Biological Journal of the Linnean Society (2000), 70: 597-612. With 3 figures.

doi:10.1006/bijl.1999.0419, available online at http://www.idealibrary.com on IDENL®

Decoupled evolution of display morphology and display behaviour in phrynosomatid lizards

JOHN J. WIENS

Section of Amphibians and Reptiles, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213–4080, U.S.A

Received 10 May 1999; accepted for publication 30 October 1999

A widespread trend in animals is the evolution of morphological ornaments and behaviours that are involved in aggressive and courtship displays. These display traits are important from the standpoint of communication, sexual selection, and speciation. Previous authors have suggested that the evolution of display morphology and display behaviour should be closely linked. In this study, I tested for this association with behavioural and morphological data for 59 taxa of phrynosomatid lizards using phylogenetic comparative methods (Maddison's concentrated changes test and Felsenstein's independent contrasts). The results showed little significant association between features of display morphology and behaviour, suggesting that the evolution of these traits is not tightly coupled. This decoupling is particularly evident in the genus *Sceloporus*, in which several species have lost the display coloration but retain unmodified display behaviour. The results also suggest that display morphology is more evolutionarily labile than display behaviour in this group.

© 2000 The Linnean Society of London

ADDITIONAL KEY WORDS:---phylogeny - character evolution - sexual selection - comparative methods.

CONTENTS

Introduction										597
Material and methods										599
Results										605
Discussion										608
Acknowledgements .										610
References										610

INTRODUCTION

Some of the most beautiful and bizarre products of morphological evolution are those ornaments associated with male courtship and aggressive displays (Darwin, 1871). These include the plumage of peacocks and birds-of-paradise, the horns of

597

E-mail: wiensj@carnegiemuseums.org

0024-4066/00/080597+16 \$35.00/0

ungulate mammals, and the brightly coloured dewlaps of Anolis lizards (Andersson, 1994). These unusual morphologies typically originate in the common ancestor of a monophyletic group and then diversify as the group radiates, and the diversity of display morphology in these groups is often accompanied by a diversity of elaborate display behaviours (e.g. Geist, 1966 [bovid mammals]; Cooper & Forshaw, 1977 [birds of paradise]; Jenssen, 1977 [Anolis]). Understanding the evolution of display traits is important to studies of sexual selection, communication, species recognition, and speciation (Darwin, 1871; Lande, 1981; West-Eberhard, 1983; Ryan & Rand, 1993; Andersson, 1994). A major focus of recent research by evolutionary biologists has been on explaining the evolution of female preferences for these elaborate morphological and behavioural traits (Kirkpatrick & Ryan, 1991Andersson, 1994; Ryan, 1998). However, relatively little attention has focused on how the evolution of display morphologies may be related to the evolution of display behaviours and vice versa. For example, do the unusual display ornaments in males evolve in response to particular behaviours (or vice versa), or do they evolve independently? Does a functional coupling between these traits mean that they should evolve together on the phylogeny?

Previous authors (e.g. Geist, 1966; Prum, 1990; Endler, 1992; Marchetti, 1993; McLennan, 1996) have proposed that the evolution of male display ornaments should be closely tied to the evolution of display behaviour, but this idea has never been rigorously tested. A close relationship between these variables makes intuitive sense; a visual display is not simply an isolated movement or morphological character, but a combination of the two. Thus, they appear to be functionally linked, at least in general. Phylogenetic evidence for a close relationship between the evolution of display behaviour and morphology has been found in studies of birds (Prum, 1990) and fish (McLennan, 1991, 1996), in that seemingly related characters of display morphology and display behaviour were found to change on the same branch of the phylogeny, or else behavioural changes preceded morphological changes (implying that behaviour drives the evolution of morphology; Prum, 1990). However, the association between traits was not tested for statistically in these studies. Martins (1993) used statistical comparative methods to examine the relationship between various components of display behaviour with each other and with display morphology, in the phrynosomatid lizard genus Sceloporus, but failed to find any significant association between morphology and behaviour. That study was problematic, however, in that the tree used was based on a phenetic analysis of (mostly) skull measurements (Larsen & Tanner, 1974), and this phenogram has since been contradicted by a recent parsimony analysis based on a diversity of molecular, morphological, and chromosomal characters (Wiens & Reeder, 1997).

Phrynosomatid lizards are an excellent model system for studying the relationship between display morphology and display behaviour because there is now both phylogenetic information (Reeder & Wiens, 1996; Wiens & Reeder, 1997) and published data on male display behaviour (e.g. Carpenter, 1962, 1963, 1978; Clarke, 1965; Lynn, 1965) available for a large number of taxa. Phrynosomatid lizards, formerly known as sceloporine iguanids, consist of approximately 120 species and 9 genera, found in a variety of habitats from Canada to Panamá (Frost & Etheridge, 1989). Display morphology in phrynosomatid lizards consists of conspicuously coloured patches (blue in most species) on the belly and throat of males of many species. The behavioural display typically consists of lateral presentation of the body (with males facing in opposite directions), raising up the body on two or four legs,

and further extension and flexion of the legs to generate a series of movements resembling push-ups. The displays also typically involve extension of the dewlap and lateral compression of the body, behaviours that increase the exposure of the throat and belly patches, respectively. A close functional relationship between the colour patches and display behaviour seems particularly likely because the patches are on the ventral surfaces of these lizards and may only be visible when actively displayed. The push-up displays are known to function in aggressive encounters and courtship (Carpenter, 1978; Cooper & Greenberg, 1992). The pattern of head bobs has been shown to be important in species recognition among closely-related phrynosomatid lizards (Hunsaker, 1962). There is evidence that belly patches are important in sexual discrimination (Cooper & Burns, 1987), and that throat colouration is important in male-male competition (Hover, 1985; Sinervo & Lively, 1996).

In this study, I test for associations between the evolution of display morphology and display behaviour in phrynosomatid lizards using statistical phylogenetic methods. Contrary to expectations, the results suggest that the evolution of display behaviour and display morphology are not closely coupled, and that phrynosomatid lizards frequently lose their display colouration with little corresponding change in display behaviour. These results also show that display morphology is relatively labile, whereas many aspects of display behaviour are relatively conservative.

MATERIAL AND METHODS

Data on display morphology were obtained from alcohol-preserved museum specimens. The presence or absence of the throat and belly patches is generally a striking and obvious character, and my observations on live, fresh-preserved, and older-preserved specimens of many species suggest that there are no significant changes between living and preserved specimens (Wiens unpubl. data). Museum specimens examined are listed in Reeder & Wiens (1996) and Wiens & Reeder (1997). The taxonomic distribution of conspicuously coloured throat patches largely parallels that of the belly patches, and for the sake of simplicity, belly patches were scored as the sole indicator of display coloration.

The taxonomic distribution of belly patches is somewhat ambiguous in that the species of *Holbrookia*, *Uma*, and *Uta* examined have dark ventrolateral spot(s) that may or may not be homologous to the belly patches of other phrynosomatids. This ambiguity was treated by running all analyses assuming either that these traits are homologous (assuming maximum homology, MAXHOM hereafter) or that dark ventrolateral spots are not homologous to the belly patches of other species (minimum homology, MINHOM). One species of *Sceloporus (S. utiformis)* has unusual reduced, ventrolateral markings in males that may not be homologous to those in other species; belly patches were treated as present in this species assuming MAXHOM and as absent under MINHOM.

Some intraspecific variation in the presence/absence of belly patches was observed, and these polymorphisms were coded for qualitative analyses using the majority method (Wiens, 1995). Thus, the condition found in more than half the individuals sampled was coded as present. When two states were present in a species at equal frequencies, the species was coded as polymorphic (both states present), but putative

6. Body movement: (0) head bobs only; (1) head neck and anterior portion of body moved during display.

9. Confrontation during display: (0) face-off; (1) no face-off.

11. Body orientation: (0) tilt towards other lizard; (1) no tilting.

14. Display sequence: (0) indeterminate; (1) determinate.

changes within polymorphic taxa were not counted. Although methods that use more detailed information on trait frequencies have desirable properties for coding intraspecific variation for phylogenetic and comparative analyses (Wiens, 1999b), the use of Maddison's (1990) method requires treating characters as binary (two states), which disallows frequency coding (but not majority coding). The majority method shares some of the useful features of frequency methods, and often gives similar results (Wiens, 1995).

Data on display behaviour were obtained from the following sources: Carpenter (1978) for 42 species of Sceloporus; Carpenter (1962) for representatives of Petrosaurus, Uta, and Urosaurus; Carpenter (1963) for Uma; Clarke (1965) for Callisaurus, Cophosaurus, and Holbrookia; and Lynn 1965) for Phrynosoma. These authors did not deal explicitly with intraspecific variation (within or between individuals), but their characterizations presumably reflect the patterns seen in the majority of sequences and individuals observed for a given species (Carpenter, 1978), and these data have been used in other comparative studies (Martins, 1993). Many of the distinctive subspecies of Sceloporus may represent different species (Wiens & Reeder, 1997) and were treated as separate taxa in this study. Although Carpenter (1978) did not treat these subspecies as distinct taxa in his analysis, behavioural data usually could be assigned to subspecies when locality data were available. A total of 15 qualitative characters were scored (Table 1), the distribution of these characters and the belly patch character among taxa is given in Table 2. Comparable data on three quantitative characters (Table 3) were available only for species of Sceloporus. Correlations between display colouration and some of the display behaviours are not intuitively obvious (e.g. 'jerkiness' of the push-up display), but all behavioural variables were included in these analyses for the sake of completeness.

The phylogeny used (Fig. 1) was from Reeder & Wiens (1996; outside *Sceloporus*) and Wiens & Reeder (1997; within *Sceloporus*). Taxa for which behavioural data were unavailable were pruned from these trees. These phylogenies are based on combined analyses of molecular, morphological, and chromosomal data (>300 parsimony-informative characters each). The analysis by Reeder & Wiens (1996) also included several characters of display behaviour, and both studies included characters that describe variation in display coloration. Inclusion of these 'characters'

TABLE 1. Qualitative behavioural characters used to test the relationship between display behaviour and morphology. See Carpenter (1978) for further explanation of these characters

^{1.} Neck display: (0) dewlap extension; (1) no dewlap extension.

^{2.} Body presentation: (0) lateral presentation; (1) no lateral presentation.

^{3.} Compression of body: (0) lateral compression; (1) no lateral compression.

^{4.} Body elevation during display: (0) present; (1) absent.

^{5.} Push ups during display: (0) present; (1) absent.

^{7.} Body elevation during display: (0) four legs; (1) front legs only.

^{8.} Push-ups: (0) front legs only; (1) four legs.

^{10.} Back posture: (0) arches back; (1) does not arch back.

^{12.} Body expansion: (0) bloating; (1) no bloating.

^{13.} DAP (display action pattern) graph: (0) jerky, without plateaus; (1) with plateaus (pauses).

^{15.} Display site: (0) raised area; (1) on ground.

TABLE 2. Qualitative behavioural and morphological data for 59 species of phrynosomatid lizards.Characters 1–15 are described in Table 1 and literature sources are listed in the Material and Methods.Characters 16 and 17 refer to the presence (1) or absence (0) of male belly patches, under MAXHOM(character 16) and MINHOM (character 17) coding. P indicates cases of intraspecific variation that
were coded using the polymorphic method because trait frequencies were unknown

	Character			
Species	1 5 10 15			
Sceloporus acanthinus	0000010010110011			
S. asper	0000010010100011			
S. bicanthalis	0000010001101100			
S. cautus	0?000010111110?11			
S. chrysostictus	0000010111101000			
S. clarkii	0000010000110011			
S. couchii	0000010011101111			
S. cozumelae	00000010111101100			
S. cryptus	00000010111110011			
S. cupreus	0000000001100P00			
S. dugesü dugesü	0000000000101011			
S. dugesii intermedius	0000000000101011			
S. edwardtaylori	00000010000110000			
S. formosus	0000000100110011			
S. graciosus	0000000011110011			
S. grammicus	0000001001110?P11			
S. norridus divientris	00000010000110000			
S. norriaus norriaus	00000010000110011			
S. jauapae	0000001110111111			
S. Junou	00000010011100011			
S. lundelli	00000010010110011			
S. raculosus	00000010000110011			
S. maximusus S. magister	00000010000110011			
S megaletidurus	02000010112110000			
S. melanorhinus	0000010000110011			
S. merriami	00000011010102011			
S. mucronatus mucronatus	00000010011101011			
S. nelsoni	000000110101?0011			
S. occidentalis	0000010011110011			
S. olivaceus	?0?000?00?0110011			
S. orcutti	0000010000110011			
S. ornatus caeruleus	0000010011100011			
S. ornatus ornatus	0000010011100011			
S. parvus	0000000011101011			
S. poinsettii	0000010011001011			
S. pyrocephalus	0000001101011?011			
S. scalaris scalaris	00000010011101111			
S. scalaris slevini	00000010011101111			
S. sunferus	0000000001100P00			
S. spinosus caerulopunctatus	0000010000110011			
S. spinosus spinosus	00000010000110011			
S. teapensis	000000100101010111			
S. windulatus torquatus	00000010010110011			
S. undulatus nyacinintinus S. autiformic	0000001010110011			
S. utijonius S. nariabilis nariabilis	0000001111101P10			
S. variabilis variabilis	000000000000000000000000000000000000000			
Petrosaurus mearna	02000010111102011			
I toosaaras meansi Urosaaras graciosus	000000101110.011			
U. ornatus	0000001010112011			
Uta stansburiana	0000000010101110			
Uma notata	000000001010?110			
Callisaurus draconoides	000000000000000000000000000000000000000			
Cophosaurus texanus	000000000010?P11			
Holbrookia maculata	000000000011?110			
Phrynosoma douglasi	111111??11?1?1100			
P. cornutum	111111??11?1?1100			
P. modestum	111111??11?1?1100			

TABLE 3. Quantitative behavioural data and frequency of male belly patches in 42 species of *Sceloporus*. Values for head-bobs were taken from the text of Carpenter (1978) rather than the figures (see Martins, 1993)

	Character									
Taxon	Head-bobs	Pause	Duration	Belly patch						
Sceloporus acanthinus	3	0.440	4.75	100						
S. asper	8	0.641	7.57	90						
S. bicanthalis	2	2.880	4.57	33						
S. cautus	6	0.220	3.70	100						
S. chrysostictus	3	2.220	11.25	0						
S. clarkii	5	0.392	7.98	100						
S. couchii	8	0.807	14.09	100						
S. cozumelae	3	1.505	9.08	0						
S. cryptus	5	0.378	7.02	100						
S. dugesii	4	0.940	7.39	100						
S. edwardtaylori	8	0.757	11.07	0						
S. formosus	7	0.167	8.44	100						
S. graciosus	9	0.878	8.52	100						
S. grammicus	5	1.083	7.88	100						
S. horridus	11	0.364	13.59	100						
S. jalapae	12	0.790	11.44	100						
S. jarrovii	5	0.980	5.33	67						
S. lunaei	9	0.563	7.38	100						
S. lundelli	9	0.391	8.10	100						
S. maculosus	13	0.261	8.42	100						
S. magister	11	0.214	7.15	100						
S. megalepidurus	9	0.690	7.89	20						
S. melanorhinus	7	0.592	12.33	100						
S. merriami	7	1.147	19.19	100						
S. mucronatus	4	1.233	11.33	100						
S. nelsoni	9	0.477	11.64	100						
S. occidentalis	15	0.441	13.18	100						
S. olivaceus	6	0.188	5.52	100						
S. orcutti	8	0.242	5.95	100						
S. ornatus	7	0.476	7.08	100						
S. parvus	5	1.797	13.93	88						
S. poinsettii	10	0.250	6.14	100						
S. pyrocephalus	11	1.203	18.85	100						
S. scalaris	2	1.250	3.25	100						
S. siniferus	15	0.438	11.65	0						
S. spinosus	9	0.338	11.28	100						
S. teabensis	10	1.250	21.25	100						
S. torquatus	6	0.450	14.82	100						
S. undulatus	13	0.440	9.47	100						
S. utiformis	3	3.035	8.83	100/0						
S. variabilis	6	1.324	18.00	100						
S. woodi	7	0.165	3.74	100						
	•	0.100	0.71							

of interest' in estimating the tree is controversial, and the best approach for character inclusion or exclusion will depend on the specific question being asked (de Queiroz, 1996). In this study, including these characters should provide the best estimate of phylogeny (i.e. the tree based on the largest sample of characters), but should not bias the comparative analyses either for or against finding an association between display morphology and behaviour.

Maddison's (1990) concentrated changes test was used to test for significant associations between display coloration and qualitative behavioural characters, and



Figure 1. Phylogeny of phrynosomatid lizards used in this study. S = Sceloporus.

was implemented using MacClade (Maddison & Maddison, 1992). The concentrated changes test determines whether the presence of a given state of one character (the independent variable) significantly enhances changes in another (the dependent

variable). Specifically, the test evaluates whether the number of changes in the dependent variable is significantly greater (or less) on the 'distinguished branches' of the phylogeny (those branches reconstructed as having the state of interest of the independent character) than expected by chance, given a null model in which gains and/or losses on any of the branches is equally likely (Maddison, 1990). Because I consider it possible that display morphology might influence the evolution of display behaviour as well as vice versa, one set of analyses tested if particular behavioural phenotypes increase or decrease the gain and/or loss of male display colouration, and another set of analyses tested whether the reconstructed absence of male belly patches increases or decreases changes in any of the behavioural characters. In each case, the choice of a particular state of the independent character chosen for the 'distinguished branches' has no impact on the results of the test (because an unusually large or small number of changes on these branches should both give significant results). Changes in both dependent and independent characters were reconstructed using both ACCTRAN and DELTRAN optimization routines (Swofford & Maddison, 1987). Although these routines may not represent all the possible reconstructions for a given character (Maddison & Maddison, 1992), they were treated as relatively extreme outcomes from among the range of possible reconstructions, and associations between characters were considered significant only if they were insensitive to the particular optimization routine used. For most comparisons there was a large number of changes in the dependent characters (making exact probability calculations difficult), and simulations were therefore used to obtain the null distribution. For the simulations, 1000 replicates were generated for each test, using the 'actual changes' and 'either state ancestral' options of MacClade. The concentrated changes test is not strictly a test of correlation (i.e. two characters changing on the same branches of the phylogeny), but it can potentially detect such correlations, as well as more diffuse associations between characters (i.e. relationship between a given state of one character and changes in another). The concentrated changes test is a widely used and easily implemented approach for examining the relationship between discrete characters, although alternate methods may also have desirable properties (e.g. Sillén-Tullberg, 1993; Pagel, 1994; Werdelin & Sillén-Tullberg, 1995).

Previous authors (e.g. Prum, 1990) have suggested that display behavior drives the evolution of display morphology, and that the gain of ornaments will therefore be preceded by the evolution of particular behavioral phenotypes. Maddison's (1990) method cannot test for gains without including losses also. I therefore reconstructed changes in discrete behavioral characters using MacClade to qualitatively determine if behavior changes before or after the gain of belly patches.

Three quantitative behavioural characters were scored for males of 42 species of *Sceloporus* by Carpenter (1978). These were (1) the number of head bobs per push up display, (2) the mean duration of pauses between head-bobs (in seconds), and (3) the total sum of the duration of all head-bobs and pauses. Head bobs are generally synonymous with push ups; but in a few species the head may be the only part of the body that is moved. Correlations between these variables and the frequency of male belly patches were tested using the independent contrasts method (IC; Felsenstein, 1985). IC requires the specification of branch lengths, and these were generated in two ways. First, I used parsimony estimates of branch lengths for the morphological data of Wiens & Reeder (1997) using PAUP* (Swofford, 1998), following Garland, Harvey & Ives (1992). Although molecular data may be preferable

for estimating branch lengths for comparative analyses, only morphological data were available for all 42 taxa. Branch length estimates obtained using both the ACCTRAN and DELTRAN optimization routines were used and analyzed separately. However, these two optimizations gave extremely similar IC results, and only results using ACCTRAN are presented. Second, I set all branches to equal length ('punctuational model' of Martins, 1993). To verify that the independent contrasts were adequately standardized by their branch lengths, the absolute values of each independent contrast for each node were regressed on their standard deviations (the square root of the sum of the branch lengths for that contrast), following Garland *et al.* (1992). *P*-values for the regression coefficients were >0.05, and the contrasts were therefore considered to be standardized.

Independent contrasts for each branch and character were obtained using the 'Contrasts' package in PHYLIP, version 3.57c (Felsenstein, 1995). The relationship between the contrasts for belly patches and each of the behavioural characters was examined using simple regression (using the StatviewTM software package), forcing the model through the origin (as recommended by Garland *et al.*, 1992). Although the presence of belly patches is a qualitative character, it was treated as continuous by using the frequency of patch presence within each species as the raw data. I consider this to be a reasonable approach because evolutionary change in quantitative trait values and frequencies of qualitative variables may both be modeled using the Brownian motion model assumed by the IC method (Felsenstein, 1988). Because the 'Contrasts' package does not allow taxa with identical trait values, several of the subspecies that were treated as separate taxa in the qualitative analyses were combined in the IC analyses.

This study involved a large number of statistical comparisons, and large numbers of statistical tests require adjusting the *P*-value necessary for results to be considered significant (Rice, 1989). However, none of the comparisons between characters consistently approached a standard, uncorrected significance level of 0.01, and so a Bonferroni correction is not discussed. Although a large number of behavioural characters were tested, a significant relationship between display morphology and any of the qualitative or quantitative display behavior characters was considered potential evidence that these traits can be coupled in their evolution.

The relative lability of morphological and behavioural display traits was evaluated by finding the consistency index (ci; fit of the characters to the tree; Kluge & Farris, 1969) of each character using MacClade and comparing the average ci's of these sets of characters.

RESULTS

In general, there was little significant association between changes in display morphology (belly patches) and particular display behaviour phenotypes (Fig. 2). Only one comparison—between changes in belly patches and elevation of the body on two legs only—yielded a P < 0.01 and then only when both characters were optimized under DELTRAN. Thus, behavioural characters do not appear to drive changes in display morphology. Similarly, there was no significant relationship between the absence of belly patches and changes in any of the qualitative behavioural characters (Fig. 2); these results apply also to patch presence. This suggests that the



Figure 2. Results from statistical analyses of the association between display colouration (male belly patches) and 15 qualitative behavioural characters (described in Table 1). Each box represents the comparison between a behavioural character and the morphological character. The relationship between a pair of characters was tested under both ACCTRAN (A) and DELTRAN (D) optimizations for each character. Different shadings represent ranges of probability values from Maddison's concentrated changes test, with white indicating a significant result. Results on the left side of the figure are with the behavioural character as the independent variable, whereas the morphological character is the independent variable on the right side. A, MAXHOM coding of belly patches. B, MINHOM coding.



Figure 3. Regressions of independent contrasts of three quantitative characters of display behaviour (y-axis) and display morphology (x-axis). The gradual model refers to the use of branch lengths estimated from morphology (Wiens & Reeder, 1997), whereas the punctuational model refers to the assumption of equal branch lengths.

presence or absence of belly patches has no significant impact on display behaviour. The non-statistical analysis of whether behaviour drives only the gain of belly patches showed that behavioural changes generally occurred after the acquisition of belly patches and/or that patches are acquired in the sand lizard clade (*Uma, Callisaurus, Cophosaurus, Holbrookia*) without any associated behavioural synapomorphies (results not shown). This result suggests that behavioural characters do not drive the gain of display coloration, or at least not at the taxonomic level investigated in this study (see Discussion).

Quantitative behavioural characters (within *Sceloporus*) showed no significant association with display morphology (Fig. 3). The relationship between pause duration and display coloration approached significance, which might suggest that the absence of belly patches drives the evolution of longer pauses between push ups, but only

under one combination of coding method and branch lengths (MINHOM, gradual).

The consistency index of the male belly patch character is 0.11 or 0.10 (MAXHOM or MINHOM), whereas the average consistency index of the 15 qualitative behavioural characters is 0.514. The morphological ci is outside of the 99% confidence interval for the mean ci of the behavioural characters. This results shows that display morphology is generally more evolutionarily labile or plastic than display behaviour in phrynosomatid lizards.

DISCUSSION

The results of this study show no consistent statistically significant associations between the evolution of display morphology and display behaviour in phrynosomatid lizards (in agreement with the results of Martins, 1993). The absence of this relationship is surprising, because one would expect display morphology and behaviour to be functionally linked (Prum, 1990; Endler, 1992), and because a relationship has been found (albeit not statistically) in manakins (Prum, 1990) and sticklebacks (McLennan, 1991, 1996). There are several possible explanations for the lack of association. One is that male belly patches and the various display behaviours tested may have different social functions (e.g. sexual discrimination vs. species discrimination), and may not be as functionally linked as expected. Conversely, some of the display traits may have the same function, and this redundancy in the signals may obviate the need for tightly correlated evolution, as suggested by Williams & Rand (1977) for displays in *Anolis* lizards. Testing these hypotheses will require studies of the social function of the belly patches and specific components of display behaviour in a diversity of phrynosomatid species; except in a few species, the specific function(s) of these signals remain poorly known. Another potential explanation for the lack of association is that display behaviour and display morphology generate different kinds of neurological information for the receiver (movement versus colour and shape; Fleishmann, 1992), and thus may not be expected to be tightly linked in their evolution. Finally, it is possible that the influence of display behaviour on the evolution of display morphology (or vice versa) may exist but may be too weak (or evolve too slowly) to be detected by the methods used or the sample of taxa. For example, it may be that the behavioural display does drive the evolution of belly patches, but that the major features of the behavioural display are relatively ancient (plesiomorphic for Iguania; see the following paragraph), whereas the evolution of throat and belly patches is relatively recent (evolving within Phrynosomatidae).

The results of this study suggest the possibility that the gain of male display coloration may be driven by display behaviours that evolved prior to the diversification of the Phrynosomatidae, whereas the loss of display morphology is uncoupled from display behaviour within the family. Different patterns of correlation associated with gain and loss of display coloration may explain the difference between the results of this study and previous analyses, which addressed mostly origins of display morphologies and behaviours (e.g. Prum, 1990; McLennan, 1991). Examining the distribution of male display behaviour and display morphology outside the Phrynosomatidae suggests that certain display behaviours may indeed drive changes in display morphology (although there is no evidence that the behavioural characters

that are gained within the family drive the gain of belly patches). Many basic behavioural components of the display of phrynosomatid lizards occur in other families of iguanian lizards (the larger clade to which the Phrynosomatidae belongs; Frost & Etheridge, 1989), including lateral presentation and compression of the body, head bobs/push-ups, and dewlap extension (Crotaphytidae [Sanborn & Loomis, 1979], Iguanidae [Carpenter, 1982], Opluridae [Blanc & Carpenter, 1969], Polychrotidae [Jenssen, 1977], Tropiduridae [Carpenter, 1977]; see Carpenter [1986] for a bibliography); within the family these traits vary only in that they are lost in the genus *Phrynosoma*. Within other families of iguanians, some clades have evolved conspicuous coloration on the throat and/or belly (and/or structural modifications of the dewlap), seemingly to accentuate these behavioural displays, particularly Anolis (Polychrotidae; Fitch & Hillis, 1984). These apparently widespread and conserved display behaviours may drive the evolution of conspicuous display morphology in various groups of iguanian lizards, including phrynosomatids. An analysis of display behaviour and display morphology at a higher taxonomic scale might show a significant relationship, but such an analysis is currently difficult because of limited behavioural and phylogenetic information.

In contrast, within the Phrynosomatidae, the results of this study show that the loss of display morphology is seemingly unrelated to display behaviour. Of the 9–10 changes in display morphology among the 59 species included in this study, 60–78% of these changes are losses of coloration in the genus Sceloporus (variation in these numbers comes from different coding and optimization methods). Species of Sceloporus that have lost the patches retain all of the basic elements of the behavioural display seen in species with patches (characters 1-6), and there are no changes in display behaviour unambiguously associated with these losses. Thus, many basic components of the display behaviour seem to be highly conserved within Phrynosomatidae regardless of whether patches are present or absent. A number of different processes have been suggested to drive the repeated loss of belly patches, including reduced female preference, higher predation in terrestrial habitats, and/or genetic drift (Wiens, 1999a). It is unclear why patches should be lost without any corresponding change in display behaviour. Possible explanations include a higher costs for display morphology than display behaviour, weaker female preferences for or male response to display coloration, or simply a higher rate of change in the display coloration.

The results mentioned above suggest that display morphology is more labile than display behaviour in phrynosomatids, and in support of this idea it was found that the qualitative behavioural characters have a higher average consistency index than the morphological character. This finding may contradict conventional wisdom that behaviour is more evolutionarily plastic than morphology, but is consistent with the results of de Queiroz & Wimberger (1993). These authors found that behaviour and morphology exhibit similar levels of homoplasy (with behaviour slightly less homoplastic on average). Prum (1997) also found more homoplasy in characters of display morphology than display behaviour in piprid birds (manakins).

The evolution of display morphology and behaviour in the horned lizards (*Phrynosoma*) shows an interesting contrast with the general results of this study. All species of *Phrynosoma* lack male display coloration and also lack many display behaviours that are present in all other phrynosomatids (characters 1–6), possibly supporting the idea that changes in display morphology and behaviour may actually be related. In addition to being the only genus with highly reduced display behaviour, *Phrynosoma* seems to be the only genus of phrynosomatid lizards in which males are

not territorial (Stamps, 1983; Zamudio, 1998 [and references therein]). As far as is known, species of *Sceloporus* in which the patches are lost are territorial (e.g. *S. chrysostictus, S. siniferus*; Carpenter, 1978). The lack of territoriality and the general social structure of *Phrynosoma* may obviate the need for male displays. Although it is difficult to draw conclusions from the singular co-occurrence of reduced territoriality and display behaviour in phrynosomatid lizards, a relationship between territoriality and displays has been suggested previously (e.g. West-Eberhard, 1983), and should be explored in other groups of organisms.

There is an incredible diversity of morphological and behavioural features of sexually selected displays in animals (Darwin, 1871; Andersson, 1994), and evolutionary biologists and ethologists seek general rules to explain this diversity (e.g. Endler, 1992). Based on previous studies (e.g. Prum, 1990; McLennan, 1996) and theory (Endler, 1992), it was expected that the evolution of display morphology and display behaviour should be closely coupled. Surprisingly, in this study it was found that display morphology and behaviour are not tightly associated, and can evolve independently of each other. Thus, the results suggest that constraints or biases imposed by display behaviour on the evolution of display morphology may be weak or absent, and vice versa. The results also suggest that display morphology may be surprisingly labile relative to display behaviour, and that display morphology and display behaviour may show very different patterns of evolution. The generality of these conclusions should be tested in other groups of organisms. Finally, the results raise the possibility that there may be different patterns of association between a pair of characters when one of the traits is lost versus gained (i.e. gain of display morphology may be related to behaviour, but loss may not be), and these different patterns should be considered in phylogenetic studies of correlation between characters.

ACKNOWLEDGEMENTS

I thank Marguerite Butler, Ellen Censky, Phil Chu, Brad Livezey, Jonathan Losos, Emília Martins, Debra McLennan, Molly Morris, Rick Prum, Matt Rand, Gil Rosenthal, Michael Ryan, and Maria Servedio for useful discussions, access to literature, and/or helpful comments on various versions of the manuscript. This paper began as a chapter of my Ph.D. dissertation at the University of Texas at Austin, where I was supported by an NSF graduate fellowship. I thank my coadvisors David Cannatella and David Hillis and the other members of my dissertation committee (Mike Ryan, Jim Bull, and Tim Rowe) for their comments, support, and encouragement.

REFERENCES

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

- Blanc CP, Carpenter CC. 1969. Studies on the Iguanidae of Madagascar III. Social and reproductive behavior of *Chalarodon madagascariensis*. *Journal of Herpetology* 3: 125–134.
- Carpenter CC. 1962. A comparison of the patterns of display behavior of Urosaurus, Uta, and Streptosaurus. Herpetologica 18: 145–152.

- Carpenter CC. 1963. Patterns of behavior in three forms of the fringe-toed lizards (*Uma*-Iguanidae). *Copeia* 1963: 406–412.
- Carpenter CC. 1977. The aggressive displays of three species of South American iguanid lizards of the genus *Tropidurus*. *Herpetologica* 33: 285–289.
- Carpenter CC. 1978. Comparative display behavior in the genus Sceloporus (Iguanidae). Mikwaukee Public Museum Contributions in Biology and Geology 18: 1–71.
- Carpenter CC. 1982. The aggressive displays of iguanine lizards. In: Burghardt GM, Rand AS, eds. Iguanas of the world: their behavior, ecology, and conservation. Park Ridge, New Jersey: Noyes Publications, 215–231.
- Carpenter CC. 1986. An inventory of the display-action-patterns in lizards. Smithsonian Herpetological Information Service No. 68.
- Clarke RF. 1965. An ethoecological study of the iguanid lizard genera *Callisaurus, Cophosaurus*, and *Holbrookia. Emporia State Research Studies* 13: 1–66.
- Cooper WE Jr, Burns N. 1987. Social significance of ventrolateral coloration in the fence lizard, Sceloporus undulatus. Animal Behavior 35: 526–532.
- Cooper WE Jr, Greenberg N. 1992. Reptilian coloration and behaviour. In: Gans C, Crews D, eds. Biology of the Reptilia. Volume 18. Hormones, brain, and behaviour Illinois: University of Chicago Press, 298–422.
- Cooper WT, Forshaw JM. 1977. The birds of paradise and bowerbirds. Sidney: Collins.

Darwin C. 1871. The descent of man and selection in relation to sex. London: Murray.

- de Queiroz A, Wimberger PH. 1993. The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. *Evolution* **47**: 46–60.
- de Queiroz K. 1996. Including the characters of interest during tree reconstruction and the problems of circularity and bias in studies of character evolution. *American Naturalist* 148: 700–708.
- Endler JA. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139: s125-s153.
- Felsenstein J. 1985. Phylogenies and the comparative method. American Naturalist 125: 1-15.
- Felsenstein J. 1988. Phylogenies and quantitative characters. Annual Review of Ecology and Systematics 19: 445–471.
- Felsenstein J. 1995. PHYLIP: phylogeny inference package. Version 3.57c. Department of Genetics, University of Washington, Seattle, Washington.
- Fitch HS, Hillis DM. 1984. The Anolis dewlap: Interspecific variability and morphological associations with habitat. Copeia 1984: 315–323.
- Fleishmann LJ. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist* 139: s36–s61.
- Frost DR, Etheridge R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Miscellaneous Publications of the University of Kansas Museum of Natural History 81: 1–65.
- Garland TG Jr, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41: 18–32.
- Geist V. 1966. The evolution of horn-like organs. Behaviour 27: 175–214.
- Hover EL. 1985. Differences in aggressive behavior between two throat colour morphs in a lizard, Urosaurus ornatus. Copeia 1985: 933–940.
- Hunsaker D. 1962. Ethological isolating mechanisms in the *Sceloporus torquatus* group of lizards. *Evolution* 16: 62–74.
- Jenssen TA. 1977. Evolution of anoline lizard display behavior. American Zoologist 17: 203–215.
- Kirkpatrick M, Ryan MJ. 1991. The evolution of mating preferences and the paradox of the lek. *Nature* 350: 33–38.
- Kluge AG, Farris JS. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18: 1–32.
- Lande R. 1981. Models of speciation by sexual selection on polygenic characters. Proceedings of the National Academy of Sciences, USA 78: 3721–3725.
- Larsen KR, Tanner WW. 1974. Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. *Great Basin Naturalist* 34: 1–41.
- Lynn RT. 1965. A comparative study of display behavior in *Phrynosoma* (Iguanidae). *Southwestern Naturalist* 10: 25–30.
- Maddison WP. 1990. A method for testing the correlated evolution of two binary characters: Are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44: 539–557.
- Maddison WP, Maddison DR. 1992. MacClade Ver. 3.0. Analysis of Phylogeny and Character Evolution. Sunderland, Massachussetts: Sinauer Associates.

- Marchetti K. 1993. Dark habitat and bright birds illustrate the role of the environment in species divergence. *Nature* 362: 149–152.
- Martins EP. 1993. A comparative study of the evolution of *Sceloporus* push-up displays. *American Naturalist* 142: 994–1018.
- McLennan DA. 1991. Integrating phylogeny and experimental ethology: From pattern to process. *Evolution* **45**: 1773–1789.
- McLennan DA. 1996. Integrating phylogenetic and experimental analyses: the evolution of male and female nuptial colouration in the stickleback fishes (Gasterosteidae). *Systematic Biology* **45:** 261–277.
- Pagel MD. 1994. Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London, Series B* 255: 37–45.
- Prum RO. 1990. Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves: Pipridae). *Ethology* 84: 202–231.
- Prum RO. 1997. Phylogenetic tests of alternative intersexual selection mechanisms: trait macroevolution in a polygynous clade (Aves: Pipridae). American Naturalist 149: 668–692.
- Reeder TW, Wiens JJ. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. *Herpetological Monographs* 10: 43–84.
- Rice WR. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.
- Ryan MJ. 1998. Sexual selection, receiver biases, and the evolution of sex differences. Science 281: 1999–2003.
- Ryan MJ, Rand AS. 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution* 47: 647–657.
- Sanborn SR, Loomis RB. 1979. Systematics and behavior of collared lizards (Crotaphytus, Iguanidae) in southern California. Herpetologica 35: 101–107.
- Sillén-Tullberg B. 1993. The effect of biased inclusion of taxa on the correlation between discrete characters in phylogenetic trees. *Evolution* 47: 1182–1191.
- Sinervo B, Liveley CM. 1996. The rock-paper scissors game and the evolution of alternative male strategies. *Nature* 380: 240–243.
- Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TR, eds. *Lizard ecology: studies of a model organism*. Cambridge: Harvard University Press, 169–204.
- Swofford DL, Maddison WP. 1987. Reconstructing ancestral character states under Wagner parsimony. *Mathematical Biosciences* 87: 199–229.
- Werdelin L, B. Sillén-Tullberg B. 1995. A comparison of two methods to study correlated discrete characters on phylogenetic trees. *Cladistics* 11: 265–277.
- West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58: 155–183.
- Wiens []. 1995. Polymorphic characters in phylogenetic systematics. Systematic Biology 44: 482–500.
- Wiens JJ. 1999a. Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proceedings of the Royal Society of London, Series B* 266: 1529–1535.
- Wiens JJ. 1999b. Polymorphism in systematics and comparative biology. Annual Review of Ecology and Systematics 30: 327–362.
- Wiens JJ, Reeder TW. 1997. Phylogeny of the spiny lizards (Sceloporus) based on molecular and morphological evidence. Herpetological Monographs 11: 1–101.
- Williams EE, Rand AS. 1977. Species recognition, dewlap function, and faunal size. American Zoologist 17: 261–270.
- Zamudio KR. 1998. The evolution of female-biased sexual size dimorphism: A population-level comparative study in horned lizards (*Phrynosoma*). *Evolution* 52: 1821–1833.