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Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards

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The evolution of conspicuous male display ornaments is a common trend in diverse groups of organisms and a continuing challenge to studies of sexual selection. A phylogenetic approach was used to examine macro-evolutionary patterns of change in sexually dichromatic display coloration (distinctively coloured belly patches) among 130 taxa of phrynosomatid lizards. The results showed repeated losses of sexual dimorphism, which occur through losses of conspicuous male coloration or gains of conspicuous female coloration. The frequent loss of male traits is surprising, given that sexual selection presumably drives their evolutionary origin and maintenance, but is consistent with a recently proposed hypothesis suggesting that females may lose responsiveness to male traits over macro-evolutionary time-scales. The observation of repeated losses of male traits in phrynosomatid lizards (and other groups) may have implications for testing among competing models for the evolution of female preferences. A concentrated changes test showed that changes in male display coloration are significantly associated with the use of ground-dwelling habitat, as opposed to rock- or tree-dwelling habitats. This result suggests a role for natural selection in the loss of male display traits in phrynosomatid lizards, but habitat type alone may be insufficient to explain these losses.

Keywords: phylogeny; character evolution; sexual selection; display ornaments; phrynosomatid lizards

1. INTRODUCTION

A long-standing problem in evolutionary biology is explaining why elaborate ornaments involved in male aggressive and courtship displays have evolved in diverse groups of organisms, given that these traits do not enhance male survival and bring no obvious benefits to females (Darwin 1871; Andersson 1994). These ornaments are typically sexually dimorphic and are thought to evolve via sexual selection (Darwin 1871). Comparative studies can provide valuable insights into the evolution of these characters (Wright 1993; Emerson 1994; Basolo 1996; McLennan 1996; Prum 1997; Burns 1998). Most fundamentally, comparative studies identify and describe the evolutionary patterns that theoretical and experimental studies strive to explain. However, there have been surprisingly few rigorous phylogenetic studies of the evolution of these traits and there have been no such studies in non-avian reptiles. In this paper, I examine the evolution of sexually dichromatic display coloration in phrynosomatid lizards in a phylogenetic context.

Given a group in which some species are sexually dimorphic for male display ornaments and others are not, the most basic evolutionary question is what are the evolutionary transitions among these conditions? For example, do dimorphism and monomorphism evolve by losses or gains of conspicuous male and/or female traits? A few previous analyses have attempted to address these questions, but have been largely restricted to studies of plumage dimorphism in birds. These studies have suggested that there is a bias towards losses rather than gains of dichromatism (Peterson 1996; Price & Birch 1996; Omland 1997), which may be related to loss of conspicuous male coloration (Peterson 1996; Burns 1998) and/or acquisition of conspicuous female coloration (Irwin 1994; Peterson 1996; Burns 1998). The idea that conspicuous male traits may be lost in some species has received relatively little attention in the micro-evolutionary literature of sexual selection, although constraints on the evolution of male traits have been discussed (see the review in Andersson 1994). Some within-species experimental studies have suggested that conspicuous male coloration may be lost because of increased predation pressure in certain habitats (Endler 1980; Reimchen 1989). However, the relationship between habitat type and display coloration has rarely been tested in a phylogenetic framework (but see Marchetti 1993).

Phrynosomatid lizards offer an excellent system for phylogenetic studies of the evolution of male display ornaments. There is detailed phylogenetic information available for 130 taxa (Reeder & Wiens 1996; Wiens & Reeder 1997), representing most species within the family. In many species of phrynosomatids, males have conspicuously coloured (usually blue) patches on the sides of the belly and on the throat (see Wiens & Reeder 1997, fig. 27). These patches are considered to enhance the aggressive and courtship displays of males (e.g. Carpenter 1978). Experiments have shown the patches to be important in sexual discrimination and in aggressive encounters between males in various phrynosomatids and female

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choice seems to be important in the evolution of display coloration in the larger group (Iguania) to which phrynosomatid lizards belong (see the review in Cooper & Greenberg 1992). Many phrynosomatid lizards are known to be territorial and polygynous (reviewed by Stamps 1983), which further supports the idea that sexual selection may be important in the group.

2. MATERIAL AND METHODS

Data on display coloration were obtained from museum specimens listed in Reeder & Wiens (1996) and Wiens & Reeder (1997). There is little difference in these patches between living and preserved specimens (J. J. Wiens, unpublished data). The distribution of throat patches largely parallels that of belly patches and was not treated as a separate character. The data matrix is available as Appendix A on the Royal Society Web site at www.pubs.royalsoc.ac.uk/publish/pro_bs/rpb1428.htm.

The phylogeny used (figure 1) was from the combined data tree of Reeder & Wiens (1996) for taxa outside the speciose genus *Sceloporus* and the phylogeny within *Sceloporus* was based on Wiens & Reeder (1997). These phylogenies are each based on a large number of molecular, morphological and chromosomal characters (>300 parsimony-informative characters). Both analyses included some characters of display coloration. The inclusion of these characters in the tree-making process should provide the best estimate of phylogeny but should not bias the results in favour of any particular pattern of gains and losses (see de Queiroz (1996) for a discussion of this issue).

Characters were mapped onto the tree using MacClade (Maddison & Maddison 1992). For the purposes of tracing character evolution, it was assumed that gains and losses of traits were equally probable, because other weighting schemes (e.g. Omland 1997) would potentially bias the results. The number of gains and losses of sexual dichromatism was estimated by initially coding species as either dichromatic (distinct belly patches present in males and absent in females) or monochromatic (distinct patches absent in both males and females or present in both males and females). However, because monochromatism was found to evolve in at least two ways (loss of male patches and gain of female patches), male and female belly patches were also treated as separate characters.

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. Sets of analyses were run assuming either that these spots are homologous (MAXHOM hereafter) or not homologous to the belly patches of other species (MINHOM). Similarly, males of *Sceloporus utiformis* have faint ventrolateral markings of unclear homology and this species was alternately coded as having (MAXHOM) or lacking (MINHOM) belly patches. The effects of coding these ambiguous taxa as unknown ('?') were also examined.

Indistinct patches are present in females of several species of *Sceloporus*. Distinct female patches that are similar in their level of expression to that seen in conspecific males occur in several taxa and these taxa were considered to be sexually monomorphic for patch presence. Species in which female patches are faint or indistinct (relative to conspecific males) were considered to be sexually dichromatic.

A few instances of intraspecific variation in the presence or absence of belly patches were observed and these polymorphisms were coded using a majority approach (commonest condition coded as present; Wiens 1995). When two states were present in a species at equal frequencies, the species was coded using the polymorphic method (*sensu* Wiens 1995), but putative changes within polymorphic taxa were not counted.

The robustness of the results was examined in two ways. First, several alternative methods of coding intraspecific variation were explored (any instance, polymorphic, missing, scaled and unordered; Wiens 1995). Second, to test the sensitivity of the results to weakly supported nodes, all clades that had bootstrap values less than 70% (see Hillis & Bull 1993) were collapsed and 200 trees with random resolutions of these nodes were generated (using MacClade) and used to examine patterns of trait evolution (following Losos 1994).

The hypothesis that changes in belly patches are associated with certain habitat types was tested using Maddison's (1990) concentrated changes test; male and female patches were tested separately and were coded using the majority method. This test examines whether there are significantly more changes in one character (the independent variable, belly patches) on branches having the state of interest of a second character (the dependent variable, habitat) than expected by chance, given a null model in which changes are equally probable on any branch. A significance level of 0.01 was used (Maddison 1990). Qualitative summaries of general habitat preference for each species were obtained from Fitch (1978), Guillette *et al.* (1980), Stebbins (1985), Conant & Collins (1991), Wiens (1993) and references therein. The concentrated changes test is designed for binary (two-state) characters. Therefore, the three types of habitat were treated as three binary characters rather than a single three-state character (character 1, 0 = not arboreal and 1 = arboreal (trees and/or bushes); character 2, 0 = not terrestrial and 1 = terrestrial (ground dwelling); and character 3, 0 = not saxicolous and 1 = saxicolous (rock dwelling)). Species that use more than one habitat were coded as present for whichever characters applied. Although other variables besides habitat may be related to changes in display morphology (e.g. mating system; Darwin 1871), current knowledge of their distribution in phrynosomatid lizards was considered too limited to include them in this study.

3. RESULTS

The evolution of sexual dichromatism has been active in phrynosomatid lizards, with at least 21 changes distributed among the 130 taxa sampled (table 1). On average these changes are biased towards losses rather than gains of sexual dichromatism (table 1). However, many instances of monomorphism are non-homologous across taxa, because monomorphism can be due to the presence of belly patches in both sexes or the absence of patches in both sexes. Examining the number of gains and losses of male belly patches (table 1) shows few gains and many losses, with the loss of male patches always resulting in species that are monochromatic for patch absence. Distinct female belly patches are frequently gained and rarely (if ever) lost (table 1) and their appearance always resulted in species that are monochromatic for patch presence. These general results are robust for different methods of coding intraspecific variation (table 2) and different resolutions of weakly supported branches (table 3). Coding the taxa of ambiguous homology as unknown also gives similar results (average number of gains of sexual dichromatism

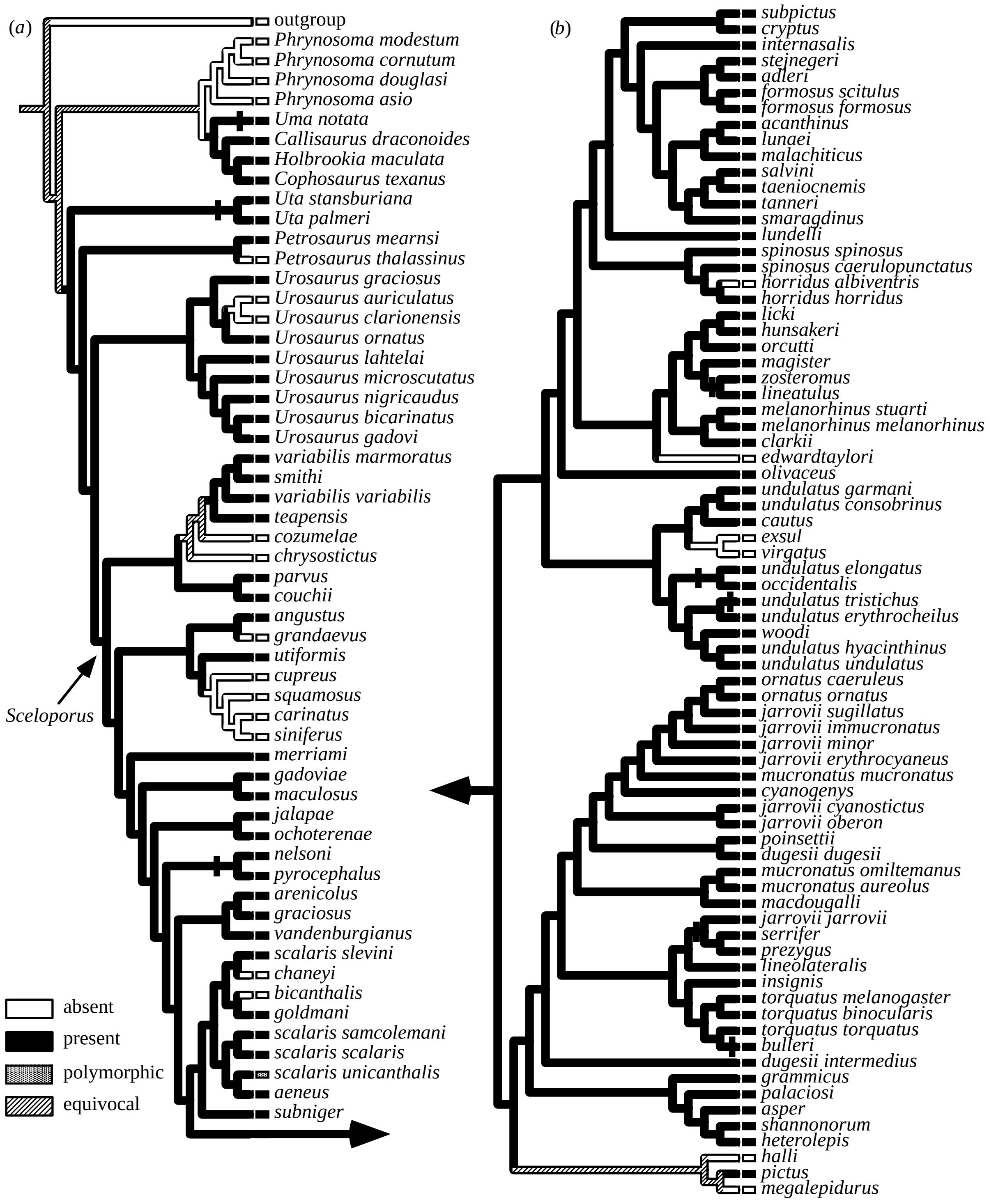

Figure 1. Phylogeny of phrynosomatid lizards. Male belly patches (MAXHOM coding) are mapped onto the tree and distinct female belly patches are shown with bars (MAXHOM coding and ACCTRAN optimization). (*a*) Generic level relationships and phylogeny of basal *Sceloporus*. (*b*) Relationships of other *Sceloporus*.

across equally parsimonious reconstructions = 3.38 and losses = 17.62; average male belly patch gains = 3.38 and losses = 11.62; and average female belly patch gains = 6.0 and losses = 0).

The concentrated changes test suggests that gains and losses of male belly patches are significantly associated with a terrestrial habitat, but not an arboreal or saxicolous habitat (table 4). There was no significant association between habitat and changes in female belly patches (results not shown).

4. DISCUSSION

This study represents the first to explore macroevolutionary patterns of change in a sexually dimorphic character system in non-avian reptiles. Although much of the literature in the field of sexual selection addresses the gain of conspicuous secondary sex characters in males (and the evolution of female preferences that drive these gains; Kirkpatrick & Ryan 1991; Andersson 1994), the results of this study suggest that losses of these traits may

Table 1. *Gains and losses of display coloration in phrynosomatid lizards*

(Unambiguous changes are those that are the same across all equally parsimonious reconstructions. The minimum and maximum numbers refer to the largest and smallest numbers of gains and losses possible across reconstructions. The average is the mean number of gains and losses across reconstructions.)

	sexual dichromatism		male belly patches		female belly patches	
	gains	losses	gains	losses	gains	losses
MAXHOM						
unambiguous	1.00	3.00	0.00	9.00	6.00	0.00
minimum	2.00	16.00	0.00	11.00	8.00	0.00
maximum	5.00	19.00	4.00	15.00	8.00	0.00
average	3.50	17.50	2.00	13.00	8.00	0.00
MINHOM						
unambiguous	0.00	11.00	0.00	6.00	5.00	0.00
minimum	2.00	9.00	2.00	9.00	6.00	0.00
maximum	13.00	20.00	7.00	14.00	6.00	0.00
average	4.89	17.11	4.89	11.11	6.00	0.00

Table 2. *Gains and losses of display coloration in phrynosomatid lizards, showing robustness to different methods for coding within-species variation*

(The results are averages from among multiple equally parsimonious reconstructions.)

	sexual dichromatism		male belly patches		female belly patches	
	gains	losses	gains	losses	gains	losses
MAXHOM						
any instance	4.00	14.00	1.50	10.50	10.50	1.50
majority	3.50	17.50	2.00	13.00	8.00	0.00
missing	4.00	14.00	1.50	10.50	10.50	1.50
polymorphic	5.50	26.50	2.00	18.00	14.50	1.50
scaled	3.56	14.44	1.57	18.44	10.30	1.70
unordered	4.92	14.00	5.56	17.03	11.84	0.75
MINHOM						
any instance	4.50	14.50	3.50	9.50	8.50	1.50
majority	4.89	17.11	4.89	11.11	6.00	0.00
missing	4.50	14.50	3.50	9.50	5.50	0.50
polymorphic	6.00	27.00	4.00	17.00	12.50	1.50
scaled	3.89	15.12	3.66	17.34	8.30	1.70
unordered	5.42	14.47	8.11	15.57	9.84	0.75

actually be the more common evolutionary event, at least in some taxonomic groups. Other phylogenetic analyses have also reconstructed losses or reductions in male display ornaments, including studies of mammals (Wright 1993), birds (Hill 1994; Peterson 1996; Burns 1998) and fishes (Meyer *et al.* 1994; Basolo 1996; McLennan 1996). Two studies in birds also compared the frequency of different types of transitions and also found that losses of conspicuous male coloration occurred more often than gains (Peterson 1996; Burns 1998). These results suggest that the pattern found in phrynosomatid lizards may be widespread.

Why are there frequent losses of male display characters in phrynosomatid lizards and other groups? Given a stochastically evolving trait that arises early in a phylogeny, a preponderance of losses should be expected (Sanderson 1993). Yet, the frequent loss of male traits seems paradoxical, if sexual selection is driving their evolutionary origin and maintenance. As part of their 'chase-away' model of sexual selection, Holland & Rice (1998) proposed that females may lose sensitivity to the male traits that supposedly evolved to stimulate them. As support, they cited data from a number of studies (in spiders, birds and fish) in which females exhibited little or no preference for exaggerated display traits in conspecific males. The results of Omland (1996) and Basolo (1998) are also suggestive of this pattern. Omland (1996) found no significant female preference for distinctive male plumages in the mallard duck, a species belonging to a clade in which there are believed to be repeated losses of these conspicuous plumages (Omland 1997). Basolo (1998) found results possibly suggesting the evolution of reduced female preference for swords in swordtail fish, a group in which swords have been lost in some taxa (Basolo 1996). The evolution of diminished female sensitivity and weakened sexual selection for the male traits

Table 3. *Sensitivity of results to different resolutions of weakly supported clades*

(For each of the 200 randomly resolved trees, the number of unambiguous gains and losses and the minimum, maximum and average number of gains and losses (from among the equally parsimonious reconstructions for a given tree) were determined and the mean values for each of these variables for the 200 trees are presented.)

	sexual dichromatism		male belly patches		female belly patches	
	gains	losses	gains	losses	gains	losses
MAXHOM						
unambiguous	1.17	15.39	0.12	11.50	7.97	0.01
minimum	1.00	14.67	1.00	11.25	7.50	0.00
maximum	10.33	27.00	4.57	16.00	11.00	2.50
average	4.46	22.24	1.74	14.93	10.53	0.20
MINHOM						
unambiguous	3.57	13.29	3.26	7.78	6.86	0.01
minimum	2.83	14.45	3.00	7.50	7.00	0.00
maximum	11.33	23.88	10.50	14.50	9.00	1.50
average	6.73	19.48	6.06	11.72	8.58	0.21

Table 4. *Results of a concentrated changes test for male display coloration* (*dependent character*) *and habitat* (*independent character*)

(Given the null model in which gains and losses of the dependent character are randomly distributed on the phylogeny, each value represents the probability of obtaining numbers of gains and losses of belly patches (on those branches having a given habitat type) equal to or greater than the numbers observed on those branches. The very low values for the terrestrial habitat indicate a non-random association with changes in belly patches. Probabilities were estimated with simulations (1000 replicates) using MacClade.)

	belly patch			
	MAXHOM		MINHOM	
	ACCTRAN	DELTRAN	ACCTRAN	DELTRAN
terrestrial				
ACCTRAN	0.008	0.005	0.007	0.025
DELTRAN	0.007	0.004	0.002	0.009
arboreal				
ACCTRAN	0.722	0.766	0.712	0.482
DELTRAN	0.792	0.850	0.741	0.490
saxicolous				
ACCTRAN	0.913	0.946	0.631	0.362
DELTRAN	0.887	0.920	0.525	0.325

might help explain the repeated loss of male traits seen in phrynosomatid lizards and other groups, despite potentially strong sexual selection associated with their origin.

Natural selection from predation in certain environments (Endler 1980; Reimchen 1989) and genetic drift in small populations (Hill 1994; Peterson 1996) have also been suggested as forces that could drive the loss of male traits. The results of this study support a significant association between changes in belly patches and the use of a terrestrial habitat by phrynosomatid lizards. This association may be due to potentially higher predation pressures on ground-dwelling lizards as opposed to rock- or tree-dwelling species and raises the possibility that natural selection (against conspicuous coloration) may outweigh sexual selection (favouring conspicuous coloration) to drive the repeated loss of belly patches in many terrestrial species. Yet, character state reconstruction shows that the terrestrial habitat is the ancestral condition for phrynosomatid lizards and either all (MAXHOM) or most (MINHOM) of the gains of male display coloration occur on branches reconstructed as terrestrial. This pattern suggests that habitat alone may be insufficient to explain the repeated loss of male coloration, without postulating additional factors (e.g. reduced female preference and genetic drift). Furthermore, belly patches have been lost in some rock- and tree-dwelling species (e.g. *Sceloporus edwardtaylori*). However, the characterization of habitat in this study was relatively broad and changes in display morphology may be related to aspects of habitat that were not tested (e.g. brightness; Marchetti 1993).

A major emphasis in research on sexual selection is testing among alternate models for the evolution of female preferences for male display traits (e.g. Fisherian runaway, good genes and direct selection; Kirkpatrick & Ryan 1991; Andersson 1994). Most theoretical and experimental studies of sexual selection have not addressed the macro-evolutionary loss of male traits, nor have macro-evolutionary studies addressed the implications of these losses for micro-evolutionary models of sexual selection. Holland & Rice (1998) argued that their chase-away model is the only one that predicts the evolutionary reduction or loss of female attraction to male display traits (a possible factor in trait loss), whereas the runaway, good genes and direct benefits models predict only increased attraction (sensory bias predicts neither increased nor decreased attraction). Given this, a useful line of research for future studies may be to test for reductions in female preference for male traits in groups (such as phrynosomatid lizards) in which the male traits have been repeatedly lost. Reduction or loss of female preference preceding the loss of the male trait would be consistent with this aspect of the chase-away model. The presence of a universally strong female preference for the male trait would be consistent with other models (e.g. good genes and direct benefits) and would suggest other factors driving trait loss (e.g. natural selection). However, it should be noted that the chase-away model actually predicts that male traits should not be lost, given that males should continually exaggerate their traits to overcome diminishing female responsiveness and the absence of any male trait would cause females to be understimulated (Holland & Rice 1998). Thus, while the chase-away model may explain reduced female preference, the observation of repeated losses actually appears to reject (or call for modification of) this model (see Rosenthal & Servedio (1999) for further critique). Schluter & Price (1993) proposed a model in which females may switch their preferences from one male trait to another (e.g. display coloration to body size). This model might account for reduced female preferences for certain male traits and is consistent with the observation that male traits are often lost.

Apart from the repeated loss of male display traits, the results of this study also show that gains (or exaggeration) of conspicuous female coloration may occur more frequently than gains of conspicuous male coloration (table 1). Similarly, Irwin (1994) found that most changes in sexual dichromatism in New World blackbirds are due to changes in female brightness and Burns (1998) found that changes in female coloration (resulting in gains or losses of sexual dimorphism) occur more frequently than changes in male plumage in tanagers. However, in phrynosomatid lizards, there are more changes overall in male coloration than female coloration, largely because of the repeated loss of male belly patches. Conspicuous female coloration may evolve through male mate choice (Hill 1993) or female–female aggression or territoriality (Trail 1990; Irwin 1994). Male mate choice has not been reported in phrynosomatid lizards, but females are known to be territorial and to perform displays (e.g. Carpenter 1978; Stamps 1983).

The concordant results in lizards (this study) and birds (Irwin 1994; Peterson 1996; Price & Birch 1996; Omland 1997; Burns 1998) suggest the intriguing possibility that there are general macro-evolutionary patterns of change in sexually selected characters. What is particularly interesting is that the two commonest changes in both groups (loss of traits in males and gain in females) differ from those emphasized in most micro-evolutionary studies (gain of traits in males and associated female preferences). These macro-evolutionary patterns, particularly the frequent loss of male traits, may have implications for testing micro-evolutionary models of sexual selection and suggest new lines of inquiry for theoretical and experimental studies.

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