming parsimony. Species are represented by numerals (see Fig. 1). Data were obtained from a variety of sources (see Appendix). ■ = trait present, □ = trait absent, ▥ = equivocal reconstruction. Large repertoire size was assumed to be absent following outgroup analysis at the ancestral node (see Ord *et al.*, 2001).

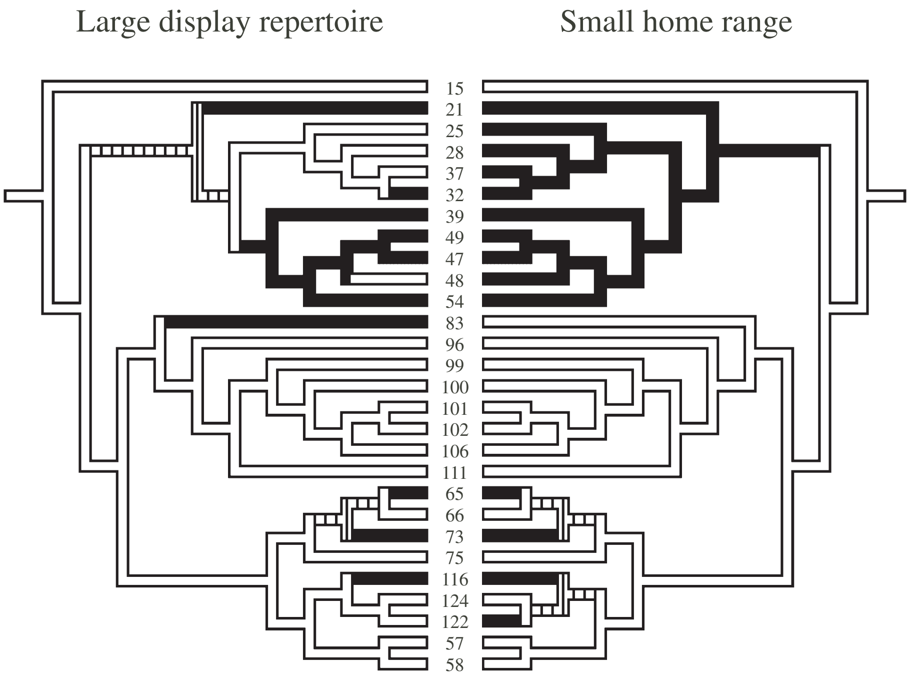


Figure 3. The evolution of large display repertoires and small home range size in iguanian lizards. See Fig. 2 legend for details.

reflect historical constraints on the visual system of each species.

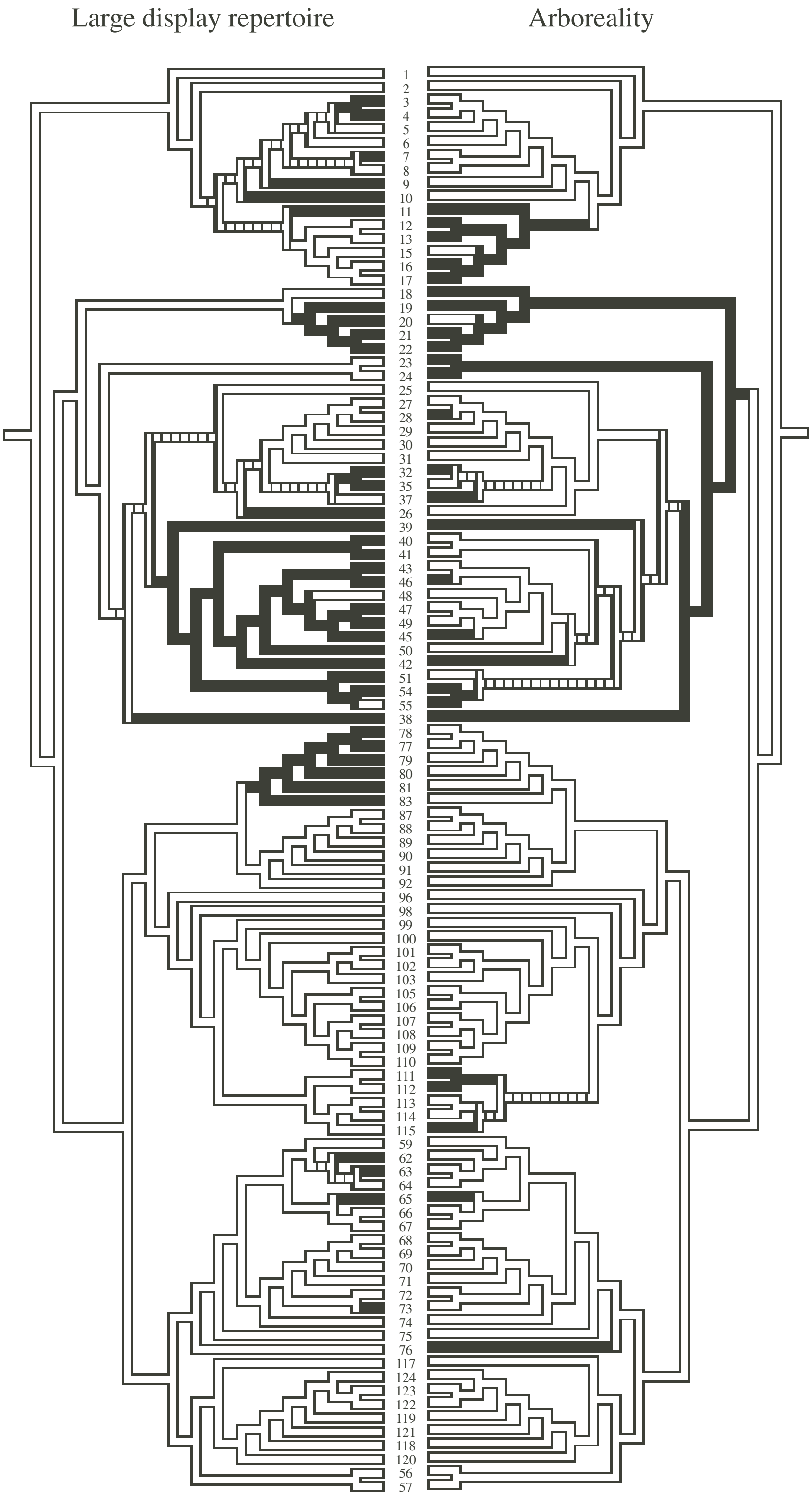
Alternatively, the closed habitat species in our analyses are largely anoles (Fig. 2) that occur in tropical environments. Some tropical habitats support a diversity of species, in part because of the opportunity to partition a complex environment (Brooks & McLennan, 1991). There is thus the potential for species groups living in such environments to possess considerable diversity in 'microhabitat' preference. Adaptation to microhabitats is known to produce differences in anoline morphology and behaviour (Losos, 1990a,b). It is hence conceivable that, as overall habitat complexity increases, the proliferation of potential microhabitats leads to a greater range of selective forces acting on signal design, resulting in the observed variation in modifier repertoire size evolution.

SIGNAL COMPLEXITY

Selection has apparently favoured the coevolution of complex signalling behaviour with small home range size (Fig. 6). We have previously found that increased male–male competitive intensity (as reflected by SSD) is also associated with an increasingly elaborate modifier repertoire (Ord *et al*., 2001). It is therefore tempting to speculate that species possessing small home ranges will consequently experience high levels of male–male competition, at least when habitats are saturated. The maximum distance at which a visual display can be detected is correlated with territory size in at least one species (*A. auratus*; Fleishman, 1992). Display rate has consistently been found to increase dramatically with decreases in inter-male distance (Hover & Jenssen, 1976; Scott, 1984; Losos, 1985a; Decourcy & Jenssen, 1994). The perceptual constraints on signal design are relaxed at short range, and complex signals may consequently have evolved in species that often interact in this way.

However, while high densities cause some reduction in the home range size of male lizards (Stamps, 1990), the principal effect is of greater home range overlap (Stamps, 1977, 1990; Stamps & Krishnan, 1998). We suggest that a direct test of the relationship between modifier use and population density will be necessary to evaluate the probability that complex signals have evolved in response to demographic pressures.

The traits of arboreality and feeding on mobile prey both facilitate the evolution of complex signals (Fig. 6). Motion perception (i.e. the ability to detect and localize moving objects) is critical for feeding on small fast-moving prey items (Jenssen & Swenson, 1974; Fleishman, 1992; Fleishman *et al*., 1995). Similarly, the need quickly to negotiate a complex habitat (Jenssen & Swenson, 1974) is likely to select for enhanced sensory processing. Analyses of retinal structure in anoles have revealed that they possess both a temporal and a central fovea (Fite & Lister,


Large display repertoire

Arboreality

Figure 4. The evolution of large display repertoires and arboreality in iguanian lizards. See Fig. 2 legend for details.

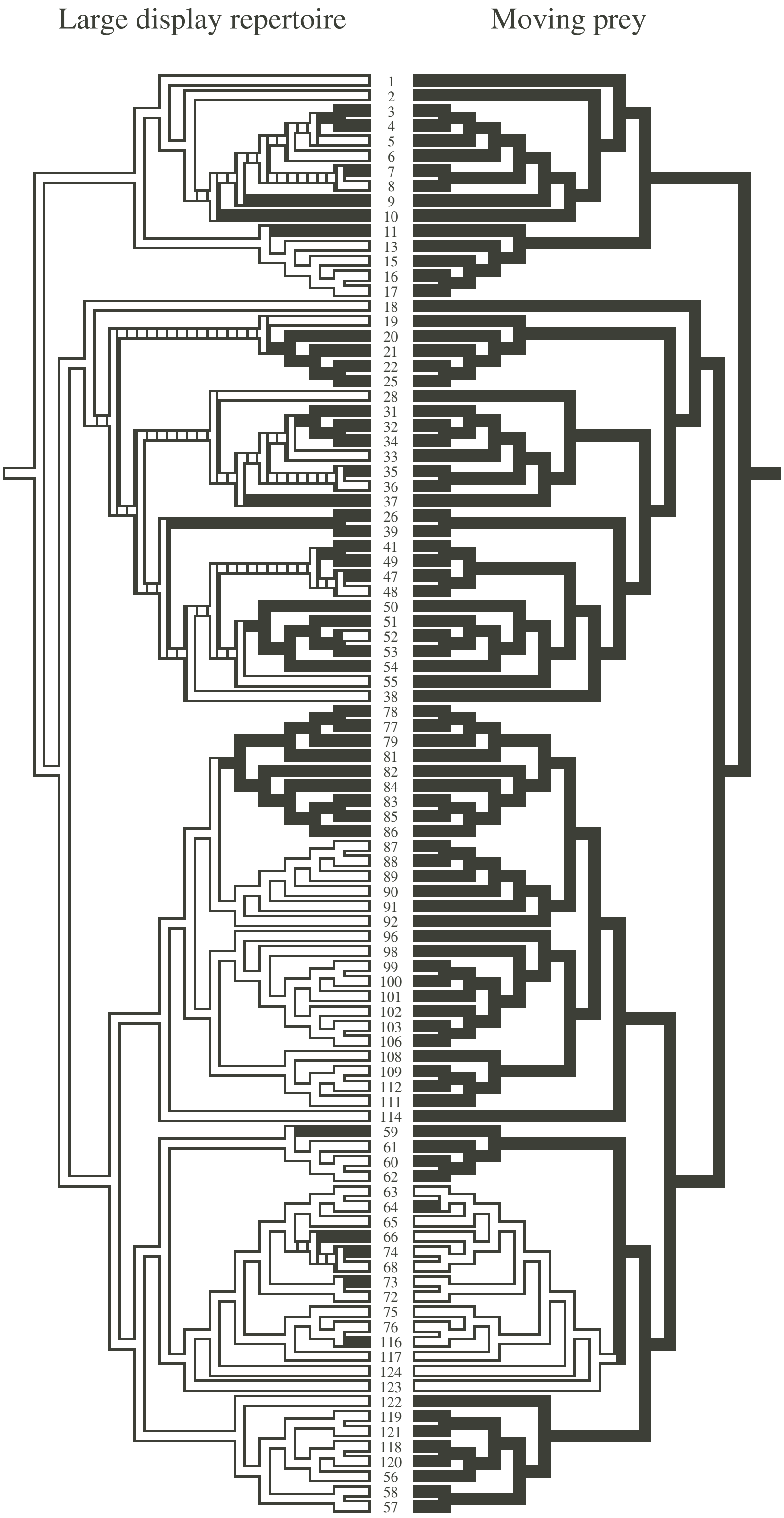


Figure 5. The evolution of large display repertoires and feeding on moving prey in iguanian lizards. See Fig. 2 legend for details.

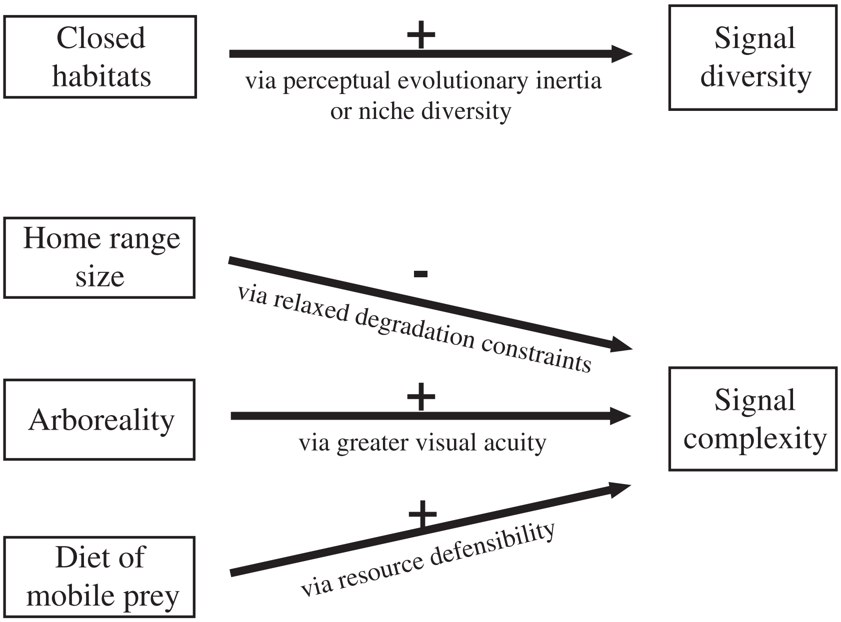


Figure 6. Summary of ecological forces acting on visual signal evolution in lizards. + indicates a positive influence, while – denotes a negative influence.

1981). Such bifoveal vision is believed to maximize spatial resolution and visual acuity, allowing capture of small prey, and has otherwise only been reported in raptors (Fite & Lister, 1981). Signals are designed to exploit the perceptual characteristics of receivers (Guilford & Dawkins, 1991; Bradbury & Vehrencamp, 1998). For example, in lizards, the motion pattern of introductory display components is tailored to effectively stimulate the periphery of the visual field and attract the receiver's attention before the more information-rich portion of the display is delivered (Fleishman, 1988a, b, 1992). Visual system performance will similarly influence the design of other display components by defining the visual cues that can be efficiently detected or discriminated. Improvements in the resolution and/or acuity of the visual system may thus have enabled the evolution of more complex display patterns.

Alternatively, the association between repertoire complexity and diet may reflect differences in sociality. Food abundance for insectivores is relatively uniform compared to the typically fluctuating food resources of many herbivores (see Stamps, 1983 and references therein). This patchiness, and the consequent difficulty in defending food resources for herbivores, may have limited the evolution of territoriality, promoting instead non-aggressive aggregations for exploiting clumped resources (Stamps, 1977, 1983). The low frequency of aggressive interactions in herbivores may have relaxed selection for complex signals to mediate territorial disputes.

In closing, we note that, while it is important to identify all of the selective forces acting on signal design, the mechanisms through which these act must be explored if we are to develop a truly comprehensive model to explain the evolution of communicative systems. Comparative studies of lizard displays reveal that ecological factors sometimes act directionally, but that they can also promote greater lability in signal evolution (Fig. 6). We anticipate the possibility of similar processes occurring in other taxa.

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APPENDIX

SOURCES CONSULTED FOR SPECIES DATA

Species	Repertoire size	Habitat preference	Home range size (m^2)	Body size (mm SVL)	Locomotion	Diet	References*
Acanthocercus atricollis	0	nd	nd		arboreal	moving prey	1–2
Agama agama	4	other	nd		arboreal	moving prey	2
Amblyrhynchus cristatus	5	other	nd		semiarboreal/terrestrial	non-moving prey	3–6
Amphibolurus muricatus	2	other	nd		semiarboreal/terrestrial	moving prey	7–10
Anolis acutus	2	closed	11	66	arboreal	moving prey	11–13
A. aeneus	5	closed	7	60	arboreal	moving prey	14–21
A. auratus	3	other	10	51	semiarboreal/terrestrial	moving prey	13,22–24
A. brevirostris	1	closed	nd		semiarboreal/terrestrial	nd	25
A. carolinensis	8	closed	nd		arboreal	moving prey	13,26–41
A. carpenteri	5	other	nd		semiarboreal/terrestrial	nd	42
A. caudalis	3	closed	nd		semiarboreal/terrestrial	nd	25
A. chlorocyanus	4	nd	nd		arboreal	nd	43,44
A. coelestinus	3	nd	nd		arboreal	nd	44
A. conspersus	3	nd	nd		nd	moving prey	36
A. cooki	6	nd	nd		nd	moving prey	45
A. cristatellus	6	closed	1	70	arboreal	moving prey	11,13,45
A. cupreus	5	closed	35	55	semiarboreal/terrestrial	moving prey	12,13,42
A. cybotes	4	nd	nd		semiarboreal/terrestrial	moving prey	46–50
A. distichus‡	2	other	16	50	arboreal	moving prey	12,13,50,51
A. equestris	4	nd	nd		arboreal	moving prey	31,52
A. evermanni	6	nd	nd		nd	moving prey	45
A. grahami	4	closed	nd		arboreal	moving prey	36,51
A. gundlachi	6	closed	nd		semiarboreal/terrestrial	moving prey	13,45,51
A. humilis	5	closed	nd		semiarboreal/terrestrial	moving prey	13,45
A. intermedius	5	nd	nd		arboreal	nd	42
A. limifrons	5	closed	nd		semiarboreal/terrestrial	moving prey	13,42,53,54
A. lineatopus	5	other	45	70	arboreal	moving prey	12,13,51,55
A. luciae	5	nd	nd		arboreal	moving prey	21,51
A. marcanoi	5	nd	nd		semiarboreal/terrestrial	moving prey	46–48
A. monensis	6	nd	nd		nd	moving prey	45
A. nebulosus	5	closed	2	42	semiarboreal/terrestrial	moving prey	13,56–59
A. opalinus	8	other	nd		semiarboreal/terrestrial	moving prey	13,51,60,61
A. pentaprion	5	nd	nd		arboreal	nd	42
A. roquet‡	6	other	nd		arboreal	moving prey	21,51
A. sagrei‡	6	other	18	55	arboreal	moving prey	12,13,27,32,36, 41,49,51
A. sericeus	5	nd	nd		arboreal	nd	42
A. townsendi	5	closed	nd		nd	nd	62,63
A. trinitatis	6	other	nd		semiarboreal/terrestrial	moving prey	20,21,51
A. tropidolepis	5	closed	nd		semiarboreal/terrestrial	nd	42
A. valencienni†	0	nd	nd		nd	moving prey	64
A. websteri	1	closed	nd		semiarboreal/terrestrial	nd	25
Brachylophus fasciatus	3	closed	nd		arboreal	non-moving prey	5,38,51,65
Callisaurus draconoides	5	other	nd		nd	moving prey	51,66
Chalarodon madagascariensis	5	other	79	87	nd	moving prey	67
Chamaelinorops barbouri	2	closed	1	41	semiarboreal/terrestrial	moving prey	68
Conolophus pallidus	4	other	nd		semiarboreal/terrestrial	non-moving prey	5,69
C. subcristatus	6	other	nd		semiarboreal/terrestrial	non-moving prey	5,69
Cophosaurus texanus	5	other	nd		nd	moving prey	66
Crotaphytus collaris	4	other	nd		semiarboreal/terrestrial	moving prey	38,51,70–72
Ctenophorus decresii	5	other	nd		semiarboreal/terrestrial	moving prey	8,73
C. fionni	5	other	nd		semiarboreal/terrestrial	moving prey	8,73
C. fordi	1	other	nd		semiarboreal/terrestrial	moving prey	8,74,75
C. maculosus	4	other	801	69	semiarboreal/terrestrial	moving prey	76,77
C. nuchalis	5	other	nd		semiarboreal/terrestrial	moving prey	7,10
C. pictus	2	other	nd		semiarboreal/terrestrial	moving prey	10,78

APPENDIX *Continued*

Species	Repertoire size	Habitat preference	Home range size (m^2)	Body size (mm SVL)	Locomotion	Diet	References*
C. vadnappa	5	other	nd		semiarboreal/terrestrial	moving prey	8,10,73
Ctenosaura hemilopha	4	other	nd		nd	non-moving prey	5,79,80
C. quiquecarinata	0	other	nd		nd	moving prey	5,51
C. similis	1	other	nd		semiarboreal/terrestrial	non-moving prey	5,38,51,81
Cyclura carinata	5	other	1924	267	semiarboreal/terrestrial	non-moving prey	5,6,12,82–84
C. collei	0	nd	nd		semiarboreal/terrestrial	nd	6,82
C. cornuta	2	other	nd		semiarboreal/terrestrial	non-moving prey	5,6,38,51,82,85
C. cychlura	3	nd	nd		semiarboreal/terrestrial	nd	5,6,82
C. nubila	1	nd	nd		semiarboreal/terrestrial	non-moving prey	5,6,38,82,86
C. ricordi	0	nd	nd		semiarboreal/terrestrial	non-moving prey	6,82,85
C. rileyi	0	nd	nd		semiarboreal/terrestrial	nd	5,6,82
Dipsosaurus dorsalis	3	other	1069	144	semiarboreal/terrestrial	non-moving prey	5,12,84,87–89
Draco spilopterus	1	closed	nd		arboreal	nd	4,51
Gambelia sila	4	other	2100	97	nd	moving prey	12,90,91
G. wislizenii	3	other	23 205	102	semiarboreal/terrestrial	moving prey	12,38,51,91,92
Holbrookia lacerata	5	other	nd		nd	moving prey	66
H. maculata	5	other	2205	60	semiarboreal/terrestrial	moving prey	66,84
H. propinqua	5	other	nd		nd	moving prey	66,93–96
Hydrosaurus pustulatus	5	closed	nd		arboreal	moving prey	51,96
Iguana iguana	7	closed	1333	360	arboreal	non-moving prey	5,12,97–100
Leiocephalus carinatus	3	other	nd		semiarboreal/terrestrial	moving prey	38,51,101
Lophognathus temporalis	1	other	nd		semiarboreal/terrestrial	moving prey	8,10,102
Lyriocephalus scutatus†	0	other	nd		arboreal	moving prey	31,51
Microlophus albemarlensis	4	other	374	104	semiarboreal/terrestrial	moving prey	12,38,51,103
M. bivittatus	4	other	nd		semiarboreal/terrestrial	moving prey	38,51,103
M. delanonis	4	other	252	129	semiarboreal/terrestrial	moving prey	12,38,51,103
M. duncanensis	4	other	nd		semiarboreal/terrestrial	moving prey	38,51,103
M. grayii	4	other	nd		semiarboreal/terrestrial	moving prey	38,51,103
M. habelii	4	other	nd		semiarboreal/terrestrial	moving prey	38,51,103
M. pacificus	4	other	nd		semiarboreal/terrestrial	moving prey	38,51,103
Petrosaurus mearnsi	2	other	nd		semiarboreal/terrestrial	moving prey	51,104–107
Phrynocephalus arabicus†	0	other	nd		nd	nd	108
P. maculatus†	0	other	nd		semiarboreal/terrestrial	moving prey	109
Phrynosoma cornutum	0	other	nd		semiarboreal/terrestrial	moving prey	72,110
P. coronatum	0	other	nd		semiarboreal/terrestrial	moving prey	72,110
P. douglassii	0	other	nd		semiarboreal/terrestrial	moving prey	72,110
P. modestum	0	other	nd		semiarboreal/terrestrial	moving prey	72,110
P. platyrhinos	0	other	nd		semiarboreal/terrestrial	moving prey	72,110
P. solare	0	other	nd		semiarboreal/terrestrial	moving prey	72,110
Pogona barbata	6	other	nd		semiarboreal/terrestrial	moving prey	7,8,31,111,112
Sauromalus ater	1	other	nd		semiarboreal/terrestrial	nd	5,6,38
S. obesus	4	other	12 610	164	semiarboreal/terrestrial	non-moving prey	5,6,12,38,113
Sceloporus cyanogenys	2	other	nd		semiarboreal/terrestrial	moving prey	51,114
S. dugesii	2	other	nd		semiarboreal/terrestrial	nd	114
S. graciosus	4	other	47	57	semiarboreal/terrestrial	moving prey	115–119
S. jarrovii	4	other	489	97	semiarboreal/terrestrial	moving prey	12,51,114,119–122
S. magister	2	other	nd		semiarboreal/terrestrial	moving prey	51,123
S. merriami	4	other	201	58	semiarboreal/terrestrial	moving prey	24,106,119,122,124,125
S. mucronatus	2	other	nd		semiarboreal/terrestrial	nd	114
S. occidentalis	2	other	6801	70	semiarboreal/terrestrial	moving prey	12,51,107,119,121,126–128
S. ornatus	2	other	nd		semiarboreal/terrestrial	nd	51,106,114
S. poinsetti	2	other	nd		semiarboreal/terrestrial	moving prey	51,114
S. torquatus	2	other	nd		nd	nd	114
S. undulatus‡	3	other	446	83	semiarboreal/terrestrial	moving prey	49,84,117–119,121,129–131
Uma exsul	7	other	nd		semiarboreal/terrestrial	moving prey	132

APPENDIX *Continued*

Species	Repertoire size	Habitat preference	Home range size (m^2)	Body size (mm SVL)	Locomotion	Diet	References*
U. inornata	6	other	nd		semiarboreal/terrestrial	moving prey	132,133
U. notata	6	other	nd		semiarboreal/terrestrial	moving prey	132,133
U. paraphygas	7	other	nd		semiarboreal/terrestrial	nd	132
U. scoparia	6	other	nd		semiarboreal/terrestrial	moving prey	132,133
Urosaurus bicarinatus	0	nd	nd		arboreal	nd	105,106
U. graciosus	2	other	nd		arboreal	moving prey	51,104–106
U. microscutatus	0	other	nd		semiarboreal/terrestrial	moving prey	51,105,106
U. nigricaudus	0	other	nd		semiarboreal/terrestrial	nd	105,106
U. ornatus	2	other	154	53	arboreal	moving prey	84,105,125, 134–142
Uta antigua	2	other	nd		nd	nd	51,105,143
U. nolascensis	2	other	nd		nd	nd	51,105,143
U. palmeri	2	other	nd		nd	nd	51,105,143
U. squamata	3	other	nd		nd	nd	105,121,143, 144
U. stansburiana	4	other	1033	54	semiarboreal/terrestrial	moving prey	12,51,84,104, 105,143–145

'nd' = no data, all traits defined in text.

*1. Cowles (1956); 2. Harris (1964); 3. Carpenter (1966a); 4. Schmidt (1935); 5. Carpenter (1982); 6. De Queiroz (1987); 7. Carpenter, Badham & Kimble (1970); 8. Cogger (1996); 9. Groom (1973); 10. Wilson & Knowles (1988); 11. Philibosian (1975); 12. Stamps (1983); 13. Andrews (1979); 14. Stamps & Barlow (1973); 15. Stamps (1978); 16. Stamps & Crews (1976); 17. Stamps (1976); 18. Stamps (1973); 19. Stamps & Krishnan (1994); 20. Gorman (1969); 21. Gorman (1968); 22. Fleishman (1988a); 23. Fleishman (1992); 24. Fleishman (1988c); 25. Jenssen & Gladson (1984); 26. Cooper (1977); 27. Tokarz & Beck (1987); 28. Jenssen, Greenberg & Hovde (1995); 29. Evans (1935); 30. McMann (1993); 31. Bels (1992); 32. Evans (1938a); 33. Greenberg & Noble (1944); 34. Crews (1975); 35. Greenberg (1977); 36. Macedonia & Stamps (1994); 37. Mason & Adkins (1976); 38. Ackerman (1998); 39. Greenberg, Chen & Crews (1984); 40. Decourcy & Jenssen (1994); 41. Evans (1938b); 42. Echelle *et al*. (1971); 43. Bels (1986); 44. Garcea & Gorman (1968); 45. Ortiz & Jenssen (1982); 46. Losos (1985a); 47. Losos (1985b); 48. Macedonia, Evans & Losos (1994); 49. Noble & Teale (1930); 50. Jenssen (1983); 51. Rogner (1997); 52. Font & Kramer (1989); 53. Jenssen & Hover (1976); 54. Hover & Jenssen (1976); 55. Rand (1967); 56. Jenssen (1970a); 57. Jenssen (1971); 58. Jenssen (1970b); 59. Lister & Aguayo (1992); 60. Jenssen (1979a); 61. Jenssen (1979b); 62. Jenssen & Rothblum (1977); 63. Carpenter (1965); 64. Hicks & Trivers (1983); 65. Greenberg & Jenssen (1982); 66. Clarke (1965); 67. Blanc & Carpenter (1969); 68. Jenssen & Feely (1991); 69. Carpenter (1969); 70. Yedlin & Ferguson (1973); 71. Fitch (1956); 72. Greenberg (1945); 73. Gibbons (1979); 74. Webber (1981); 75. Cogger (1978); 76. Mitchell (1973); 77. Greer (1989); 78. Mayhew (1963); 79. Carothers (1981); 80. Brattstrom (1974); 81. Henderson (1973); 82. Martins & Lamont (1998); 83. Iverson (1979); 84. Christian & Waldschmidt (1984); 85. Carey (1975); 86. Buide (1951); 87. Carpenter (1961a); 88. Norris (1953); 89. Parker (1972); 90. Montanucci (1965); 91. Tollestrup (1983); 92. Montanucci (1967); 93. Cooper (1985); 94. Cooper & Guillette (1991); 95. Cooper (1988); 96. Gonzales (1974); 97. Dugan (1982); 98. Distel & Veazey (1982); 99. Lazell (1973); 100. Swanson (1950); 101. Evans (1953); 102. Blamires (1998); 103. Carpenter (1966b); 104. Carpenter (1962); 105. Purdue & Carpenter (1972a); 106. Wiens (1993); 107. Stebbins (1966); 108. Ross (1995); 109. Ross (1989); 110. Lynn (1965); 111. Brattstrom (1971); 112. Lee & Badham (1963); 113. Nagy (1973); 114. Hunsaker (1962); 115. Martins (1991); 116. Martins (1993a); 117. Ferguson (1971); 118. Ferguson (1973); 119. Martins (1994); 120. Ruby (1977); 121. Ransom (1981); 122. Martins (1993b); 123. Vitt *et al*. (1974); 124. Carpenter (1961b); 125. Milstead (1970); 126. Tarr (1982); 127. Fitch (1940); 128. Purdue & Carpenter (1972b); 129. Cooper & Burns (1987); 130. Rothblum & Jenssen (1978); 131. Roggenbuck & Jenssen (1986); 132. Carpenter (1967); 133. Carpenter (1963); 134. Carpenter & Grubitz (1961); 135. Mahrt (1998); 136. Thompson & Moore (1992); 137. Carpenter & Grubitz (1960); 138. Zucker (1987); 139. M'Closkey, Deslippe & Szpak (1990); 140. Zucker (1989); 141. Deslippe *et al*. (1990); 142. M'Closkey, Biana & Russell (1987); 143. Ferguson (1970a); 144. Ferguson (1970b); 145. Ferguson (1966).

†Species not possessing core displays.

‡Species typically found in numerous habitats.