SEXUAL SELECTION AND THE EVOLUTION OF COMPLEX COLOR PATTERNS IN DRAGON LIZARDS

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Many species have elaborate and complex coloration and patterning, which often differ between the sexes. Sexual selection may increase the size or intensity of color patches (elaboration) in one sex or drive the evolution of novel signal elements (innovation). The latter potentially increases color pattern complexity. Color pattern complexity may also be influenced by ecological factors related to predation and environment; however, very few studies have investigated the effects of both sexual and natural selection on color pattern complexity across species. We used a phylogenetic comparative approach to examine these effects in 85 species and subspecies of Australian dragon lizards (family Agamidae). We quantified color pattern complexity by adapting the Shannon–Wiener diversity index. There were clear sex differences in color pattern complexity, which were positively correlated with both sexual dichromatism and sexual size dimorphism, consistent with the idea that sexual selection plays a significant role in the evolution of color pattern complexity. By contrast, we found little evidence of a link between environmental factors and color pattern complexity on body regions exposed to predators. Our results suggest that sexual selection rather than natural selection has led to increased color pattern complexity in males.

KEY WORDS: Agamidae, color pattern complexity, phylogenetic generalized least squares, sexual dichromatism, sexual dimorphism, signal evolution.

Color patterns are a key component of many animal ornaments, playing an important role in social communication as well as being an adaptation to diverse habitats (Darwin 1859; Wallace 1879). The evolution of these patterns has therefore been shaped by both sexual and natural selection. Many studies on the evolution of animal color patterns have focused on selection on specific colors or pattern elements (Andersson 1994; Badyaev and Hill 2000; Grether et al. 2004; Caro 2005). By contrast, very little attention has been paid to color pattern complexity, which is a key aspect of signal design (Badyaev and Young 2004; Endler et al. 2005). We define color pattern complexity as the diversity of colors and patterns found within individuals of a species. To understand signal design, we need to understand why some species have relatively few types of colors or patterns whereas others have numerous combinations of colors and patterns on different body regions.

Identifying the selective forces that drive the evolution of complex signals is a currently a focus of much research (for recent overviews see Hebets 2011; Ord and Garcia-Porta 2012). From an interspecific perspective, many studies have focused on acoustic signals and visual behavioral displays and used intuitive measures of complexity such as repertoire size (e.g., Read and Weary 1992; Ord et al. 2001). Quantifying color pattern complexity is more challenging and has rarely been attempted. Endler

and Mielke (2005) developed a mathematically sophisticated multivariate method that uses knowledge of photoreceptor properties to analyze entire color patterns, thereby giving an indicator of the number of different colors. Although ingenious, the method requires intensive measurement of spectrometer readings across the body of live specimens, which makes it impractical for large-scale comparative analyses. Allen et al. (2011) quantified complexity in felid coat patterns by getting observers to match wildlife pictures with computer-generated patterns of differing complexity (defined as the formation of multiple pattern elements within the same space). However, their approach considered only pattern and not color. In this article, we propose a novel method, based on a well-established method for analyzing diversity in community ecology, for quantifying color pattern complexity.

Signal complexity may arise through sexual selection because of the need to convey multiple types of information on individual quality (multiple messages) to potential mates or rivals (Møller and Pomiankowski 1993; Johnstone 1996). In the case of animal coloration, sexual selection has resulted in widespread sexual dichromatism, where males and females differ in coloration (e.g., Badyaev and Hill 2003). Color patterns may be enhanced by evolving larger or more intensely colored patches (elaboration) or by evolving additional, novel colors, and patterns (innovation) (Endler et al. 2005). Both elaboration and innovation of color patterns in one sex result in greater sexual dichromatism but only innovation increases color pattern complexity. A link between sexual dichromatism and color pattern complexity is not inevitable. Species may have highly complex color patterns but be sexually monomorphic. For example, the characteristic and attractive collection of alternating yellow, red, and black bands found on coral snakes (genus *Micrurus*) are typical of both sexes. Likewise, sexual dichromatism need not be associated with any difference in color pattern complexity, as is seen in the Gouldian finch (*Erythrura gouldiae*) where, although both males and females have very similar complexity to their color patterns, the males have unmistakably brighter coloration. This example shows also that sexual dichromatism may be solely the result of elaboration, which generates sexual dichromatism without sex differences in complexity. Alternatively, sex differences in color pattern complexity may be the result of environmental or behavioral factors affecting males and females in different ways, particularly where females may have more complex patterns to be camouflaged from potential predators, as can be observed in the barred plumage patterns only found on females in many bird species (Gluckman and Cardoso 2010). In other words, the decoupling of color pattern complexity and sexual dichromatism may result if natural selection rather than sexual selection drives color pattern evolution.

Natural selection is known to influence signal complexity. Environmental conditions such as vegetation type, ambient light,

background motion, and microhabitat structure affect the detectability of signals to receivers and hence shape signal type and structure (Endler 1992, 1993). For example, in anole lizards, species in closed habitats have less-complex dewlap displays, which could be due to relatively low signal transmission efficacy in low light habitat (Ord and Martins 2006). Yet, within closed habitats, arboreal species, which may experience more complex motion backgrounds due to windblown vegetation, utilize more complex visual signals (Endler 1992; Ord et al. 2002). Just as ecologically generalist species that use diverse substrate types may evolve color polymorphism (Bond 2007), species that live in a variety of habitats may exhibit higher complexity in coloration either because they are less reliant on camouflage (e.g., in moths—Endler 1984) or because that optimizes cryptic coloration in heterogeneous environments (Merilaita et al. 1999).

Here, we perform a correlative study to examine the role of sexual selection and natural selection on the evolution of color pattern complexity via a phylogenetic comparative study of color pattern complexity in Australian dragon lizards (Sauria: Agamidae). We focus specifically on complexity and address the evolution of individual color and pattern elements elsewhere. The Australian members of the family Agamidae, representing 69 recognized species, comprise a monophyletic lineage with diverse color patterns and ecological niches. In addition to gathering detailed morphological and ecological information, we have produced a new well-resolved molecular phylogeny for the group, updating a previous analysis (Hugall et al. 2008) to include almost all Australian agamids for which we have color pattern data. To assess the role of sexual selection, we tested whether color pattern complexity was associated with sexual dichromatism, sexual body size dimorphism, and sexual head size dimorphism, all of which have been widely used as indicators of the strength of sexual selection in comparative studies (Andersson 1994; Stuart-Fox and Ord 2004; Ord and Martins 2006; Fairbairn et al. 2007) and which have been empirically shown to be associated with sexual selection in lizards in general (Kratochvíl and Frynta 2002; Cox et al. 2003) and Australian agamids in particular (Stuart-Fox and Johnston 2005; Healey et al. 2007). To assess the role of natural selection, we tested for a relationship between color pattern complexity and habitat openness, arboreality and microhabitat generalism. As body size may constrain signal complexity (Ord and Blumstein 2002), we also tested for a relationship between body size and color pattern complexity.

Methods
DATA COLLECTION
We collated morphological and ecological data for Australian dragon lizards, including color and pattern types in addition to

habitat information and morphometric data. The sources for these data were field guides and primary literature (Mitchell 1948; Storr 1964, 1966, 1974, 1977, 1981, 1982; Witten 1972; Houston 1974, 1977, 1998; Badham 1976; Storr et al. 1983; Witten and Coventry 1984; James and Shine 1988; Shine 1989, 1990; Johnston 1992; Christian et al. 1995; Manthey and Shuster 1996; Greer and Smith 1999; Cogger 2000; Harlow and Taylor 2000; Stuart-Fox and Ord 2004; Swan et al 2004; Wilson 2005; Cuervo and Shine 2007; Doughty et al. 2007; Wilson and Swan 2008; Cronin 2009) and museum specimens. The dataset comprised 69 species, belonging to 13 genera. The subspecies and subpopulations with recognized geographic color pattern variants were also included, which resulted in a sample size of 85 taxa used for this study. The dataset used in the analyses is provided in Table S1.

COLOR PATTERN SCORING AND COMPLEXITY ESTIMATION

Color pattern types were scored into five categories: (1) uniform, (or "flush"); (2) striped: including chevrons, bars, and streaks; (3) mottled: flecked, peppered, stippled, or spotted; (4) blotched: with a patch, large single spot or rhomb; and (5) reticulated: net-like or variegated. Types of colors were recorded from the direct descriptions in the literature as yellow, red, orange, gray, brown, black, green, white, and blue. Ambiguous descriptions such as maroon and brick red were scored as brown; cream and pale were scored into white or gray after cross-checking with available photographs. We unambiguously scored individual color patterns (e.g., "brown mottled," "red uniform") as present or absent for each of nine body regions for each species: (1) side of head, (2) shoulder (including side of neck), (3) dorso-vertebral, (4) dorso-lateral (upper flank), (5) lower flank, (6) groin (including thigh and base of tail), (7) throat (including gular region, chin, jaw), (8) chest, and (9) belly (Fig. S1). We scored adult coloration for both males and females. For species where males experience seasonal changes in coloration, we scored the breeding coloration.

We verified the scored patterns from the literature, and supplemented data for species descriptions that did not include complete information for all body regions using ethanol-preserved museum specimens (Museum Victoria, South Australian Museum and Western Australian Museum). We did not score colors from museum specimens as these fade with preservation; however, patterns are still evident in museum specimens. In the few cases where there was disagreement between literature descriptions and museum specimens, we used the latter. In cases where published descriptions of coloration for a species differed, we used the source that resulted in the greatest color pattern complexity score (see below), as we were specifically interested in the maximum color pattern complexity known for each species. Male and female color pattern data for each species were taken from the same source, where possible.

The simplest measure of complexity would be to count the number of different color patterns; however, this measure ignores the distribution of those color patterns across the body. One species may have one small patch of a color pattern, a, on an otherwise uniform color background, b, whereas the second species has a psychedelic mixture of color patterns a and b over the body. Both species have the same number of color patterns, but the latter is intuitively more complex. The problem has an ecological analogy with the use of species richness as an indicator of diversity: two sites can have the same species richness, but one may dominated almost entirely by one species whereas the other has equal numbers of each species, representing a more diverse (complex) assemblage. We therefore used an index to quantify color pattern complexity which adopts a standard method for dealing with this analogous problem in community ecology: the Shannon–Wiener species diversity index (Shannon and Weaver 1949), which traditionally calculates diversity based on species richness and species equitability. We replaced species richness with the number of different color pattern types (i_1, i_2, i_3, i_4 .... i_n) on a body, and species equitability with the relative abundance of these different color pattern types. Thus, we calculated complexity as:

$$H = -\sum p_i \cdot \ln(p_i),$$

where p_i is the proportion (out of all color patterns across the nine body regions) of color pattern i. We scored color pattern complexity for the entire animal and for the exposed (dorsal and lateral) regions alone, which we assume to be under more intense natural selection than ventral body regions. These exposed regions encompass five areas visible to both predators and conspecifics: (1) side of head, (2) shoulder, (3) dorso-vertebral, (4) dorso-lateral, and (5) lower flank. In some species, color patterns extended continuously from dorsal to ventral regions, whereas in others, the same color pattern was found in distinct noncontinuous patches on the different body regions. Intuitively, the latter is a more complex form of color patterning, however the Shannon–Wiener diversity index scores both as the same complexity. Therefore, to account for this, we scored noncontinuous color patterns found on both ventral and dorsal body regions as distinct types of color pattern for calculating complexity.

ECOLOGICAL DATA

The ecological factors examined in this study were habitat openness, lifestyle (arboreal or semiarboreal vs. primarily terrestrial), and microhabitat generalism. Habitat openness comprised two categories, open and forested, based on habitat classifications used by Stuart-Fox and Ord (2004). Microhabitats or substrates were classified into nine major types: (1) ground, (2) fallen timber, (3) grass/tussocks, (4) stony soil/gibber desert, (5) trees, (6) shrubs/bushes, (7) sand, (8) riparian, and (9) rocks/boulders.

We quantified microhabitat generalism as the number of different microhabitat types in which a species has been recorded as active. The index of ecological generalism therefore ranges from 1 to 9 (mean ± SD: 2.31 ± 0.114).

SEXUAL DICHROMATISM AND SEXUAL SIZE DIMORPHISM

We scored the degree of sexual dichromatism for each body region, where $0 =$ no difference, $1 =$ difference in color intensity or in pattern only, and $2 =$ entirely different color or difference in both color and pattern. Color types that may be generated by the same mechanism (e.g., red, orange, and yellow are generated by carotenoid and/or pteridine pigments whereas black, gray, and brown are generated by melanins), or that may reflect descriptive ambiguities in field guides, were scored as differences in color intensity ($= 1$). We summed these scores across the nine body regions to derive a measure of overall sexual dichromatism ranging from 0 to 18.

Our indices of sexual size dimorphism were based on body size (snout-vent length) and on relative head size (consisting of head length, head width, and head depth). We estimated sexual size dimorphism using the index of Lovich and Gibbons (1992), where SDI (sexual dimorphism index) is calculated as:

$$\text{SDI} = [(\text{mean size of male})/(\text{mean size of female})] - 1.$$

A positive value of SDI indicates male-biased size dimorphism. In this study, we were primarily interested in SDI as an indirect measure of the strength of sexual selection. As female-biased sexual dimorphism has been shown to reflect selective forces other than sexual selection in lizards including Australian agamids (specifically fecundity selection—Shine 1989; Stuart-Smith et al. 2007), we set negative values of SDI to 0. An analysis where we included raw SDI values (including negative values) produced qualitatively the same results, except in one case (see Results).

We obtained morphometric data from museum specimens and the published literature (see Table S1). We only used species for which there were sufficient samples (>3 individuals of each sex). The great majority of taxa (51 out of 56 taxa $= 91\%$) had measurements for at least five individuals for each sex. As sexual dimorphism in the three head dimensions (the Lovich–Gibbons ratios for length, width, and depth) was strongly intercorrelated, a single new variable reflecting total head size dimorphism was obtained by principal components analysis. PC1 accounted for 67.77% of the total variation (eigenvalue $= 2.033$) in the original dataset and was used in the subsequent analyses.
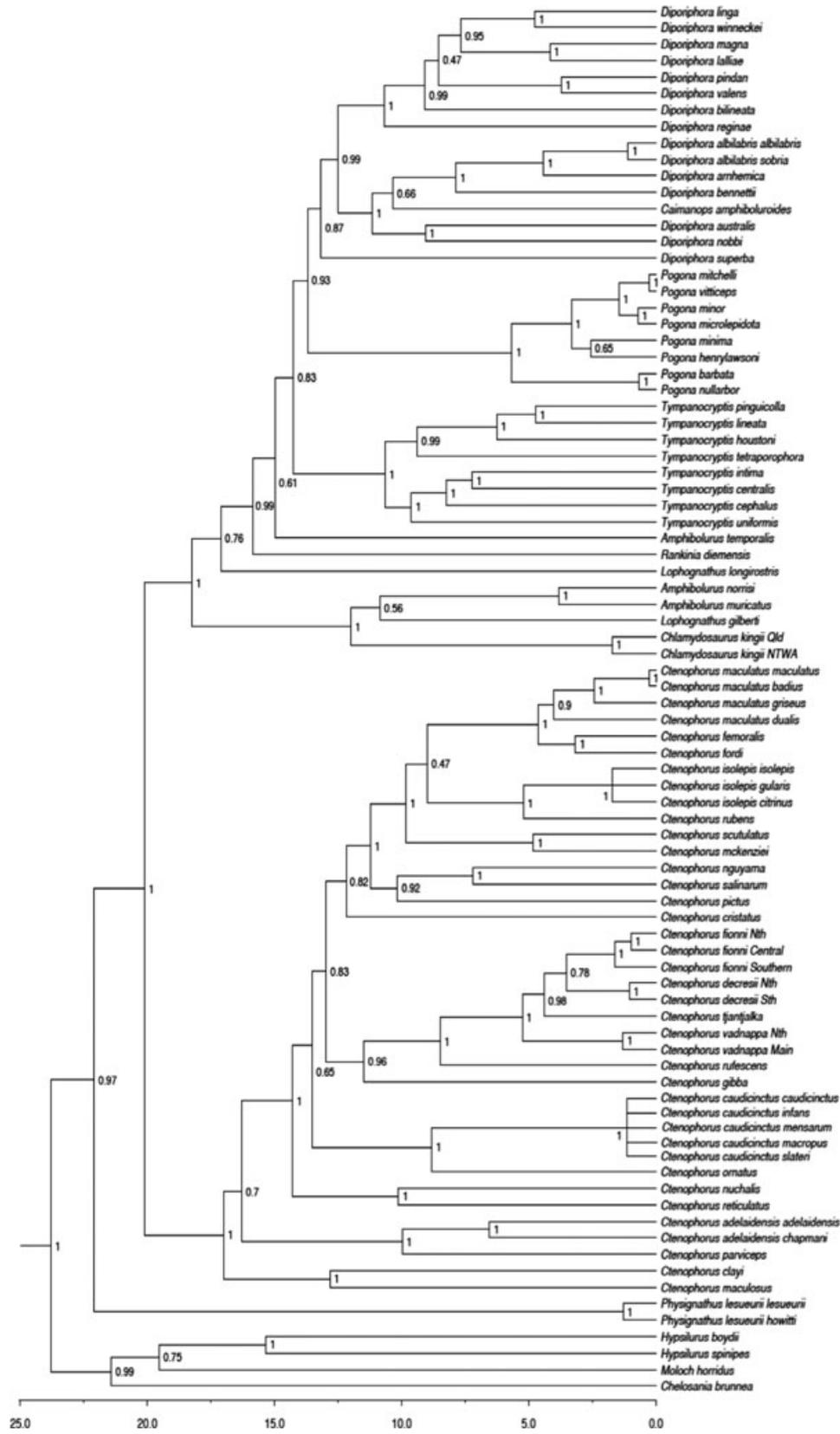
PHYLOGENY

We constructed a phylogeny based on alignment of 1664 sites spanning the ND1-COI region, including the complete protein-coding mitochondrial ND2 gene as this has the most comprehensive coverage of species and faithfully reproduces best estimates of topology and relative branch length from combined nuclear and mitochondrial data of a subset of species (Hugall et al. 2008). The data are largely those used in a previous analysis (Hugall et al. 2008), incorporating new sequences and information from more recent analyses (see below). Trees were inferred with the Bayesian relaxed-clock program BEAST v1.5.4 package (Drummond and Rambaut 2007). The datamatrix comprised 102 Australasian ingroup species and subspecies, with 26 outgroups for rooting and divergence calibration. Nine taxa with no sequence data were a priori interpolated into the consensus phylogeny based on knowledge from other phylogenetic information (Melville et al. 2001; Melville et al. 2008; Melville et al. 2011; Smith et al. 2011) and expert opinion. Likewise, estimates of relative ages of these species were likewise imposed based on expert knowledge of likely divergence dates. Insertion of these taxa was done via topological constraints and node height priors (with a minimum ≥ 0.1 Mya to exclude the possibility of zero age estimates). Further subspecies of *Ctenophorus isolepis* and *C. caudicinctus*, for which there was no information, were designated as polytomies within the relevant species. In the subsequent comparative analysis, the existence of these polytomies had very little weight on the final result. The phylogeny is shown in Figure 1, and the GenBank sequences and other information regarding the assignment of species in the phylogeny are given in Table S2.

BEAST analyses were run using the GTR-G-inv model of sequence evolution, uncorrelated lognormal rate variation model, Yule speciation prior, and dating calibrated as per Hugall et al. (2008). These models were determined as best for these data using information-theoretic model selection approaches (see Hugall et al. 2008 for details). Duplicate runs of 10 million steps each with 10% burn-in (both with all parameter ESS >100), which produced congruent phylogenies and posterior probability support. We then pooled to construct a maximum clade credibility posterior consensus tree with median node heights. This tree was then pruned down to the final set of 85 taxa for the comparative analyses and represents the current best knowledge of the systematics of this group.

COMPARATIVE ANALYSIS

To control for the nonindependence of species data resulting from their shared common ancestry, we used phylogenetic generalized least-squares (PGLS) regression. The phylogenetic variance–covariance matrix, where the diagonal represents the branch-length distance from root to each tip, was generated in R (R Development Core Team 2011) using the "Analyses in Phylogenetics and Evolution" (APE) package (Paradis et al. 2004) for comparative analyses in Regressionv2.m (Lavin et al. 2008). The fitting procedure calculates and incorporates Pagel's

Figure 1. Bayesian consensus phylogeny of Australian agamid species and subspecies used in the comparative analyses after pruning down to 85 taxa and enforcing polytomies with *Ctenophorus isolepis* and *C. caudicinctus* (see Methods and Table S2). Posterior probabilities are shown at nodes. Time scale is Mya.

Table 1. Phylogenetic general linear models predicting aspects of color pattern complexity in Australian dragon lizards. These best models were selected by a backwards selection method (see Methods for details).

(A) Male color pattern complexity		
Best-approximating model: $\lambda = 0.00$, $R^2 = 0.17$, df = 46, Akaike weight = 0.73		
Independent variable	Coefficient ($\pm$SE)	Parameter weight
Head size dimorphism	-0.03 (± 0.03)	1.00
Sexual dichromatism	0.03 (± 0.01)	1.00
(B) Male–female sexual dimorphism in color pattern complexity		
Best-approximating model: $\lambda = 0.60$, $R^2 = 0.16$, df = 54, Akaike weight = 0.81		
Independent variable	Coefficient ($\pm$SE)	Parameter weight
Body size dimorphism	0.79 (± 0.32)	1.00
Sexual dichromatism	0.01 (± 0.01)	1.00

transformation parameter, λ (Pagel 1997, 1999), by restricted maximum likelihood. Lambda (λ) is a constant between 0 and 1, where a value close to 1 implies a strong effect of phylogeny and 0 indicates no phylogenetic signal.

We examined the relationship between factors that are likely to reflect sexual selection (sexual dichromatism and dimorphism) and color pattern complexity in males and females separately. Likewise, in separate models, we also assessed whether color pattern complexity in either sex was associated with factors likely to be linked to natural selection (habitat openness, arboreal lifestyle, or microhabitat generalism). In both analyses, body size (SVL) was also initially included as a factor. We derived "best" multivariate PGLS models using backward selection on the basis of the model's Akaike information criterion (AIC) (Burnham and Anderson 2002). Lower AIC values indicate better approximating models; therefore, starting with the full model, we eliminated the predictor that had the least effect on reducing the AIC score. We continued this process removing terms until there was no further drop in AIC. The predictors retained in the final model represent the best approximating model for our data.

gularis) did females have more complex color patterns than males (for the entire body). The remaining taxa ($\approx$31%; $n = 26$) showed no sexual differences in color pattern complexity (see Table S1).

CORRELATES OF COLOR PATTERN COMPLEXITY

Color pattern complexity of exposed body regions in males and females was not associated with habitat openness, arboreal lifestyle, or ecological generalism. However, two indirect indicators of sexual selection (head size dimorphism and sexual dichromatism) were retained in the model predicting male overall color pattern complexity whereas no measures of dimorphism predicted female color pattern complexity (Table 1A; Fig. 2A). Sexual body size dimorphism and sexual dichromatism also predicted sex differences in color pattern complexity (male color pattern complexity minus female color pattern complexity; Table 1B; Fig. 2B). However, in the analysis that included all raw values of SDI (including the negative, female-biased values), only sexual dichromatism was retained. Body size was not retained in any of the models.

Results

SUMMARY OF COLOR PATTERN COMPLEXITY

Females of two taxa (*C. caudicinctus macropus* and *Pogona microlepidota*) had a single color pattern over the whole body, resulting in a 0 value for the Shannon–Wiener diversity index. As these were clear outliers and cannot be distinguished from species which would have no color patterns at all, we removed these two taxa from the analyses of color pattern complexity in females. In $\approx$65% of taxa that could be compared ($n = 54$ of 83 taxa), males had more complex color patterns than females, and average color pattern complexity was higher in males ($\male$ $n = 85$, mean = 1.791, SD = 0.398; $\female$ $n = 83$, mean = 1.610, SD = 0.341). In only three taxa (*P. vitticeps*, *C. maculosus*, *C. isolepis*

Discussion

Our results suggest that sexual selection has had greater influence on the evolution of more complex color patterns in Australian dragon lizards than has natural selection. Male (but not female) color pattern complexity was significantly associated with sexual dichromatism, suggesting that it is likely to be associated with selection for male sexual signals. Further, sex differences in color pattern complexity were associated with sexual size dimorphism and sexual dichromatism when male-biased dimorphism only was considered, but not when both female- and male-biased dimorphism were considered. In these species, greater sexual dichromatism appears to be achieved in part by the use of different types of color patterns, thereby increasing color pattern complexity. This
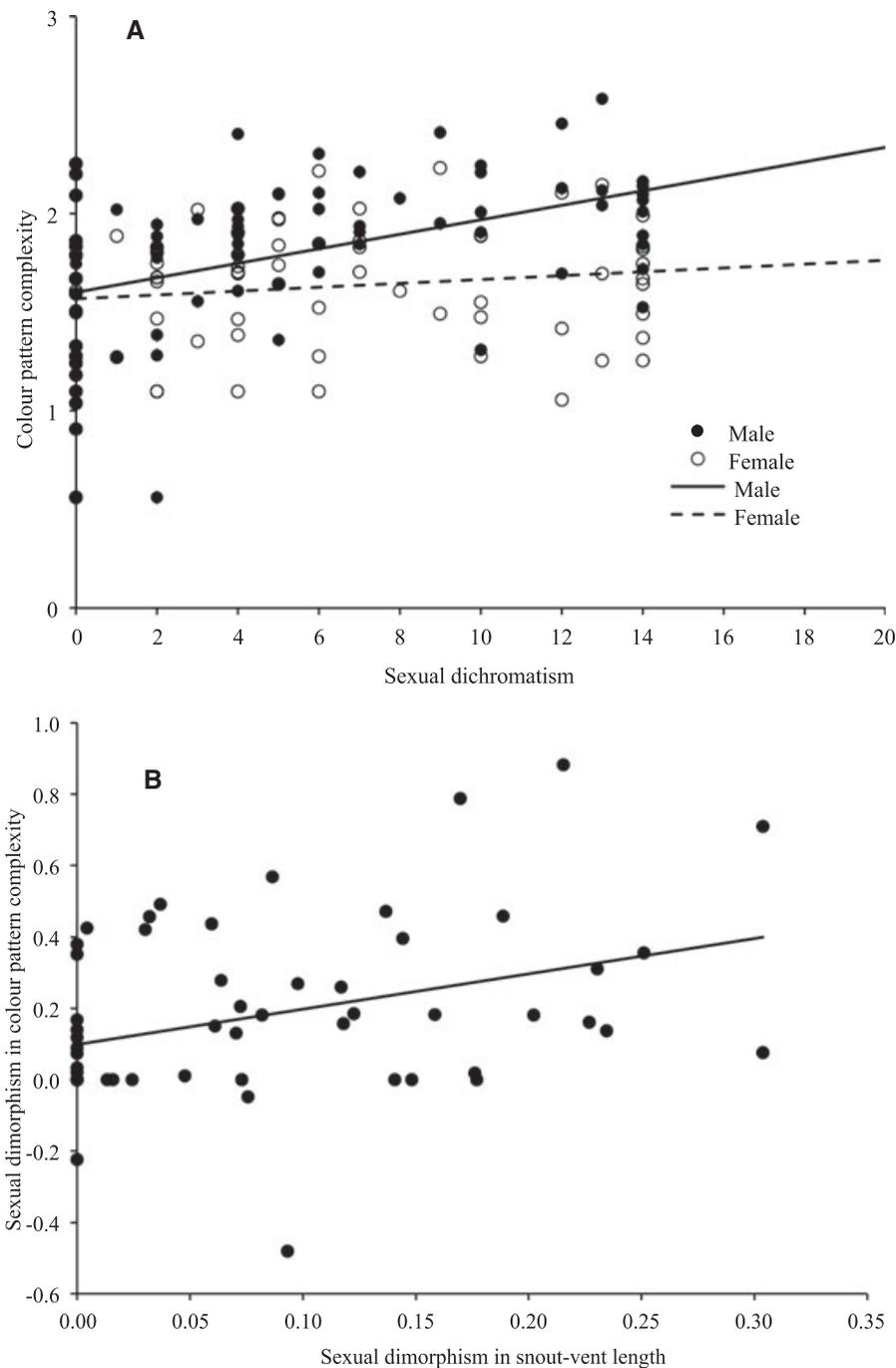
Figure 2. (A) Relationship between color pattern complexity in males (filled circles, solid line) and females (open circles, dotted line) and degree of sexual dichromatism across Australian dragon lizard species. Nonphylogenetically corrected least-squares best-fit regression lines are displayed. The relationship for males is statistically significant ($P < 0.01$). (B) Relationship between sexual dimorphism in color pattern complexity and sexual dimorphism in body size (snout-vent length) across Australian dragon lizard species. Nonphylogenetically corrected least-squares best-fit regression line displayed. The relationship is statistically significant ($P < 0.05$).

association suggests that sexual selection has resulted in signal innovation (the addition of novel color patterns) either with, or instead of, elaboration (the generation of larger or more intensely colored signals).

Our results are concordant with other comparative studies showing a positive correlation between visual signal complexity and indices of sexual selection. In iguanian lizards (agamids and iguanids), male behavioral display complexity (number of display

elements) is positively correlated with male-biased size dimorphism. Since male-biased size dimorphism and sexual dichromatism are typically associated with sexual selection (Badyaev and Hill 2003; Cox et al. 2003), our results strongly suggest that the evolution of color patterns in these lizards is strongly influenced by sexual selection. Ord et al. (2001) found a similar correlation between sexual dimorphism and behavioral display complexity in lizards. Our results therefore provide evidence of sexual selection acting on static visual signals in addition to the dynamic visual signals found in Ord et al.'s work. Comparative studies of different taxa and signal modalities have similarly shown a correlation between signal complexity and sexual selection. For instance, bird song complexity (measured as syllable repertoire size) is associated with polygyny and male parental care (Read and Weary 1992). This pattern is supported by empirical studies demonstrating a sexual advantage of complex signals. For example, warblers with larger song repertoires mate earlier (Catchpole 1980), túngara frogs with elaborate elements (chucks) in their mating calls are preferred by females (Ron 2008) as are wolf spiders with morphological ornaments (tufts) which are used in leg-waving displays (Hebets and Uetz 2000). Although there is evidence that coloration influences contest success in Australian agamid lizards (Stuart-Fox and Johnston 2005; Healey et al. 2007), empirical studies demonstrating an influence of color pattern complexity on pre- or postcopulatory sexual selection are required to confirm the pattern we identify.

The visual environment can strongly affect the efficacy of visual signals and select for more complex or less-complex signals dependent on background and light levels (Endler 1992, 1993; Ord et al. 2002; Ord and Martins 2006). For instance, felid species living in closed habitats are more likely to have complex coat patterns, suggesting selection for camouflage in patchier light environments (Allen et al. 2011). However, none of the ecological factors we examined, namely, habitat openness, lifestyle, and microhabitat generalism were associated with color pattern complexity in Australian dragon lizards. The lack of relationship between habitat openness and color pattern complexity on exposed body regions suggests that predation pressure does not drive selection on color pattern complexity. However, light environment may have a stronger influence on the use of specific types of color and pattern (Chen 2011) rather than on complexity per se. It is also possible, though, that habitat openness is a poor proxy for light environment or predation pressure. Our index of color pattern complexity does not reflect visual contrast against the background and it is not clear whether complexity might differentially influence conspicuousness to predators in open and closed habitats. Finer scale analysis of the influence of color pattern complexity on conspicuousness against different backgrounds and in different light environments is needed to understand the role of natural selection in the evolution of color pattern complexity.

If sexual selection drives the evolution of visual signal complexity why might complexity confer a reproductive advantage? One potential answer is that color pattern complexity has evolved to enable males to convey various types of information to facilitate female choice or opponent assessment ("multiple messages"—Møller and Pomiankowski 1993; Johnstone 1996). For example, in the American goldfinch (*Carduelis tristis*), carotenoid-based yellow color reflects physical and disease condition, whereas melanin-based (black) color reflects social status (McGraw and Hill 2000). Alternatively, some signals may be redundant or serve as "backup signals," each reflecting the same rather than different aspects of mate or opponent quality with some error (Møller and Pomiankowski 1993; Johnstone 1996).

In addition to signal content (the information being conveyed), novel color pattern elements may also influence signal efficacy (the detectability of the signal) by affecting the contrast within the color patterns as well as against the background (Endler et al. 2005). Therefore, it is likely that the use of multiple types of color pattern results in different or novel visual contrasts to optimize social communication. Other functions associated with sexual selection such as species recognition and reproductive isolation may also explain the evolution of more complex/novel signals (Andersson 1994; Candolin 2003; Hebets and Papaj 2005). However, these mechanisms remain to be tested at the macroevolutionary level.

We propose that sexual selection plays the more significant role compared to natural selection in the evolution of color pattern complexity in Australian dragon lizards. As sexual dichromatism is positively associated with sexual dimorphism in color pattern complexity, we suggest that sexual selection has led to signal innovation, involving the use of additional and/or novel signal types, which has resulted in increased complexity in males. By using a novel measure of color pattern complexity, derived from the field of community ecology (the Shannon–Weiner index), we not only demonstrate sexual selection on color pattern complexity, but also present a method for assessing the evolution of color pattern complexity in other lineages in a phylogenetic comparative context.

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Supporting Information

The following supporting information is available for this article:

Figure S1. The nine body regions for which color patterns were scored, shown in lateral (left image) and ventral (right image) view. Note that the groin region is indicated on both views.
Table S1. Data for agamid lizard species used in the analyses.
Table S2. GenBank accession numbers and other sources of information for the agamid phylogeny.

Supporting Information may be found in the online version of this article.

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