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Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards

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Both sexual selection and natural selection can influence the form of dimorphism in secondary sexual traits. Here, we used a comparative approach to examine the relative roles of sexual selection and natural selection in the evolution of sexually dimorphic coloration (dichromatism) and ornamentation in agamid lizards. Sexual dimorphism in head and body size were used as indirect indicators of sexual selection, and habitat type (openness) as an index of natural selection. We examined separately the dichromatism of body regions 'exposed to' and 'concealed from' visual predators, because these body regions are likely to be subject to different selection pressures. Dichromatism of 'exposed' body regions was significantly associated with habitat type: males were typically more conspicuously coloured than females in closed habitats. By contrast, dichromatism of 'concealed' body regions and ornament dimorphism were positively associated with sexual size dimorphism (SSD). When we examined male and female ornamentation separately, however, both were positively associated with habitat openness in addition to snout-vent length and head SSD. These results suggest that natural selection constrains the evolution of elaborate ornamentation in both sexes as well as sexual dichromatism of body regions exposed to visual predators. By contrast, dichromatism of 'concealed' body regions and degree of ornament dimorphism appear to be driven to a greater degree by sexual selection.

Keywords: sexual dichromatism; habitat openness; sexual size dimorphism; predation; light environment

1. INTRODUCTION

Sexual selection and natural selection can interact in complex ways to influence the form of secondary sexual traits. For instance, sexual selection is thought to favour conspicuous coloration or ornamentation, while natural selection often favours cryptic coloration and reduced ornamentation (Endler 1983; Andersson 1994). Populations and species can vary greatly in the form and extent of sexual dimorphism in coloration and ornamentation depending on the relative importance of these selective pressures. It is now both theoretically and empirically well established that the evolutionary interaction or trade-off between sexual selection and natural selection can generate phenotypic variation (Andersson 1982; Endler 1983, 2000; Lande & Kirkpatrick 1988; Price 1998). However, the extent to which such trade-offs generate predictable patterns in the form of sexual dimorphism in secondary sexual traits remains largely unexplored (but see Promislow *et al.* 1992, 1994; Cuervo & Møller 1999).

Differences in coloration or ornamentation between the sexes, with males typically possessing the more elaborate phenotype, have traditionally been thought to result from sexual selection (Darwin 1859; Andersson 1994). This view has received support from comparative studies showing a strong relationship between sexual dimorphism in coloration or ornamentation and other indices of sexual selection, such as mating system (Owens & Hartley 1998;

Figuerola & Green 2000; Dunn *et al.* 2001) and extra-pair paternity (Møller & Birkhead 1994; Owens & Hartley 1998). Recent models of signal evolution, however, emphasize the interaction between signal function, properties of the signal environment, the sensory system of receivers and the presence of unintended receivers that may exploit signals for their own purposes (e.g. predators; Endler 1992; Espmark *et al.* 2000; Boughman 2002). The environment can influence the form of signals by defining the cues that are most readily perceived by the sensory system of a receiver. For instance, habitat openness or vegetation cover affects light conditions, which may exert strong selection on visual signals such as colour patches or ornaments to maximise conspicuousness (Marchetti 1993; Endler & Thery 1996; Zahavi & Zahavi 1997; Andersson 2000). Predators may also exploit signals to localize prey (Endler 1980; Ryan 1987), and habitat openness can in turn determine the vulnerability of signallers to visual predators. Habitat type, through its influence both on properties of the signalling environment and predation pressure, can thus play an important role in the evolution of conspicuous male coloration and ornamentation (Endler 2000).

In this study, we investigated whether variation in coloration and ornamentation is more tightly coupled with indices of natural selection or sexual selection in agamid lizards. However, the relative influence of these selective forces may differ according to the location of the signal. For instance, 'private' signals revealed to conspecifics only during bouts of display might be subject to lower levels of natural selection via predation than are signals that are always visible (Espmark *et al.* 2000). Thus, the location of signals, particularly those that are static and/or obvious to predators, is likely to be an important target of selection.

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Previous comparative studies examining the evolution of dichromatism have not considered the effects of signal location. We therefore also examined the influence of natural and sexual selection on dichromatism of regions of the body 'exposed to' and 'concealed from' visual predators. We expected that these two forms of dichromatism are likely to be the focus of very different selective pressures.

We used habitat openness as an index of natural selection, and measures of sexual dimorphism in head and body size as indices of sexual selection. Sexual size dimorphism (SSD) has been used widely as an indirect measure of sexual selection in comparative studies (e.g., Björkland 1990; Badyaev & Hill 2000; Ord *et al.* 2001; Morrow & Pitcher 2003) because there is strong empirical evidence that SSD often results from competition over mates and other resources (Andersson 1994). Comparative studies have also demonstrated associations between SSD and a wide variety of other indicators of sexual selection, such as mating system (Lindenfors & Sillén-Tullberg 1998; Owens & Hartley 1998; Dunn *et al.* 2001; Lindenfors *et al.* 2002), population density (Stamps *et al.* 1997) and territoriality (Cox *et al.* 2003). In lizards, sexual dimorphism in both body and head size has been shown to be primarily the result of intrasexual selection (Vitt & Cooper 1985; Anderson & Vitt 1990; Olsson 1992; Kratochvil & Frynta 2002). Indeed, some authors have even suggested that head dimorphism may be a better indicator of the strength of intrasexual selection than body SSD in lizards (Anderson & Vitt 1990; Kratochvil & Frynta 2002). Thus, we used both head and body SSD as indirect indicators of sexual selection in agamid lizards.

The Agamidae is an old-world-distributed, monophyletic family with over 370 currently recognized species (Macey *et al.* 2000). The species vary greatly in the type and extent of sexual dimorphism. For example, the group includes the colourful, highly sexually dichromatic garden lizards (*Calotes*), the Sri Lankan horned lizards (*Ceratophora*) in which males have rostral appendages, and the monomorphic thorny devil (*Moloch*). Agamid lizards also occupy a diverse range of habitats: they can be found in the harshest deserts, as well as tropical rainforest and montane cloud forest. Agamid lizards thus represent an excellent group within which to conduct a comparative test of how sexual selection and natural selection interact in the evolution of conspicuous coloration and ornamentation.

2. MATERIAL AND METHODS

(a) *Data collection*

We compiled a database of morphological and habitat information from museum specimens and the published literature (see Stuart-Fox & Owens (2003) for details). We obtained data on two types of secondary sexual traits expressed in agamid lizards: (i) sexual dichromatism; and (ii) ornament dimorphism. Information on dichromatism or ornamentation and at least one independent variable (i.e. snout-vent length (SVL), head SSD, body SSD or habitat—see below) were obtained for 253 species covering 48 genera, which equates to 67% of all recognized agamid lizards (see electronic Appendix A). Museum specimens were used to obtain some of the data on body size, head dimensions and ornament dimorphism (a total of 624 specimens belonging to 155 species were examined). The list of museum specimens examined and complete

morphometric data are available from D.M.S.-F. on request. Dichromatism and habitat were scored exclusively from the literature.

Dichromatism was measured as a count of the number of body regions for which the sexes were dichromatic, ranging from 0 to 11 (Stuart-Fox & Owens 2003). The 11 body regions used were: crown, lateral region of the head, throat, chest, ventral region, anterior dorsal, posterior dorsal, flanks (dorso-lateral region), forelimbs, hindlimbs and tail. Body regions were scored as dichromatic only if they differed in colour (hue), not merely intensity. This index of dichromatism is conservative and does not rely on subjective assessments of differences in intensity of coloration between the sexes, which may vary greatly among individuals. We also calculated separately the dichromatism for body regions 'exposed to' and 'concealed from' visual predators because these two types of body region are likely to be subject to different selective pressures. The lateral region of the head, and the throat, chest and ventral region were classed as 'concealed', whereas the remaining body regions were classed as 'exposed'. We did not score 'conspicuousness' or 'colourfulness' of males and females separately, because decisions regarding what constitutes a conspicuous colour patch are necessarily subjective and dependent on environmental context (background colour).

Ornament dimorphism was measured as a weighted index of the number of physical features (ornaments) that differed between the sexes (Stuart-Fox & Owens 2003). If the ornament was present in both sexes, but larger in the male, it was given a value of 1. If only the male possessed the ornament, it was given a value of 2. Total ornament dimorphism was calculated as the sum of the values of seven ornament types, and thus ranged between 0 and 14. The seven categories of ornaments were: nape crest/spines, dorsal crest/spines, tail crest/spines, enlarged cheeks, gular pouch, rostral appendage and supra-ocular spines/ridges. We also calculated total male and female ornamentation as a simple count of the number of ornament types possessed by each sex, respectively.

We used two surrogates for sexual selection: sexual dimorphism in body size (body SSD) and head size (head SSD). We defined body SSD as the ratio of mean male to mean female body size (snout-vent length) because ratio measures of SSD are intuitive and widely used in comparative studies on lizards (e.g. Stamps *et al.* 1997; Butler *et al.* 2000; Ord *et al.* 2001; Cox *et al.* 2003). Where females were larger, we set body SSD to one, because processes other than sexual selection, such as fecundity selection, are more likely to be responsible for larger female than male size (reviewed in Shine (1989)). In addition, to be conservative, all values below 1.05 were set to one to control for potential measurement error, since data from the literature or museum specimens were often based on small sample sizes. Head size dimorphism was measured as the maximum of the ratio of mean male to female relative head width or head depth. Mean relative head width and depth were calculated as the mean head width or depth divided by mean SVL for each sex separately. In lizards, SSD is typically associated with overall species body size. To account for possible body size effects in analyses, we obtained additional measures of average species SVL. Both SSD and body size were log-transformed to ensure normality.

Our proxy measure for natural selection was an index of habitat openness. Species were scored as occurring in either open (0) or closed (1) habitats. The following habitat types were considered open: stony desert, sandy desert, rock outcrops, semi-desert, savannah, arid acacia woodlands, open woodlands, human inhabited/highly disturbed areas and coastal heath/dunes. Riparian vegetation, rainforest edges/ecotones, seasonally dry (monsoon) rainforest, montane cloud forest, primary rainforest and

Table 1. Associations among measures of dichromatism and ornamentation, controlling for phylogeny. (Regression correlations are based on independent contrasts. Values below the diagonal are r -values, while those above the diagonal are p -values. Asterisks indicate significance at $p < 0.05$ after Bonferroni correction for multiple tests. $n = 151$.)

	total dichromatism	'concealed' dichromatism	'exposed' dichromatism	ornament dimorphism	male ornamentation	female ornamentation
total dichromatism	—	< 0.001*	< 0.001*	0.191	0.785	0.662
'concealed' dichromatism	0.83	—	< 0.001*	0.070	0.961	0.818
'exposed' dichromatism	0.93	0.58	—	0.453	0.711	0.620
ornament dimorphism	0.11	0.10	0.07	—	< 0.001*	< 0.001*
male ornamentation	−0.02	−0.004	−0.03	0.64	—	< 0.001*
female ornamentation	−0.04	−0.02	−0.04	0.40	0.84	—

secondary rainforest were considered to be closed habitats. Twenty-four species occurred in both open and closed habitat types (electronic Appendix A). Twelve of these occurred in one or more types of rainforest (closed) as well as human-inhabited/disturbed areas (open). Because their natural habitat is forested, we classified these species as occurring in closed habitats. The remaining 12 species occurred in more than one open habitat type in addition to seasonally dry (monsoon) rainforest (closed), a forest type that occurs primarily within an open woodland/grassland mosaic in northern Australia. These species were classified as occurring in open habitat because they occur in such environments more often and over a greater part of their natural range. However, we repeated all analyses with these twenty-four species removed. There was no qualitative difference in the results, and we present analyses with all species included.

(b) Comparative analyses

We first examined correlations among dependent variables (ornamentation and dichromatism) and then used multiple regression with backward model selection to test for associations between these secondary sexual traits and predictor variables. We followed the method of Purvis *et al.* (2000) whereby we sequentially removed variables explaining the least variation. As variables were dropped, new sets of contrasts were generated for the remaining variables. This often led to an increase in sample size, so we followed the heuristic procedures described by Purvis *et al.* (2000) to ensure that important predictors were not dropped from the model early on. The criterion for remaining within the model was set at $p = 0.1$ significance level.

To control for potential non-independence of species data through common ancestry, regression calculations were conducted on values transformed by the widely used standardized independent contrast method (Felsenstein 1985), using the software COMPARE 4.5 (Martins 2003). All regressions were forced through the origin (Garland *et al.* 1992). To calculate contrasts, we gathered additional information on phylogenetic relationships from the literature. No single phylogenetic tree included all species of interest. Initially, mitochondrial DNA-based phylogenies were used to construct a composite tree covering 128 species. When conflicts between trees arose, we favoured those with the most complete species representation, followed by year of publication. Specifically, genera positions and most species were placed following Schulte *et al.* (2002, 2003) and Macey *et al.* (2000). Publications by Pang *et al.* (2003) and McGuire & Heang (2001) were used to infer relationships within *Phrynocephalus* and *Draco*, respectively. Finally, Moody's (1980) morphological hypothesis was used to place *Gonocephalus grandis*, *G. chameleontinus* and *Agama hispida*. Species that were not represented in any phylogeny were left as polytomies (i.e. where the precise

relationship between species is unknown) within their respective genera. Branch lengths of the phylogeny were assumed to be equal because branch length information was not available and simulation studies have shown that setting branches to equal lengths yields acceptable type I error rates for larger sample sizes (Ackerly 2000). Species synonyms were checked using the EMBL reptile database (<http://www.embl-heidelberg.de/~uetz/LivingReptiles.html>).

3. RESULTS

No measure of dichromatism was correlated with any measure of ornamentation (table 1). However, the three measures of dichromatism were intercorrelated, as were the three measures of ornamentation (table 1). Overall dichromatism was more strongly associated with dichromatism of 'exposed' body regions than of 'hidden' body regions, and these in turn were significantly, though more weakly correlated with each other. Male and female ornamentation were highly correlated and each was also more weakly correlated with ornament dimorphism (table 1).

Overall sexual dichromatism was positively associated with habitat openness (table 2). This relationship was weak and marginally non-significant. However, when we examined dichromatism of 'exposed' and 'concealed' body regions separately, we found that for 'exposed' body regions this relationship became significant. Thus species that are more dichromatic in 'exposed' body regions tend to occupy closed habitats. Dichromatism of 'concealed' body regions was positively associated with head SSD rather than habitat openness (table 2).

Ornament dimorphism was positively and strongly associated with body SSD and weakly with SVL (table 2). When we looked at male and female ornamentation separately, both were positively associated with SVL and head SSD, as well as with habitat openness (table 2). Thus, species with more-ornamented males and females tend to occur in closed habitats, but these species may be monomorphic, resulting in a lack of association between habitat type and ornament dimorphism.

4. DISCUSSION

In agamid lizards, both sexual selection and natural selection influence the form of dimorphism in secondary sexual traits. However, our results suggest that in these lizards, dimorphism in coloration and ornamentation evolve independently and are influenced by natural and sexual selection in very different ways. In addition, our results highlight the importance of considering signal location. Dichromatism of 'exposed' body regions was significantly

Table 2. Multiple regression results using phylogenetically corrected data.

(Independent variables initially included in all models were: SVL, head SSD (maximum dimorphism in head width or depth), body SSD, habitat openness.)

dependent variable	overall model and independent variables remaining within the model after backwards elimination	<i>n</i>	<i>r</i> for the model or partial <i>r</i> for each variable	coefficient	two-tailed <i>p</i> -value
total dichromatism	overall	127	0.16		0.065
	habitat openness		0.16	1.51	0.065
'exposed' dichromatism	overall	127	0.20		0.027
	habitat openness		0.20	1.19	0.027
'concealed' dichromatism	overall	65	0.37		0.01
	head SSD		0.30	8.93	0.015
	body SSD		0.22	4.44	0.085
ornament dimorphism	overall	149	0.34		< 0.001
	SVL		0.15	1.78	0.065
	body SSD		0.23	8.23	0.006
male ornamentation	overall	62	0.55		< 0.001
	SVL		0.37	2.67	0.004
	head SSD		0.29	9.96	0.025
	habitat openness		0.19	1.22	0.039
female ornamentation	overall	62	0.66		< 0.001
	SVL		0.45	2.54	< 0.001
	head SSD		0.37	9.93	0.003
	habitat openness		0.38	1.35	0.003

associated with habitat openness: species occupying open habitats were less sexually dichromatic than species in more closed habitats. By contrast, dichromatism of 'concealed' body regions showed a positive association with head SSD. Neither of the indices of sexual and natural selection could explain the variation in overall dichromatism because signals located in 'concealed' and 'exposed' body regions are influenced by different processes, yet both contribute to the overall score. Furthermore, while ornament dimorphism was positively associated with body size (SVL) and body SSD, total male and female ornamentation were associated with habitat openness, as well as SSD. Taken together, these results suggest that natural selection constrains dichromatism of 'exposed' body regions and overall level of ornamentation in both sexes, whereas dichromatism of 'concealed' body regions and dimorphism in ornamentation are driven primarily by sexual selection.

Habitat openness can influence the evolution of dichromatism in two ways. First, differences in the light environment between closed and open habitats may select for different types of colour pattern for efficient communication (Marchetti 1993; Endler & Thery 1996; Zahavi & Zahavi 1997; Andersson 2000; McNaught & Owens 2002). Specifically, low ambient light conditions characteristic of closed habitats could select for 'bright' colours to maximize conspicuousness (Marchetti 1993) in males, thereby influencing the degree of dichromatism. Second, the predation hypothesis suggests that species occupying open habitats will be more vulnerable to visual predators (Cott 1940; Endler 1980). Natural selection for crypsis may therefore override or constrain sexual selection for conspicuous coloration in males, resulting in less sexual dichromatism in species occupying more open habitats (i.e. both sexes are cryptic). The predation hypothesis predicts that the extent

of sexual dichromatism should be related to habitat openness only for body regions exposed to visual predators. By contrast, the light environment hypothesis makes no such distinction, because light conditions should affect any colour patch used in intraspecific communication equally. Although not usually visible, body regions classed as 'concealed' are important in intraspecific communication, as most agamid species flash dewlaps or perform head bobs in social interactions (Cooper & Greenberg 1992). In agamid lizards, only dichromatism of body regions 'exposed' to visual predators showed an association with habitat openness, suggesting that natural selection acts primarily via the mechanism of differential predation pressure. Substantial comparative and empirical evidence already exists for a predation cost associated with conspicuous coloration (Endler 1983; Promislow *et al.* 1992, 1994; Huhta *et al.* 2003; Stuart-Fox *et al.* 2003). This study provides broad comparative support for the view that the evolution of sexual traits results from a trade-off between sexual selection for conspicuous coloration and natural selection via differential predation pressure.

Species that occupy closed habitats were also more ornamented than those in open habitats. In these species, both sexes are apparently highly ornamented (male and female ornamentation being highly correlated), resulting in monomorphism and a lack of association between ornament dimorphism and habitat. There are at least two reasons why agamids occupying closed habitats might be more ornamented. First, ornamentation may increase conspicuousness in visually simple, open environments, but may affect conspicuousness to a lesser degree, or even increase crypsis, in structurally complex, closed habitats. For instance, the rostral appendages of *Ceratophora* spp. make animals resemble a twig or leaf (at least to a human

observer; Pethiyagoda & Manamendra Arachchi 1998). Similarly, crests and spines can be cryptically coloured and blend into a structurally complex background. Second, species occupying open habitats often seek refuge in rock crevices or burrows, constraining the evolution of projecting ornaments such as spines, ridges and rostral appendages. By contrast, species occupying closed habitats are often arboreal; they may rely on staying out of view on the far side of a trunk or branch, or they may glide (e.g. *Draco*) as their main predator escape mechanisms. Arboreality could therefore place less ecological constraint on the evolution of elaborate ornamentation.

We can expect a multitude of factors to influence the evolution of signals. For example, physiology, development, diet and the sensory processing abilities of receivers have all been identified as important in determining signal form in iguanian lizards (Hews & Moore 1995; Sinervo *et al.* 2000; see also Ord & Blumstein (2002) and Ord *et al.* (2002) for discussion). Nevertheless, in addition to associations with habitat, we have found a consistent relationship between indices of sexual selection and the evolution of elaborate ornamentation in both sexes, ornament dimorphism and dichromatism of 'concealed' body regions. This implies that these traits convey fitness benefits when sexual selection is high. In lizards, SSD is most probably the product of intrasexual selection (Anderson & Vitt 1990; Ord *et al.* 2001; Kratochvil & Frynta 2002). In a previous study of iguanian lizards, signal complexity was found to increase with SSD and was argued to improve opponent assessment in species where males compete intensely for resources (Ord *et al.* 2001). We suggest that a similar phenomenon may also account for variation in static colour signals and other forms of ornamentation. The evolution of elaborate secondary sexual traits might also be facilitated by the occupation of habitats that present communicating lizards with a visually difficult signal environment. However, when lizards occupy more open habitats, the associated increase in predation risk appears to constrain the evolution of conspicuous coloration and ornamentation, and instead selects for more 'private' signals.

Studies addressing the interaction between sexual selection and natural selection at macroevolutionary scales are rare (but see Carranza (1996); Lindenfors (2002)). Our study demonstrates that the trade-off between sexual and natural selection has predictable consequences on signal evolution, and that this is dependent on both the type and location of signals. However, our analysis is necessarily coarse, given the available data. Patterns of signal evolution may differ among individual body regions (e.g. dewlaps/gular region versus flanks) and analyses using indices of overall dichromatism and ornament dimorphism may mask such patterns. More accurate estimates of habitat variation and/or direct measures of predation pressure (e.g. type and abundance of visual predators) may also help to explain more of the variation in secondary sexual traits. Another limitation of this study is that the precise evolutionary relationships of several species are currently unknown. Contrasts calculated using a tree that is not fully resolved reduce the power of subsequent statistical tests. However, while the net result limits the overall fit of variables in regression models, by being conservative in both data collection and analysis we are confident that observed trends in colour dichromatism and ornamentation reflect particularly prominent evolutionary

patterns. Better-resolved phylogenetic relationships may also allow a more detailed examination of patterns of trait evolution. For example, changes in dichromatism or ornament dimorphism may result from both gains and losses of either male or female coloration or ornaments (Wiens 2001). Similarly, coloration or ornaments may be lost with occupation of open habitats or gained with occupation of closed habitats.

Finally, we have examined only one environmental measure: habitat openness. There are many other environmental factors, however, that may influence the form of sexual dimorphism. For instance, ornaments such as long tail feathers or large crests and spines may decrease manoeuvrability in structurally complex environments (Møller & Hedenstrom 1999). Similarly, adopting different types of lifestyle, such as terrestriality or arboreality, or using different types of shelter, such as crevices or burrows, may exert selection on sexually dimorphic traits (Wiens 1999; Butler & Losos 2002). Improved comparative tests of the association between sexually selected traits and aspects of the environment or species' ecology may reveal how natural selection can constrain or even enhance the actions of sexual selection in a broad range of taxa.

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