Ecology and signal evolution in lizards

TERRY J. ORD1*, DANIEL T. BLUMSTEIN2 and CHRISTOPHER S. EVANS3

1Department of Biological Sciences, Macquarie University, Sydney NSW 2109, Australia
2Department of Organismic Biology, Ecology, and Evolution, University of California, Los Angeles, CA 90095–1606 USA
3Department of Psychology, Macquarie University, Sydney NSW 2109, Australia.

Received 13 February 2002; accepted for publication 10 June 2002

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.

ADDITIONAL KEYWORDS: Agamidae – arboreality – comparative method – diet – display behaviour – habitat – home range – Iguanidae – repertoire size – visual communication.

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, 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

*Correspondence. Present address: Department of Biology, Indiana University, Bloomington, IN 47405 USA.
E-mail: tord@bio.indiana.edu.
Marten typically given (Morton, 1975; Marten & Marler, 1977; mission range in bird song is maximized by tailoring of acoustic communication have shown that 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 signaler 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 habitats (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 sig-
nals 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 iguanid 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 m². 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 predominantly 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/~netz/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. carperteri, A. intermedius, A. sericus, 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. mcroronatus 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.
ECOLOGICAL INFLUENCES ON SIGNAL EVOLUTION

© 2002 The Linnean Society of London, Biological Journal of the Linnean Society, 2002, 77, 127–148
equal to this number were scored as having small modifier repertoires, while those with less 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).
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

| Trait            | No. of speciesa | Reconstruction | Directional change | Variable change |
|------------------|-----------------|----------------|-------------------|-----------------|
|                  |                 |                | Tree 1            | Tree 2          | Tree 1          | Tree 2          |
|                  |                 |                | No. of gains and lossesb | P | No. of gains and lossesb | P | No. of gains and lossesc | P |
|                  |                 |                | No. of gains and lossesb | P | No. of gains and lossesc | P |
| Closed habitat   | 103             | Linear parsimony | MINSTATE G10 L8/G2 ns | G9 L8/G2 ns | G10 L8/G2 ns | G9 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 | G11 L5/G3 L3 0.013 | G9 L6/G3 L4 0.002 |
|                  |                 |                | ACCTRAN G11 L5/G3 ns | G9 L6/G3 ns | G13 L3/G3 L3 0.002 | G13 L8/G3 L3 0.033 | G10 L6/G2 L3 0.037 |
|                  |                 |                | DELTRAN G13 L3/G3 ns | G12 L3/G4 0.087 | G13 L8/G3 L3 0.033 | G10 L6/G2 L3 0.037 |
|                  |                 |                | 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 | G2 L7/G1 L3 ns | G5 L3/G4 L2 0.020 | G3 L5/G2 L5 0.004 |
|                  |                 |                | MAXSTATE G2 L7/G1 ns | G6 L2/G5 0.050 | G5 L3/G4 L2 0.020 | G3 L5/G2 L5 0.004 |
|                  |                 |                | ACCTRAN G5 L3/G4 ns | G3 L5/G2 ns | G6 L2/G5 0.050 | G5 L3/G4 L2 0.020 | G3 L5/G2 L5 0.004 |
|                  |                 |                | DELTRAN G7 L1/G6 0.111 | G7 L1/G6 0.111 | 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 | G9 L5/G4 L2 0.035 |
|                  |                 |                | MAXSTATE G10 L6/G5 0.052 | G9 L5/G4 ns | G14 L2/G4 L1 0.065 | G9 L5/G4 L2 0.035 |
|                  |                 |                | ACCTRAN G11 L6/G5 0.039 | G10 L4/G5 0.068 | G13 L8/G4 L2 0.069 | G9 L7/G3 L3 0.036 |
|                  |                 |                | DELTRAN G15 L2/G5 0.112 | G11 L3/G5 0.101 | G13 L8/G4 L2 0.069 | G9 L7/G3 L3 0.036 |
|                  |                 |                | 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 | G18 L2/G14 L2 ns |
|                  |                 |                | MAXSTATE G8 L12/G5 0.016 | G10 L8/G7 0.061 | G18 L2/G14 L2 ns | G18 L2/G14 L2 ns |
|                  |                 |                | ACCTRAN G9 L10/G7 0.089 | G11 L6/G8 0.107 | G18 L2/G14 L2 ns | G18 L2/G14 L2 ns |
|                  |                 |                | DELTRAN G19 L1/G15 0.028 | G13 L4/G9 0.044 | G18 L2/G14 L2 ns | G18 L2/G14 L2 ns |
|                  |                 |                | Squared-change parsimony G12 L12/G9 0.105 | G12 L9/G8 0.034 | G18 L2/G14 L2 ns | G18 L2/G14 L2 ns |

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.

aTotal number of species with available data.
bTotal 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.
cTotal 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).
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, 1995).

---

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

ACKNOWLEDGEMENTS

We thank Jon Losos, Emília Martins and John Wiens for advice on iguanid phylogeny and comments on our phylogenetic selection criteria; Scott Hocknull for advice on agamid phylogeny and Allen Greer for sharing unpublished phylogenetic hypotheses; Charlie Nunn for advice on concentrated-changes test methodology; and Linda Evans for comments on a previous version of the manuscript. We are also indebted to the staff of the Macquarie University Library for tracking down and obtaining many sources used in this study. T.J.O. was supported by a Macquarie University postgraduate award, the Macquarie University postgraduate research fund, the Australian Geographic Society, a Sigma Xi Grant-in-Aid of Research and Rufunsa Technology Services, D.T.B. by an Australian Research Council postdoctoral fellowship and C.S.E. by an Australian Research Council grant. This
research was conducted as partial fulfillment of a doctoral thesis for T.J.O at Macquarie University.

REFERENCES

Ackerman DV. 1998. The biology of reptiles: the biology, husbandry and health care of reptiles. Neptune City: TFH Publications.

Adest GA. 1977. Genetic relationships in the genus Uma (Iguanidae). Copeia 1977: 47–52.

Alexander RD. 1962. Evolutionary change in cricket acoustical communication. Evolution 16: 443–467.

Andersson M. 1994. Sexual selection. Princeton: Princeton University Press.

Andrews RM. 1979. Evolution of life histories: a comparison of Anolis lizards from matched island and mainland habitats. Breviora 454: 1–51.

Bels VL. 1986. Analysis of the display-action-pattern of Anolis chlorocyanus (Sauria: Iguanidae). Copeia 1986: 963–970.

Bels VL. 1992. Functional analysis of the ritualized behavioral motor pattern in lizards: Evolution of behaviour and the concept of ritualization. Zoologische Jabrabuecher Anatony 122: 141–159.

Benton MJ. 1999. The history of life: Large databases in paleontology. In: Harper, DAT, ed. Numerical paleontology. Chichester: John Wiley & Sons, 249–283.

Blamires SJ. 1998. Circumbution and head bobbing in the agamid lizard Lophognathus temporalis. Herpetofauna 28: 51–52.

Blanc CP, Carpenter CC. 1969. Studies on the Iguanidae of Madagascar. III. Social and reproductive behavior of Chabaredon madagascariensis. Journal of Herpetology 3: 125–134.

Blumstein DT, Armitage KB. 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling scurid alarm calls. American Naturalist 150: 179–200.

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland: Sinauer Associates.

Brattstrom BH. 1971. Social and thermoregulatory behavior of the bearded dragon, Amphibolurus barbatus. Copeia 1971: 484–497.

Brattstrom BH. 1974. The evolution of reptilian social behavior. American Zoologist 14: 35–49.

Brooks DR, McLennan DA. 1991. Phylogeny, ecology, and behavior. Chicago: University of Chicago Press.

Buide MS. 1951. Observation on habits of the Cuban iguana. Herpetologica 7: 124.

Burnell KL, Hedges SB. 1990. Relationships of West Indian Anolis (Sauria: Iguanidae): An approach using slow-evolving protein loci. Caribbean Journal of Science 26: 7–30.

Carey WM. 1975. The rock iguana, Cyclura pinguis, on Anegada, British Virgin Islands, with notes on Cyclura ricordi and Cyclura cornuta on Hispaniola. Bulletin of the Florida State Museum, Biological Sciences 19: 189–234.

Carothers JH. 1981. Dominance and competition in a herbivorous lizard. Behavioral Ecology and Sociobiology 8: 261–266.

Carpenter CC. 1961a. Patterns of social behavior in the desert iguana, Diposaurus dorsalis. Copeia 1961: 396–405.

Carpenter CC. 1961b. Patterns of social behavior of Merriam’s canyon lizard Sceloporus m. merriami – Iguanidae. Southwestern Naturalist 6: 138–148.

Carpenter CC. 1962. A comparison of the patterns of display of Urosaurus, Uta, and Stenopelmas. Herpetologica 18: 145–152.

Carpenter CC. 1963. Patterns of behavior in three forms of the fringe-toed lizards Uma-Iguanidae. Copeia 1963: 406–412.

Carpenter CC. 1965. The display of the Cocos Island anole. Herpetologica 21: 256–260.

Carpenter CC. 1966a. The marine iguana of the Galapagos islands, its behavior and ecology. Proceedings of the California Academy of Sciences 34: 329–376.

Carpenter CC. 1966b. Comparative behavior of the Galapagos lava lizards Tropidurus. In: Bowman, R, ed. The Galapagos: Proceedings of the Galapagos International Scientific Project. Berkeley: University of California Press, 269–273.

Carpenter CC. 1967. Display patterns of the Mexican iguanid lizards of the genus Uma. Herpetologica 23: 285–293.

Carpenter CC. 1969. Behavioural and ecological notes on the Galapagos land iguanas. Herpetologica 25: 155–164.

Carpenter CC. 1978. Ritualistic social behaviors in lizards. In: Greenberg, N, MacLean, PD, eds. Behavior and neurology of lizards. Washington: National Institute of Mental Health, 253–267.

Carpenter CC. 1982. The aggressive displays of iguanine lizards. In: Burghardt, GM, Rand, AS, eds. Iguanas of the world: their behavior, ecology and conservation. New Jersey: Noyes Publications, 215–231.

Carpenter CC, Badham JA, Kimble B. 1970. Behavior patterns of three species of Amphibolurus (Agamidae). Copeia 1970: 497–505.

Carpenter CC, Grubitz G. 1960. Dominance shifts in the tree lizard Urosaurus ornatus – Iguanidae. Southwestern Naturalist 5: 123–128.

Carpenter CC, Grubitz GG. 1961. Time-motion study of a lizard. Ecology 42: 199–200.

Christian KA, Waldschmidt S. 1984. The relationship between lizard home range and body size: a reanalysis of the data. Herpetologica 40: 68–75.

Clarke RF. 1965. An ethological study of the iguanid lizard genera Callisaurus, Cophosaurus, and Holbrookia. Emporia State Research Studies 13: 1–66.

Cogger HG. 1978. Reproductive cycles, fat body cycles and socio-sexual behavior in the mallee dragon, Amphibolurus fordi (Lacertilia: Agamidae). Australian Journal of Zoology 26: 653–672.

Cogger HG. 1996. Reptiles and amphibians of Australia. Port Melbourne: Reed Books.

Cooper WE Jr. 1977. Information analysis of agonistic behavioural sequences in male iguanid lizards, Anolis carolinensis. Copeia 1977: 721–735.

Cooper WE Jr. 1985. Female residency and courtship intensity in a territorial lizard, Holbrookia propinqua. Amphibia-Reptilia 6: 63–69.
Cooper WE Jr. 1988. Aggressive behaviour and courtship rejection in brightly and plainly colored female keeled earless lizards Holbrookia propinqua. Ethology 77: 265–278.

Cooper WE Jr, Burns N. 1987. Social significance of ventrolateral colouration in the fence lizard, Sceloporus undulatus. Animal Behaviour 35: 529–532.

Cooper WE Jr, Guillette LJ. 1991. Observations on activity, display behavior, coloration and androgen levels in the keeled earless lizard, Holbrookia propinqua. Amphibia-Reptilia 12: 57–66.

Cowles RB. 1956. Notes on natural history of a South African agamid lizard. Herpetologica 12: 297–302.

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

Daniel JC, Blumstein DT. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. Animal Behaviour 56: 1517–1528.

Dawkins MS. 1993. Are there general principles of signal design? Philosophical Transactions of the Royal Society of London, Series B 340: 251–255.

De Queiroz K. 1987. Phylogenetic systematics of Iguanidae lizards: a comparative osteological study. University California Publications in Zoology 118: 1–203.

Decourcy KR, Jenssen TA. 1994. Structure and use of male territorial headbob signals by the lizard Anolis carolinensis. Animal Behaviour 47: 251–262.

Deslippe RJ, M'Closkey RT, Dajczak SP, Szpak CP. 1990. A quantitative study of the social behavior of tree lizards, Urosaurus ornatus. Journal of Herpetology 24: 337–341.

Distel H, Veazey J. 1982. The behavioral inventory of the green iguana, Iguana iguana. In: Burghardt, GM, Rand, AS, eds. Iguanas of the world: their behavior, ecology and conservation. New Jersey: Noyes Publications, 252–270.

Dugan B. 1982. A field study of the headbob displays of male green iguanas Iguana iguana: variation in form and context. Animal Behaviour 30: 327–338.

Dusenbery DB. 1992. Sensory ecology. New York: W.H. Freeman.

Echelle AA, Echelle AF, Fitch HS. 1971. A comparative analysis of aggressive display in nine species of Costa Rican Anolis. Herpetologica 27: 271–288.

Endler JA. 1987. Predation, light intensity and courtship behavior in Poecilia reticulata (Pisces: Poeciliidae). Animal Behaviour 35: 1376–1382.

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist, Supplement 139: S125–S153.

Endler JA, McLellan T. 1988. The processes of evolution: towards a newer synthesis. Annual Review of Ecology and Systematics 19: 395–421.

Evans LT. 1935. Winter mating and fighting behavior of Anolis carolinensis as induced by pituitary injections. Copeia 1935: 3–6.

Evans LT. 1938a. Courtship behavior and sexual selection of Anolis. Journal of Comparative Psychology 26: 475–492.

Evans LT. 1938b. Cuban field studies on territoriality of the lizard, Anolis sagrei. Journal of Comparative Psychology 35: 97–123.

Evans LT. 1953. Tail display in an iguanid lizard, Liocranopus carinatus coryi. Copeia 1953: 50–54.

Felsenstein J. 1985. Phylogenies and the comparative method. American Naturalist 125: 1–15.

Ferguson GW. 1966. Releasers of courtship and territorial behavior in the side blotted lizard Uta stansburiana. Animal Behaviour 14: 89–92.

Ferguson GW. 1970a. Variation and evolution of the push-up displays of the side-blotched lizard genus Uta (Iguanidae). Systematic Zoology 19: 79–101.

Ferguson GW. 1970b. Mating behaviour of the side-blotched lizards of the genus Uta (Sauria: Iguanidae). Animal Behaviour 18: 65–72.

Ferguson GW. 1971. Observations on the behavior and interactions of two sympatric Sceloporus in Utah. American Midland Naturalist 86: 190–196.

Ferguson GW. 1973. Character displacement of the push-up displays of two partially-sympatric species of spiny lizards, Sceloporus (Sauria: Iguanidae). Herpetologica 29: 251–284.

Fitch HS. 1940. A field study of the growth and behavior of the fence lizard. University of California Publications in Zoology 44: 151–172.

Fitch HS. 1956. An ecological study of the collared lizard Crotophysurus collybirs. University of Kansas Publications, Museum of Natural History 8: 213–274.

Fite KV, Lister BC. 1981. Bifoveal vision in Anolis lizards. Brain, Behaviour and Evolution 19: 144–154.

Fleishman LJ. 1988a. Sensory influences on physical design of a visual display. Animal Behaviour 36: 1420–1424.

Fleishman LJ. 1988b. Sensory and environmental influences on display form in Anolis auratus, a grass anole from Panama. Behavioral Ecology and Sociobiology 22: 309–316.

Fleishman LJ. 1988c. The social behavior of Anolis auratus, a grass anole from Panama. Herpetologica 22: 13–23.

Fleishman LJ. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anole lizards and other vertebrates. American Naturalist 139: 836–861.

Fleishman LJ, Marshall CJ, Hertz PE. 1995. Comparative study of temporal response properties of the visual system of three species of anole lizards. Copeia 1995: 422–431.

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

Garcea R, Gorman G. 1968. A difference in male territorial display behavior in two sibling species of Anolis. Copeia 1968: 419–420.

Garland T Jr. 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Vitt, LJ, Pianka, ER, eds. Lizard ecology: historical and experimental perspectives. Princeton: Princeton University Press, 248–249.

Gibbons JR. 1979. The hind leg pushup display of the Amphibolurus decresii species complex (Lacertilia: Agamidae). Copeia 1979: 29–40.
correlates of agonistic displays of Anolis limifrons (Sauria, Iguanidae). Behaviour 58: 173–191.

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

Iverson JB. 1979. Behavior and ecology of the rock iguana Cyclura carinata. Bulletin of the Florida State Museum, Biological Sciences 24: 1–358.

Jackman TR, Larson A, de Queiroz K, Losos JB. 1999. Phylogenetic relationships and tempo of early diversification in Anolis lizards. Systematic Biology 48: 254–285.

Jenssen TA. 1970a. The ethoecology of Anolis nebulosus (Sauria, Iguanidae). Journal of Herpetology 4: 1–38.

Jenssen TA. 1970b. Female response to filmed displays of Anolis nebulosus (Sauria, Iguanidae). Animal Behaviour 18: 640–647.

Jenssen TA. 1971. Display analysis of Anolis nebulosus (Sauria, Iguanidae). Copeia 1971: 197–209.

Jenssen TA. 1977. Evolution of anoline lizard display behavior. American Zoologist 17: 203–215.

Jenssen TA. 1978. Display diversity in anoline lizards and problems of interpretation. In: Greenberg, N, MacLean, PD, eds. Behavior and neurology of lizards. Washington: National Institute of Mental Health. 269–285.

Jenssen TA. 1979a. Display behavior of male Anolis opalinus (Sauria, Iguanidae): a case of weak display stereotypy. Animal Behaviour 27: 173–184.

Jenssen TA. 1979b. Display modifiers of Anolis opalinus (Lacertilia, Iguanidae). Herpetologia 35: 21–30.

Jenssen TA. 1983. Display behavior of two Haitian lizards, Anolis cybotes and Anolis distichus. In: Rhodin, AGJ, Miyata, K, eds. Advances in herpetology and evolutionary biology. Cambridge: Museum of Comparative Zoology. 552–569.

Jenssen TA, Feely CF. 1991. Social behavior of the male anoline lizard Chamaeleonorhops barbouri, with comparison to Anolis. Journal of Herpetology 25: 454–462.

Jenssen TA, Gladson NL. 1984. A comparative display analysis of the Anolis brevirostris complex in Haiti. Journal of Herpetology 18: 217–230.

Jenssen TA, Greenberg N, Havre KA. 1995. Behavioural profile of free-ranging male lizards, Anolis carolinensis, across breeding and post-breeding seasons. Herpetological Monographs 9: 41–662.

Jenssen TA, Hover EL. 1976. Display analysis of the signature display of Anolis limifrons (Sauria: Iguanidae). Behaviour 57: 227–240.

Jenssen TA, Rothblum LM. 1977. Display repertoire analysis of Anolis townsendi (Sauria: Iguanidae) from Cocos Island. Copeia 1977: 103–109.

Jenssen TA, Swenson B. 1974. An ecological correlate of critical flicker-fusion frequencies for some Anolis lizards. Vision Research 14: 965–970.

Lazell JD. 1973. The lizard genus Iguana in the Lesser Antilles. Bulletin of the Museum of Comparative Zoology 145: 1–28.

Lee AK, Badham JA. 1963. Body temperature, activity, and behavior of the agamid lizard, Amphibolurus barbatus. Copeia 1963: 387–394.
Lister BC, Aguayo AG. 1992. Seasonality, predation, and the behavior of a tropical mainland anole. Journal of Animal Ecological 61: 717–733.

Lorch PD, Eadie JA. 1999. Power of the concentrated changes test for correlated evolution. Systematic Biology 48: 170–191.

Losos JB. 1985a. Male aggressive behavior in a pair of sympatric sibling species. Breviora 484: 1–30.

Losos JB. 1985b. An experimental demonstration of the species-recognition role of Anolis dewlap colour. Copeia 1985: 905–910.

Losos JB. 1990a. Concordant evolution of locomotor behavior, display rate and morphology in Anolis lizards. Animal Behaviour 39: 879–890.

Losos JB. 1990b. Ecomorphology, performance capability, and scaling of West Indian Anolis lizards: An evolutionary analysis. Ecological Monographs 60: 369–388.

Losos JB, Chu LR. 1998. Examination of factors potentially affecting dewlap size in Caribbean anoles. Copeia 1998b: 430–438.

Lynn RT. 1965. A comparative study of display behavior in Phrynosoma (Iguanidae). Southwestern Naturalist 10: 25–30.

McCloskey RT, Baia KA, Russell RW. 1987. Defense of mates: a territory departure rule for male tree lizards following sex-ratio manipulation. Oecologia 73: 28–31.

McCloskey RT, Deslippe RJ, Szpak CP. 1990. Tree lizard distribution and mating system: the influence of habitat and food resources. Canadian Journal of Zoology 68: 2083–2089.

Macedonia JM, Evans CS, Losos JB. 1994. Male Anolis lizards discriminate video-recorded conspecific and heterospecific displays. Animal Behaviour 47: 1220–1223.

Macedonia JM, Stamps JA. 1994. Species recognition in Anolis grahami (Sauria, Iguanidae): evidence from recombination. Evolution 50: 57–69.

Macedonia JM, Evans CS, Losos JB. 1994. Male Anolis lizards discriminate video-recorded conspecific and heterospecific displays. Animal Behaviour 47: 1220–1223.

Macedonia JM, Stamps JA. 1994. Species recognition in Anolis grahami (Sauria, Iguanidae): evidence from recombination. Evolution 50: 57–69.

Macey JR, Schulte JA, Larson A, Ananjeva NB, Wang Y, Pethiyagoda R, Rastegar-Pouyani N, Papenfuss TJ. 2000. Evaluating trans-tethys migration: An example using arodont lizard phylogenetics. Systematic Biology 49: 233–256.

Maddison WP. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution 44: 539–557.

Maddison WP. 1991. Scaled-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. Systematic Biology 40: 304–314.

Maddison WP, Maddison DR. 1992. MacClade: analysis of phylogeny and character evolution. Sunderland: Sinauer Associates.

Maddison WP, Maddison DR. 1999. MacClade, Version 3.08a upgrade. Available free from http://phylogeny.arizona.edu/macclade/macclade.html

Mahrt LA. 1998. Territorial establishment and maintenance by female tree lizards, Urosaurus ornatus. Journal of Herpetology 32: 176–182.

Marchetti K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature 362: 149–152.

Marten K, Marler P. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behavioral Ecology and Sociobiology 2: 271–290.

Marten K, Quine D, Marler P. 1977. Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. Behavioral Ecology and Sociobiology 2: 291–302.

Martins EP. 1991. Individual and sex differences in the use of the push-up display by the sagebrush lizard, Sceloporus graciosus. Animal Behaviour 41: 403–416.

Martins EP. 1993a. Contextual use of the push-up display by the sagebrush lizard, Sceloporus graciosus. Animal Behaviour 45: 25–36.

Martins EP. 1993b. A comparative study of the evolution of Sceloporus push-up displays. American Naturalist 142: 994–1018.

Martins EP. 1994. Phylogenetic perspectives on the evolution of lizard territoriality. In: Vitt, Lj, Pianka, ER, eds. Lizard ecology: historical and experimental perspectives. Princeton: Princeton University Press, 117–144.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149: 646–667.

Martins EP, Lamont J. 1998. Estimating ancestral states of a communicative display: a comparative study of Cyclura rock iguanas. Animal Behaviour 55: 1685–1706.

Mason P, Adkins EK. 1976. Hormones and social behavior in the lizard, Anolis carolinensis. Hormones and Behavior 7: 75–86.

Mayhem WW. 1963. Observations on captive Amphibolurus pictus an Australian agamid lizard. Herpetologica 19: 81–88.

McGregor PK, Krebs JR. 1984. Sound degradation as a distance cue in great tit (Parus major) song. Behavioral Ecology and Sociobiology 16: 49–56.

McMan S. 1993. Contextual signalling and the structure of dyadic encounters in Anolis carolinensis. Animal Behaviour 45: 657–668.

Milstead WW. 1970. Late summer behavior of the lizards Sceloporus merriami and Urosaurus ornatus in the field. Herpetologica 26: 343–354.

Mindell DP, Sites JW, Graur D. 1989. Speciation evolution: a phylogenetic test with allozymes in Sceloporus (Reptilia). Cladistics 5: 49–61.

Mitchell FJ. 1973. Studies on the ecology of the agamid lizard Amphibolurus maculosus (Mitchell). Transactions of the Royal Society of South Australia 97: 47–76.

Mittleman MB. 1942. A summary of the iguanid genus Urosaurus. Bulletin of the Museum of Comparative Zoology 91: 106–181.

Moermond TC. 1979. Habitat constraints on the behavior, morphology, and community structure of Anolis lizards. Ecology 60: 152–164.

Montanucci RR. 1965. Observations on the San Joaquin leopard lizard, Crotaphytus wislizenii silus Stejneger. Herpetologica 21: 270–283.

© 2002 The Linnean Society of London, Biological Journal of the Linnean Society, 2002, 77, 127–148
Montanucci RR. 1967. Further studies on leopard lizards, Crotaphytus wislizeni. Herpetologica 23: 119–126.

Moody SM. 1980. Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). PhD Dissertation. Michigan: University of Michigan.

Morton ES. 1975. Ecological sources of selection on avian sounds. American Naturalist 109: 17–34.

Morton ES. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99: 65–86.

Nagub M, Wiley RH. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Animal Behaviour 62: 825–837.

Nagy KA. 1973. Behavior, diet and reproduction in a desert lizard, Sauromalus obsesus. Copeia 1973: 93–102.

Noble GK, Teale HK. 1930. The courtship of some iguanid and teiid lizards. Copeia 1930: 54–56.

Norris KS. 1953. The ecology of the desert iguana Diposaurus dorsalis. Ecology 34: 265–287.

Nunn CL, Barton RA. 2001. Comparative methods for studying primate adaptation and allometry. Evolutionary Anthropology 10: 81–98.

Ord TJ, Blumstein DT, Evans CS. 2001. Intra-sexual selection predicts the evolution of signal complexity in lizards. Proceedings of the Royal Society of London, Series B. 268: 737–744.

Ortiz PR, Jenssen TA. 1982. Interspecific aggression between lizard competitors, Anolis cooki and Anolis cristatellus. Zeitschrift für Tierpsychologie 60: 227–238.

Ortolani A, Caro TM. 1996. The adaptive significance of color patterns in carnivores: phylogenetic tests of classic hypotheses. In: Gittleman, JL, ed. Carnivore behavior, ecology and evolution. Ithaca: Cornell University Press, 132–188.

Pagel M. 1999. Inferring the historical patterns of biological evolution. Nature 401: 877–884.

Parker WS. 1972. Notes on Diposaurus dorsalis in Arizona. Herpetologica 28: 226–229.

Philibosian R. 1975. Territorial behavior and population regulation in the lizards, Anolis acutus and A. cristatellus. Copeia 1975: 428–443.

Purdue JR, Carpenter CC. 1972a. A comparative study of the display motion in the iguanid genera Sceloporus, Uta, and Urosaurus. Herpetologica 28: 137–141.

Purdue JR, Carpenter CC. 1972b. A comparative study of the body movements of displaying males of the lizard genus Sceloporus (Iguanidae). Behaviour 41: 68–81.

Purvis A, Rambaut A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. Computer Applied Biology 11: 247–251.

Rand AS. 1967. Ecology and social organization in the iguanid lizard Anolis lineatopus. Proceedings of the United States National Museum 122: 1–77.

Ransom JE. 1981. Harper & Row’s complete field guide to North American wildlife. New York: Harper & Row.

Reeder TW, Wiens JJ. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. Herpetological Monographs 10: 43–84.

Roggenbuck ME, Jenssen TA. 1986. The ontology of display behavior in Sceloporus undulatus (Sauria: Iguanidae). Ethology 71: 153–165.

Rogner M. 1997. Lizards. Malabar: Krieger Publishing Co.

Ross W. 1989. Notes on ecology and behaviour with special reference to tail signalling in Phrynocephalus maculatus (Reptilia: Agamidae). Fauna of Saudi Arabia 10: 417–422.

Ross W. 1995. Tail signaling in populations of Phrynocephalus arabicus (Anderson, 1894) (Reptilia: Agamidae). Reptilia 11: 63–71.

Rothblum L, Jenssen TA. 1978. Display repertoire analysis of Sceloporus undulatus haecynthinus (Sauria: Iguanidae) from South-Western Virginia. Animal Behaviour 26: 130–137.

Roughgarden JJ, Pacala S. 1989. Taxon cycle among Anolis lizard populations: review of evidence. In: Otte, D, Endler, JA, eds. Speciation and its consequences. Sunderland: Sinauer Associates, 403–432.

Ruby D. 1977. The function of shudder displays in the lizard Sceloporus jarrovi. Copeia 1977: 110–114.

Ryan MJ, Rand AS. 1993. Sexual selection and signal evolution: the ghost of biases past. Philosophical Transactions of the Royal Society of London, Series B 340: 187–195.

Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126: 87–100.

Ryan MJ, Cocroft RB, Wilczynski W. 1990. The role of environmental selection in intraspecific divergence of mate recognition signals in the cricket frog, Acris crepitans. Evolution 44: 1869–1872.

Schmidt KP. 1935. Notes on the breeding behavior of lizards. Zoological Series of the Field Museum of Natural History 20: 71–76.

Schulte JA, Macey JR, Larson A, Papenfuss TJ. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using four subfamilies of the lizard family Iguanidae. Molecular Phylogenetics and Evolution 10: 367–376.

Scott MP. 1984. Agonistic and courtship displays of male Anolis sagrei. Breviora 479: 1–22.

Sites JW, Davis SK, Guerra T, Iverson JB, Snell HL. 1996. Character congruence and phylogenetic signal in molecular and morphological data sets: a case study in the living iguanas (Squamata, Iguanidae). Molecular Biology and Evolution 13: 1087–1105.

Stamps JA. 1973. Displays and social organization in female Anolis aeneus. Copeia 2: 264–272.

Stamps JA. 1976. Rainfall, activity and social behavior in the lizard, Anolis aeneus. Animal Behaviour 24: 603–608.

Stamps JA. 1977. Social behavior and spacing patterns in lizards. In: Gans, C, Tinkle, DW, eds. Biology of the Reptilia: ecology and behavior. New York: Academic Press, 265–334.

Stamps JA. 1978. A field study of the ontogeny of social behavior in the lizard Anolis aeneus. Behaviour 68: 1–31.

Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Huey, RB, Pianka, ER, Schoener, TW, eds.
Lizard ecology: studies of a model organism. Cambridge: Harvard University Press, 169–204.

Stamps JA. 1990. The effect of contender pressure on territory size and overlap in seasonally territorial species. American Naturalist 135: 614–632.

Stamps JA, Barlow GW. 1973. Variation and stereotypy in the displays of Anolis aeneus (Sauria: Iguanidae). Behaviour 47: 67–94.

Stamps JA, Crews DP. 1976. Seasonal changes in reproduction and social behavior in the lizard Anolis aeneus. Copeia 3: 467–476.

Stamps JA, Krishnan VV. 1994. Territory acquisition in lizards. I. First encounters. Animal Behaviour 47: 1375–1385.

Stamps JA, Krishnan VV. 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Animal Behaviour 55: 461–472.

Stamps JA, Losos JB, Andrews RM. 1997. A comparative study of population density and sexual size dimorphism in lizards. American Naturalist 149: 64–90.

Stebbins RC. 1966. A field guide to Western reptiles and amphibians. Boston: Houghton Mifflin Company.

Stoddard PK. 1999. Predation enhances complexity in the evolution of electric fish signals. Nature 400: 254–256.

Swanson PL. 1950. The iguana Iguana iguana iguana (L). Herpetologica 6: 187–193.

Swofford DL, Maddison WP. 1987. Reconstructing ancestral character states under Wagner parsimony. Mathematical Bioscience 87: 199–229.

Tarr RS. 1982. Species typical display behavior following stimulation of the reptilian striatum. Physiology and Behavior 29: 615–620.

Thompson CW, Moore MC. 1992. Behavioural and hormonal correlates of alternative reproductive strategies in a polygynous lizard: tests of the relative plasticity and challenge hypotheses. Hormones and Behavior 26: 568–585.

Tokarz RR, Beck JW. 1987. Behavior of the suspected lizard competitors Anolis sagrei and Anolis carolinensis: an experimental test for behavior interference. Animal Behaviour 35: 722–734.

Tollestrup K. 1983. The social behavior of two species of closely related leopard lizards, Gambelia silus and Gambelia wislizenii. Zeitschrift für Tierpsychologie 62: 307–320.

Trivers RL. 1976. Sexual selection and resource-accruing abilities in Anolis garmani. Evolution 30: 253–269.

Turner FB, Jennrich RI, Weintraub JD. 1969. Home ranges and body size of lizards. Ecology 50: 1076–1081.

Upton DE, Murphy RW. 1997. Phylogeny of the side-blotched lizards Phrynosomatidae: Uta based on mtDNA sequences: support for a midpeninsular seaway in Baja California. Molecular Phylogenetics and Evolution 8: 104–113.

Vitt LJ, Congdon JD, Hulse AC, Platz JE. 1974. Territorial aggressive encounters and tail breaks in the lizard Sceloporus magister. Copeia 1974: 990–993.

Webber P. 1981. To spy on a desert skink. Australian Natural History 19: 270–275.

Whitehead JM. 1987. Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys, Alouatta palliata palliata. Animal Behaviour 35: 1615–1527.

Wiens JJ. 1993. Phylogenetic systematics of the tree lizards genus Urosaurus. Herpetologica 49: 399–420.

Wiens JJ, Hollingsworth BD. 2000. War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. Systematic Biology 49: 143–159.

Wiens JJ, Reeder TW. 1997. Phylogeny of the spiny lizards Sceloporus based on molecular and morphological evidence. Herpetological Monographs 11: 1–44.

Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal communication. Behavioural Ecology and Sociobiology 3: 69–94.

Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma, DE, Miller, EH, Ouellet, H, eds. Acoustic communication in birds. New York: Academic Press, 131–181.

Wilson SK, Knowles DG. 1988. Australia’s Reptiles. Sydney: Collins Books.

Yang SY, Soule M, Gorman GC. 1974. Anolis lizards of the eastern Caribbean: a case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the Roquet group. Systematic Zoology 23: 387–399.

Yedlin IN, Ferguson GW. 1973. Variations in aggressiveness of free-living male and female collared lizards, Crotaphytus collaris. Herpetologica 29: 268–275.

Zucker N. 1987. Behavior and movement patterns of the tree lizard Urosaurus ornatus (Sauria: Iguanidae) in seminatural enclosures. Southwestern Naturalist 32: 321–333.

Zucker N. 1989. Dorsal darkening and territoriality in a wild population of the tree lizard, Urosaurus ornatus. Journal of Herpetology 23: 389–398.
## APPENDIX

### SOURCES CONSULTED FOR SPECIES DATA

| Species                        | Repertoire size | Habitat preference | Home range size (m²) | 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                   | semi-arboreal/terrestrial | non-moving prey               | 3–6                         |             |
| Amphibolurus muricatus         | 2               | other              | nd                   | semi-arboreal/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                | semi-arboreal/terrestrial      | moving prey                 | 13,22–24    |
| A. brevirostris                | 1               | closed             | nd                   | semi-arboreal/terrestrial | nd                             | 25                          |             |
| A. carolinensis                | 8               | closed             | nd                   | arboreal          | moving prey                    | 13,26–41                    |             |
| A. carpenteri                  | 5               | other              | nd                   | semi-arboreal/terrestrial | nd                             | 42                          |             |
| A. caudalis                    | 3               | closed             | nd                   | semi-arboreal/terrestrial | nd                             | 25                          |             |
| A. chlorocyanus                | 4               | nd                 | nd                   | arboreal          | nd                             | 44                          |             |
| A. coelestinus                 | 3               | nd                 | nd                   | nd                | moving prey                    | 36                          |             |
| A. conspersus                  | 3               | nd                 | nd                   | nd                | moving prey                    | 45                          |             |
| A. cupreus                     | 6               | closed             | 1                    | 70                | arboreal                       | moving prey                 | 11,13,45    |
| A. cybotes                     | 5               | closed             | 35                   | 55                | semi-arboreal/terrestrial      | moving prey                 | 12,13,42    |
| 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                   | semi-arboreal/terrestrial | moving prey               | 13,45,51                    |             |
| A. humilis                     | 5               | closed             | nd                   | semi-arboreal/terrestrial | moving prey               | 13                           |             |
| A. intermedius                 | 5               | nd                 | nd                   | arboreal          | nd                             | 42                          |             |
| 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                   | semi-arboreal/terrestrial | moving prey               | 46–48                       |             |
| A. monensis                    | 6               | nd                 | nd                   | nd                | moving prey                    | 45                          |             |
| A. nebulosus                   | 5               | closed             | 2                    | 42                | semi-arboreal/terrestrial      | moving prey                 | 13,56–59    |
| A. opalinus                    | 8               | other              | nd                   | semi-arboreal/terrestrial | moving prey               | 13,51,60,61                |             |
| A. pentaptron                  | 5               | nd                 | nd                   | semi-arboreal/terrestrial | moving prey               | 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                | moving prey                    | 62,63                       |             |
| A. tristis                     | 6               | other              | nd                   | semi-arboreal/terrestrial | moving prey               | 20,21,51                    |             |
| A. tropidolepis                | 5               | closed             | nd                   | semi-arboreal/terrestrial | nd                             | 42                          |             |
| A. valencienni†                | 0               | nd                 | nd                   | nd                | moving prey                    | 64                          |             |
| A. websteri                    | 1               | closed             | nd                   | semi-arboreal/terrestrial | nd                             | 25                          |             |
| Brachylophus fasciatus         | 3               | closed             | nd                   | arboreal          | non-moving prey                | 5,38,51,65                  |             |
| Callosaurus draconoides        | 5               | other              | nd                   | moving prey                    | 51,66                       |             |
| Chalarodon madagascariensis    | 5               | other              | 79                   | 87                | moving prey                    | 67                          |             |
| Chamaeleonator barbouri        | 2               | closed             | 1                    | 41                | semi-arboreal/terrestrial      | moving prey                 | 68                       |
| Conolophus pallidus            | 4               | other              | nd                   | semi-arboreal/terrestrial | non-moving prey               | 5,69                       |             |
| C. sabristatus                 | 6               | other              | nd                   | semi-arboreal/terrestrial | non-moving prey               | 5,69                       |             |
| Cophosaurus texanus            | 5               | other              | nd                   | moving prey                    | 66                          |             |
| Crotaphytus collaris           | 4               | other              | nd                   | semi-arboreal/terrestrial      | moving prey               | 38,51,70–72                |             |
| Ctenophorus decresci           | 5               | other              | nd                   | semi-arboreal/terrestrial      | moving prey               | 8,73                       |             |
| C. fionii                      | 5               | other              | nd                   | semi-arboreal/terrestrial      | moving prey               | 8,73                       |             |
| C. fordi                       | 1               | other              | nd                   | semi-arboreal/terrestrial      | moving prey               | 8,73                       |             |
| C. macalosus                   | 4               | other              | 801                  | 69                | semi-arboreal/terrestrial      | moving prey                 | 76,77        |
| C. nuchalis                    | 5               | other              | nd                   | semi-arboreal/terrestrial      | moving prey               | 7,10                       |             |
| C. pictus                      | 2               | other              | nd                   | semi-arboreal/terrestrial      | moving prey               | 10,78                      |             |

© 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **77**, 127–148
### APPENDIX Continued

| Species                     | Repertoire size | Habitat preference | Home range size (m²) | Body size (mm SVL) | Locomotion                  | Diet                        | References* |
|-----------------------------|-----------------|-------------------|----------------------|--------------------|-----------------------------|-----------------------------|-------------|
| *C. vadnappa*               | 5               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 8,10,73                     |             |
| *Ctenosaura hemilopha*      | 4               | other             | nd                   | semiarboreal/terrestrial | non-moving prey              | 5,79,80                     |             |
| *C. quiquecarinata*         | 1               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 5,51                        |             |
| *C. similis*                | 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. cyehliara*              | 3               | nd                | nd                   | semiarboreal/terrestrial | nd                           | 5,6,82                      |             |
| *C. nubila*                 | 1               | nd                | nd                   | semiarboreal/terrestrial | non-moving prey             | 5,6,38,82,86               |             |
| *Cyclura carinata*          | 5               | other             | 1069                 | 144                | semiarboreal/terrestrial    | non-moving prey             | 5,12,84–87–89 |
| *C. collei*                 | 0               | nd                | nd                   | semiarboreal/terrestrial | nd                           | 5,6,82                      |             |
| *C. cornuta*                | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 5,6,38,82,85               |             |
| *C. similis*                | 5               | other             | 2100                 | 97                 | nd                           | moving prey                 | 12,90,91               |
| *C. quiquecarinata*         | 3               | other             | 23 205               | 102                | semiarboreal/terrestrial    | moving prey                 | 12,38,51,91,92 |
| *C. simillata*              | 5               | other             | 2205                 | 60                 | semiarboreal/terrestrial    | moving prey                 | 66,84                   |
| *C. propinquus*             | 5               | other             | 374                  | 104                | semiarboreal/terrestrial    | moving prey                 | 12,38,51,103 |
| *C. opalinus*               | 1               | other             | 1333                 | 360                | arboreal                    | moving prey                 | 5,12,97–100 |
| *C. delanas*                | 4               | other             | 252                  | 129                | semiarboreal/terrestrial    | moving prey                 | 12,38,51,103 |
| *C. duncanensis*            | 4               | other             | 252                  | 129                | semiarboreal/terrestrial    | moving prey                 | 38,51,101               |
| *C. grayii*                 | 4               | other             | 252                  | 129                | semiarboreal/terrestrial    | moving prey                 | 8,10,102               |
| *C. kelaari*                | 4               | other             | 252                  | 129                | semiarboreal/terrestrial    | moving prey                 | 38,51,103               |
| *C. pacificus*              | 4               | other             | 252                  | 129                | semiarboreal/terrestrial    | moving prey                 | 38,51,103               |
| *C. maculatus*              | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 108                        |             |
| *C. mexicanus*              | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 109                        |             |
| *C. ornatus*                | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 72,110                     |             |
| *C. coronatum*              | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 72,110                     |             |
| *C. douglassii*             | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 72,110                     |             |
| *C. modestum*               | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 72,110                     |             |
| *C. platyrhinos*            | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 72,110                     |             |
| *C. solare*                 | 0               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 7,8,31,111,112             |             |
| *C. rubescens*              | 6               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 7,8,31,111,112             |             |
| *C. ornatus*                | 1               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 5,6,38                     |             |
| *C. sceloporus cyanogenys*   | 4               | other             | 12 610               | 164                | semiarboreal/terrestrial    | non-moving prey             | 5,6,12,38,113 |
| *S. andersonii*             | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 51,114                     |             |
| *S. ferruginea*             | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 115–119                    |             |
| *S. neomexicanus*           | 4               | other             | 120                  | 114                | semiarboreal/terrestrial    | moving prey                 | 12,119,114,119–122       |             |
| *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. auropalpebris*          | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 51,106,114               |             |
| *S. occidentalis*           | 2               | other             | 6801                 | 70                 | semiarboreal/terrestrial    | moving prey                 | 12,51,107,119,121,126–128 |
| *S. ornatus*                | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 51,106,114               |             |
| *S. poindatti*              | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 51,114                     |             |
| *S. torquatus*              | 2               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 114                        |             |
| *S. undulatus*              | 3               | other             | 446                  | 83                 | semiarboreal/terrestrial    | moving prey                 | 49,84,117–119,121,128–131 |
| *Uma exsul*                 | 7               | other             | nd                   | semiarboreal/terrestrial | moving prey                 | 132                        |             |

© 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 127–148
### APPENDIX

| Species              | Repertoire size | Habitat preference | Home range size (m²) | 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. paraphysgas*     | 7               | other              | nd                   | semiarboreal/terrestrial | nd           | 132,133                   |             |
| *U. scoparia*        | 6               | other              | nd                   | semiarboreal/terrestrial | moving prey | 132,133                   |             |
| *U. bicarinatus*     | 0               | other              | 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. Tekarz & 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. Hosos (1985a); 47. Hosos (1985b); 48. Macedonia, Evans & Hosos (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. Blanch & 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. Bratstrom (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. Tollesstrup (1993); 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. Purdu & Carpenter (1972a); 106. Wiens (1993); 107. Stebbins (1966); 108. Ross (1995); 109. Ross (1989); 110. Lynn (1965); 111. Bratström (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. Witt et al. (1974); 124. Carpenter (1961b); 125. Milstead (1970); 126. Tarr (1982); 127. Fitch (1940); 128. Purdu & 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, Desloge & Szpak (1990); 140. Zucker (1989); 141. Desloge 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.