



Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour

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Within species, natural and sexual selection work together to shape the design of animal communicative systems, and sometimes act differentially on alternate components to produce a single elaborate phenotype that works well in several contexts. Here, we show a similar pattern at the interspecific level, and describe how an intricate selective regime can shape diversification of a complex behaviour across species. Using four phylogenetic comparative methods, alternative phylogenetic hypotheses, and a data set compiled from over 50 different sources representing 53 taxa, we test the relative importance of different ecological variables on the evolution of anole visual displays. Our study makes use of the inherent complexity of these signals and the availability of published descriptions in the form of display-action-patterns. Results indicate that different selective forces are linked to change in different display components. Whereas evolutionary changes in display duration appear to be linked to sexual size dimorphism, measures of display complexity (number and uniformity of display components) were more tightly associated with the need to facilitate species recognition and the type of light environment in which the display is typically performed. We also found some evidence that ecomorph distinctions, a major force in morphological evolution of anoles, have had an impact on the evolution of display structure. We use our findings to highlight areas for future research and discuss the similarities and differences between display evolution in anoles and in other lizard genera.

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As with most complex phenotypes, myriad factors have been implicated in directing the evolution and design of animal communicative systems (e.g. Bradbury & Vehrencamp 1998; Uetz & Roberts 2002; Seddon 2005). For example, signals that help animals to recognize, obtain access to, and/or attract appropriate mates will experience considerable selective advantage (e.g. Proctor 1991; Fleishman 1992; Ryan & Rand 1993; Rodd et al. 2002). Properties of the signal environment have also been shown to be critical, with habitat structure often dictating those components that can be readily perceived by receivers (Morton 1975; Endler 1992; Marchetti 1993; Peters & Evans 2003a, b). Yet adaptation is not the only process by which signal design can change over evolutionary time. Diversification can also be expected through

stochastic forces, such as mutation and random genetic drift, and genetic correlations between different elements of a phenotype. Identifying exactly which evolutionary processes are responsible for the diversity of animal signals observed across species today is complicated by the fact that most animal signals are made up of several components, each responding semi-independently to different evolutionary pressures. In this study, we apply modern phylogenetic comparative methods (PCMs) to explore the impact of phylogenetic and ecological factors on the interspecific diversification of a multifaceted signal, the dynamic visual displays of anoles. We show how comparative data from a variety of sources can be combined to help infer the evolutionary mechanisms responsible for signal diversity, and identify promising avenues for further empirical study.

With close to 400 recognized species, *Anolis* is one of the largest genera of vertebrates on the planet (Losos 1994; Nicholson 2002). This remarkable species richness has resulted from separate adaptive radiations on each of the four islands of the Greater Antilles (Jackman et al.

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1997) and following the colonization of mainland Central America and northern South America (Nicholson et al. 2005). The group has been the subject of intense research activity and is an important model system in ecology, evolutionary biology and island biogeography (e.g. Calsbeek & Smith 2003; Glor et al. 2003, 2004; Harmon et al. 2003; Kolbe et al. 2004; Losos et al. 2004; reviewed in: Losos 1994, 2004; Thorpe et al. 2004). Consequently, there is a great deal of interspecific data available for this group, including morphological, ecological and phylogenetic information. Most importantly for our purposes, the displays of an unusually large number of species have been the subject of detailed frame-by-frame analyses required to quantify the complex motion characteristics of anole headbob and dewlap displays (e.g. Jenssen 1977a; Carpenter 1986; Fig. 1). Headbob displays (pushups and/or headnods) are almost ubiquitous throughout the iguanian superfamily, suggesting an early evolutionary origin leading to subsequent homology in the gross form of communicative behaviour across extant species. Displays

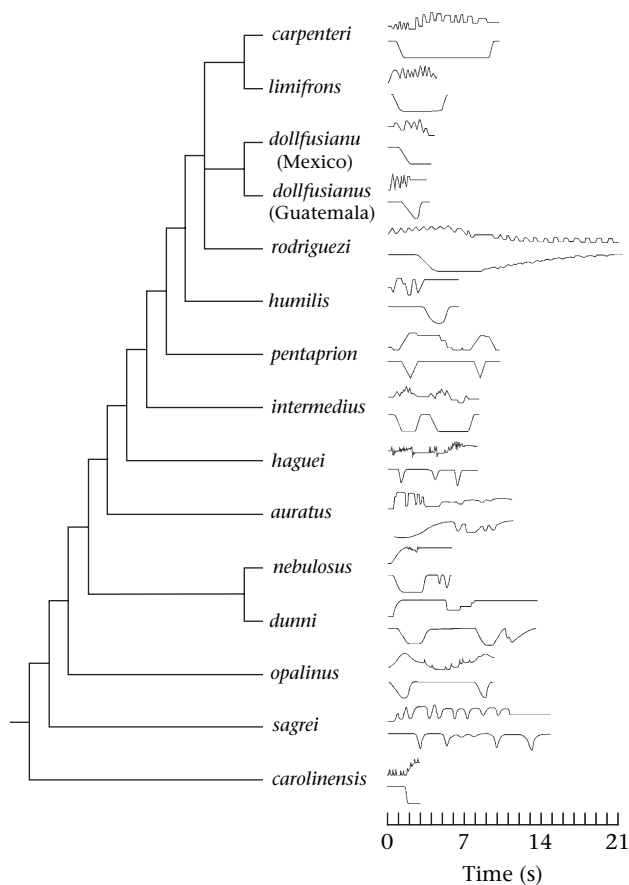


Figure 1. Examples of headbob and dewlap display for a subset of anoles. Plots are display-action-pattern graphs (DAP-graphs; sensu Carpenter & Grubitz 1961) depicting the up-and-down or extension-and-retraction over time of headbob (top line) and dewlap (bottom line) movements, respectively. The highest and lowest points within each sequence are standardized across species and do not represent absolute amplitude. Sources for DAP-graphs were: Echelle et al. (1971); Jenssen (1979); Fitch et al. (1976); Scott (1984); Fleishman (1988b); Decourcy & Jenssen (1994). Phylogenetic relationships are based on Tree 1 (see Methods; Fig. 2).

consist of a complex series of up-and-down motions and are used primarily during the establishment and maintenance of territories (Trivers 1976; Carpenter & Ferguson 1977; Carpenter 1978b). There is, however, considerable diversity in the motion characteristics of these displays (Martins 1993; Martins & Lamont 1998; Martins et al. 2004), and, in anoles, headbobs are also frequently accompanied by an extendible throat fan or 'dewlap', which is often large and exquisitely coloured. The extensive literature cataloguing the behaviour, ecology and phylogenetic relationships of anole lizards offers fertile ground for exploring the processes underlying the evolution of a complex communicative signal.

We begin our investigation by examining the evolutionary relationships between different signal characteristics making up displays (e.g. the number, timing and form of headbob and dewlap movements). Next, we explore the role of evolutionary forces such as stabilizing selection, selective response to fluctuating environments and other types of long-term influences (Felsenstein 1988; Hansen & Martins 1996; Hansen 1997) on shaping display structure using the phylogenetic generalized least squares (PGLS) approach proposed by Martins & Hansen (1997). We also apply the phylogenetic mixed model (PMM; Lynch 1991; Housworth et al. 2004) to identify display components that are more or less 'phylogenetically heritable' (i.e. the degree to which components are influenced by phylogeny). Finally, we examine how species ecology has directed signal evolution and we discuss the potential role of sexual selection, species recognition and habitat use in producing evolutionary change in the design of anole display structure.

Ecological Influences on Signal Design

There appears to be little, if any, female mate choice in iguanian lizards (reviewed in Tokarz 1995; see also Jenssen & Nunez 1998; Tokarz 1998; LeBas & Marshall 2001; Hamilton & Sullivan 2005). Instead, sexual selection manifests primarily through competition between males over territories that influence access to mates (and, subsequently, male reproductive success). There is strong empirical evidence in many animals that male-biased sexual size dimorphism (SSD) results when males compete vigorously for resources (Andersson 1994). Size dimorphism has therefore been used to estimate the intensity of male-male competition (see Ord et al. 2001 and references therein). Studies of bird song reveal the evolution of increasingly shorter territorial displays as competitive intensity increases in species (e.g. Price & Lanyon 2004). In lizards, male-male competition has been found to be a powerful force directing the evolution of complex communication, producing large signal repertoires (Ord et al. 2001) and elaborate colour signals and other ornamentation (Stuart-Fox & Ord 2004). We test whether SSD is correlated with the evolution of shorter, more complex signals (e.g. rapid displays with many headbobs), which is predicted when rivals must assess each other quickly and accurately before committing to a fight they are

unlikely to win (Zahavi 1977; Ord et al. 2001). However, in at least some anoles, the origin of SSD may also reflect natural selection driving the sexes into different ecological niches to minimize intersexual competition for resources (e.g. Schoener 1967, 1968). If habitat partitioning accounts for sex differences in size, there should be little relationship between dimorphism and aspects of signal design, and a closer association with habitat use or ecomorph type (see below).

Signals may also diversify over long periods of evolutionary time through their role in species recognition (e.g. Jenssen 1978; Córdoba-Aguilar 2002; Magurran & Ramnarine 2004), which is thought to be an important function of anole displays, particularly dewlaps (Williams & Rand 1977; Losos 1985; Macedonia & Stamps 1994; Macedonia et al. 1994). Consequently, one recurring hypothesis is that regular encounters with sympatric congeners have facilitated much of the divergence in signal structure (Ferguson 1973; Leal & Fleishman 2002, 2004). We test this by examining whether species found in sympatry with other anoles produce longer, more diverse displays to facilitate species recognition (e.g. temporally different dewlap pulses given in a long stereotyped sequence) compared to allopatric species. Although data on encounter rate between congeners are difficult to obtain, the co-occurrence of different species is frequently reported by researchers and provides a ready (albeit rough) estimate of the number of sympatric congeners that lizards may potentially interact with.

For animals to communicate efficiently, they must produce signals that not only convey their message reliably, but are also obvious to receivers in the environment. Several environmental variables are likely to be important in determining signal efficiency (reviewed in Endler 1992). For example, the degree of background motion produced by windblown vegetation determines the conspicuousness of motion-based displays in lizards (e.g. Fleishman 1988a, b; Peters & Evans 2003a), as does the number of visual obstructions between signaller and receiver in cluttered habitats. In anoles, particular attention has focused on the light environment and its influence on the evolution of dewlap colour (Fleishman et al. 1997; Fleishman & Persons 2001; Leal & Fleishman 2004). Habitat lighting will also dictate the conspicuousness of display motion (Endler 1992). Specifically, the ability to perceive a rapidly moving object, such as a headbobbing lizard, will be more difficult under low light (Fleishman et al. 1995). We test whether displays produced by anoles in shaded habitats show higher levels of redundancy (e.g. long display sequences with headbobs of uniform amplitude and duration) to facilitate signal perception compared to lizards living in sunnier habitats.

Finally, anoles are well-known microhabitat specialists, with distantly related species invading similar ecological niches and showing dramatic convergences in morphology and behaviour (i.e. 'ecomorphs'; Williams 1983; Losos 1996). The unique selective pressures associated with each ecomorph might also produce subtle differences in signal design. For example, we might expect that performing an elaborate display on a perch high up in a tree is difficult for canopy-affiliated ecomorphs (e.g. the loss of 'jerky'

displays in arboreal *Sceloporus* lizards; Martins 1993). We test this idea by examining whether highly arboreal ecomorphs have converged on a signal design typified by slow and/or few movements (e.g. longer/fewer headbobs or dewlap pulses).

To summarize, we explore the influence of four ecological variables thought to affect interspecific diversification in signal design directly or indirectly. (1) As the intensity of male–male competition increases, more complex and/or faster displays are predicted to evolve to facilitate opponent assessment and rapid dispute resolution. (2) The diversity in displays produced by sympatric species should be greater than that of allopatric species, and should be proportional to the number of congeners each species is likely to encounter. (3) Species that occupy shady habitats are predicted to produce more uniform and/or longer display sequences to enhance signal detection relative to species communicating in sunny habitats. (4) Highly arboreal ecomorphs are likely to have converged on a signal design consisting of slow and few display movements. Hypotheses (1) and (2) deal with influences likely to promote signal complexity or diversity, while (3) and (4) emphasize forms of selective constraint on signal elaboration.

METHODS

Data Collection and Categorization

Information on anole signal design was collected from published display-action-pattern (DAP)-graphs that illustrate the motion of headbobs and dewlaps over time (Fig. 1, Appendix). In a few cases, DAP-graphs were also available for populations within species and were included wherever possible (i.e. *A. grahami*: Negril and Kingston on Jamaica; *A. dollfusianus*: Mexico and Guatemala; *A. distichus*: Petionville and Montrouis in Haiti). Many anoles have a repertoire of display sequences (Jenssen 1978). To standardize the analysis, data collection was focused on those termed in the literature as 'type A', 'broadcast' or 'signature' displays, which are considered species typical. The data set includes information on 15 features (Table 1) scored from the headbob and dewlap displays of 53 taxa (50 species), compiled from over 50 sources (see Appendix). When compiling data, particular attention was made to concentrate on display characteristics that would not be confounded by the method used by authors to construct DAP-graphs, which is likely to vary between sources. For example, when scoring bob/dewlap amplitude, a 'relative' measure of amplitude variation between components within the display itself (see Table 1) was taken rather than literal distance moved (data of which was rarely given in the literature and usually then in units not directly comparable across sources; e.g. pixels on a video monitor).

Published data was also gathered on sexual size dimorphism (SSD; ratio of male to female snout–vent length, SVL) and species body size (maximum SVL, log₁₀-transformed), sympatry, habitat use and ecomorph class (see Appendix for data and sources used). Quantitative data on

Table 1. Signal measures scored from published DAP-graphs

Signal parameter	Description
Headbob duration or Dewlap duration	Total duration (s) of headbob or dewlap display sequences, from start of first headbob or dewlap pulse to end of last headbob or dewlap pulse, respectively.
Average headbob duration or Average dewlap duration	Average duration (s) of all individual headbobs or dewlap pulses in the display.
Headbob uniformity or Dewlap uniformity	Absolute value of the number of short headbobs (<0.5 s) or short dewlap pulses (<1.0 s) minus the number of long headbobs (≥0.5 s) or long dewlap pulses (≥1.0 s) divided by total of number headbob/dewlap pulses, respectively.
Average headbob pause duration or Average dewlap pause duration	Average duration (s) of all pauses between individual headbobs or dewlap pulses.
Headbob number or Dewlap number	Total number of individual headbobs or dewlap pulses in the display.
Headbob amplitude variation or Dewlap amplitude variation	Number of headbobs or dewlap pulses with different amplitudes divided by total number of headbobs/dewlap pulses. This parameter is a measure of amplitude variation relative to the headbobs/dewlap pulses within the display, and not a literal quantification of amplitude per se.
Dewlap latency	Time (s) from start of first headbob to start of first dewlap pulse. Negative values indicate dewlap pulses precede headbobs.
% Overlap	Time (s) that each dewlap pulse overlaps with a headbob, divided by the duration of the dewlap pulse, multiplied by 100, and averaged across all dewlap pulses. Small values indicate that headbobs and dewlap pulses alternate, whereas large values indicate that headbobs and dewlap pulses are performed simultaneously.
Dewlap/headbob ratio	Total duration of dewlap sequences divided by total duration of headbob sequences. Low values indicate that headbobs make up the majority of display, whereas large values indicate that dewlap pulses make up the majority of display.

encounter rate between congeners is difficult to obtain. However, there are a number of reports of sympatric species putatively engaging in interspecific agonistic behaviour (Schwartz & Henderson 1985) and several examples of interspecific mating between sympatric anoles (e.g. Gorman 1969; Jenssen 1977b). The number of anoles reported to co-occur with species was therefore used as a rough estimate of the potential for interspecific interaction. Available information on sympatry was taken from published accounts listing the number of sympatric congeners for each species and \log_{10} -transformed following inspection

of distribution plots. Habitat use was defined as sunny or shady depending on descriptions given in the literature (e.g. sunny habitats were described as 'sunny', 'open' or 'grassland' environments; shady habitats were described as 'shaded', 'closed' or 'forest' environments). *Anolis distichus*, *A. grahami* and *A. conspersus* have been reported in both sunny and shaded habitats and were excluded from habitat analyses. Finally, representatives of eight ecomorph types for which display data were available were identified from the literature (generalist, ground, grass-bush/bush-ground, trunk-ground, trunk, trunk-crown, crown-giant and canopy; no published DAP-graphs for any two twig anole were found). Differences in morphology and perch use exist between species within ecomorph types depending on whether anoles are island or mainland in origin (Irschick et al. 1997). Analyses were first conducted on all species, taking advantage of the increased sample size to identify prominent relationships between display variables and ecomorph. Any trends found were confirmed by repeating analyses on island and mainland ecomorphs separately. There was no qualitative difference in the results, and we present analyses with island and mainland species pooled.

Ecomorph types are represented by species in both sunny and shady habitats. Habitat use, as defined by light environment, is therefore considered to be independent of ecomorph type. The degree of SSD shown by species, however, is related to ecomorph type (e.g. trunk-ground or trunk-crown anoles of the Greater Antilles are often, but not exclusively, highly sexual dimorphic; Butler et al. 2000) and findings are interpreted with this relationship in mind.

Phylogenetic Comparative Analyses

Our analyses were focused around two complementary and evolutionarily explicit approaches. First, we applied the phylogenetic generalized least squares (PGLS) method described in Martins & Hansen (1997; see also Martins & Lamont 1998; Martins et al. 2002). Like other phylogenetic methods based on least squares statistics, PGLS can be used to estimate ancestral states and relationships between evolutionary changes in two or more traits and/or environments. However, in contrast to other statistical approaches, including those on which PGLS was based (e.g. Felsenstein 1985; Grafen 1989), PGLS (as applied here) assumes phenotypic evolution can be explained by a stationary Ornstein–Uhlenbeck model of constrained evolution. This assumption has been described for phenotypic evolution of quantitative traits under random genetic drift and several types of natural selection (Felsenstein 1988; Hansen & Martins 1996). To avoid specifying too many details of the evolutionary process, a single α parameter was estimated for each regression model, describing a composite constraint that can be interpreted in a variety of ways (Hansen & Martins 1996; Hansen 1997; Martins & Hansen 1997; see below).

Second, we applied the phylogenetic mixed model (PMM; Lynch 1991; Housworth et al. 2004). The PMM envisions interspecific phenotypes as the sum of evolutionary changes inherited along a phylogeny (similar to the

Brownian motion model underlying Felsenstein's (1985) independent contrasts) and bursts of change that may occur at all points in the evolutionary history of a clade, but which descendant taxa do not inherit from their ancestors. The PMM measures the relative contributions of these phylogenetically heritable (h^2) and nonheritable ($1 - h^2$) factors.

Although PGLS and PMM offer fundamentally different views of phenotypic evolution, both can be set to estimate the same types of parameters (e.g. correlations between traits, ancestral states). When PGLS α is forced to approach 0 and PMM $h^2 = 1$, both methods give results identical to Felsenstein's (1985) independent contrasts (FIC), in which phylogeny is the primary factor accounting for trait similarities between taxa. In this scenario, traits evolve along a lineage via random genetic drift and/or in response to selection, in which the direction of selection varies randomly over the long periods of time represented by the phylogeny. At the other extreme, when PGLS α is set to be very large and PMM $h^2 = 0$, results are consistent with ignoring phylogeny or assuming species radiated instantaneously from a single common ancestor (TIPS). Under PGLS, this scenario describes traits undergoing stabilizing selection constraining them to remain near a fixed optimum. Phylogenetic effects are unimportant or even completely erased as traits track that optimum. Under PMM, the same results are obtained for very different reasons. Here, phylogenetic effects are erased because evolutionary shifts are not passed on between parent and descendant taxa, perhaps because the traits are not genetically inherited or because daughter taxa evolve quickly to adapt to different selective regimes. Statistically, whereas extreme applications of the two methods (TIPS and FIC) have been shown to give very poor results in simulation studies (Martins et al. 2002; Housworth et al. 2004), applications that allow PGLS to estimate α via maximum likelihood and PMM to estimate h^2 using restricted maximum likelihood (REML), perform reasonably well in most conditions tested (Martins et al. 2002; Housworth et al. 2004). Results that are consistent across all four methods (TIPS, FIC, PGLS with estimated α , and PMM with estimated h^2) are likely to reflect particularly robust and prominent evolutionary trends, regardless of one's preferred view of phenotypic evolution.

Phylogeny

No published phylogenetic hypothesis for anoles includes all species of interest. Instead, the two most recent and comprehensive phylogenies developed by Poe (2004) and Nicholson et al. (2005) were combined. However, neither study lists *A. extremus*, *A. anisolepis* or *A. haguei*. For *A. extremus*, we followed Giannasi et al. (2000), but in the case of *A. anisolepis* and *A. haguei*, which are not reported in any published phylogeny, we used the taxonomic classification suggested by Nicholson (2002). Species synonyms were checked using the EMBL reptile database (<http://www.embl-heidelberg.de/~uetz/Living-Reptiles.html>).

Phylogenetic positions within the *Anolis* group have proven to be notoriously difficult to resolve. In general,

recent divergences are robustly supported, but nodes deeper in the tree are less certain, perhaps reflecting periods of rapid diversification (Jackman et al. 1999). There are some disagreements between the sources we consulted. To incorporate these different hypotheses in our analysis, we constructed two alternative topologies using the following criteria (Fig. 2): Tree 1 was collated favouring the molecular Bayesian and parsimony trees presented in Nicholson et al. (2005), while the morphology/molecular parsimony tree of Poe (2004) was favoured in Tree 2. Although the positions of several taxa vary (Fig. 2), inferences within major clades are generally well supported (e.g. bootstrap values >80%, Bayesian posterior probabilities >90%; Poe 2004; Nicholson et al. 2005).

As described elsewhere (Martins & Hansen 1997; Martins & Housworth 2002), branch lengths in a phylogenetic comparative analysis represent the amount of phenotypic change expected for the specific trait of interest, quantities that are almost never known. Fortunately, both PGLS and PMM use their respective α and h^2 parameters to calculate branch lengths that maximize the fit of data, thereby offering some protection against inaccurate branch length information (Martins et al. 2002; Housworth et al. 2004). Branch length information was not available for our composite phylogenies. Instead, we chose to rely on the robust properties of PGLS and PMM, setting all branch lengths equal to each other before beginning analyses.

Identifying Patterns in Comparative Data

We began by applying principal components analysis (PCA; using varimax rotation) to the 15 display measures (both raw data and Felsenstein contrasts) to identify biologically meaningful traits (i.e. several of our trait categorizations could actually be alternative measures of the same signal parameter) or trait complexes that appear to have evolved together over long periods. Not all species had data for every signal parameter (Appendix). Therefore, separate analyses were conducted on the available headbob (52 taxa) and dewlap (35 taxa) data, and on a combined data set of both display types (33 taxa), to highlight consistent trait relationships. To minimize the potential pitfalls of multiple statistical comparisons, only the most striking patterns were confirmed using PGLS pairwise correlations on the combined data set (33 taxa). Instead of relying on a specific phylogenetic hypothesis, the procedures outlined in Martins (1994) were used to conduct analyses under the assumption that each phylogeny is equally likely to be the true tree.

Based on results from PCA and pairwise comparisons, subsequent analyses were focused on a smaller number of representative signal parameters likely to reflect those aspects of signal design predicted to be influenced by ecological factors. This approach was chosen instead of using principal components, or other composite variables, to simplify the evolutionary interpretation of results. To describe the relative evolutionary lability of representative traits, two model-specific parameters were

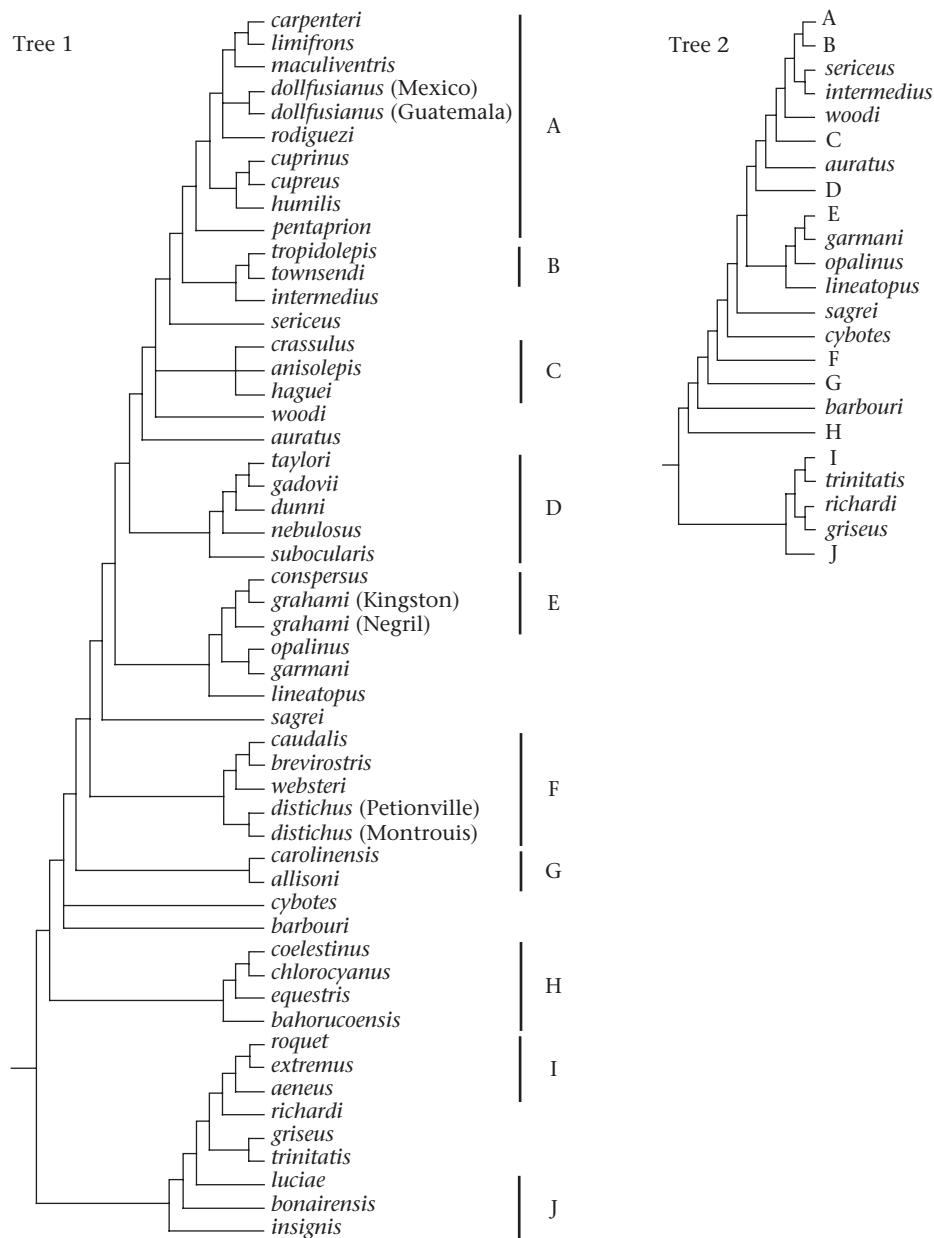


Figure 2. Species and phylogenetic hypotheses used to conduct comparative analyses. See Methods for details.

estimated from bivariate regression: PGLS α and PMM h^2 . (Note that as applied here, PGLS estimates a single α parameter for each bivariate model, whereas PMM estimates separate h^2 values for response and predictor variables.) Large values of PGLS α and small values of PMM h^2 indicate that phylogeny has left little, if any, signal in the interspecific phenotypes, whereas small α and large h^2 indicate the presence of a considerable phylogenetic effect.

Finally, potential adaptive evolution in signal design was examined by estimating pairwise relationships between display traits, morphology and ecology using four methods: TIPS, FIC, PGLS and PMM. Again, to minimize the possible complications of conducting multiple comparisons or Bonferroni-style corrections (see Nakagawa 2004), significance tests were conducted only for PGLS,

using the technique proposed in Martins (1994) to construct 95% confidence intervals (CI) around regression slopes that reflect the uncertainty of two phylogenies. Regression slopes (and in turn correlation coefficients) were considered to be significantly different from zero if their CIs did not include zero (henceforth, $P < 0.05$). We focus on PGLS because it is more robust to branch length errors than are FIC and TIPS, and unlike PMM, it does not suffer problems associated with small sample sizes. We did not use multiple regressions to consider relative impact of all ecological variables in the same statistical model because complete data were available for only 11 taxa.

To estimate relationships between continuous display measures and categorical factors of ecomorphs, we formulated PGLS ANOVAs as general linear models,

regressing each display measure (y) on a series of eight dichotomous dummy variables (x ; e.g. is/is not a 'ground' anole, is/is not a 'grass-bush' anole). Because PMM estimators have not yet been developed for more than two traits, PMM could not be applied to ecomorph data. Tests (across two phylogenies) were calculated separately for each of the resulting regression slopes, and the square root of the overall coefficient of determination (R) is reported as roughly comparable to the absolute value of the Pearson correlation coefficients reported for bivariate relationships.

All regression analyses were conducted in COMPARE 4.6 (Martins 2004). Several analyses (i.e. PCAs and residual analysis of SSD regressed on SVL) also relied on SPSS 11.5 (SPSS, Chicago, Illinois, U.S.A.).

RESULTS

Describing Anole Displays

Several display measures were tightly associated with each other (Table 2), suggesting they either represent the same biological trait or quantify distinct traits that have changed in concert over long periods of evolutionary time. PCA showed measures of duration (total headbob and dewlap duration, average headbob and dewlap duration) were strongly, positively associated and nearly always combined into a single, composite variable that explained 19–27% of the interspecific variation. This general pattern was consistent regardless of how data were treated (TIPS or FIC), phylogeny used, or data set analysed (headbob only: 52 taxa; dewlap only: 35 taxa; or combined data: 33 taxa). All pairwise correlations among these four traits (estimated from the 33-taxon data set using PGLS and assuming the true phylogeny was equally likely to be either of the two composite trees) were significantly greater than zero ($0.47 < R < 0.95$, $P < 0.05$ in all cases).

Average duration of headbob pauses also correlated weakly with total headbob duration and average dewlap duration ($R = 0.31$ and 0.42 , respectively, the latter $P < 0.05$), but not with other measures of duration ($R < 0.20$, $P > 0.05$), and hence was only sometimes grouped in PCAs (Table 2). Pause durations (especially between dewlaps) were more likely to form a third axis with dewlap latency and percentage of overlap (Table 2); displays with longer average dewlap pauses also tend to have shorter dewlap latencies and more overlap between headbob and dewlap sequences. Only the negative relationship between dewlap pause durations and dewlap latency was significantly different from zero ($R = -0.42$, $P < 0.05$).

A second axis often combined counts (headbob and dewlap number), but also included measures of dewlap amplitude variation, while a fourth or fifth axis formed around the relationship between uniformity, headbob amplitude variation and dewlap/head ratio (Table 2). Displays including more dewlaps tended to show less variation in the relative amplitude of dewlaps ($R = -0.37$, $P < 0.05$). Displays that consisted primarily

of headbob rather than dewlap motions tended to be less uniform (showing a disproportionate number of short- versus long-duration components; $R = -0.48$, $P < 0.05$; Table 1).

Using the above information, we chose headbob duration, dewlap duration, headbob number, dewlap number, headbob uniformity, dewlap uniformity and dewlap latency as representative variables for further analyses. Collectively, these parameters encompass each of the principal component axes presented in Table 2 and are likely to reflect signal traits predicted to be affected by ecological factors (i.e. SSD, sympatry, habitat and ecomorph type).

Patterns of Phylogenetic Signal

Estimated values of PGLS α and PMM h^2 provide an index of phylogenetic signal exhibited in traits (i.e. the extent that traits tend to be correlated with phylogeny). When α is 0 and h^2 approaches 1, a trait is considered to have considerable phylogenetic signal, whereas high values of α and an h^2 of 0 represents little or no phylogenetic signal. Dewlap uniformity and dewlap latency exhibited more evidence of phylogenetic signal than did other display measures when calculated using both PGLS α and PMM h^2 . The PMM also found evidence of phylogenetic signal in several of the nondisplay measures, specifically sexual size dimorphism and sympatry (Table 3). Habitat use and ecomorph showed little relationship with phylogeny, in agreement with findings from other comparative studies on anoles (e.g. Losos et al. 1998, 2003).

Ecological Influences on Signal Design

Sexual size dimorphism

Headbob duration was strongly, negatively correlated with SSD (ratio of male/female snout-vent length) regardless of phylogenetic hypothesis and in most comparative methods used ($-0.36 > R > -0.62$, $P < 0.05$ when tested using PGLS and broad confidence intervals reflecting two possible phylogenies; Table 4). There was little, if any, evidence of a relation between any of the other display traits and SSD. Overall, species that are highly sexually size dimorphic tend to possess displays that are shorter in total duration (Fig. 3). Interestingly, this does not seem to have been achieved by decreasing headbob number in display sequences (see Tables 2, 4).

Species body size is often positively correlated with SSD in anoles (e.g. Butler et al. 2000). To control for this, we repeated regressions using mass-free residuals of SSD (residuals generated from a regression of SSD on SVL), which produced similar results ($-0.37 > R > -0.44$).

Sympatry

There was a negative trend between the number of sympatric congeners and headbob uniformity

Table 2. Principal component loadings for major axes (defined as eigenvalues >1.0, calculated with varimax rotation and Kaiser normalization) resulting from analyses of raw species data (TIPS) and Felsenstein's (1985) contrasts (FIC)

Signal parameters	TIPS					FIC									
						Tree 1					Tree 2				
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
Headbob data only (52 taxa)															
Headbob duration*	0.78	0.43	0.26			0.86	0.15				0.70	0.51			
Av. headbob duration	0.92	-0.16	-0.11			0.70	-0.58				0.07	0.92			
Av. headbob pause dur.	0.09	-0.25	0.82			0.46	0.14				0.47	0.15			
Headbob uniformity*	-0.04	0.21	0.66			0.33	0.45				0.55	-0.06			
Headbob number*	-0.13	0.90	0.20			-0.08	0.85				0.61	-0.58			
Headbob amp. variation	-0.10	-0.40	0.11			-0.20	-0.50				-0.48	0.07			
Total variance explained (%)	24.7	21.4	20.6			26.6	25.8				27.0	24.7			
Dewlap data only (35 taxa)															
Dewlap duration*	0.77	-0.10	0.31	0.31		0.28	0.25	0.85	0.07		0.29	0.74	0.44	0.10	
Av. dewlap duration	0.89	0.11	-0.16	-0.29		-0.03	-0.52	0.78	-0.12		-0.02	0.92	-0.25	-0.07	
Av. dewlap pause dur.	-0.11	-0.10	0.78	0.10		0.70	0.29	0.18	-0.06		0.68	0.07	0.16	-0.08	
Dewlap latency*	-0.55	0.29	-0.61	0.17		-0.80	0.17	-0.37	-0.08		-0.74	-0.46	0.10	-0.08	
% Overlap	0.22	0.32	0.69	0.05		0.89	-0.004	-0.13	0.004		0.85	-0.09	-0.01	-0.02	
Dewlap number*	0.07	-0.12	-0.06	0.86		-0.09	0.83	-0.13	0.26		-0.10	-0.04	0.83	0.26	
Dewlap amp. variation	0.13	-0.07	-0.13	-0.75		-0.16	-0.80	-0.10	0.21		-0.18	0.03	-0.76	0.28	
Dewlap/headbob ratio	0.16	-0.88	-0.08	-0.11		-0.07	-0.08	0.21	0.82		-0.09	0.18	-0.04	0.77	
Dewlap uniformity*	0.11	0.83	-0.07	-0.17		-0.10	-0.13	0.24	-0.84		-0.05	0.18	-0.06	-0.87	
Total variance explained (%)	20.2	19.0	17.8	17.3		23.0	20.1	18.3	16.7		20.6	18.7	17.4	16.9	
Headbob and dewlap data combined (33 taxa)															
Headbob duration*	0.84	0.09	0.19	0.12	0.33	0.93	0.16	0.15	-0.07	-0.04	0.89	0.32	0.12	-0.04	-0.04
Dewlap duration*	0.86	0.26	0.16	-0.14	0.20	0.92	0.16	0.25	0.07	-0.01	0.87	0.32	0.23	0.12	-0.05
Av. headbob duration	0.57	0.02	-0.52	-0.17	0.33	0.55	-0.62	0.29	-0.11	-0.09	0.63	-0.40	0.36	-0.11	-0.21
Av. dewlap duration	0.85	0.22	-0.35	0.07	-0.07	0.77	-0.46	-0.05	0.28	0.26	0.84	-0.27	-0.04	0.39	0.16
Av. headbob pause dur.	0.54	-0.37	0.10	0.22	-0.26	0.51	-0.02	-0.48	-0.06	0.23	0.52	-0.08	-0.48	-0.07	0.29
Av. dewlap pause dur.	0.06	0.05	0.12	0.02	-0.01	0.11	0.12	-0.74	-0.24	-0.02	0.12	0.02	0.71	-0.27	0.12
Dewlap latency*	-0.23	-0.83	0.08	0.26	0.04	-0.29	0.08	-0.78	-0.32	-0.07	-0.29	0.01	-0.73	-0.42	-0.01
% Overlap	0.01	0.72	0.08	0.31	0.29	0.05	0.09	0.82	0.05	-0.01	0.05	0.12	0.74	0.12	0.04
Headbob number*	0.07	0.32	0.78	0.16	0.28	0.17	0.88	0.12	0.008	0.05	0.18	0.87	0.08	0.09	0.15
Dewlap number*	0.00	-0.02	0.65	-0.28	0.59	0.04	0.81	-0.11	-0.19	-0.38	0.14	0.79	-0.14	-0.17	-0.34
Headbob amp. variation	0.15	0.82	0.13	-0.02	-0.28	-0.23	0.02	0.22	0.81	0.23	0.17	0.10	0.15	0.88	0.07
Dewlap amp. variation	-0.02	0.09	-0.77	0.00	0.13	0.006	-0.73	-0.21	-0.007	-0.18	0.08	-0.71	-0.21	-0.05	-0.19
Dewlap/headbob ratio	0.06	0.15	-0.03	-0.84	-0.35	0.02	-0.009	-0.04	0.65	-0.59	-0.05	-0.01	-0.08	0.53	-0.67
Headbob uniformity*	0.28	-0.03	0.02	0.16	0.70	0.41	0.14	0.22	-0.62	0.24	0.50	-0.19	0.13	-0.49	0.27
Dewlap uniformity*	0.10	0.09	0.02	0.84	-0.14	0.08	0.02	-0.04	0.01	0.91	0.02	0.10	0.03	0.12	0.89
Total variance explained (%)	19.7	15.2	14.2	12.2	10.4	21.6	17.8	16.0	11.9	10.5	22.3	16.0	14.2	12.0	11.1

Bold indicates relatively heavy loading on an axis.

*Signal parameters chosen for subsequent analyses.

Table 3. The degree to which phylogeny explained interspecific phenotypic variation, as estimated by phylogenetic generalized least squares (PGLS) α and phylogenetic mixed model (PMM) h^2

Variable	PGLS: α^*		PMM: h^2 †	
	Mean	Range	Mean	Range
Headbob duration	12.38	8.87–15.50+	0.25	0.00–0.61
Dewlap duration	15.34	13.36–15.50+	0.09	0.00–0.54
Headbob number	12.99	6.66–15.50+	0.05	0.00–0.28
Dewlap number	15.33	13.23–15.50+	0.02	0.00–0.10
Headbob uniformity	14.85	13.45–15.50+	0.19	0.11–0.28
Dewlap uniformity	8.91	3.37–10.32	0.60	0.00–0.71
Dewlap latency	6.19	2.54–12.58	0.90	0.39–1.00
SSD	13.82	8.87–15.50+	0.86	0.81–0.92
Sympatry	12.15	7.69–15.50+	0.64	0.49–0.82
Sunny vs shady habitats	11.60	3.37–15.50+	0.00	n/a
Ecomorph				
Multiple regression	12.85	6.66–15.50+	n/a	n/a
Pairwise comparisons	12.11	2.54–15.50+	0.38	0.00–0.97

Means and ranges describe estimates derived using two phylogenies and from five regression models (see text for details).

* α values between 0 (approaching FIC) and 15.5 (approaching TIPS) were tested, where low values indicate more phylogenetic signal.

† h^2 values range from 0 (approaching TIPS) to 1 (approaching FIC), where low values indicate less phylogenetic signal.

($-0.29 > R > -0.33$, $P < 0.05$; Table 4). Species that are likely to encounter congeners seem to produce headbob displays that are more diverse in the temporal pattern of elements used (Fig. 4).

Table 4. Average relationships (Pearson correlation coefficients) for ecological traits estimated across two possible phylogenies

	N	TIPS	FIC	PGLS	PMM
SSD					
Headbob duration	42	-0.39	-0.23	-0.36*	-0.62
Dewlap duration	28	-0.10	-0.12	-0.11	-0.07
Headbob number	42	-0.17	-0.08	-0.15	-0.21
Dewlap number	28	0.06	-0.09	0.04	0.06
Headbob uniformity	42	0.15	0.00	0.13	0.25
Dewlap uniformity	28	-0.01	0.17	0.07	-0.17
Dewlap latency	28	0.08	-0.12	0.01	0.45
Sympatry					
Headbob duration	37	0.28	0.14	0.26	0.45
Dewlap duration	23	0.17	0.17	0.17	0.11
Headbob number	37	-0.12	-0.25	-0.17	0.20
Dewlap number	23	-0.10	-0.19	-0.11	0.02
Headbob uniformity	37	-0.32	-0.29	-0.32*	-0.33
Dewlap uniformity	23	-0.16	-0.28	-0.20	0.23
Dewlap latency	23	0.10	-0.03	0.07	0.49
Sunny vs shady habitats					
Headbob duration	29	0.19	0.16	0.19	0.19
Dewlap duration	20	-0.06	-0.04	-0.06	-0.07
Headbob number	29	0.08	0.09	0.08	0.08
Dewlap number	20	-0.44	-0.40	-0.44*	-0.46
Headbob uniformity	29	-0.06	0.07	-0.04	-0.04
Dewlap uniformity	20	0.46	0.46	0.46*	0.43
Dewlap latency	20	0.12	0.14	0.15	0.05

Significance tests were conducted only for PGLS, with asterisks referring to estimates considered reliably different from zero based on 95% confidence intervals. See Methods for variable and analysis details.

N = number of species; TIPS, phylogenetically uncorrected regression; FIC, Felsenstein's (1985) independent contrasts; PGLS, phylogenetic generalized least squares regression; PMM, phylogenetic mixed model.

Sunny versus shady habitats

In all cases, species that occupy shaded environments use displays with fewer ($-0.40 > R > -0.46$, $P < 0.05$), but more uniform ($0.43 < R < 0.46$, $P < 0.05$) dewlap pulses (Table 4, Fig. 5). Conversely, lizards communicating in sunny habitats produce more pulses, which are also more temporally variable, during display sequences.

Ecomorph

Both headbob duration and dewlap latency were closely associated with ecomorph categories (Table 5). In all cases, canopy species tend to produce longer headbob displays than other ecomorphs, while trunk and crown-giant

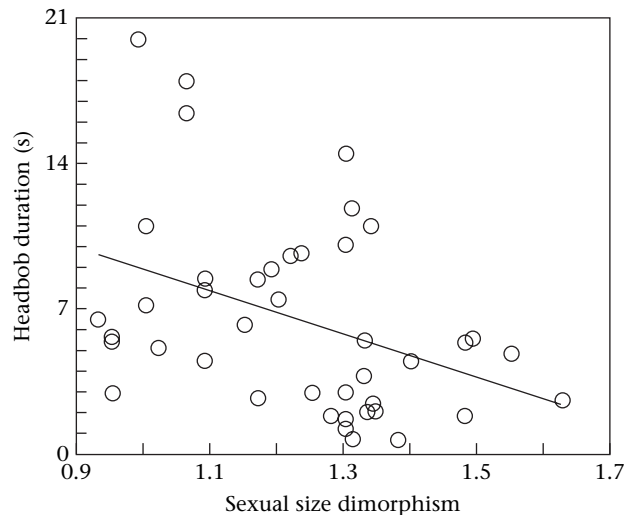


Figure 3. The relation between the length of headbob displays and sexual size dimorphism (male:female snout-vent length; values of 1 indicate sexes of equal size, those greater than 1 male-biased dimorphism and those less than 1 female-biased dimorphism). Data presented are uncorrected for phylogeny (i.e. TIPS).

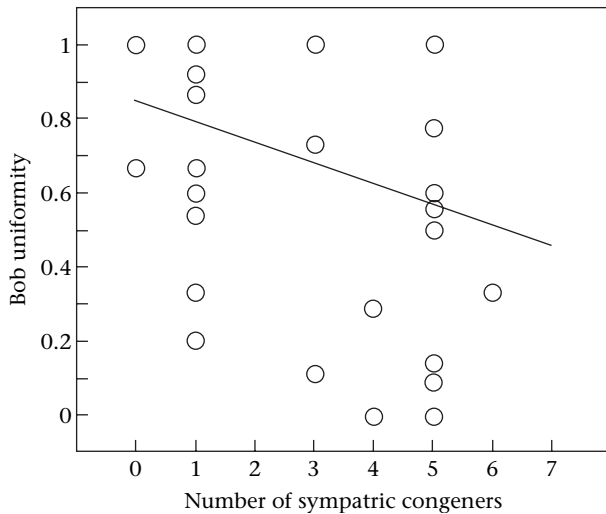


Figure 4. The relation between the proportion of short versus long headbobs used in displays (values of 1 indicate bobs of similar duration and values less than 1 indicate bobs of different duration) and the number of sympatric congeners likely to be encountered by species. Data presented are uncorrected for phylogeny (i.e. TIPS).

anoles introduce dewlaps later in display sequences (Fig. 6). Although sample sizes were small for individual ecomorph types, trends were robust regardless of phylogeny or comparative method used, or how data were treated (island and mainland ecomorphs pooled or separate). There was also a tendency for canopy anoles to produce longer dewlap displays, but the relationship was not statistically significant.

DISCUSSION

Recent studies have shown that complex phenotypes such as communicative displays are often the product of an equally complex selective regime, with elements of a signal responding differently to separate selective pressures (e.g. Marchetti 1998; Andersson et al. 2002; Stuart-Fox & Ord 2004; Martins et al. 2005; Seddon 2005). The structure of animal signals can be influenced by sexual selection (Andersson 1994; Ord et al. 2001), properties of the environment (Peters & Evans 2003a, b), the need to convey species identity (Seddon 2005), physical constraints and phylogeny (Bradbury & Vehrencamp 1998; Seddon 2005). Our study confirms that long-term patterns of display evolution in anoles carry the imprint of multiple, interacting forces. Intraspecific competition (via sexual selection or resource competition between the sexes), sympatry, habitat use (light environment and ecomorph), constraints imposed by close evolutionary ties between signal parameters, and phylogenetic history have all played some part in the diversification of anole displays. Moreover, each factor seems to have affected different signal components. Whereas evolutionary changes in total headbob duration are linked to SSD, changes in headbob uniformity (whether a display consists of components with similar duration; Table 1) are more closely related to species recognition. The environment seems to have influenced evolutionary changes in the number and

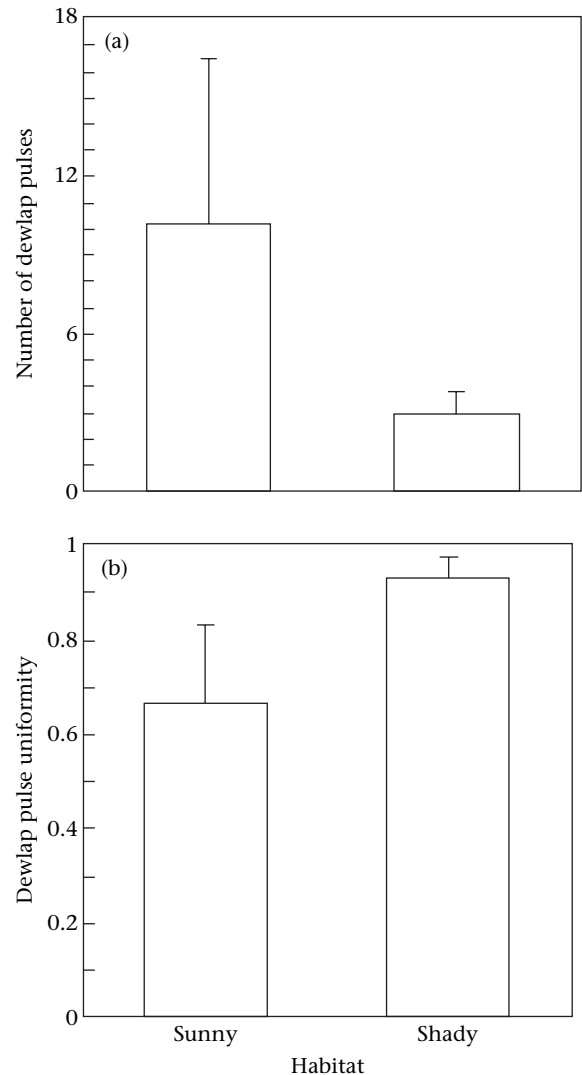


Figure 5. Differences in the (a) number of dewlap pulses and (b) proportion of short versus long dewlap pulses used by anoles living in sunny and shady habitats. Data presented are uncorrected for phylogeny (i.e. TIPS).

uniformity of dewlap pulses, and ecomorph distinctions associated with such dramatic convergences in anole lizard morphology and lifestyle (Losos 1990; Losos et al. 1998) have also had a potential impact on the evolution of signal design. Below, we use these results to identify areas for future research and contrast patterns of anole display evolution with other lizard groups.

Evolution of Complex Signals

The duration of headbob displays was closely associated with SSD; species that are highly sexually size dimorphic typically produce short territorial displays. There was no evidence for a relation between the number of headbobs and either SSD or the length of display sequences. Instead, shorter displays have evolved by the inclusion of faster signal elements and shorter pauses between them, rather than fewer display components (Table 2). This suggests

Table 5. Relationships (correlation of determination and regression slopes) for ecomorph types estimated across two possible phylogenies

	N	TIPS		FIC		PGLS	
		R ²	B (95% CI)	R ²	B (95% CI)	R ²	B (95% CI)
Headbob duration	47	0.33		0.34		0.32*	
			Ground		−5.17 (−12.60, 2.26)		−0.94 (−7.27, 5.39)
			Grass-bush		−4.76 (−10.95, 1.43)		−1.04 (−6.45, 4.37)
			Trunk-ground		−1.55 (−7.43, 4.33)		0.53 (−4.12, 5.18)
			Trunk		−4.71 (−11.88, 2.46)		0.14 (−5.45, 5.73)
			Trunk-crown		−3.04 (−9.47, 3.39)		0.52 (−5.69, 6.73)
			Crown-giant		−4.04 (−8.67, 0.59)		−3.52 (−8.07, 1.03)
			Canopy		7.37 (0.29, 14.45)		10.08 (3.02, 17.14)
Dewlap duration	30	0.36		0.43		0.37	
Headbob number	47	0.15		0.33		0.22	
Dewlap number	30	0.14		0.34		0.16	
Headbob uniformity	47	0.18		0.25		0.18	
Dewlap uniformity	30	0.14		0.13		0.13	
Dewlap latency	30	0.61		0.45		0.55*	
			Ground		3.51 (−0.10, 7.12)		2.41 (−1.20, 6.02)
			Grass-bush		2.54 (−0.97, 6.05)		1.19 (−2.20, 4.58)
			Trunk-ground		2.53 (−0.68, 5.74)		1.54 (−1.48, 4.56)
			Trunk		3.96 (0.43, 7.49)		3.87 (0.32, 7.42)
			Trunk-crown		2.52 (−1.11, 6.15)		2.95 (−0.62, 6.52)
			Crown-giant		6.80 (2.96, 10.64)		8.30 (4.42, 12.18)
			Canopy		0.58 (−2.42, 3.58)		0.10 (−3.57, 3.77)

N = total number of species included in analysis; TIPS, phylogenetically uncorrected regression; FIC, Felsenstein's (1985) independent contrasts; PGLS, phylogenetic generalized least squares regression; PMM, phylogenetic mixed model. 'Generalist' was dropped from the analyses because this variable was summarized by the combined effect of the other seven dummy variables.

*PGLS estimates considered reliably different from zero based on 95% confidence intervals (CI); PGLS regression slopes of note are highlighted in bold.

that shorter displays are potentially information-packed and energetically costly. If SSD is the product of sexual selection acting through male–male competition (Ord et al. 2001; Stuart-Fox & Ord 2004), then this supports our hypothesis that competitive intensity promotes the evolution of short, complex displays, a finding that also bears some resemblance to the evolution of bird song (Read & Weary 1992; MacDougall-Shackleton 1997; Bradbury & Vehrencamp 1998; Price & Lanyon 2004). When anoles advertise the continued occupation of a territory, the repetition of such a signal during prolonged bouts of display may present a reliable cue of physiological condition and help to deter territorial intrusions from neighbours and other rivals. Future studies that focus on the detailed interaction between individuals during competitive interactions (e.g. McMann 1993) and the energetic cost of display behaviour (e.g. Brandt 2003) may help to explain the precise evolutionary significance of rapid, stereotyped displays. Furthermore, we know little about the functional relation between the structure of headbob and dewlap displays and the frequent evolution of other visual components, such as colour signals, body postures and other motions (Ord et al. 2001; Stuart-Fox & Ord 2004; Martins et al. 2005).

The origin of SSD in anoles is in itself likely to be the result of multiple forces, such as intersexual habitat partitioning and foraging mode, in addition to intrasexual selection (Butler et al. 2000; Butler & Losos 2002). We found some evidence that ecomorph distinctions, which typically group into classes of either high or low SSD (Butler et al. 2000), also tend to predict similarities in signal

design; specifically, longer headbob displays in canopy anoles, and the introduction of dewlaps much later in the displays of trunk and crown-giant lizards, all 'low SSD' ecomorphs (Butler et al. 2000). The relationship between SSD and display evolution is therefore likely to be complex, possibly reflecting differences in habitat use as well as sexual selection. We predicted that highly arboreal ecomorphs would suffer more constraints on signal design, and the tendency for canopy anoles to perform longer displays supports this to an extent. However, a similar relationship is absent in crown-giants, which also tend to display from perches high up in the canopy. Furthermore, it is unclear how habitat constraints on display form might have led to the observed differences in dewlap latency between ecomorphs. Empirical studies that explore how differences in habitat use between ecomorph types affect social behaviour and signal production are therefore warranted.

More intuitive is the finding that displays incorporating more than one type of headbob seem to have evolved when species recognition is likely to be important. Specifically, bobs are more temporally diverse (i.e. less uniform) in headbob sequences with increasing numbers of sympatric congeners (where there is a greater need for interspecific discrimination). A reduction in headbob uniformity appears to be linked to an increase in variation of relative bob amplitude (Table 2), further supporting our hypothesis that displays produced by sympatric species are generally more diverse or complex in structure. It is important to reiterate that the displays examined in this study are species typical and highly stereotyped within

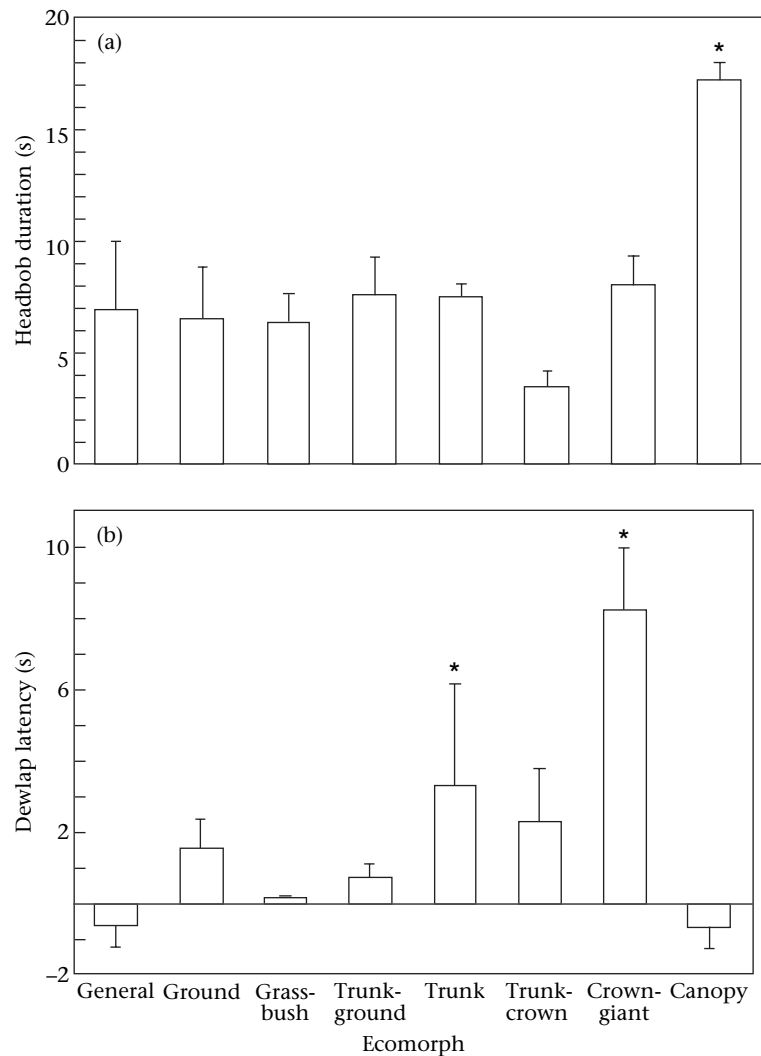


Figure 6. Ecomorph differences in (a) total headbob duration and (b) time to start of dewlap display following (positive values) or preceding (negative values) onset of headbob display. Data presented are uncorrected for phylogeny (i.e. TIPS). *Categories with 95% confidence intervals not overlapping zero.

and between individuals. 'Variation' and 'diversity' in display structure refer to the inclusion of bobs of different appearance, but that are nevertheless performed in a stereotyped sequence. For example, *A. opalinus* occurs with as many as four anoles and performs a stereotypical display that includes a mixture of long and short bobs of different amplitude, whereas *A. rodriguezii* is typically sympatric with only one congener and uses bobs of more uniform duration and amplitude (Appendix; see Fig. 1). In the presence of many congeners, diverging from the more 'generic' signal design of uniform display elements by introducing greater temporal and amplitude diversity, presumably renders a display more distinct and recognizable to conspecifics.

There was a similar (be it weak) relation with dewlap uniformity, but sympatry could not reliably predict the structure of dewlap sequences. Instead, less uniform dewlap pulses were found in species frequenting open, brightly lit environments (as opposed to greater dewlap

uniformity in shaded habitats, which is consistent with our prediction of greater redundancy when lighting conditions are low). Species in sunnier habitats also typically produce more dewlap pulses, and generally have more dewlaps than headbobs in their displays (Table 2). Previous studies have argued that dewlap colour encodes important cues on species identity (e.g. Rand & Williams 1970; Williams & Rand 1977; Losos 1985; Leal & Fleishman 2004). Furthermore, lizards seem to gain little benefit from the use of dewlaps during aggressive encounters with conspecifics (Tokarz et al. 2003, 2005). Dewlaps might therefore serve a more prominent role in species recognition in brightly lit, open areas, where visual signals are potentially perceived over greater distances and cues obtained from gross morphology (which are presumably important in conspecific identification) are more difficult to assess. Alternatively, or in addition, flashing a dewlap may help to orient distant receivers to display broadcasts.

We also found some evidence that those anoles using fewer dewlap extensions (i.e. those in shaded habitats) compensate by extending the average duration of pulses. Producing only one or two sustained dewlap pulses might provide a better strategy for enhancing conspicuousness in darker habitats. This strategy would be further facilitated with the evolution of larger dewlaps, which appears to be a general trend in anoles living in dimly lit environments (Losos & Chu 1998). Regardless, dewlap movement is in itself an important aspect of anole signal design, and its relationship with dewlap colour and interaction with the properties of environment, a promising avenue for continued study (e.g. Persons et al. 1999; Fleishman & Persons 2001).

Signal Evolution in Iguanian Lizards

Anole displays are perhaps not as variable as they appear at first glance. Using PCMs to identify evolutionarily meaningful trait complexes from DAP-graphs (which is only one method for quantifying display structure; see Peters et al. 2002; Peters & Ord 2003), we found several strong associations between display measures that suggest that interspecific variation in signal design can be described reasonably well by three headbob and dewlap parameters (duration, number of units and uniformity) and one parameter representing the interaction between headbobs and dewlaps (dewlap latency). The tendency for increases in the number of units to be accompanied by decreases in relative amplitude variation, especially in dewlap displays, is particularly interesting. This relationship supports the conclusion that iguanian lizard displays have increased in complexity in two fundamentally different ways (Martins 1993): some species are increasing the number of regular up-and-down motions, whereas others are evolving displays that reduce the overall number of these elements, but increase their relative variance in vertical amplitude. Studies into the genetic, neural and endocrine bases of lizard headbob displays may shed light on the underlying mechanisms that direct evolutionary changes in display structure along these paths.

Anole headbob displays are also strikingly similar to those of *Sceloporus* lizards, in both the number of up-and-down motions (mean \pm SE = 6.5 ± 0.74 for anoles, 6.9 ± 0.36 for *Sceloporus*) and total duration (9.2 ± 1.04 s for anoles, 9.8 ± 0.67 s for *Sceloporus*). The *Sceloporus* genus, a distantly related iguanid group found throughout North America, is also species rich like the anoles (Carpenter 1978a; Martins 1993; Warheit et al. 1999). Anoles may show more interspecific diversity in signal form than *Sceloporus*, but whether this reflects varying rates of phenotypic evolution or differences in the relative number of species in the two genera, requires a more precise knowledge on the evolutionary timing of speciation events in the two groups (see Warheit et al. 1999 for a comparison of morphological diversification between the two genera). Headbob displays of both anoles and *Sceloporus* are somewhat longer and involve more up-and-down motions than do the displays of South American *Liolaemus* lizards (Martins et al. 2004) and some *Cyclura* iguanas (Martins

& Lamont 1998). An obvious difference between the visual signals of anoles and other iguanian lizards is their use of dewlap displays. *Sceloporus* have a simple gular flap that can be engorged to inflate the throat, but is not used in complex, stereotyped motions. Other lizard taxa are poorly studied, but seem to rely on different components to elaborate headbob displays, such as body coloration, ornamentation, arm-waves and tail-flicks (e.g. Carpenter et al. 1970; Macedonia et al. 2002; Ord et al. 2002; Ord & Blumstein 2002; Peters & Ord 2003; Stuart-Fox & Owens 2003; Stuart-Fox & Ord 2004). Although Wiens (2000) was unable to find evidence for an evolutionary interaction between colour patches and dynamic displays in *Sceloporus*, the combination of colour and motion in anole dewlap displays offers a more promising place to look.

Identifying the Evolutionary Forces Shaping Complex Behaviour

Phylogenetic comparative methods (PCMs) are often described as a powerful tool for generating predictions, and we outline several areas for future research resulting from our analyses on anole signal design. Although PCMs offer the potential to infer a great deal about the details of the evolutionary process (e.g. Martins 2000), further theoretical development has been restrained by concerns about the large sample sizes needed to obtain decent parameter estimates (e.g. Housworth et al. 2004). Our study illustrates the utility of PCMs to uncover interesting patterns from intermediate-sized, realistic data sets. Although our comparative data represents a huge amount of empirical research (compiling the results of over 50 studies published over nearly four decades), the sample sizes are still quite small from a statistical perspective.

Nevertheless, we were able to show that changes in several aspects of dewlap structure appear to track the phylogeny more closely than do other display measures, implying that these features are constrained by some aspect of morphology or another trait inherited along a phylogeny. Relating individual differences in display duration (e.g. Jenssen 1971; Crews 1975; Jenssen & Hover 1976; Bels 1986) to their functional consequences, or identifying the underlying genetic and physiological mechanisms dictating intraspecific variation in signal production, may be particularly effective at drawing a direct link between microevolutionary process and the resulting macroevolutionary pattern shown in signal structures. Most aspects of signal design were largely unrelated to phylogeny, revealing that anole display evolution is typified by extremely rapid and/or recent evolutionary change, to the point that extant phenotypes retain few of the elements inherited from their immediate ancestors.

Using several different PCMs and phylogenetic hypotheses, we show how sexual size dimorphism predicts the evolution of rapid displays, perhaps reflecting male–male competitive intensity or a by-product of differences in habitat use. The need to distinguish heterospecifics from conspecific rivals or mates also appears to have created more complex displays by increasing the diversity of head

movements incorporated into displays. We also provide the first comparative evidence to support empirical research (Fleishman 1988a; Peters & Evans 2003a, b) demonstrating that habitat structure can shape the dynamic properties of lizard visual displays. In general, the homology issues confronted by investigations of the evolution of dynamic visual signals are more complex than those confronted by studies of acoustic and static signals (Prum 1990, 1994, 1997; Wiens 2000). Consequently, our knowledge of the evolutionary forces shaping motion-based forms of communication has lagged. As we show here, it is only through the study of exceedingly complex communicative displays that we can gain insight into the interaction of phylogenetic, functional and environmental factors that influence display evolution.

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Appendix

Table A1. Trait data and sources consulted*

Species	Average headbob			Headbob uniformity	Headbob number	Headbob amplitude variation	Dewlap latency (s)	% Overlap	Average dewlap		Average dewlap		Dewlap/		Dewlap uniformity	SSD	SVL	Sympatry	Sunny vs shady habitats	Ecomorph class
	Headbob duration (s)	headbob duration (s)	pause duration (s)						pause duration (s)	Dewlap duration (s)	Dewlap duration (s)	Dewlap amplitude variation	Dewlap number	Dewlap/ headbob ratio						
<i>Anolis aeneus</i> ¹	4.5	0.6	0.4	0.3	3	0.3	0.0	70	0.0	7.6	3.6	1.0	2	1.7	1.0	1.40 ²³	77 ³⁴	1 ³⁸	Shady ⁴³	Generalist ³⁸
<i>A. allisoni</i> ²	2.3	0.6	0.3	0.3	3	1.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.33 ²⁴	91 ²⁴	nd	Sunny ³⁷	Trunk-crown ⁴⁷
<i>A. anisolepis</i> ³	5.8	0.3	0.6	0.9	15	1.0	4.2	100	0.0	1.3	0.3	1.0	4	0.2	1.0	0.95 ³	nd	1 ³	nd	nd
<i>A. auratus</i> ⁴	11.0	1.0	0.7	0.4	7	0.7	0.0	91	0.0	10.3	1.8	0.6	5	0.9	0.2	1.00 ²⁵	48 ²⁵	nd	Sunny ²⁵	Grass ^{†25}
<i>A. bahorucoensis</i> ⁵	9.3	0.1	0.4	1.0	49	0.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	Shady ⁴⁴	Grass-bush ³⁸
<i>A. barbouri</i> ⁶	19.0	6.2	0.0	1.0	3	1.0	-1.3	79	0.0	24.0	24.0	1.0	1	1.3	1.0	nd	nd	nd	nd	None ⁴⁸
<i>A. bonairensis</i> ⁷	3.0	0.2	0.0	1.0	16	0.9	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.25 ²⁶	75 ²⁶	0 ³⁸	nd	None ³⁸
<i>A. brevirostris</i> ⁸	9.0	0.6	0.9	0.3	6	0.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.19 ²⁷	50 ³⁵	nd	Shady ⁴³	Trunk ⁴⁷
<i>A. carolinensis</i> ⁹	2.8	0.1	0.2	1.0	9	0.7	1.6	92	0.0	1.2	1.2	1.0	1	0.4	1.0	1.34 ²⁸	64 ⁴⁹	nd	Shady ⁴⁴	Trunk-crown ³⁸
<i>A. carpenteri</i> ¹⁰	6.5	0.5	0.3	0.1	9	0.8	0.3	58	0.0	6.8	6.8	1.0	1	1.0	1.0	0.93 ²⁵	41 ^{10,25}	3 ³	Sunny ⁴³	Trunk ³⁰
<i>A. caudalis</i> ⁸	8.0	0.6	0.9	0.3	6	0.0	9.0	0	0.4	4.2	2.0	0.5	2	0.5	1.0	1.09 ²⁹	51 ²⁹	nd	Shady ⁴³	Trunk ⁴²
<i>A. chlorocyanus</i> ¹¹	3.8	0.3	0.4	1.0	9	0.7	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.33 ²⁷	70 ²⁷	nd	Shady ³³	Trunk-crown ³⁸
<i>A. coelestinus</i> ¹²	1.9	0.1	0.0	1.0	6	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.28 ²⁷	70 ²⁷	nd	Shady ³³	Trunk-crown ³⁸
<i>A. conspersus</i> ¹³	3.0	0.2	0.4	0.7	6	1.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0 ³⁸	nd	Trunk-crown ³⁸
<i>A. crassulus</i> ³	5.6	0.2	0.6	1.0	16	1.0	1.7	80	2.4	3.8	0.6	0.5	2	0.7	1.0	0.95 ³⁰	nd	nd	nd	Ground ³⁰
<i>A. cupreus</i> ¹⁰	8.4	0.7	0.4	0.5	11	0.8	0.1	60	0.9	9.5	4.2	1.0	2	1.1	1.0	1.17 ²⁵	55 ²⁵	nd	Shady ²⁵	Bush-ground ^{†25}
<i>A. cuprinus</i> ³	14.5	1.2	0.0	0.5	13	0.8	0.0	34	2.6	16.4	3.5	1.0	2	1.1	1.0	1.30 ³⁰	nd	1 ³⁰	nd	Trunk-ground ³⁰
<i>A. cybotes</i> ¹⁴	10.1	0.2	0.4	1.0	29	0.6	2.2	60	0.0	11.7	0.4	0.3	29	1.2	0.8	1.30 ²⁷	65 ²⁷	3 ^{39,40}	Sunny ⁴⁵	Trunk-ground ³⁰
<i>A. distichus</i> (Montrouis) ¹⁴	7.9	0.2	1.1	1.0	13	0.9	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	3 ^{40,41}	nd	Trunk ³⁸
<i>A. distichus</i> (Petionville) ¹⁴	6.3	0.2	1.0	1.0	10	0.9	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.15 ²⁷	50 ³⁶	3 ^{40,41}	nd	Trunk ³⁸
<i>A. dollfusianus</i> (Guatemala) ³	1.8	0.3	0.0	0.6	5	0.4	1.1	39	0.0	1.8	1.8	1.0	1	1.0	1.0	1.30 ³⁰	nd	1 ³	nd	Trunk-ground ³⁰
<i>A. dollfusianus</i> (Mexico) ³	3.1	0.6	0.3	0.2	5	1.0	0.5	93	0.0	2.8	2.8	1.0	1	0.9	1.0	nd	nd	nd	nd	Trunk-ground ³⁰
<i>A. dunni</i> ³	7.5	3.0	0.7	1.0	2	0.0	0.3	25	4.0	12.6	2.2	1.0	4	1.7	0.5	1.20 ³¹	nd	3 ³	nd	Trunk-ground ³⁰
<i>A. equestris</i> ¹⁵	8.5	0.5	0.4	0.3	12	0.3	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.09 ²⁴	181 ²⁴	6 ³⁵	Shady ⁴⁴	Crown-giant ⁴⁷
<i>A. extremus</i> ⁷	0.7	0.2	0.0	1.0	4	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.38 ²⁹	83 ³³	0 ^{38,50}	nd	Trunk-crown ³⁸
<i>A. gadovii</i> ³	3.0	0.3	0.8	1.0	7	0.9	-0.4	25	0.3	5.3	3.6	0.5	2	1.8	1.0	1.30 ³⁰	nd	1 ³	nd	Trunk-ground ³⁰
<i>A. garmani</i> ^{16,51}	5.5	0.4	0.8	0.1	7	0.3	6.5	3	0.0	3.3	3.3	1.0	1	0.6	1.0	1.33 ²⁷	105 ²⁷	4 ^{35,40}	Shady ³⁷	Crown-giant ²⁷
<i>A. grahami</i> (Negril) ¹⁶	3.7	0.3	0.6	1.0	6	0.3	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	4 ^{35,40}	nd	Trunk-crown ³⁸
<i>A. grahami</i> (Kingston) ^{16,51}	5.6	0.5	0.5	0.6	5	0.6	5.3	2	0.3	4.8	1.3	0.3	3	0.9	1.0	1.49 ²⁷	76 ²⁷	4 ^{35,40}	nd	Trunk-crown ³⁸
<i>A. griseus</i> ⁷	5.4	0.2	2.4	1.0	7	0.9	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.48 ²⁶	136 ²⁶	1 ³⁸	nd	None ³⁸

<i>A. haguei</i> ³	7.2	0.2	0.4	0.9	26	0.7	0.7	86	1.8	5.5	0.7	1.0	3	0.8	1.0	nd	nd	1 ³	nd	nd
<i>A. humilis</i> ¹⁰	3.0	1.1	0.3	1.0	2	0.5	3.0	0	0.0	2.3	2.3	1.0	1	0.8	1.0	0.95 ²⁵	38 ²⁵	5 ³²	Shady ²⁵	Ground ³⁰
<i>A. insignis</i> ³	16.5	1.1	1.4	1.0	13	0.8	-1.3	65	0.0	21.3	21.3	1.0	1	1.3	1.0	1.06 ³²	nd	5 ³²	Shady ³²	Canopy ³²
<i>A. intermedius</i> ¹⁰	7.2	0.5	1.1	0.1	11	1.0	0.3	83	0.8	7.4	3.2	0.5	2	1.0	1.0	1.00 ²⁵	54 ²⁵	5 ³²	Shady ³²	Bush-ground† ²⁵
<i>A. limifrons</i> ¹⁷	4.5	0.4	0.0	0.6	10	0.8	0.3	80	0.0	5.0	5.0	1.0	1	1.1	1.0	1.09 ²⁵	40 ²⁵	4 ³	Shady ²⁵	Bush-ground† ²⁵
<i>A. lineatopus</i> ¹⁷	1.9	0.3	0.5	1.0	5	1.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.48 ²⁹	70 ³⁴	4 ⁴⁰	Sunny ³⁷	Trunk-ground ²⁷
<i>A. luciae</i> ⁷	4.9	0.2	2.6	1.0	13	0.7	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.55 ²⁹	91 ³³	0 ³⁸	nd	Trunk-crown ³⁸
<i>A. maculiventris</i> ³	14.3	0.9	0.4	0.7	15	0.6	-0.7	100	3.5	16.0	6.4	1.0	2	1.1	1.0	nd	nd	3 ³	nd	nd
<i>A. nebulosus</i> ¹⁸	2.7	0.3	0.0	0.7	7	0.7	0.2	29	0.7	5.0	1.2	1.0	3	1.9	0.3	1.17 ²⁹	42 ²⁵	nd	Shady ²⁵	Bush-ground† ²⁵
<i>A. opalinus</i> ¹⁹	9.6	0.8	0.4	0.6	9	0.7	0.0	100	5.5	9.3	1.8	0.5	2	1.0	1.0	1.22 ²⁷	52 ²⁷	4 ³⁵	Shady ⁴⁴	Trunk-crown ⁴⁸
<i>A. pentapriion</i> ¹⁰	9.7	2.8	0.9	0.3	3	1.0	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.24 ²⁹	75 ³⁰	7 ⁴²	Shady ⁴⁶	nd
<i>A. richardi</i> ⁷	2.8	0.4	0.0	0.7	6	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.62 ²⁶	115 ²⁶	1 ³⁸	nd	None ³⁸
<i>A. rodriguezii</i> ³	20.0	0.7	0.4	1.0	23	0.7	2.5	80	0.0	19.3	1.3	0.9	16	1.0	0.9	0.99 ³	nd	1 ³	Shady ⁴⁶	Trunk-ground ³⁰
<i>A. roquet</i> ⁷	2.3	0.5	0.5	0.5	4	0.8	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.34 ³³	86 ³³	0 ³⁸	Sunny ⁴³	Trunk-crown ³⁸
<i>A. sagrei</i> ²⁰	11.0	1.9	0.4	0.8	9	0.3	2.0	83	1.3	12.0	1.1	0.7	6	1.1	0.7	1.34 ²⁹	60 ³⁷	5 ⁴²	Sunny ⁴⁴	Trunk-ground ³⁸
<i>A. sericeus</i> ¹⁷	nd	nd	nd	nd	nd	nd	0.8	66	4.3	30.8	1.5	0.7	6	1.0	0.7	nd	50 ²⁵	nd	nd	Trunk ²⁵
<i>A. subocularis</i> ³	11.9	0.4	0.0	0.3	31	1.0	-0.8	27	1.9	21.6	5.9	0.3	3	1.8	1.0	1.31 ³⁰	nd	4 ³	nd	Trunk-ground ³⁰
<i>A. taylori</i> ³	0.8	0.4	0.4	0.0	2	1.0	1.0	0	0.0	4.2	2.6	1.0	3	5.3	0.3	1.31 ³⁰	nd	4 ³	nd	Trunk-ground ³⁰
<i>A. townsendi</i> ²¹	11.3	0.3	0.3	0.7	20	0.8	0.0	100	0.6	12.0	2.0	0.2	5	1.1	1.0	nd	nd	nd	Shady ⁴³	nd
<i>A. trinitatis</i> ⁷	1.3	0.2	0.0	1.0	7	0.9	nd	nd	nd	nd	nd	nd	nd	nd	nd	1.30 ²⁶	74 ²⁶	1 ³⁸	Sunny ⁴³	Trunk-crown ³⁸
<i>A. tropidolepis</i> ¹⁰	5.2	0.7	0.3	0.0	6	1.0	0.0	74	0.0	5.0	5.0	1.0	1	1.0	1.0	1.02 ²⁵	59 ²⁵	5 ³²	Shady ³²	Trunk-ground ³⁰
<i>A. websteri</i> ⁸	10.0	0.8	1.0	0.7	6	0.0	10.0	0	0.0	2.0	2.0	1.0	1	0.2	1.0	nd	nd	nd	Shady ⁴³	Trunk ⁴²
<i>A. woodi</i> ²²	18.0	1.1	2.2	1.0	7	1.0	0.0	54	0.0	20.5	20.5	1.0	1	1.1	1.0	1.05 ³⁰	nd	5 ³²	nd	Canopy ⁴²

Display parameters are described in Table 1; all other traits are defined in the text. SSD, sexual size dimorphism (male:female snout–vent length), where values greater than 1 are male-biased SSD, those equal to 1 are sexes of equal size, and those less than 1 are female-biased SSD; SVL, maximum species snout–vent length in millimetres; Sympatry, the number of geographically overlapping congeners; nd, no data.

*Superscript numbers refer to sources of display data. ¹Stamps (1973); ²Ruibal (1965); ³Fitch et al. (1976); ⁴Fleishman (1988b); ⁵Orrell & Jenssen (1998); ⁶Jenssen & Feely (1991); ⁷Gorman (1968); ⁸Jenssen & Gladson (1984); ⁹Decourcy & Jenssen (1994); ¹⁰Echelle et al. (1971); ¹¹Bels (1986); ¹²Garcea & Gorman (1968); ¹³Macedonia & Clark (2001); ¹⁴Jenssen (1983); ¹⁵Font & Kramer (1989); ¹⁶Jenssen (1981); ¹⁷Jenssen (1978); ¹⁸Jenssen (1971); ¹⁹Jenssen (1979); ²⁰Scott (1984); ²¹Jenssen & Rothblum (1977); ²²Echelle et al. (1978); ²³Stamps et al. (1997); ²⁴Rodríguez Schettino (1999); ²⁵Andrews (1979); ²⁶Roughgarden (1995); ²⁷Butler et al. (2000); ²⁸Schoener (1977); ²⁹Ord et al. (2001); ³⁰Fitch (1976); ³¹Fitch & Hillis (1984); ³²Pounds (1988); ³³Williams (1970); ³⁴Perry & Garland (2002); ³⁵Schwartz & Henderson (1985); ³⁶Rand & Williams (1970); ³⁷Williams & Rand (1977); ³⁸Losos & de Queiroz (1997); ³⁹Rand (1969); ⁴⁰Schoener (1970); ⁴¹Stamps (1983); ⁴²J. B. Losos, pers. comm.; ⁴³Ord (2001); ⁴⁴Loew et al. (2002); ⁴⁵Moermond (1979); ⁴⁶Stafford & Meyer (2000); ⁴⁷Knox et al. (2001); ⁴⁸Losos & Chu (1998); ⁴⁹Tinkle et al. (1970); ⁵⁰Yang et al. (1974); ⁵¹Jenssen (1977a).

†'Grass' and 'Grass-ground' categories were grouped with 'Grass-bush' species in analyses.