

## Estimating ancestral states of a communicative display: a comparative study of *Cyclura* rock iguanas

EMÍLIA P. MARTINS & JENNY LAMONT  
*Department of Biology, University of Oregon at Eugene*

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**Abstract.** In this study we describe the signature headbob displays of seven of the eight extant species of *Cyclura* iguanas using data collected from the field and from captive animals. We used phylogenetic comparative methods to estimate the ancestral states of several measures of the headbob displays, including number of headbobs and the duration of headbobs and inter-bob pauses. Divergence in the headbob display among species has been substantial, with some major changes occurring within only a few (about six) generations. Otherwise, results are consistent with those obtained previously for other lizards which suggest that there is an evolutionary limit on the total duration of headbob displays. Differences in the results obtained using different phylogenetic methods suggest that although estimates of ancestral states are reasonably robust to violations of evolutionary assumptions, we cannot determine the standard errors of those ancestral phenotypes accurately without more detailed information about the types of forces (e.g. selection, drift) underlying evolutionary change in these traits. In particular, within-species variation had a substantial impact on the standard errors of estimated ancestral states, and should be included in such estimations whenever possible. Finally, our results emphasize the importance of conserving behavioural as well as genetic diversity in trying to preserve endangered species for possible reintroduction into the wild.

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The phylogenetic comparative method has been used throughout animal behaviour, but has been particularly useful in generating hypotheses and guiding experimental studies of the evolution of communication systems (e.g. Sillén-Tullberg 1988; Basolo 1990; Prum 1994, 1997; Ryan 1995; Endler & Thery 1996). Although communicative displays are often defined by their stereotyped nature, they are also quite variable, with different species, populations, and even individuals producing remarkably different displays. This variation may be due to a number of factors, including ecological, genetic and behavioural differences. Phylogenetic comparative studies provide us with a uniquely powerful tool to begin to tease apart these possibilities and to highlight species and traits that may be particularly important in future empirical studies (see reviews in Brooks & McLennan 1991; Losos 1996; Martins 1996c). By reconstructing the communicative behaviour of

hypothetical ancestors on a phylogeny, we can determine the order of evolutionary changes and uncover any evidence of long-term trends in the evolutionary history of the displays. We can also determine the general time scale at which changes are occurring, thereby providing information on whether it would be more profitable to conduct future studies at the population, species, genus, or higher taxonomic level. In the current study, we use a phylogenetic comparative analysis of *Cyclura* lizards to consider evolutionary changes in display structure. In doing so, we illustrate the use of a new phylogenetic comparative method for estimating ancestral states (Martins & Hansen 1997), and discuss its application to the study of animal behaviour.

*Cyclura* iguanas exhibit an impressive diversity of social behaviour and communicative displays, and thus offer an excellent opportunity to study the evolution of these traits. The eight species of *Cyclura* rock iguanas are found on several islands in the Caribbean, including Cuba, Jamaica, Hispaniola and the Bahamas. These iguanas are

Correspondence: E. P. Martins, Department of Biology, University of Oregon, Eugene OR 97403, U.S.A. (email: emartins@work.uoregon.edu).

quite large (ranging from 30.6 to 74.5 cm maximum male snout-vent length, Schwartz & Henderson 1991), primarily herbivorous, and endangered due both to habitat destruction and to the introduction of exotic predators (e.g. feral cats, dogs and pigs) which prey on eggs and juvenile lizards (Iverson 1978). Studies of *Cyclura* behaviour are thus of considerable practical interest to conservation agencies raising these animals in captivity for future reintroduction into the field. Although two species of *Cyclura* are found on Hispaniola, most of the *Cyclura* are not sympatric, and the genus exhibits an impressive diversity of social behaviour types. In some species (e.g. *Cyclura cornuta stejnegeri*: Wiewandt 1977), both sexes defend all or most of their home ranges against other individuals of their sex. This is the pattern found in most lizards, and is considered to be evolutionarily primitive (Martins 1994). Other species (e.g. *Cyclura cyclura*: Windrow 1977) exhibit personal space aggression, in which individuals do not defend any particular geographical range, but will aggressively defend the area immediately around them. Still other species (e.g. the Cuban *Cyclura nubila nubila*: A. Alberts, personal communication) live in groups of up to 20 individuals which interact frequently.

Although *Cyclura* iguanas produce several visual displays including tail waves and various body postures, we concentrated entirely on their bobbing displays, in particular, the Broadcast Display (also termed 'signature bob' or 'Assertion display') for each species. Most other lizards of the Iguania group use headbob and push-up displays in both territorial defence and maintenance (e.g. Carpenter & Ferguson 1977). Although some species have more than one pattern of bobbing display, most produce a single broadcast display most often, and several studies have shown that these displays contain information about the individual identity of the animals (e.g. Crews 1975; Rothblum & Jenssen 1978; Martins 1991). During these displays, animals move their heads in a stereotyped fashion, usually raising and lowering them in a series of headbobs or tosses. Unlike some smaller lizards which produce the up-and-down motion by extending and flexing their legs (i.e. a 'push-up' display), iguanas produce the motion using primarily the muscles in their necks. In the current study, we focused on the 'bob pattern', that is, the number of times the head was

raised and lowered and the relative duration of up-and-down motions and pauses. In other species of Iguania, bobbing displays are often species-typical, with the number and type of bobs in each display containing information about the individual, sex and species identity of the animal as well as about the type of social context in which the animal is engaged (Carpenter & Ferguson 1977; Martins 1993a; DeCourcy & Jenssen 1994).

The phylogenetic comparative method is a powerful tool for inferring the evolutionary history of behavioural phenotypes (see Brooks & McLennan 1991; Harvey & Pagel 1991; or Martins & Hansen 1996 for review). Nevertheless, early techniques (e.g. parsimony) developed primarily for the analysis of molecular or morphological characters are not well suited for inferring the evolution of many behavioural traits. Behavioural traits are usually thought to be more flexible, responding quickly to the action of natural and sexual selection (but see de Queiroz & Wimberger 1993; Irwin 1996; Wimberger & de Queiroz 1996). More recently, we (Martins & Hansen 1997) developed a form of phylogenetic regression which can be used to estimate several parameters (e.g. the correlation between two traits, the rate of phenotypic evolution, ancestral states) from comparative data while applying any one of a variety of assumptions developed for the specific characters under analysis. Using this method, we can estimate various evolutionary parameters while assuming more realistic models of behavioural evolution such as the models of stabilizing selection, fluctuating directional selection and random genetic drift summarized by Hansen & Martins (1996).

In the current study, we collected information on the bobbing displays of nine populations (seven of the eight species) of *Cyclura*, filming animals in the field and in captivity and analysing videotapes gathered by other researchers. Overlaying these data on an independent phylogeny (Malone & Davis, unpublished data), we infer the sequence of evolutionary changes underlying present day diversity of communicative behaviour. We consider a variety of assumptions regarding the evolutionary processes underlying phenotypic evolution and incorporate within-species variation into the analysis using generalized least-squares regression (Martins & Hansen 1997), and thus also illustrate the application of a

new phylogenetic comparative method to the study of animal behaviour.

## METHODS

### Data Collection

We conducted behavioural observations in the field during two short trips to the Caribbean, gathered videotapes made by other researchers in the field, and observed some animals in captivity. Together, the data set consists of 204 displays produced by approximately 101 animals. All behavioural observations were made from a distance of at least 5 m during the main activity period (0900–1200 hours and 1400–1800 hours). Whenever possible, these observations were recorded on videotape and in field notes during focal animal samples. Videotaped recordings were made using a Canon L-2 Hi-8 video camera with a Canon 15 × macro zoom lens. Hand-written notes concentrated on describing bobbing displays in terms of the number and type of bobs in the display, and did not include estimates of temporal duration. The observer's (E.P.M.) ability to describe the bobbing displays in hand-written notes was tested periodically against videotaped recordings, and was found to be completely accurate in 20 of 20 trials. In most cases, individuals were easily distinguished on the basis of unique morphological features, and an attempt was made to observe as many different animals as possible. Because adult males are substantially more active than other age and sex groups in most species, more data were collected from males than from females of most species, and very few juvenile and hatchling animals are represented. Total numbers of individuals above are estimates based both on our ability to distinguish individuals and on the geographical distance between animals.

During about 20 h of observation in August 1995, we recorded 30 displays (four on videotape, 26 in hand-written notes) produced by approximately 23 individual *C. carinata* on Water Cay in the Turks and Caicos Islands. *Cyclura carinata* is rather unusual in that the typical headbob display is produced more often by females and juvenile animals than by adult males, and because the display is often produced in what appears to be an appeasement rather than an aggressive or broadcast context (Iverson 1979). Nineteen of the 30 recorded displays were produced by adult females,

an additional 10 were produced by juvenile males, and only one display was produced by a large, adult male. With the exception of the display produced by the large male, all headbob displays were produced by animals either approaching or being approached by larger individuals of either sex, as this seems to be the *C. carinata* equivalent of a signature display.

Also in August 1995, we recorded 17 displays from 15 adult male *C. nubila nubila* during about 15 h of observation on Isla Magueyes in Puerto Rico. *Cyclura nubila nubila* is native to Cuba, but a small group of animals was released from a zoo on Isla Magueyes in the mid 1960s (Christian 1986) and have been reproducing there as a free-ranging population. Alison Alberts also generously provided videotapes from her long-term field study of *C. nubila nubila* on Guantánamo Bay, Cuba (unpublished data) from which we obtained recordings of 40 displays from 24 animals. In November 1995, we observed *C. rileyi* for about 13 h on Green Cay (near San Salvador Island) in the Bahamas, recording a total of 17 displays produced by 12 individuals (11 adult males and one hatchling) on videotape.

Thomas Wiewandt provided a film he made during a long-term field study of *C. cornuta stejnegeri* on Mona Island, Puerto Rico (Wiewandt 1977, 1981). This film includes 14 displays produced by about 10 adult animals. Because these animals are sexually monomorphic (Wiewandt 1977), it is impossible to determine from the film exactly how many males and females displayed. From the narration, it appears that displays were obtained from both males and females in both aggressive interactions (males defending their mates and females defending nest sites) and courtship contexts. Thus, here, as in *C. carinata*, the displays are not necessarily all 'signature' headbobs, and may be subject to more within-species variation because of the combined contexts. Finally, it is important to note that the Mona Island iguana is quite distinct in many ways from the Hispaniolan *C. cornuta cornuta*, such that these data should not be considered necessarily representative of the species as a whole.

John Iverson also provided videotapes of *C. cyclura* made during his long-term field study on Allen's Cay, Bahamas (unpublished data). A total of 17 signature displays produced by about 11 adult males was extracted from these videotapes.

It was not possible to observe the behaviour of two exceedingly rare species (*C. collei* and *C. ricordi*) in the wild. Thus, videotapes of a very small number of individuals were obtained at the Indianapolis Zoo in March 1996. The Zoo has three juvenile (two females and one male) *C. collei*, and three *C. ricordi* (one adult male 'Robbie', and two juvenile females). All of the juvenile animals were quite wary and relatively inactive. During about 8 h of observation, we recorded only three displays produced by the juvenile male *C. collei*. In contrast, 54 displays were recorded from the adult male *C. ricordi* during about 6 h of observation. Videotapes of three individuals of the rare Grand Cayman Island subspecies, *C. nubila lewisi*, were also made at the Indianapolis Zoo. During about 3 h of observation, we recorded 10 signature displays from one adult male and one adult female. Although *C. pinguis* can still be observed on Anegada Island in the British Virgin Islands, we were unable to do so during this study. Because these animals are also not in captivity at any zoo (Christie 1995), we did not obtain any videotaped recordings at all from this species.

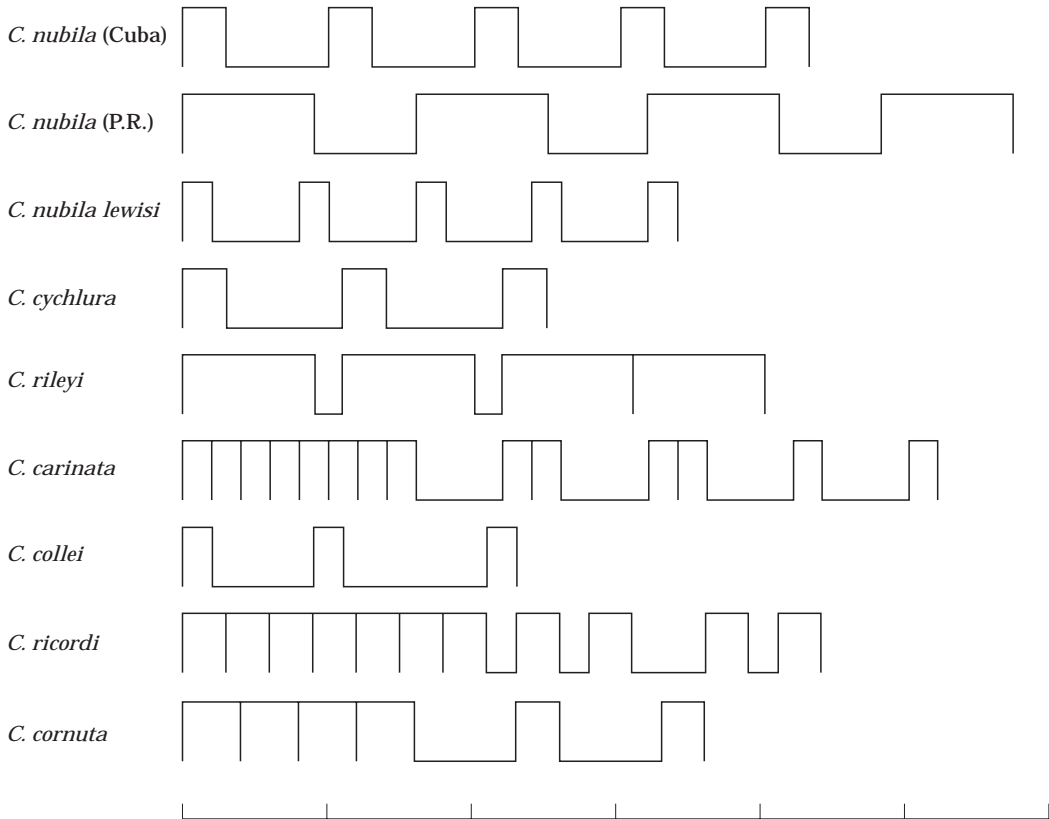
Although we tried to consider only signature headbobs, displays in this study were produced by animals in very different conditions, including animals in captivity and animals that had been subjected to a large degree of human contact. Thus, we make no attempt to interpret the function or meaning of displays from this data set. Furthermore, because the sample size of displays within any one species was small, and occasionally came from measures of a single individual, caution should be used in interpreting the fine structure of these displays in any detail. Fortunately, despite the variability among individuals and populations of lizards, interspecific differences in the bobbing displays of other lizards are usually far greater than that within species even across contexts (e.g. Martins 1993a, b). Estimates of the standard error of existing measures (see Results) show that the same is usually true of *Cyclura* iguanas. In other words, although the sample size is small, it is sufficient to discover a number of interesting evolutionary patterns.

### Videotape Analysis

Videotapes were digitized on a computer and subjected to frame-by-frame analysis. First, we

transferred clips of videotaped headbob displays onto a PowerPC using Radius Videofusion hardware to capture 15 frames/s of the image. We then recorded the vertical height of the tip of the lizard's nose (in the case of headbob displays) or the highest point of an eye ridge (in the case of head rolls, see description of *C. cornuta* displays below) for each frame of the videotape. We also recorded the vertical height of a stationary object on the film (usually a stationary part of the animal's body), and calculated the relative vertical motion of the lizard's head as vertical deviation between the stationary spot and the tip of the lizard's nose or eye ridge. We then plotted relative vertical motion against time to obtain a Display-Action-Pattern graph (DAPgraph, Carpenter & Grubitz 1961) for each display (e.g. Fig. 1) from which measures such as the number and timing of headbobs could be recorded. Note that although this procedure minimizes the effects of any small camera motion during the filming of the display, we did not record detailed information about the distance from the animal at each point in time nor the angle at which the camera was held, and thus were unable to determine absolute vertical height of the head motion from our recordings. We have schematized the DAPgraphs primarily to emphasize the lack of accuracy in our measurements of the vertical height of display components.

The term 'headbob' in this paper refers to an up-and-down motion in which the tip of the nose is raised vertically until the jaw forms an angle of at least 30° with the substrate the animal is standing on. The nose may be held up for a short time before again being lowered to the horizontal position and pulled in towards the body. Each up-and-down motion ('headbob') takes slightly less than 1 s to complete, and may occur in a series of two or more produced in rapid succession. The term 'bout' will be used to refer to each series of up-and-down motions, separated from other headbobs by pauses of at least 0.13 s (two frames of the digitized videotape). A bout might thus be a double headbob, triple headbob, or even a long trill of up to 15 up-and-down motions separated by pauses of no more than 0.07 s (one frame of the videotape). Thus, each display consists of one or more bouts of headbobs. Iguanas often hold their mouths open, raise their tails, or adopt other special body postures while producing headbobs, but during



**Figure 1.** Examples of 'typical' displays for the seven species of *Cyclura* observed in this study. Horizontal axis is time (in seconds), and vertical axis is a schematic depiction of the height of the animal's nose or eye ridge (for *C. cornuta stejnegeri*) during the display. These figures are comparable to DAPgraphs (Carpenter & Grubitz 1961).

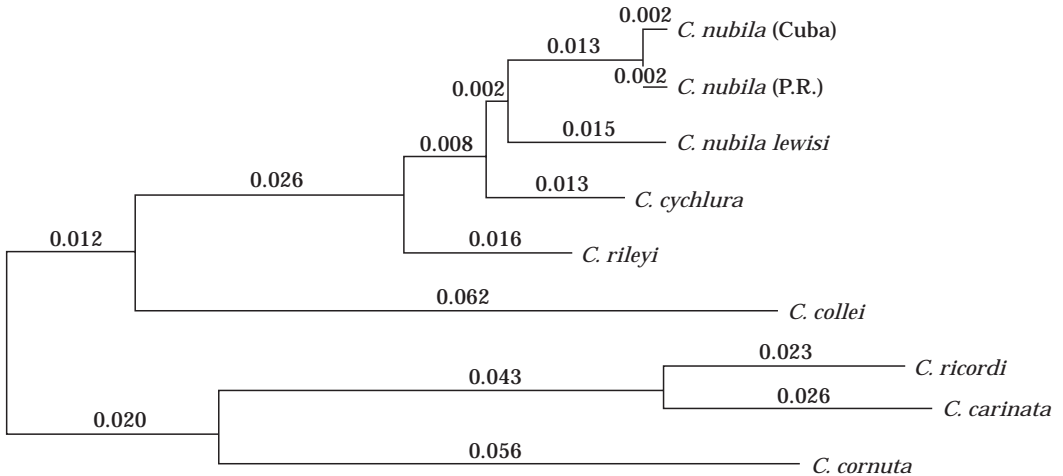
the headbob display, the rest of the body is held quite still.

### Phylogenetic Comparative Analyses

We used phylogenetic comparative analyses to reconstruct ancestral states of various measures of the headbob pattern (headbob, pause, and total durations, total number of up-and-down motions and bob type), and also to estimate correlation coefficients between these measures. Given the variation in headbob displays present even within a species, parsimony methods do not seem appropriate for reconstructing ancestral states. Instead, we applied a generalized least-squares approach to estimating ancestral phenotypes (Martins & Hansen 1997). This method offers flexibility as to the assumptions underlying a phylogenetic statistical analysis. Because the original paper

(Martins & Hansen 1997) leaves out many of the details for estimating ancestral states, we go through this procedure in some detail below.

This generalized least-squares approach (Martins & Hansen 1997) requires first that we describe the questions of interest in terms of standard regression models. Thus, we estimated ancestral states using the model:  $\mathbf{A} = \mathbf{W}\mathbf{Y} + \boldsymbol{\varepsilon}$ , where  $\mathbf{A}$  is a vector of the ancestral states,  $\mathbf{Y}$  is a vector of the extant species phenotypes relative to the grand mean,  $\mathbf{W}$  is a matrix derived from the phylogeny, and  $\boldsymbol{\varepsilon}$  is vector of error terms (see Martins & Hansen 1997, equations 3, 10–12 for details). Specifically, we measured the traits ( $\mathbf{Y}^0$ ) in nine populations of *Cyclura* and calculated the grand mean for each trait across the whole clade ( $M_G$ ) using  $M_G = (\mathbf{J}'\mathbf{Var}[\mathbf{Y}]^{-1}\mathbf{J})^{-1}\mathbf{J}'\mathbf{Var}[\mathbf{Y}]^{-1}\mathbf{Y}^0$ , where  $\mathbf{J}$  is a column of 1 s, and  $\mathbf{Var}[\mathbf{Y}]$  is a matrix of the expected similarities among extant taxa



**Figure 2.** Phylogeny from Malone & Davis (unpublished data) based on parsimony analysis of mtDNA sequences. Numbers refer to branch lengths in units of per cent nucleotide sequence divergence. Bootstrap values for all nodes are over 90%.

(discussed below). The standard error of this grand mean is given by the square roots of the elements of  $\mathbf{J}\mathbf{Var}[\mathbf{Y}]^{-1}\mathbf{Y}^0$ . We then transform the empirical measures ( $\mathbf{Y}^0$ ) into deviations from the grand mean to form  $\mathbf{Y}$  ( $=\mathbf{Y}^0 - \mathbf{M}_C$ ), and calculate  $\mathbf{W}$  as the product of the expected similarity between extant and ancestral phenotypes ( $\mathbf{Var}[\mathbf{A}, \mathbf{Y}]$ , see below for details) and the inverse of  $\mathbf{Var}[\mathbf{Y}]$  (such that  $\mathbf{W} = \mathbf{Var}[\mathbf{A}, \mathbf{Y}]\mathbf{Var}[\mathbf{Y}]^{-1}$ ). The vector  $\mathbf{A}$  (containing the estimated ancestral states) is calculated as the product of  $\mathbf{W}$  and  $\mathbf{Y}$ , and we add the grand mean to back transform each estimated ancestor to the scale of  $\mathbf{Y}^0$ . Variances (and therefore, standard errors) for these ancestral states were estimated using generalized least squares, specifically:

$$\mathbf{Var}[\hat{\mathbf{A}}] = \mathbf{Var}[\mathbf{A}] - \mathbf{Var}[\mathbf{A}, \mathbf{Y}]\mathbf{Var}[\mathbf{Y}]^{-1}\mathbf{Var}[\mathbf{Y}, \mathbf{A}]$$

where these variance matrices are calculated from the phylogeny and error variance as discussed below.

In calculating both  $\mathbf{W}$  and the standard errors, we need to calculate three variance-covariance matrices describing the expected degree of similarity between different taxon phenotypes ( $\mathbf{Var}[\mathbf{Y}]$ ,  $\mathbf{Var}[\mathbf{A}, \mathbf{Y}] = \mathbf{Var}[\mathbf{Y}, \mathbf{A}]$ , and  $\mathbf{Var}[\mathbf{A}]$ ). Expected similarities between taxon phenotypes are due to at least three factors: (1) within species variability or measurement error ( $\epsilon_M$ ); (2) error due to shared, stochastic evolution of taxa along a phylogenetic

tree ( $\epsilon_S$ ); and (3) error due to incorrect specification of the phylogeny ( $\epsilon_P$ ). First, to include measurement error, we calculated the within-species variance for each character and taxon for which data were available from more than one individual. We used these within-species variances to create an error variance matrix,  $\mathbf{Var}[\epsilon_M]$ , for each trait with variances on the diagonals and all other elements set equal to zero.

Second, we used a preliminary phylogeny (C. L. Malone & S. K. Davis, unpublished data; Fig. 2) to calculate the expected similarity due to shared, stochastic evolution ( $\mathbf{Var}[\epsilon_S]$ ). Malone & Davis' phylogeny is part of a larger study examining relationships among several genera of iguanas (Sites et al. 1996) using a parsimony analysis of mitochondrial DNA data (ND4 and three tRNA genes). It is completely independent of the behavioural information presented in the current study, and although the phylogeny is a preliminary estimate, nodes are quite well supported, with bootstrap values exceeding 90% in all cases. Branch lengths on the phylogeny are also available in units of DNA sequence divergence. The fact that branch lengths at the tips do not all line up at one end of the phylogeny suggest that there is some rate heterogeneity in the molecular sequence data, and that measures of sequence divergence provide only rough estimates of relative time. In the present study, however, we assume that sequence divergence is a reasonable

estimate of time, and that the behavioural characters evolved along this phylogeny using one of two possible forms of phenotypic evolution: (1) such that phenotypic divergence is linearly related to phylogenetic distance; and (2) such that phenotypic divergence is exponentially related to phylogenetic distance. As shown by Hansen & Martins (1996), these two possibilities describe the result of phenotypic evolution under a wide variety of scenarios, including random genetic drift, directional selection and stabilizing selection. Note that since we consider a variety of possibilities and focus on the robustness of our results across these options, small errors in the original branch lengths or in the assumption that branch lengths are reasonable estimates of relative time, are likely to have little impact on the conclusions of this study.

For a linear relationship between phenotypic and phylogenetic divergence, we calculated the matrix  $\mathbf{Var}[\varepsilon_S]$  with each element corresponding to a constant ( $\sigma_S^2$ ) multiplied by the phylogenetic distance ( $d$ ) from the root of the tree to the most recent common ancestor of the taxon pair. This model is often used to describe phenotypic evolution under random genetic drift or under directional selection when the direction of selection varies randomly over time. The constant  $\sigma_S^2$  is a function of the mutation rate and other forces causing taxa to diversify. For an exponential relationship, we calculated each element of  $\mathbf{Var}[\varepsilon_S]$  as  $\sigma_S^2 \exp(-\alpha t)$  for each pair of taxa, where  $\alpha$  and  $\sigma_S^2$  are estimated constants, and  $t$  is the phylogenetic distance between the two taxa. This latter model is most often used to describe the evolution of phenotypes subjected to a restraining force, such as stabilizing selection pushing the character towards a fixed optimum. The parameter,  $\alpha$ , can be interpreted as a measure of the strength of that restraining force.

We estimated  $\sigma_S^2$  using an iterative Fisher scoring procedure. We began by calculating the Fisher information matrix,  $\mathbf{F}$ , as one-half the trace of the matrix  $\mathbf{P}\mathbf{V}^{-1}\mathbf{P}\mathbf{V}^{-1}$ , where  $\mathbf{P}$  equals  $\mathbf{V}^{-1}(\mathbf{I} - \mathbf{H}\mathbf{V}^{-1}[\mathbf{J}\mathbf{V}^{-1}\mathbf{J}])$ ,  $\mathbf{V}^{-1}$  is the inverse of the total error matrix ( $\mathbf{Var}[\varepsilon_S] + \mathbf{Var}[\varepsilon_M]$ ),  $\mathbf{I}$  is an identity matrix,  $\mathbf{H}$  is a matrix of 1s, and  $\mathbf{J}$  is a vector of 1s. We calculated each new value of  $\sigma_S^2$  using the following equation:

$$\sigma_{S(t+1)}^2 = \sigma_{S(t)}^2 - \frac{1}{2} \mathbf{F}^{-1} [-\text{tr}[\mathbf{P}\mathbf{V}_2] + \mathbf{Y}\mathbf{P}\mathbf{V}_2\mathbf{P}\mathbf{Y}]$$

where  $\sigma_{S(t)}^2$  is the present, estimated value of  $\sigma_S^2$  and  $\sigma_{S(t+1)}^2$  is the next value. The trace of a matrix ( $\mathbf{P}\mathbf{V}_2$ ) is denoted by  $\text{tr}[\mathbf{P}\mathbf{V}_2]$ , where  $\mathbf{V}_2$  is  $\mathbf{Var}[\varepsilon_S]$  divided by  $\sigma_S^2$ . Most times, this iterative procedure converged on a single value of  $\sigma_S^2$  within a few hundred iterations. When it did not converge, it was usually because the values bounced between two or more peak values that were fairly similar in magnitude (i.e. within 10) and thus had little impact on estimates of the standard error. At very high or very low levels of  $\alpha$ , values for  $\sigma_S^2$  may never converge at all, making it impossible to estimate the standard error. Note that estimates of  $\sigma_S^2$  cancel out of the equation for estimating ancestral states. Therefore, their only impact is on estimates of the standard errors of the ancestral states. Unfortunately, with the relatively small number of taxa in this study, we were not able to estimate  $\alpha$  effectively from the measured data at all. Instead, we applied a range of possible  $\alpha$ s, as a way of determining the robustness of our estimates to different  $\alpha$  values (i.e. different assumptions about the strength of stabilizing selection and the phenotypic response to that selection).

For each character, we estimated the phenotypes of hypothetical ancestors and the standard errors of those phenotypes using forms of  $\mathbf{Var}[\varepsilon_S]$  to create the  $\mathbf{Var}[\mathbf{Y}]$ ,  $\mathbf{Var}[\mathbf{A}, \mathbf{Y}]$  and  $\mathbf{Var}[\mathbf{A}]$  matrices. We also conducted separate analyses using the sum of  $\mathbf{Var}[\varepsilon_S]$  and  $\mathbf{Var}[\varepsilon_M]$  matrices to form the  $\mathbf{Var}[\mathbf{Y}]$  matrix. Doing both analyses allows us to illustrate the difference in results obtained by incorporating within-species variation in the analyses versus assuming that within-species variation is negligible. The matrix  $\mathbf{Var}[\mathbf{Y}]$  consists of the expected similarities between all possible pairs of the extant taxon phenotypes,  $\mathbf{Y}$ , whereas  $\mathbf{Var}[\mathbf{Y}, \mathbf{A}]$  consists of the expected similarities between extant taxon phenotypes and ancestral states and  $\mathbf{Var}[\mathbf{A}]$  contains the expected similarities between ancestral taxa. We assumed that within-species variation in extant taxa was independent of such variation in ancestral taxa, and included within-species variability only in estimates of the expected similarity between extant taxa ( $\mathbf{Var}[\mathbf{Y}]$ ). In both cases, expected similarities were calculated as linear or exponential functions of phylogenetic distance (as discussed above). Note that this analysis does not take error due to incorrect specification of the phylogeny ( $\varepsilon_p$ ) into account, simply because no good estimates of this

error were available, and randomization tests (e.g. Martins 1996a) which are appropriate for generating confidence intervals, may not be as appropriate for obtaining the best estimates of evolutionary parameters. Fortunately, generalized least squares ensures that our estimates will still be unbiased, although perhaps not quite as accurate as we might prefer. All analyses were conducted using Mathematica (Wolfram 1991) to implement the generalized least-squares equations. For comparison, we also estimated ancestral states using the sum-of-squared-changes parsimony algorithm (Huey & Bennett 1987; Maddison 1991; McArdle & Rodrigo 1994), weighting estimates by the branch lengths on the phylogeny (as in ME1G of Martins & Garland 1991). Programs to conduct these and similar analyses are also available in COMPARE (Martins 1996b).

We also applied phylogenetic comparative analyses to estimate the correlations between measures of the headbob pattern. Again, we used a generalized least-squares approach (Martins & Hansen 1996), but now applied the model  $\mathbf{Y} = \beta\mathbf{X} + \varepsilon$ , where  $\mathbf{Y}$  and  $\mathbf{X}$  are various measures of the headbob pattern, considered individually in separate models. With only nine taxa, estimation and power of evolutionary relationships are small. Thus, we aimed primarily to obtain a general picture of the patterns of relationship rather than detailed and accurate parameter estimates or confidence intervals. As above, we created error covariance structures based on assumptions that phenotypic divergence is linearly or exponentially related to phylogenetic divergence, but considered only the case when  $\alpha$  is assumed to equal one. We then estimated correlation coefficients using the 'contrast' module of COMPARE (Martins 1996b) which implements several variants of the independent contrasts method (e.g. Felsenstein 1985; Grafen 1989) for incorporating phylogenetic information. Although we did not include within-species variability in this analysis, we did calculate alternative confidence intervals using the 'randtree' module of COMPARE. To do this calculation, we generated a set of 1000 possible phylogenies assuming only that speciation can be described as a standard Markovian branching process (e.g. Slowinski & Guyer 1989), calculated correlation coefficients using each phylogeny, and combined the results using the procedure described in Martins (1996a) to construct conservative confidence intervals for our hypothesis

tests. This final procedure incorporates the error due to mis-specification of the phylogeny ( $\varepsilon_p$ ) into the analysis.

## RESULTS

### Headbob Displays

#### *Cyclura carinata*

Most of the 30 *C. carinata* headbob displays we observed consisted of a series of alternating single and double headbobs (Fig. 1). Each display usually began with one or two single headbobs (13/30 displays) or a fast trill of 6–15 bobs (7/30 displays). These were then followed by a set of between one and six double headbobs, which were then followed again by another single headbob or two. In some cases (10/30 displays), the display began without preamble at the set of double headbobs. Of the four displays recorded on videotape and for which durations were thus available, three did not include a trill and lasted an average ( $\pm$  SE) of  $0.5 \pm 0.10$  s. The fourth display included a trill of 11 bobs and lasted 7.4 s. Thus, durations calculated as averages of these four displays had rather high standard errors (Table I). *Cyclura carinata* also produces head nods and tail raises typical of other iguanas.

#### *Cyclura collei*

Two of the *C. collei* headbob displays observed during this study consisted of one single headbob each. The third display (Fig. 1) consisted of three single headbobs with pauses of 0.7 s and 1.0 s between them (Table I).

#### *Cyclura cornuta*

*Cyclura cornuta* are unusual in that they are the only *Cyclura* species that produces 'rolls' as well as headbobs (Wiewandt 1977). In a roll, one side (left or right) of the head is raised, and when it is lowered, the opposite side of the head (left or right) is raised. The motion is often repeated multiple times, raising one side of the head and then the other in a back and forth motion. In most cases, rolls were produced in long series, with virtually no pause (less than 0.07 s) between successive back-and-forth motions. Rolls could not be analysed in detail without a camera observing the animal from above. By recording the relative

**Table I.** Means ( $\pm$  SE) of several measures of the headbob display for seven species of *Cyclura*

	Total duration (s)	Pause duration (s)	Headbob duration (s)	Number of bouts	Number of bobs
<i>C. carinata</i>	2.20 (1.735)	0.63 (0.129)*	0.34 (0.086)	1.97 (0.215)	6.00 (4.673)
<i>C. collei</i>	0.98 (0.953)	0.87 (0.133)*	0.24 (0.058)	1.67 (0.667)	1.67 (0.667)
<i>C. cornuta</i>	2.83 (0.447)	0.75 (0.139)	0.38 (0.027)	2.14 (0.206)	5.50 (0.489)
<i>C. cyclura</i>	1.98 (0.399)	0.82 (0.118)	0.30 (0.023)	2.35 (0.242)	2.88 (0.193)
<i>C. nubila nubila</i> (Cuba)	3.22 (0.406)	0.67 (0.048)	0.28 (0.058)	3.63 (0.344)	4.85 (0.540)
<i>C. nubila nubila</i> (P.R.)	4.23 (0.711)	0.74 (0.053)	0.98 (0.415)	3.77 (0.474)	4.29 (0.520)
<i>C. nubila lewisi</i>	3.43 (0.896)	0.59 (0.104)	0.22 (0.022)	3.50 (0.749)	5.50 (1.851)
<i>C. ricordi</i>	3.37 (0.243)	0.30 (0.021)	0.27 (0.006)	3.48 (0.239)	9.72 (0.590)
<i>C. rileyi</i>	3.14 (0.556)	0.22 (0.060)	0.88 (0.007)	3.17 (0.345)	5.22 (0.721)

\*Standard errors based on variation within one display by a single lizard.

height of one eye ridge, though, we were able to determine the number of times each side of the head was raised or lowered during each roll and describe these motions in much the same way as we described headbobs.

Rolls occurred at the beginning of nine of the 14 displays, at the end of one display, and not at all in four displays. In all but one case, rolls were accompanied by one or two series of standard headbobs. There was an average ( $\pm$  SE) of  $4.0 \pm 0.42$  back and forth motions per roll (Fig. 1), and up to six up and down motions per headbob series (mean  $\pm$  SE =  $2.0 \pm 0.42$ ). Average durations were obtained by treating up-and-down headbobs and back-and-forth rolls as equivalent units (Table I). Again, these data were obtained only from *C. c. stejnegeri*. Some observations of *C. c. cornuta* at the Indianapolis Zoo show that these animals also produce head rolls, but detailed measures of the cadence of these displays were not available.

#### *Cyclura cyclura*

The 17 *C. cyclura* headbob displays obtained from Iverson's videotapes (unpublished data) consisted of short bouts of mostly single, but occasionally double, headbobs (mean  $\pm$  SE =  $1.2 \pm 0.07$ ; Fig. 1, Table I), with no obvious pattern to the choice of single or double headbobs.

#### *Cyclura nubila*

*Cyclura nubila* is unique among *Cyclura* in that it produces an S-roll similar to the 'roll' (Dugan 1982), or 'rotary head nodding' (Distel & Veazey

1982; Dugan 1982) of green iguanas. In an S-roll, the nose is raised and lowered as in a headbob, but is also moved in a horizontal plane during the lowering motion. Although some individuals appeared to be producing standard headbobs in addition to the S-rolls, the twisting motion is not as dramatic as the full rolling motion produced by *C. cornuta*, and can hardly be seen from a lateral view. Thus, we scored all up-and-down motions produced by *C. nubila* as S-rolls.

Displays for the two different subspecies and two populations of the same subspecies did not differ substantially in most measures. All *C. nubila* produced series of about five S-rolls separated by pauses of about 0.7 s, leading to a total duration of about 4 s (Table I, Fig. 1). The one exception was that headbobs produced by animals in the Puerto Rican population lasted more than twice as long (mean  $\pm$  SE =  $1.0 \pm 0.42$ ) as those from the other two populations (mean  $\pm$  SE =  $0.3 \pm 0.06$  for Cuban *C. n. nubila*; mean  $\pm$  SE =  $0.2 \pm 0.02$  for *C. n. lewisi* at the zoo).

#### *Cyclura ricordi*

The headbob displays of the single *C. ricordi* male consisted of long series of headbobs with progressively longer pauses between them (Fig. 1, Table I). The display usually began with a series of about seven headbobs (mean  $\pm$  SE =  $6.6 \pm 0.37$ ) with virtually no pauses. The initial series was usually followed by an additional set of about three single headbobs (mean  $\pm$  SE =  $2.5 \pm 0.24$ ) with inter-bob pauses of about 0.2 s each (mean  $\pm$  SE =  $0.2 \pm 0.02$  s). Frequently, these would

be followed by one long pause (mean  $\pm$  SE duration =  $0.5 \pm 0.03$  s), and then another series of about two headbobs (mean  $\pm$  SE =  $1.7 \pm 0.12$ ). Thus, inter-bob pauses slowly increased in duration throughout the display. Sometimes, the entire series of headbobs was followed immediately by another set, and it was difficult to distinguish the end of one display and the start of the next.

### *Cyclura rileyi*

The 17 displays recorded for *C. rileyi* in this study consisted of series of up to seven single and double headbobs (Table I, Fig. 1). These headbobs were mixed, with no obvious pattern to the choice of single or double headbobs.

### Phylogenetic Analyses

Overlaying measures of the headbob displays on the phylogeny, we found that headbob displays have evolved frequently and dramatically among the *Cyclura*, with major changes in the display occurring in almost every branch leading to a tip species (Fig. 3, Table II). Some aspects of the display are less malleable than others, evolving only once in the genus. For example, three species produced series of fast up-and-down motions ('trills'), and in all three cases, these trills were produced at the beginning (rather than in the middle or at the end) of displays. Because the three species that exhibit trills are also their own closest relatives, it seems likely that trills have evolved a single time in the ancestor leading to *C. ricordi*, *C. carinata* and *C. cornuta*. In contrast, although many species of *Cyclura* exhibit some slight horizontal motion in their headbob displays, the S-rolls of *C. nubila* and the long rolls of *C. cornuta* are clearly quite different from each other and those of any other species of *Cyclura*. Given the phylogenetic distance between these two taxa, it would seem that the roll has evolved at least twice within *Cyclura*. Because green iguanas also use rolling motions in their displays, it may be that iguanas in general have some evolutionary predisposition towards using horizontal motion in their head-bob displays.

Pause duration was remarkably constant throughout the genus in an absolute sense, ranging between 0.2 and 0.9 s, and not undergoing any evolutionary shifts greater than one standard error in magnitude (Fig. 3c). All other measures

(total duration, headbob duration, and the number of bouts or headbobs per display) underwent three to seven major evolutionary changes (at least one standard error) within the genus (Fig. 3). These measures of the headbob display increased and decreased through evolutionary time in various lineages, but there were no long-term trends holding steady throughout the phylogeny. In fact, the most striking pattern is that all of these changes are concentrated among the tips of the phylogeny, with none occurring near the root of the tree. This suggests that change is happening quite quickly, with phenotypes rarely remaining intact past a speciation event. Focusing, for example, on the headbob displays of the two populations of *C. nubila*, we find major differences in the total duration, headbob duration and number of headbobs. The introduced population at Isla Magueyes (Puerto Rico) hold their heads up for an unusually long period of time during each headbob, leading to a much longer headbob display, even though it contains fewer headbobs. This difference has happened quite recently, no longer than the time separating two populations of animals on Cuba, and possibly as recently as when the Puerto Rican population was established (30 years ago).

### Evolutionary Assumptions

Estimates of ancestral states were remarkably consistent, whether calculated using the linear or exponential models, and regardless of the value of the restraining force ( $\alpha$ ) in the exponential model (Table II). For ancestors of the most recently diverged taxa (the two *C. nubila* populations), these estimates were often identical for all models, and never differed by more than 5% of the trait value. Differences among results for different models were more apparent when considering estimates of ancestral states deeper in the phylogeny. These estimates occasionally varied by as much as 50% of the trait value. Not surprisingly, standard errors of estimated ancestral states also usually increased upon approaching the root of the phylogeny.

Measures of the fit of the statistical models also depended in large part on the underlying choice of evolutionary assumptions (i.e. linear versus exponential) and whether or not within-species variation was included. Most dramatically, the residual sum of squares often decreased substantially

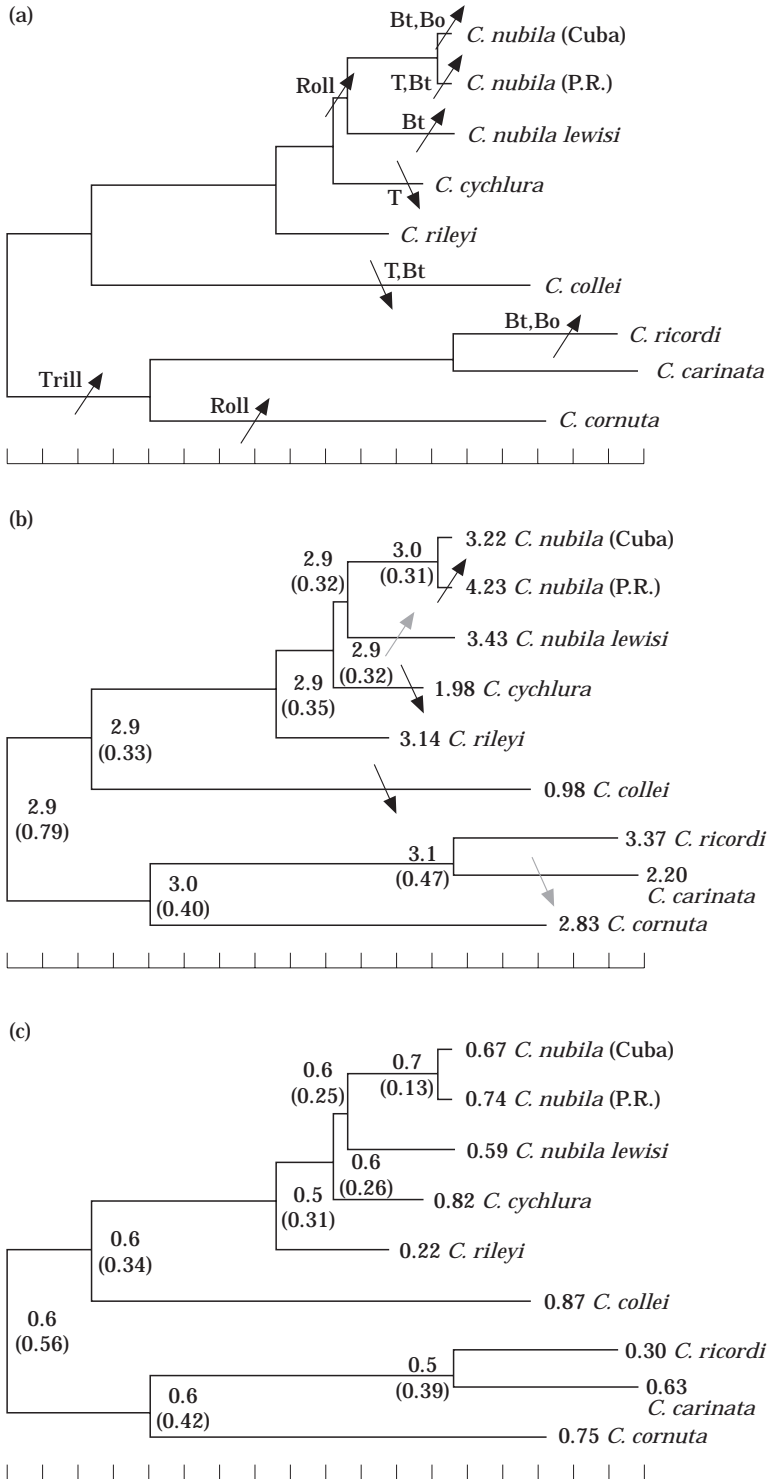


Figure 3. (a)–(c).

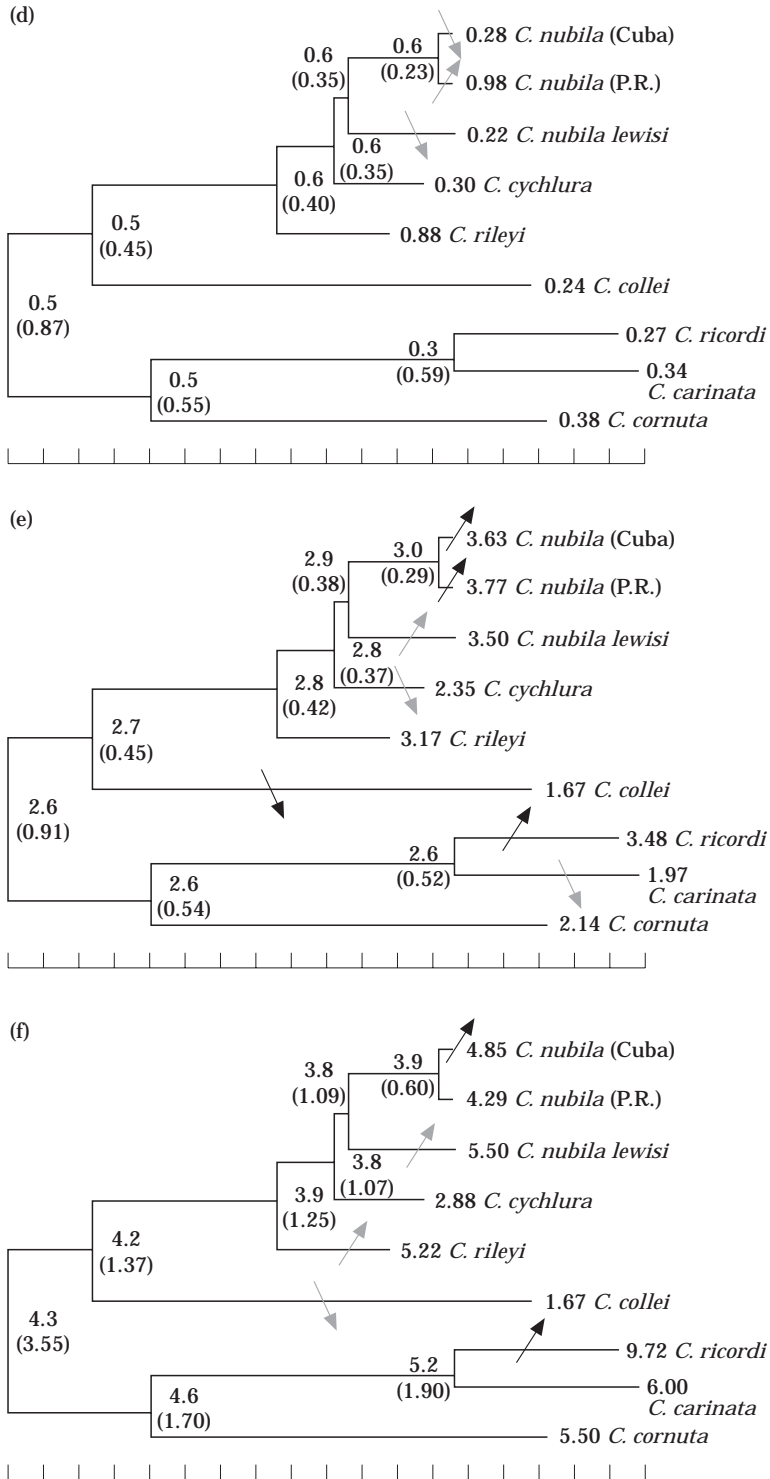


Figure 3. (d)–(f).

when within-species variability was included (Table II). This is probably due to the small sample size of individuals measured within each species (and the correspondingly large standard errors), and to the many cases in which taxa with the largest standard errors (i.e. least reliable measures) were also the most influential in estimating ancestral states.

As expected, the small number of taxa led to relatively flat likelihood surfaces for these models, and it was not possible to distinguish readily between the relative fits of the linear and exponential models or between exponential models with different values of the restraining force,  $\alpha$ . Still, the linear model often provided the best fit, and never did worse than all of the exponential models with different values of  $\alpha$ .

### Relationships Among Variables

There were positive relationships between evolutionary changes in total duration and number of bouts per display, and between changes in the number of bouts and the number of headbobs whether assuming a linear or an exponential relationship between phenotypic and phylogenetic divergence (Table III). The latter relationship was relatively small when phylogeny was not taken into account, and is a good example of how phylogenetic comparative methods can clarify patterns obscured by historical relationships. There was also a strong inverse relationship between the number of headbobs (or bouts) and the duration of inter-bob pauses. None of these patterns was entirely obvious when looking at the reconstruction of ancestral states (Fig. 3), illustrating the importance of applying statistical techniques that are specifically designed to address each evolutionary question.

Other correlation coefficients that had large absolute values when linear divergence was assumed were small or even opposite in direction

when exponential divergence was assumed (Table III). Thus, although they provide tantalizing suggestions of a pattern, it is unclear how much faith we should have in these potential relationships. None of the correlation coefficients in Table III was significantly different from zero when randomization tests were applied to determine confidence intervals as if no phylogenetic information were available.

## DISCUSSION

*Cyclura iguanas* show a remarkable degree of diversification in their headbob displays. Although some aspects of the headbob display have remained relatively stable throughout the evolution of the genus, others differ radically among species or even populations, sometimes dwarfing the differences previously found among other groups of lizards (e.g. *Sceloporus*: Carpenter 1978; Martins 1993b). These evolutionary changes are spread throughout the genus, with many occurring recently in the history of particular taxa. The phylogenetic comparative methods in this study do not distinguish between genetic and non-genetic causes of change, leaving open the possibility of phenotypic plasticity and recent responses to environmental fluctuation. There also seem to be strong positive evolutionary relationships between total duration and the number of bouts per display, and a strong negative relationship between number of headbobs and the duration of inter-bob pauses.

### Display Evolution

In general, our measures of the headbob display coincide with the bits of information available about *Cyclura* from other studies. Not surprisingly, our descriptions of *C. cornuta* displays (derived from Wiewandt 1981) match those of

**Figure 3.** Summary of reconstructed evolutionary changes in the headbob display of *Cyclura iguanas* calculated using a linear model and including within-species variation (Table II). Numbers at each node are the estimated ( $\pm$  SE) ancestral state for that node. Grey arrows depict at least  $\pm 1$  SE of phenotypic change; black arrows denote changes of at least  $\pm 2$  SE. Up arrows indicate increases, whereas down arrows indicate decreases. (a) Summarizes evolutionary changes in the headbob display (T: changes in total duration; P: pause duration; H: headbob duration; Bt: number of bouts; Bo: number of headbobs). (b–f) Detail the evolutionary changes in each measure: (b) depicts evolution of total duration; (c) depicts pause duration; (d) depicts headbob duration; (e) depicts number of bouts; and (f) depicts number of headbobs.

**Table II.** Estimates of phenotypes for hypothetical ancestors within the genus *Cyclura* calculated using models of phenotypic evolution that assume either linear or exponential relationships between phenotypic and phylogenetic divergence

Trait	Alpha	$\epsilon_M$	RSS	Root	A	B	C	D	E	F	G	$\sigma^2$	
Total duration	0.01	=0	22505.4	2.49 (1.578)	3.67 (0.230)	3.05 (0.486)	2.91 (0.490)	2.89 (0.603)	2.44 (0.946)	2.78 (0.765)	2.65 (1.015)		
	0.50	=0	2253.3	2.49 (1.586)	3.67 (0.230)	3.05 (0.486)	2.91 (0.491)	2.89 (0.603)	2.44 (0.947)	2.78 (0.766)	2.65 (1.017)		
	1.00	=0	228.2	2.49 (1.664)	3.68 (0.232)	3.06 (0.491)	2.91 (0.496)	2.90 (0.610)	2.45 (0.962)	2.79 (0.775)	2.65 (1.033)		
	2.00	=0	115.7	2.49 (1.753)	3.68 (0.234)	3.06 (0.496)	2.92 (0.502)	2.90 (0.617)	2.45 (0.978)	2.79 (0.785)	2.66 (1.051)		
	linear	=0	450.0	2.52 (1.055)	3.68 (0.218)	3.05 (0.456)	2.91 (0.459)	2.89 (0.551)	2.44 (0.621)	2.78 (0.710)	2.65 (0.763)		
				2.56 (0.989)	3.68 (0.292)	3.05 (0.292)	2.91 (0.288)	2.89 (0.321)	2.44 (0.420)	2.75 (0.402)	2.64 (0.432)		
	parsimony	$\neq 0$	9.6	3.03 (0.989)	3.03 (0.292)	3.02 (0.292)	3.02 (0.288)	3.02 (0.321)	3.03 (0.420)	3.03 (0.402)	3.03 (0.432)		
	0.01	$\neq 0$	8.9	3.02 (0.983)	3.00 (0.301)	2.99 (0.306)	2.99 (0.302)	2.99 (0.339)	3.00 (0.453)	3.06 (0.467)	3.02 (0.467)		
	0.50	$\neq 0$	6.9	2.94 (1.034)	3.00 (0.330)	2.90 (0.365)	2.88 (0.361)	2.89 (0.417)	2.87 (0.589)	3.13 (0.555)	2.97 (0.615)		
	1.00	$\neq 0$	6.1	2.89 (1.082)	3.05 (0.346)	2.88 (0.405)	2.85 (0.401)	2.86 (0.469)	2.81 (0.678)	3.14 (0.631)	2.93 (0.713)		
	2.00	$\neq 0$	6.2	2.95 (0.790)	2.97 (0.313)	2.92 (0.325)	2.91 (0.320)	2.92 (0.350)	2.92 (0.330)	3.11 (0.472)	2.99 (0.402)		
	Pause duration	0.01	=0	800.8	0.69 (0.829)	0.70 (0.043)	0.64 (0.092)	0.64 (0.093)	0.52 (0.114)	0.62 (0.178)	0.49 (0.144)	0.61 (0.191)	
		0.50	=0	80.2	0.69 (0.832)	0.70 (0.043)	0.64 (0.092)	0.64 (0.093)	0.52 (0.114)	0.62 (0.179)	0.49 (0.145)	0.61 (0.192)	
		1.00	=0	8.2	0.68 (0.870)	0.70 (0.044)	0.64 (0.093)	0.64 (0.094)	0.52 (0.116)	0.62 (0.182)	0.49 (0.147)	0.61 (0.196)	
2.00		=0	4.2	0.67 (0.912)	0.70 (0.044)	0.64 (0.094)	0.64 (0.095)	0.52 (0.117)	0.61 (0.186)	0.48 (0.149)	0.60 (0.200)		
linear		=0	16.0	0.61 (0.549)	0.70 (0.041)	0.64 (0.086)	0.64 (0.087)	0.52 (0.104)	0.62 (0.117)	0.49 (0.134)	0.61 (0.144)		
				0.63 (1.000)	0.70 (0.052)	0.65 (0.094)	0.65 (0.096)	0.55 (0.111)	0.64 (0.167)	0.49 (0.134)	0.62 (0.183)		
parsimony		$\neq 0$	7.9	0.67 (1.005)	0.66 (0.052)	0.65 (0.095)	0.65 (0.096)	0.64 (0.112)	0.68 (0.168)	0.54 (0.135)	0.62 (0.184)		
0.01		$\neq 0$	7.9	0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		
0.50		$\neq 0$	7.9	0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		
				0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		
				0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		
				0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		
				0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		
				0.66 (1.005)	0.67 (0.052)	0.61 (0.095)	0.60 (0.096)	0.55 (0.112)	0.62 (0.168)	0.49 (0.135)	0.59 (0.184)		

Table II. Continued

Trait	Alpha	$\epsilon_M$	RSS	Root	A	B	C	D	E	F	G	$\sigma_S^2$
Pause duration (cont.)	1.00	$\neq 0$	6.9	0.67 (1.054)	0.69 (0.055)	0.63 (0.102)	0.62 (0.104)	0.52 (0.122)	0.61 (0.185)	0.49 (0.148)	0.60 (0.202)	1.0
	2.00	$\neq 0$	6.7	0.67 (1.109)	0.70 (0.056)	0.63 (0.105)	0.63 (0.107)	0.52 (0.125)	0.61 (0.192)	0.48 (0.153)	0.60 (0.209)	0.5
	linear	$\neq 0$	1.0	0.61 (0.559)	0.69 (0.125)	0.62 (0.254)	0.61 (0.257)	0.52 (0.305)	0.61 (0.342)	0.49 (0.391)	0.60 (0.421)	15.8
Headbob duration	0.01	= 0	6973.9	0.32 (0.569)	0.62 (0.128)	0.45 (0.270)	0.46 (0.273)	0.57 (0.336)	0.44 (0.527)	0.32 (0.426)	0.39 (0.565)	
	0.50	= 0	697.6	0.32 (0.572)	0.62 (0.128)	0.45 (0.270)	0.46 (0.273)	0.57 (0.336)	0.44 (0.527)	0.32 (0.426)	0.39 (0.566)	
	1.00	= 0	70.0	0.33 (0.605)	0.62 (0.128)	0.45 (0.272)	0.46 (0.275)	0.57 (0.338)	0.45 (0.533)	0.32 (0.429)	0.39 (0.572)	
	2.00	= 0	35.2	0.33 (0.642)	0.62 (0.129)	0.45 (0.274)	0.46 (0.277)	0.58 (0.340)	0.45 (0.539)	0.32 (0.433)	0.39 (0.579)	
	linear	= 0	139.5	0.42 (0.760)	0.62 (0.121)	0.45 (0.254)	0.46 (0.255)	0.57 (0.307)	0.44 (0.346)	0.32 (0.395)	0.39 (0.425)	
	parsimony			0.42	0.62	0.45	0.45	0.57	0.44	0.32	0.38	
Number of bouts	0.01	$\neq 0$	9.3	0.51 (0.998)	0.54 (0.128)	0.54 (0.120)	0.54 (0.118)	0.54 (0.116)	0.53 (0.164)	0.49 (0.154)	0.51 (0.176)	49.5
	0.50	$\neq 0$	9.2	0.49 (1.002)	0.60 (0.130)	0.60 (0.121)	0.60 (0.120)	0.61 (0.118)	0.56 (0.168)	0.40 (0.157)	0.49 (0.180)	5.2
	1.00	$\neq 0$	7.0	0.43 (1.043)	0.57 (0.150)	0.56 (0.152)	0.56 (0.152)	0.63 (0.156)	0.54 (0.242)	0.34 (0.222)	0.44 (0.258)	1.2
	2.00	$\neq 0$	6.9	0.40 (1.091)	0.57 (0.151)	0.53 (0.156)	0.54 (0.156)	0.62 (0.161)	0.52 (0.251)	0.33 (0.229)	0.43 (0.269)	0.7
	linear	$\neq 0$	2.6	0.52 (0.875)	0.59 (0.225)	0.58 (0.346)	0.59 (0.349)	0.63 (0.399)	0.55 (0.449)	0.35 (0.594)	0.46 (0.551)	28.7
				2.50	3.67	3.17	3.05	3.00	2.57	2.71	2.51	
Number of bouts	0.01	= 0	7488.8	2.50 (1.582)	3.67 (0.133)	3.17 (0.280)	3.05 (0.283)	3.00 (0.348)	2.57 (0.546)	2.71 (0.441)	2.51 (0.586)	
	0.50	= 0	750.7	2.50 (1.589)	3.67 (0.133)	3.17 (0.281)	3.05 (0.283)	3.00 (0.348)	2.57 (0.547)	2.71 (0.442)	2.51 (0.587)	
	1.00	= 0	76.9	2.50 (1.668)	3.67 (0.135)	3.18 (0.285)	3.06 (0.288)	3.01 (0.354)	2.58 (0.558)	2.72 (0.450)	2.51 (0.600)	
	2.00	= 0	39.5	2.50 (1.757)	3.67 (0.137)	3.18 (0.290)	3.06 (0.293)	3.02 (0.361)	2.58 (0.571)	2.72 (0.458)	2.52 (0.614)	
	linear	= 0	149.7	2.55 (0.609)	3.66 (0.126)	3.17 (0.263)	3.05 (0.265)	3.00 (0.318)	2.57 (0.358)	2.71 (0.409)	2.51 (0.440)	
				2.50	3.67	3.17	3.05	3.00	2.57	2.71	2.51	

Table II. Continued

Trait	Alpha	$\epsilon_M$	RSS	Root	A	B	C	D	E	F	G	$\sigma_S^2$
Number of bouts (cont.)	parsimony 0.01	≠0	7.1	2.55	3.66	3.17	3.05	3.00	2.57	2.71	2.51	804.9
				(0.996)	(0.274)	(0.321)	(0.314)	(0.365)	(0.432)	(0.556)		
	0.50	≠0	7.0	2.64	2.77	2.74	2.74	2.73	2.67	2.63	2.62	82.0
				(1.000)	(0.275)	(0.323)	(0.316)	(0.368)	(0.436)	(0.562)		
	1.00	≠0	6.2	2.60	3.11	2.93	2.90	2.87	2.69	2.66	2.57	9.7
				(1.045)	(0.283)	(0.346)	(0.339)	(0.396)	(0.473)	(0.615)		
	2.00	≠0	5.6	2.58	3.25	2.98	2.93	2.91	2.68	2.68	2.56	5.7
				(1.097)	(0.291)	(0.369)	(0.362)	(0.426)	(0.512)	(0.671)		
	linear	≠0	6.8	2.65	2.99	2.87	2.85	2.83	2.69	2.64	2.59	17.7
				(0.902)	(0.295)	(0.376)	(0.367)	(0.421)	(0.519)	(0.542)		
Number of headbobs	0.01	=0	45290.2	5.07	4.57	4.47	4.31	4.58	4.43	7.46	5.67	4944.2
				(2.253)	(0.326)	(0.689)	(0.696)	(0.855)	(1.342)	(1.440)		
	0.50	=0	4543.4	5.07	4.57	4.47	4.31	4.58	4.43	7.47	5.67	501.6
				(2.264)	(0.327)	(0.690)	(0.697)	(0.857)	(1.345)	(1.444)		
	1.00	=0	469.1	5.08	4.56	4.46	4.31	4.58	4.43	7.49	5.68	57.7
				(2.377)	(0.332)	(0.704)	(0.711)	(0.875)	(1.379)	(1.481)		
	2.00	=0	243.1	5.09	4.56	4.45	4.30	4.57	4.42	7.51	5.70	33.5
				(2.505)	(0.339)	(0.720)	(0.727)	(0.895)	(1.417)	(1.523)		
	linear	=0	905.5	4.90	4.56	4.47	4.31	4.58	4.43	7.46	5.67	280.6
				(2.100)	(0.309)	(0.646)	(0.651)	(0.781)	(1.007)	(1.082)		
parsimony 0.01	≠0	6.6	4.90	4.56	4.47	4.31	4.58	4.43	7.46	5.67	4944.2	
			(3.89)	(0.463)	(0.741)	(0.722)	(0.866)	(1.331)	(1.402)			
0.50	≠0	6.5	4.05	3.86	3.85	3.84	3.87	3.96	4.23	4.09	501.6	
			(0.992)	(0.465)	(0.746)	(0.727)	(0.872)	(1.340)	(1.413)			
1.00	≠0	6.0	4.74	3.92	3.79	3.77	3.91	4.25	5.76	4.95	57.7	
			(1.028)	(0.481)	(0.796)	(0.777)	(0.933)	(1.426)	(1.528)			
2.00	≠0	5.5	4.96	4.02	3.81	3.77	3.96	4.33	6.40	5.25	33.5	
			(1.074)	(0.500)	(0.853)	(0.835)	(1.004)	(1.524)	(1.659)			
linear	≠0	2.7	4.34	3.86	3.80	3.79	3.89	4.16	5.17	4.64	280.6	
			(3.549)	(0.595)	(1.088)	(1.068)	(1.254)	(1.899)	(1.700)			

For non-linear models, value of  $\alpha$ , the restraining force, is given. For models including within-species variation, estimates of  $\sigma_S^2$  are given. Standard errors for estimates of ancestral phenotypes are given in parentheses.

**Table III.** Pair-wise correlation coefficients to describe the relationship between characters estimated assuming that phenotypic divergence is linearly, exponentially (with  $\alpha=1$ ), or not at all related to phylogenetic distance on the tree in Fig. 2

	Pause duration	Headbob duration	Number of bouts	Number of headbobs
Total duration				
Linear	-0.20	0.78**	0.75**	0.31
Exponential	-0.70**	0.39	0.88**	0.77**
No phylogeny	-0.44	0.53	0.89**	0.54
Pause duration				
Linear		0.35	-0.64*	-0.98**
Exponential		-0.20	-0.86**	-0.98**
No phylogeny		-0.29	-0.47	-0.72**
Bob duration				
Linear			0.22	-0.23
Exponential			0.07	-0.12
No phylogeny			0.38	-0.06
Number of bouts				
Linear				0.66*
Exponential				0.85**
No phylogeny				0.44

\* $P < 0.05$ .\*\* $P < 0.01$ .

Wiewandt (1977). Our conclusions do differ slightly from his in that we have no evidence to suggest that *C. cornuta* displays are more variable than those of other *Cyclura* species. Our descriptions of *C. carinata* displays also match those of Iverson (1979, which involved animals from a different cay from those observed in the current study) except that Iverson does not mention the rapid trill-like motions at the beginning of some displays. Further studies are needed to determine whether this difference is due to the small sample size in both studies or to true population differences. Carpenter (1982) provided data from a very small number of *C. cyclura* displays which also coincide generally with our results.

Data from other lizards are also sparse, with *Sceloporus* and *Anolis* being the only other genera for which quantitative information on a large number of species is available. Although it would also be interesting to make comparisons with the visual displays of anoles, such comparison is seriously complicated by the existence of multiple headbob and dewlap displays within each species (e.g. Janssen 1977). Thus, we make comparisons only with *Sceloporus*. Although *Cyclura* are quite diverse in the larger aspects of their headbob

displays (e.g. using headbob displays in a novel context as does *C. carinata*, and producing at least two types of rolling motions as in *C. nubila* and *C. cornuta*), *Cyclura* headbob displays are quite similar to the push-up displays of *Sceloporus* lizards (Carpenter 1978; Martins 1993b) in many small ways. *Cyclura* displays fall roughly within the range of *Sceloporus* displays in terms of pause duration (range=0.2–3 s for *Sceloporus*; 0.2–0.9 s for *Cyclura*) and the number of bobs per display (range=2–15 bobs/display for *Sceloporus*; 1–10 bobs/display for *Cyclura*). Because mutations, replication errors and responses to environmental change accumulate at each generation, variation is expected to increase with phylogenetic time. Furthermore, if the frequency of speciation is also related to time, we expect phenotypic variation to increase with increasing numbers of species. Thus, given that these species means are based on data from 42 species of *Sceloporus* and only seven species of *Cyclura*, it is not surprising that *Sceloporus* are also more variable. Even taking this difference into account, *Cyclura* displays are somewhat shorter than *Sceloporus* displays (range of species means for total duration=3–21 s for *Sceloporus* as opposed to 1–4 s for *Cyclura*).

Other similarities between *Sceloporus* and *Cyclura* lie in the positive relationship between number of headbobs and total duration and the negative relationship between number of headbobs and pause duration (cf. Martins 1993b). These relationships support the suggestion that there is an evolutionary constraint on the total duration of displays, such that animals can produce either several headbobs with short pauses between them or short series of headbobs with long inter-bob pauses. With only seven species, it was not possible to test the further suggestion (Martins 1993b) that the shape of the headbob (i.e. degree of jaggedness) is also negatively related to the number of headbobs. However, future studies considering possible anatomical or physiological mechanisms of a constraint on total display duration are warranted.

In studies of *Anolis auratus*, Fleishman (1988a, b) suggested that rapid motion at the beginning of lizard visual displays may be a means of getting the attention of conspecifics before proceeding with the information-rich body of the message. Our finding that rapid trill-like motions only occur at the beginning of headbob displays in at least some populations of *C. ricordi* and *C. carinata* support this hypothesis. That the rolling motions of *C. cornuta* also seem more likely to occur at the beginning rather than at the ends of displays also provides some evidence that an important function of the beginning of displays is to get the attention of other animals in the vicinity. The *Cyclura* system may be particularly useful in pursuing this question further because it includes some species and even populations that produce trills and others that do not. Studies of these populations could determine whether animals that produce trills (or that produce them more often) live in environments with thicker vegetation, more wind, or other factors which may increase the visual interference and the need for attention-getting devices.

### Rates of Behavioural Evolution

In several aspects, headbob displays of the Cuban population (*C. n. nubila*) are more similar to those of the Grand Cayman subspecies (*C. n. lewisii*) than they are to displays of the Puerto Rican population (*C. n. nubila*). The Puerto Rican population has been isolated from Cuban founders only since the mid 1960s (about

30 years or about six generations), but probably originated from a population that has been separated for some time from the Guantánamo Bay animals measured in this study. Although it is not known how long ago the Grand Cayman animals diverged from *C. n. nubila*, genetic differences between the two subspecies are quite large (Fig. 2), suggesting that they have been separated for quite some time.

*Cyclura n. nubila* from Puerto Rico produces much longer displays with longer and fewer headbobs than either of the other two populations. This distinction in their displays makes the Cuban animals more similar to their geographic neighbours (*C. n. lewisii*) than they are to the Puerto Rican population. One possibility is that the Puerto Rican (*C. n. nubila*) population may be evolving more rapidly than either of the other two populations due to random genetic drift. The Puerto Rican population is quite small (estimated at 157 adults in Christian 1986; Christian et al. 1986), and small island populations are subject to random genetic drift and other forces which may cause very rapid evolutionary change. Another possibility is that trait variation is subject primarily to environmental rather than genetic control, and that the differences are due either to ecological differences among the three populations (suggesting that the headbob display is far more plastic than is generally believed) or to cultural evolution (such as is often hypothesized for population differences in bird song, e.g. Lynch & Baker 1994). The phylogenetic analysis herein does not distinguish between these possibilities.

Because headbob displays are frequently used in courtship and defence of territories, major differences in the headbob display could lead to reproductive isolation and speciation. Further research is needed to determine whether iguanas can distinguish the difference between the different types of headbob displays and whether these differences have an impact on mate attraction or mating success. The finding that such dramatic changes in duration occurred between two populations, however, suggests that these variables are quite plastic, and seems in superficial conflict with our finding that only a few changes in duration have occurred across the genus as a whole. One possibility is that multiple small changes have occurred throughout the evolution of the genus, but we cannot detect them at the phylogenetic scale because most changes did not proceed in a

consistent direction through evolutionary time. Frequent evolutionary changes in which the direction of change moves back and forth at random is consistent with the linear (Brownian motion) model of phenotypic evolution applied in this study.

### Phylogenetic Analyses

In this study, we used phylogenetic comparative methods to reconstruct the ancestral states of several characters. Instead of applying the usual parsimony methods, we applied a generalized least-squares approach (Martins & Hansen 1996) which allows both for the incorporation of measurement error and for the use of a more flexible set of assumptions regarding the underlying evolutionary process. Reassuringly, we found only small differences in the ancestral states estimated by various different types of assumptions. This result suggests that when the main goal is to estimate the phenotype of a hypothetical ancestor or to uncover general trends in the evolution of a clade, most of the assumptions suggested by existing phylogenetic methods will probably give reasonably accurate results. These results coincide with the theoretical expectations of the method. Generalized least-squares regression is expected to give unbiased estimates regardless of the underlying error structure (phylogeny, model of evolutionary change, within-species variation, etc.), which affects primarily confidence intervals and hypothesis tests. On the other hand, we also found major differences in the standard errors produced by analyses with different assumptions. Thus, if the goal is to determine exactly where evolutionary changes occurred on a phylogeny, whether a single change in one trait really did precede changes in a second trait, or whether one ancestral state is significantly different from another, one must have rather precise information about the microevolutionary process underlying each trait and the types of within-species variability involved.

The incorporation of measurement error often reduced the standard errors of the ancestral states and allowed us to find some patterns that would otherwise have been totally obscured. This reduction in standard errors is probably due in part to the small sample size used in this study. Many of the species means had large standard errors, with the most unusual values being obtained for taxa that were poorly represented in the data. Incorporation of measurement error into the analysis

allowed us to weight those taxa more lightly than some of the other taxa in which we had greater confidence, and to obtain more accurate estimates. We expect that within-species variability would have a much smaller impact on the standard errors in studies that included more accurate measures of each species mean, but this remains to be shown.

We also applied two sets of assumptions (and several possible values) to span a wide range of possible microevolutionary scenarios underlying the data. In doing so, we found that a linear model usually fitted reasonably well, and often provided the best fit to the data. Thus, the linear, Brownian motion assumption seems to be a good one for headbob data, supporting the use of the independent contrasts method (Felsenstein 1985) with these data. In several cases, however, one of the exponential models provided a better fit (lower residual sum of squares), suggesting that this may also be a reasonably good model for some behavioural characters. Unfortunately, it was not possible to estimate the restraining force in the exponential model ( $\alpha$ ) effectively and choose among exponential models with so few taxa. Furthermore, all of the models we considered assume that the chosen microevolutionary scenario is constant throughout the phylogeny. Future studies might improve on the situation by considering changing scenarios, such as stabilizing selection about a fluctuating optimum (e.g. Hansen 1997).

In its simplest form (assuming a linear model of evolutionary change and excluding within-species variation), our method gives ancestral state estimates that are virtually identical to those provided by the popular sum-of-squared-changes parsimony algorithm. This result is not surprising given the similarities between the assumptions of the sum-of-squared-changes parsimony algorithm and the Brownian motion model (Maddison 1991). Our method, however, also provides estimates of the standard errors of ancestral states, allowing us to determine where relatively large, statistically significant evolutionary changes occur and to conduct hypothesis tests involving those changes. It also allows us to incorporate measures of within-species variation. Note that parsimony estimates of an ancestral state will never exceed the range of the two immediate daughters of the ancestor, whereas, ancestral estimates obtained using the generalized least-squares method and incorporating within-species variation will

occasionally do so. Furthermore, our generalized least-squares method can incorporate a wide variety of other microevolutionary models, providing a measure of the robustness of the results to possible violations of evolutionary assumptions. Thus, sum-of-squared-changes parsimony might be considered as a specific case of our method, which provides a more thorough, more flexible approach to ancestral estimation.

### Impact on Conservation Efforts

Several aspects of our results should be of interest to conservation agencies raising endangered species of lizards in captivity for possible reintroduction to the wild. First, our results generally support the idea that major changes in the headbob display exist, even at the population level. From a practical perspective, this suggests that care should be taken when mixing animals from different populations in captive situations. These animals may not interact with each other effectively, or in the same ways that they would interact with animals from their own population.

Second, such differences can occur exceedingly quickly, even in stereotyped displays which are likely to be of considerable importance to reproductive behaviour. Our results suggest that major changes in the headbob display might occur in as little as six generations (about 30 years), exhibiting far more plasticity than we might have predicted. There are several possible explanations for such plasticity, such as: (1) headbob displays may change quickly in small populations subject to random genetic drift (e.g. most captive populations); (2) headbob displays may depend substantially on ecological rather than genetic factors such that captive animals need to be presented with appropriate ecological contexts in order to preserve their behavioural phenotypes; and (3) headbob displays may be evolving culturally with dialects of the sort found in many songbirds, such that different populations of iguanas are behaviourally unique and worthy of independent conservation. Further research is needed to distinguish between these possibilities.

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