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Rapid evolution of elaborate male coloration is driven by visual system in Australian fairy-wrens (Maluridae)

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Abstract

The interplay between colour vision and animal signalling is of keen interest to behavioural ecologists and evolutionary biologists alike, but is difficult to address in terrestrial animals. Unlike most avian lineages, in which colour vision is relatively invariant among species, the fairy-wrens and allies (Maluridae) show a recent gain of ultraviolet sensitivity (UVS). Here, we compare the rates of colour evolution on 11 patches for males and females across Maluridae in the context of their visual system. We measured reflectance spectra for 24 species, estimating five vision-independent colour metrics as well as metrics of colour contrast among patches and sexual dichromatism in a receiver-neutral colour space. We fit Brownian motion (BM) and Ornstein–Uhlenbeck (OU) models to estimate evolutionary rates for these metrics and to test whether male coloration, female coloration or dichromatism was driven by selective regimes defined by visual system or geography. We found that in general male coloration evolved rapidly in comparison with females. Male colour contrast was strongly correlated with visual system and expanded greatly in UVS lineages, whereas female coloration was weakly associated with geography (Australia vs. Papua New Guinea). These results suggest that dichromatism has evolved in Maluridae as males and females evolve at different rates, and are driven by different selection pressures.

Introduction

Animal species often differ in their coloration, an evolutionary pattern that can be easily observed in many animal clades. This diversity in coloration evolves as part of a complex visual environment that is perceived by mates and competitors, but also predators (Cuthill, 2006). Sexually selected signals such as elaborate plumage can evolve in response to changes in the signalling environment, changes in the sensory system of the receiver or a combination of the two as populations adapt to novel sensory conditions (Endler & Basolo, 1998). In such cases, changes in visual system may lead females to prefer males with a novel colour phenotype (Seehausen *et al.*, 2008). However, studies are needed that examine how coloration responds to evolutionary transitions in visual systems, in particular whether ornamental traits can exploit changes in receivers' spectral sensitivity.

Birds present a tantalizing but difficult problem for the study of colour evolution in relation to visual systems; despite a long tradition of comparative studies of plumage coloration (Barlow & Flood, 1983), there remain few species whose visual system is well understood (Hart & Hunt, 2007). A key component of variation in the avian visual system is found in the spectral sensitivity of the short-wavelength-sensitive 1 visual pigment (SWS1), which in many species has a peak absorbance at the edge of the human visual spectrum, but in other species exhibits a shift towards greater sensitivity in the ultraviolet range (Wilkie *et al.*, 2000). Much of this variation is observed as a result of sequence variation at a single site in the SWS1 gene, which can produce a shift between violet sensitivity (VS) and ultraviolet sensitivity (UVS; Ödeen & Håstad, 2003; but see Hauser *et al.*,

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2014). Most avian clades show little evidence of recent transitions between UVS and VS (Ödeen & Håstad, 2010; Ödeen *et al.*, 2011), making comparative studies difficult (but see Lind & Delhey, 2015). Australian fairy-wrens and allies (Maluridae) are perhaps an exception to this pattern, in that they show a relatively recent transition from VS to UVS (Ödeen *et al.*, 2012). Consequently, they are an ideal group in which to compare the evolution of plumage coloration in the context of different visual systems.

Several studies of visual system and colour evolution in Maluridae have recently been published. Ödeen *et al.* (2012) genotyped the SWS1 locus of 16 malurid species to predict violet/ UVS. They concluded that UVS had evolved either one or two times in *Malurus* and that this shift was associated with the evolution of the elaborate short-wavelength plumage coloration seen in many fairy-wrens. Delhey *et al.* (2013) tested this suggestion by demonstrating that UVS showed better performance at discriminating short-wavelength coloration against a natural background. However, neither of these studies considers female plumage coloration in the context of visual system and thus cannot assess whether these effects are restricted to male coloration or are mirrored by changes in females.

Although changes in the degree of sexual dichromatism have historically been conflated with changes in the degree of male ornamentation, sexual dichromatism can be achieved by changes in either males or females (Amundsen, 2000). Female plumage coloration often varies considerably among birds, and in many cases, sexual dichromatism is driven primarily by losses of elaborate female coloration from a sexually monochromatic elaborate ancestor (Irwin, 1994; Burns, 1998; Hofmann *et al.*, 2008). This suggests that selection on females, either maintaining ornaments for use in territory defence (i.e. social selection; West-Eberhard, 1983) or eliminating them for the sake of crypsis (i.e. natural selection), plays an important and neglected role in the evolution of female coloration (Stutchbury & Morton, 2001). Research in blackbirds suggests that females have evolved cryptic plumage in migratory lineages, potentially as year-round territoriality is no longer maintaining selection for the ancestral elaborate coloration (Hamilton, 1961; Whittingham *et al.*, 1992; Friedman *et al.*, 2009).

Most studies of male and female colour have observed that changes in the degree of ornamentation occur predominantly in females (reviewed in Badyaev & Hill, 2003); indeed, initial observations in Maluridae have indicated that almost all such changes have occurred in females (Karubian, 2013). However, other studies have suggested that male plumage evolves more rapidly (Figuerola & Green, 2000) and even tends to diverge most rapidly in dichromatic lineages (Seddon *et al.*, 2013). A recent study in Maluridae by Johnson *et al.* (2013) showed that males and females evolve by different modes, albeit at similar rates. In that study, Johnson *et al.* (2013) showed that female plumage patterns varied primarily with geography, whereas male plumage varied stochastically. However, they measured coloration by human scoring, and their results are thus likely to underestimate both sexual dichromatism and rates of evolution in the ultraviolet range of the spectrum (Eaton, 2005). Furthermore, the authors analysed discretely scored plumage characters using methods explicitly designed for continuously varying characters, so their results should be interpreted with caution (O'Meara & Beaulieu, 2014).

Recent advances in phylogenetic comparative methods allow researchers to rapidly estimate evolutionary rate for characters and to test whether the rate or direction of change differs among lineages with different selection regimes (Butler & King, 2004; Harmon *et al.*, 2008; O'Meara & Beaulieu, 2014). Here, we combine Johnson *et al.*'s (2013) focus on the tempo and mode of evolution among sexes with the visual system data and perspective reported by Ödeen *et al.* (2012) and Delhey *et al.* (2013). Following Johnson *et al.* (2013), we also compare plumage coloration in Australia vs. Papua New Guinea (PNG). We examine (i) rates of plumage evolution across plumage patches of both males and females in Maluridae and (ii) whether UVS species have evolved an expanded range of plumage colours. We show that the rates of evolution for male plumage coloration considerably outpace female plumage and that males exhibit a broader range of colours following the evolution of UVS in Maluridae. In contrast, female plumage appears to be more conserved and potentially related to geography rather than to visual system.

Materials and methods

Colour measurement and analysis

To measure plumage reflectance, we used an Avantes AvaSpec-2048 spectrometer equipped with an Ava-Light-XE pulsed xenon light source and standardized with a WS-2 white reference. We examined vouchered museum specimens of 24 species in the family Maluridae at the Australian National Wildlife Collection (ANWC), with a sampling goal of five individuals from each (see Appendix S1, mean = 2.7 females, 3.6 males). We were unable to measure female specimens from *Chenoramphus grayi*, and this changed our total number of taxa to 23 species for analyses of female colour and dichromatism. For each specimen, we measured 11 plumage patches (Fig. 1) at a perpendicular probe angle, averaging across three repeated measurements. For species with coloration that differed between the mantle and scapulars (e.g. *M. elegans*), we measured the scapulars as well for the purposes of calculating a complete colour span. To ensure that the males we measured were adults in breeding condition, we sampled only

individuals that showed enlarged testes and complete skull ossification when such data were available (as they are for most specimens at ANWC).

There are many metrics that may be used for quantifying coloration (Montgomerie, 2006; Butler *et al.*, 2011); however, no single metric was appropriate for this study. Some metrics were avoided because they are effective for only a single mechanism of colour (e.g. λR_{50}; Friedman *et al.*, 2011), or cannot be mapped onto a phylogeny due to their circular character space (e.g. θ; Stoddard & Prum, 2008; Maia *et al.*, 2013a). As one of our aims was to test for an effect of visual system on colour evolution, it was necessary to intentionally utilize metrics that lacked explicit visual modelling so as to avoid combining the visual model and reflectance as a composite character on the phylogeny (McLennan & Brooks, 1993).

We used Endler's segment classification to describe hue (LM hue and MS hue; Endler, 1990; see Appendix S2). LM hue is the relative difference in reflectance and chroma between long- and medium-wavelength segments, and MS hue is the difference between medium- and short-wavelength segments. A limitation of this approach is that it cannot describe variation in UV reflectance. Consequently, we included analyses of UV chroma (Montgomerie, 2006) to describe this axis of variation. We also included measurements from Montgomerie (2006) that describe saturation and mean brightness. As estimates of plumage brightness are sensitive to measurement error, we performed all measurements in a darkened room at the ANWC. We performed all colour analyses in the R package *pavo* (version 0.5-1, Maia *et al.*, 2013b).

To describe the degree of chromatic contrast among patches for each species, we developed an analogue of the colour span measurement described by Endler & Mielke (2005). Our measure (hereafter PCA span) is similar to colour span in that it takes a specimen's mean pairwise Euclidean distance among the reflectance spectra for its patches in colour space. However, to avoid incorporating visual system into this measure (see above), we used a colour space derived from a principle component analysis (PCA) of our reflectance spectra (centred to remove brightness; Maia *et al.*, 2013a,b). Thus, PCA span represents the mean distance among patches in a PCA space defined by the first two principle components, which together described 92% of colour variation (see loadings in Fig. S1). We repeated the comparative analyses below using both colour span and colour volume under an average UVS visual system, which performed similarly to one another and to PCA span (Stoddard & Prum, 2008).

To describe sexual dichromatism for use in our comparative analyses, we calculated mean Euclidean distances between male and female colours as plotted in PCA space for each patch. We then took an aggregate 'net dichromatism' score that is the sum of mean Euclidean colour distances across all patches, compared between sexes.

Colour analysis using visual models

Birds have four retinal cone classes, and thus, their extent of potentially visible colours can be represented as a tetrahedron or as a spherical projection, with each axis representing the relative stimulation of a cone class (Endler & Mielke, 2005; Stoddard & Prum, 2008). We used visual models to estimate relative receptor stimulation values for each patch's reflectance spectrum in its native visual system (Vorobyev *et al.*, 1998; Maia *et al.*, 2013b), allowing us to place each measured patch in colour space as estimated for an avian UVS or VS observer.

To describe sexual dichromatism in an avian visual context, we calculated mean Euclidean distances between male and female colours as plotted in Stoddard & Prum's (2008) tetrahedral colour space based on either a UVS or VS observer model. This measure is intended to represent distance in character space, and not discriminability under ideal conditions. Following Avery *et al.* (2014), we also examined 1000 bootstrap replicates of male–female comparisons for each species to produce a confidence interval around the mean degree of dichromatism. We refer to species as 'dichromatic' below when the confidence interval of colour differences among sexes did not overlap with the extent of differences within sexes.

Phylogenetic and comparative methods

As our sampling of the Maluridae included not only *Malurus* species, but also a large proportion of *Stipiturus* and *Amytornis*, we used the more completely sampled species tree recently inferred by Lee *et al.* (2012; their fig. 5), which includes these groups. This tree was constructed using a BEST analysis (Liu, 2008) on one mitochondrial and 16 nuclear loci, and its branch lengths are proportional to time in generations as estimated by BEST's coalescent model (Liu & Pearl, 2007). Previous phylogenetic studies of *Malurus* have relied on Driskell *et al.* (2011; Ödeen *et al.*, 2012; Delhey *et al.*, 2013), whose results differ primarily in the relationships among the chestnut-shouldered group.

To test whether the evolution of male PCA span, female PCA span or net dichromatism was driven by visual system, we examined the fit of Ornstein–Uhlenbeck (OU) models as implemented in the R package *OUwie* (version 1.42; Butler & King, 2004; O'Meara & Beaulieu, 2014). This framework is capable of comparing models in which traits are (i) evolving randomly following Brownian motion (BM), (ii) evolving towards a single optimum (OU1), (iii) evolving towards several optima depending on the selective regime (OUM) or (iv) evolving towards several optima at differing rates

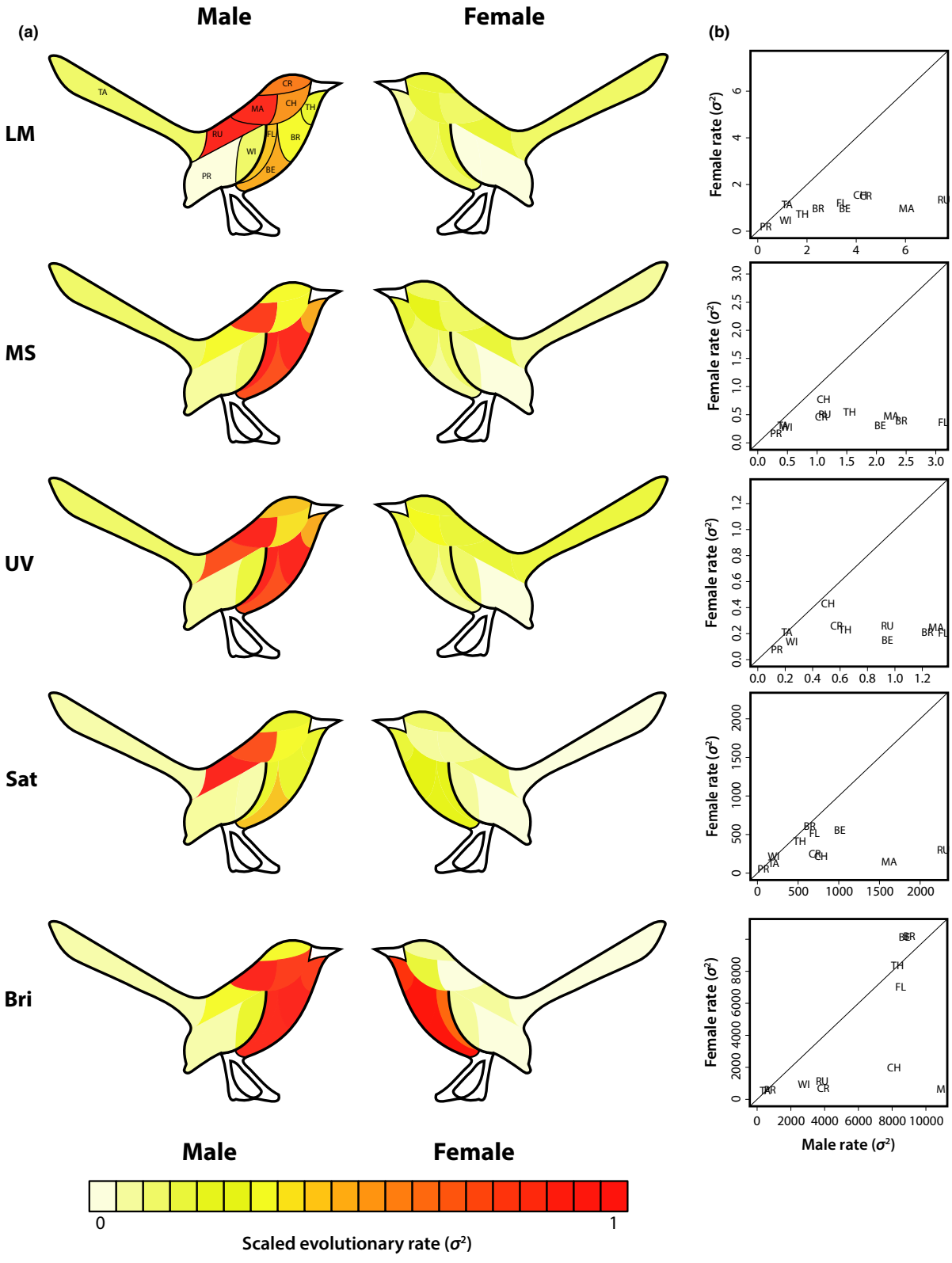

Fig. 1 (a) Evolutionary rate parameter optima for five measures of colour (LM hue, MS hue, UV chroma, saturation and brightness), illustrated across patches using the heat colour scale at bottom. (b) Plot of evolutionary rate optima, compared among males and females.

depending on the selective regime (OUMV). In this context, support for the BM and OU1 models indicates that the trait is evolving independently of selective regime, whereas support for the OUM and OUMV models indicates evidence that the trait is evolving towards different optima defined by the selective regime (Butler & King, 2004; e.g. Maia *et al.*, 2013a).

We constructed selective regimes for the species' visual system based on UV/V sensitivity reported by Ödeen *et al.* (2012). We defined a discrete character for species' geography following Johnson *et al.* (2013), scoring species as breeding in Australia or PNG based on range maps available from BirdLife (BirdLife International & NatureServe 2011). In each case, we estimated ancestral states for regimes using unordered parsimony and likelihood in *Mesquite* (version 2.75; Maddison & Maddison, 2011), and we repeated our analyses across each of the most parsimonious reconstructions (Fig. S2). Using these selective regimes, we fit each of the models described above to data on male colour span, female colour span and net dichromatism. We compared the fit of these models to our data using the Akaike information criterion corrected for sample size (AICc) and converted these AICc values to proportional Akaike weights indicating relative model support.

To compare the rates of evolution across the 11 plumage patches that we measured, we used the R package *geiger* (version 2.0.3) (Harmon *et al.*, 2008). We fit BM and OU1 models to our colour data and the tree using 100 000 MCMC generations under flat priors, and compared the posterior distributions of the model's σ^2 parameter, which is a common measure of evolutionary rate (see Adams, 2013 and refs. therein). Rate parameters estimated from BM and OU1 models were highly congruent (compare Fig. 1b, Fig. S3, Fig. S4), and thus, parameters from the BM model are reported throughout, as these require fewer assumptions (Beaulieu *et al.*, 2012).

Ancestral state reconstruction for PCA span was performed using *phytools* (Revell, 2012) and is included primarily as a visual aid.

Results

Colour space and sexual dichromatism

The major differences between the gamut of female and male plumage coloration in Maluridae are in regions of intense short-wavelength reflectance or a combination of UV and long-wavelength reflectance; we observed few female plumage spectra with these characteristics (Fig. 2). Interestingly, the whole of UVS species in *Malurus* appears to cover a similar range of potential colours as VS species. However, UVS species showed greater distances among patches as measured by PCA span (Fig. 3) and colour span. Grasswren species (*Amytornis*) exhibited a considerably smaller range of colours than other species in this study (Fig. 2) and were largely restricted to melanin-derived colours including blacks, browns and rusty reds.

Sexual dichromatism was not prevalent in the grasswrens, but was very prevalent in the fairy-wrens (*Malurus*). For example, 44% of sampled grasswren species showed high degrees of dichromatism for the breast patch, compared to 100% of fairy-wren species (Fig. S5A). Interestingly, net dichromatism was highest for two VS species, *M. cyanocephalus* and *M. leucopterus*. All *Malurus* species exhibited sexual dichromatism on the breast, cheek, crown, flank, mantle and rump patches (e.g. Fig. S5A). The degree of sexual dichromatism for each species was nearly identical when

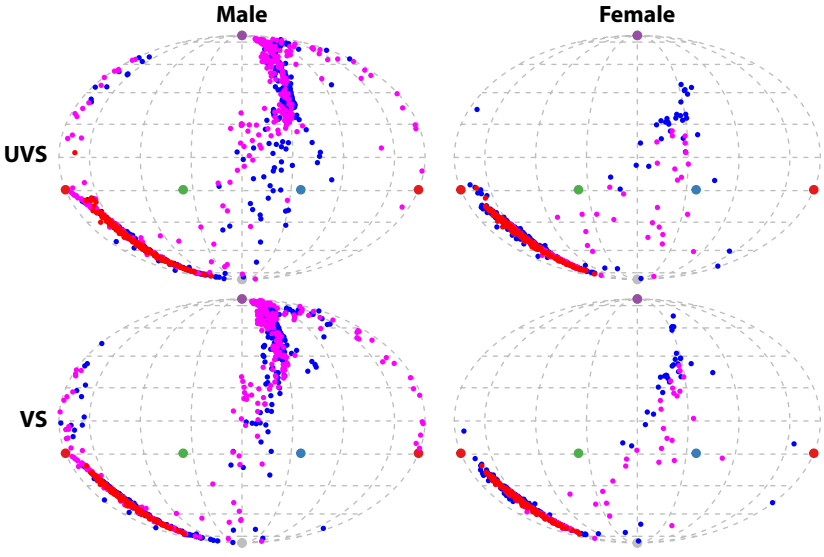

Fig. 2 Reflectance spectra for Maluridae species, mapped in Mollweide projections of avian UVS and VS colour space. *Amytornis* is depicted in red, VS fairy-wrens in blue and UVS fairy-wrens in magenta. Each point represents a reflectance spectrum for a particular species–patch combination. UVS, ultraviolet sensitivity; VS, violet sensitivity.

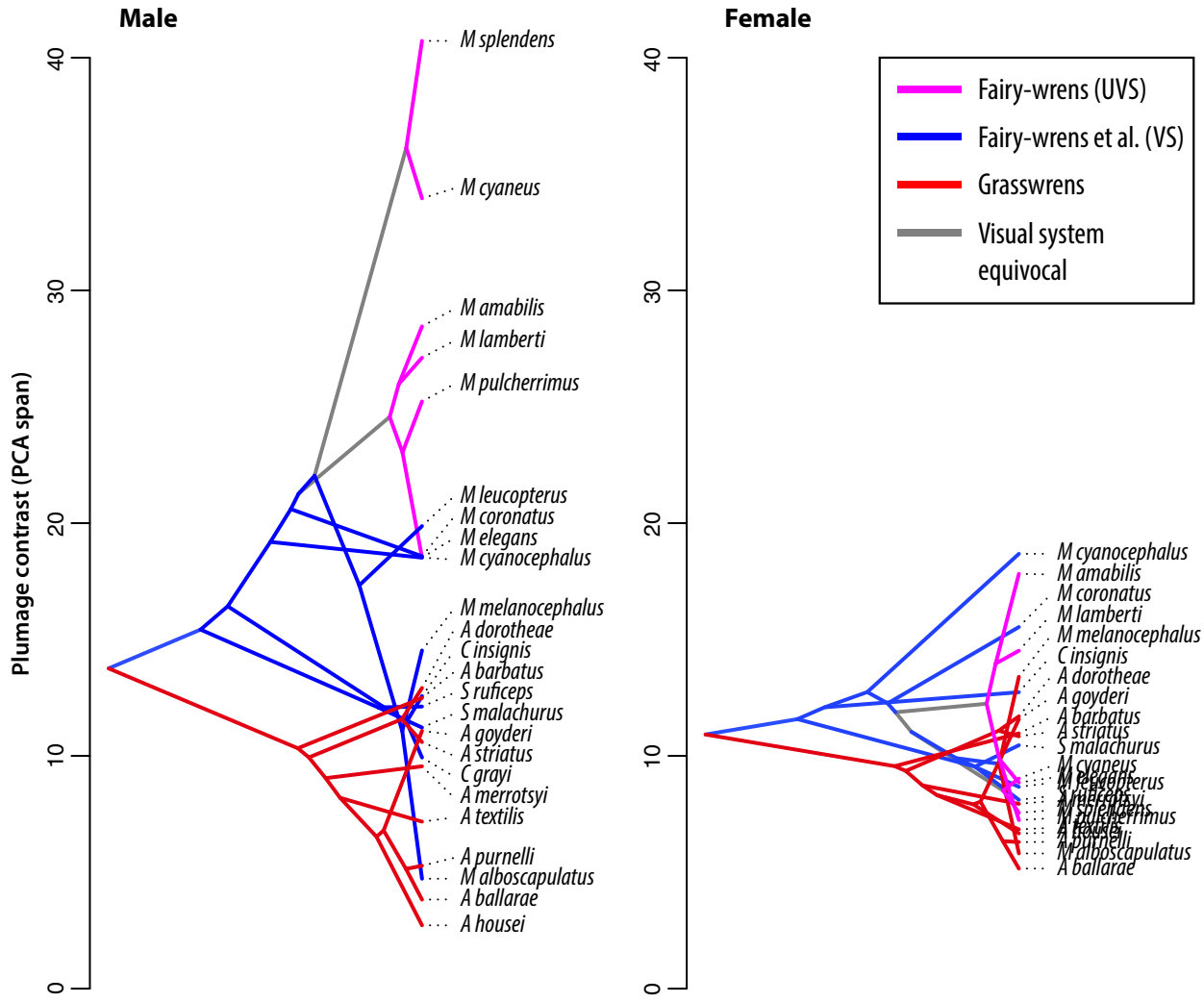

Fig. 3 Maximum-likelihood ancestral state reconstruction of PCA span for male and female Maluridae species, performed using the *phytools* package in R. PCA span is a measure of contrast among patches and is thus a composite character whose inferred ancestral states should be interpreted with care. PCA, principle component analysis.

comparing between UVS and VS observers (e.g. Figs S5A vs. S6).

Evolutionary rate

Evolutionary rate, as indicated here by the σ^2 parameter of BM models, varied considerably among patches (Fig. 1a). The primaries, tail and wing coverts were consistently the most conserved plumage patches across all colour metrics and in both males and females. Among males, rates of evolutionary change along the LM axis of hue were greatest on dorsal plumage patches, whereas rates along the MS axis were greatest on ventral plumage patches and the mantle (Fig. 1a). The rates of evolutionary change in male UV chroma were greatest on the mantle, breast and flank. Rates for saturation were greatest on the mantle and rump, whereas rates for brightness were greatest on the cheek, mantle and ventral patches. In contrast, the rates of plumage evolution were highest in females for the cheek and rump patches across measurements of hue and chroma, but highest on ventral patches when measuring saturation and brightness. The rates of evolution for the mantle patch, among the highest for males in all measurements, were uniformly low in females, despite the gain of short-wavelength dorsal plumage in females of *M. amabilis* and *M. lamberti* (Joseph *et al.*, 2013).

Rates of hue evolution were roughly three- to six-fold lower in females than in males. Overall, dorsal patches were consistently more evolutionarily labile in males than females (Figs 1B, S3 and S4). The evolution

of ventral patches largely followed this pattern for measures of hue, but evolved at equally low rates for saturation and equally high rates for brightness (Fig. 1a). Rates of colour evolution for the primaries, tail and wing coverts were similarly low in both sexes across measurements.

Modelling selective regimes: visual system and geography

To define ancestral selective regimes for use in OU analyses, we used several methods to reconstruct ancestral states for visual system and geography (see above). The unordered parsimony method showed equivocal support for two most parsimonious histories for both visual system and geography (Fig. S2), and as such, we repeated each OU analysis across both of the two most parsimonious histories for its selective regime (Fig. 4). Likelihood models in which gains and losses were equally probable (mk1) supported two independent gains of UVS in *Malurus*; however, likelihood models with unequal rates for gains and losses (mk2) showed more equivocal results (Fig. S2). However, both likelihood models supported two independent malurid radiations in PNG as in Schodde (1982).

Multi-optimum OU models based on a visual system selective regime strongly outperformed single-optimum and BM models in explaining the evolution of male coloration, but not female coloration (Fig. 4). In the OU framework, this indicates evidence for a correlation between visual system and male PCA span and was observed to a weaker extent for net dichromatism. In contrast, single-optimum OU and BM models were sufficient to explain the phylogenetic distribution of female coloration span. These results were consistent across the two most parsimonious reconstructions of UV sensitivity (Fig. S2). Furthermore, these results were supported in additional analyses conducted using male colour span and colour volume.

We conducted similar analyses with selective regimes based on geographic range following Johnson *et al.* (2013). In these analyses, multi-optimum models showed slightly better fit than single-optimum models, showing at best weak support for a correlation between geography and female coloration, and virtually none for a correlation with male coloration or sexual dichromatism (Fig. 4). These results were consistent across the two most parsimonious reconstructions of geographic range (Fig. S2). However, analyses conducted with colour span and colour volume showed stronger support for a relationship between female coloration and geography.

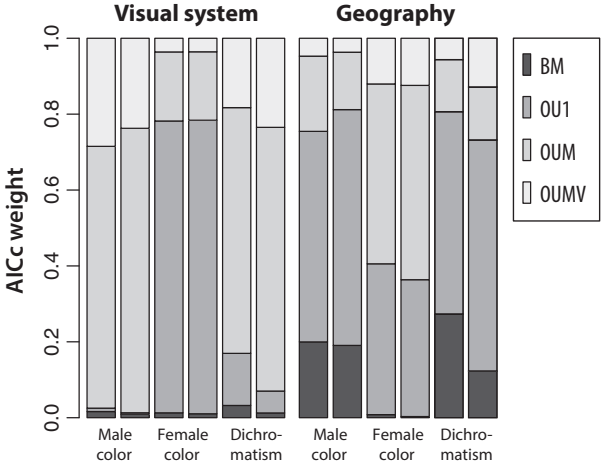

Fig. 4 Akaike weights of OU and BM models fit to visual system and geographic selection regimes. Two model sets are shown for each character: one for each of the two most parsimonious reconstructions of the selective regime. The OUM model supports separate trait optima for each selective regime, and the similar OUMV model also supports separate rates of evolution for each selective regime. In contrast, the BM and OU1 models lack separate trait optima for selective regimes. High Akaike weights show support for a relationship between male colour span and the visual system selection regime, and female colour span and the geography selective regime. OU, Ornstein–Uhlenbeck; BM, Brownian motion.

Discussion

Evolutionary rate and dichromatism

The rates of evolution were greater for male plumage coloration than for female plumage coloration across nearly every measurement and patch, often by a wide margin (Figs 1B and S3). The differential rate of male and female plumage evolution we observe suggests a greater role for sexual selection in driving phenotypic diversification of colour in males than in females. There is currently a wide body of evidence supporting rapid rates of evolution for male nuptial characters across many clades (Emlen *et al.*, 2007; Arnegard *et al.*, 2010; Martin & Mendelson, 2014; Klaczko *et al.*, 2015). Indeed, studies have implicated sexual selection in driving this divergence, showing that male and not female coloration evolves more rapidly in sexually dichromatic species (Seddon *et al.*, 2013; but see Price & Whalen, 2009). However, Price & Eaton (2014) showed that for a clade of New World blackbirds, female coloration at times evolved twice as rapidly as male coloration, often with female divergence associated with changes in mating system. Our finding of the reverse pattern is in stark contrast to that finding, and also to recent estimates that rates are similar for both sexes in Maluridae (Johnson *et al.*, 2013). When considered solely in terms of the presence or absence of ornamentation, male coloration appears constant relative to female coloration, which differs considerably among species (Karubian, 2013). However, our analyses show that when

considered in terms of the colour of that ornamentation, male ornaments are far more variable and evolving far more rapidly.

In Maluridae, most of the striking differences between the male and female range of plumage colours are in the UV (Fig. 2). Indeed, many of the intense short-wavelength colours observed in males were wholly absent in females. Thus, it is likely these were missed by the visual plumage scoring performed in preceding studies (Johnson *et al.*, 2013). This may explain why we observed a greater evolutionary rate for male colour measures rather than equal rates for both sexes, and it highlights the importance of considering the evolution of species' colour patterns in the context of their visual system (see Eaton, 2005). However, it is worth noting that for several metrics that do not include variation in the UV range (LM hue and MS hue), evolutionary rates were also substantially greater for males than for females (Fig. 1b).

We observed rapid rates of male plumage evolution on both dorsal and ventral plumage patches, whereas in females only ventral patches showed rapid rates of evolution, and only in our measure of brightness (Fig. 1). Such ventral patches are likely to be less conspicuous to predators in ground-foraging birds and should experience less intense selection for crypsis (Gomez & Théry, 2007). This suggests that dorsal plumage coloration in malurid females may be constrained by greater selection for crypsis, which is relaxed on ventral patches. However, many of the colour transitions among females for ventral patches reflect changes in the extent of rusty plumage in *Amytornis* and *Stipiturus*; in these genera, many species exhibit rusty flanks, which are likely cryptic in typical arid habitats. Such differential selection on females and males is a cornerstone of theory on sexual selection (Andersson, 1994) and has been observed to cause sexual dichromatism in many groups (Kunte, 2008; Price & Eaton, 2014).

Interestingly, the Maluridae do not appear to be a case in which dichromatism is driven by divergence in male plumage or by divergence in female plumage (Figuerola & Green, 2000; Kunte, 2008; Friedman *et al.*, 2009). Rather, our results suggest that both sexes are evolving independently: at different rates and in response to different selective regimes (Johnson *et al.*, 2013; Karubian, 2013). This is inconsistent with, but does not exclude, a genetic correlation model for the evolution of sexual dichromatism. In such a model, selection on males leads to both sexes gaining elaborate coloration that is subsequently suppressed in females (Kimball & Ligon, 1999) – this would require a monochromatic elaborate ancestor. It appears as though elaborate female coloration is suppressed in most fairy-wren species, with this suppression lost on several occasions (the alternative being that convergence with male plumage is selected or coincidental). Although an androgenic source of plumage control in females seems promising at first, previous observations have suggested that the development of sex-specific plumage coloration is under nongonadal (luteinizing hormone and/or genetic) control in many songbirds, with both plumage types expressed seasonally in gonadectomized songbirds, and expressed simultaneously in gynandromorphs (Kimball & Ligon, 1999; Agate *et al.*, 2003). These observations have been supported by experimental evidence in Maluridae, which shows that testosterone treatment is not sufficient to induce male coloration in females of *M. cyaneus* (Peters, 2007), despite being sufficient to induce this phenotype in juvenile males of *M. melanocephalus* and *M. cyaneus* (Peters *et al.*, 2000; Lindsay *et al.*, 2011). The repeated transitions between dull and elaborate female plumage in Maluridae underline the need for further genomic and experimental study of the mechanisms of sexual dichromatism in birds (Karubian, 2013).

We found that colour evolution was most conserved for patches located on the wing and tail, both in males and in females (Fig. 1). These feathers are used more in flight than the contour feathers measured in other patches (Burtt, 1986), and each was a dark brown colour that varied little between species. Previous studies have shown in laboratory and natural experiments that melanin-pigmented feathers are more resistant to abrasion and bacterial degradation (Burtt, 1979; Barraclough & Sibley, 1980; Goldstein *et al.*, 2004). Our results suggest that feather coloration was highly conserved on those patches most critical for flight and vulnerable to abrasive damage.

Visual system and coloration

We found strong support for OU models in which male PCA span was evolving dependent on visual system (Fig. 3), representing evidence of a correlation between these traits. Thus, our results further support a relationship between the evolution of a UVS visual system and the evolution of elaborate feather ornamentation in Maluridae. However, the direction of this relationship remains contentious. Ödeen *et al.* (2012) compared the use of short-wavelength plumage ornamentation to UV/V sensitivity and reported that gains of UV coloration most likely predated changes in visual system. Here, we show that the range and contrast of male colours expands in concert with the evolution of UVS (Fig. 4). Given the prevalence of extra-pair mating and sexual selection in fairy-wrens (Mulder *et al.*, 1994), it is not difficult to imagine that in this case a change in sensory system might have lead female preferences to drive male ornaments towards a new optimum. However, it is also possible that other potential differences between UVS and VS species, such as the strength or optima of female preferences, could explain the expansion of male contrast in Maluridae.

Unlike Delhey *et al.* (2013), our study is not capable of differentiating between selection for increased signal variability vs. detectability to conspecific receivers. Delhey *et al.* (2013) showed that the fairy-wrens' UVS visual system enhances the conspicuousness of elaborate male patterns, but does not enhance discriminability of intraspecific variation. Our study expands on this by showing that whereas males in species with a UVS visual system have more contrasting plumage, females tend to retain cryptic plumage and evolve at a slow rate relative to males (Higgins *et al.*, 2001). The lack of a relationship between female contrast and UVS may suggest that selection for increased signal detectability is not typically mirrored in females – this would contrast with other lineages in which elaborate female plumage coloration has been maintained due to its function in social competition (Trail, 1990; Stutchbury & Morton, 2001; Murphy *et al.*, 2009). Although this function of female colour may be largely absent in Maluridae, it could be present in several species in which females exhibit elaborate coloration. As suggested by Karubian (2013), behavioural studies are needed to address the roles of predation avoidance and crypsis for female coloration in this clade and to assess whether these differ between species in Australia and PNG.

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References

Adams, D.C. 2013. Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Syst. Biol.* **62**: 181–192.

Agate, R.J., Grisham, W., Wade, J., Mann, S., Wingfield, J., Schanen, C. *et al.* 2003. Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch. *Proc. Natl. Acad. Sci. USA* **100**: 4873–4878.

Amundsen, T. 2000. Why are female birds ornamented?. *Trends Ecol. Evol.* **15**: 149–155.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, USA.

Arnegard, M.E., McIntyre, P.B., Harmon, L.J., Zelditch, M.L., Crampton, W.G.R., Davis, J.K. *et al.* 2010. Sexual signal evolution outpaces ecological divergence during electric fish species radiation. *Am. Nat.* **176**: 335–356.

Avery, J.D., Cassey, P. & Lockwood, J.L. 2014. Contemporary divergence of island bird plumage. *J. Avian Biol.* **45**: 291–295.

Badyaev, A.V. & Hill, G.E. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Evol. Syst.* **34**: 27–49.

Barlow, J.C. & Flood, N.J. 1983. Research collections in ornithology – a reaffirmation. In: *Perspectives in Ornithology: Essays Presented for the Centennial of the American Ornithologists' Union* (A.H. Brush & G.A. Clarke Jr, eds), pp. 37–54. Cambridge University Press, Cambridge.

Barraclough, G.F. & Sibley, F.C. 1980. Feather pigmentation and abrasion: test of a hypothesis. *Auk* **97**: 881–883.

Beaulieu, J.M., Jhwueng, D.-C., Boettiger, C. & O'Meara, B.C. 2012. Modeling stabilizing selection: expanding the Ornstein-Uhlenbeck model of adaptive evolution. *Evolution* **66**: 2369–2383.

BirdLife International & NatureServe (2011) *Bird Species Distribution Maps of the World*. BirdLife International, Cambridge, UK & NatureServe, Arlington, USA.

Burns, K.J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. *Evolution* **52**: 1219–1224.

Burtt, E.H. 1979. Tips on wings and other things. In: *The Behavioral Significance of Color* (E.H. Burtt, ed.), pp. 70–123. Garland Press, New York, USA.

Burtt, E.H. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on Wood-warblers. *Ornithol. Monogr.* **38**: 1–126.

Butler, M.A. & King, A.A. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**: 683–695.

Butler, M.W., Toomey, M.B. & McGraw, K.J. 2011. How many color metrics do we need? Evaluating how different color-scoring procedures explain carotenoid pigment content in bare-part and plumage ornaments. *Behav. Ecol. Sociobiol.* **65**: 401–413.

Cuthill, I.C. 2006. Color perception. In: *Bird Coloration, Vol. 1: Mechanisms and Measurements* (G.E. Hill & K.J. McGraw, eds), pp. 3–40. Harvard University Press, Cambridge, USA.

Delhey, K., Hall, M., Kingma, S.A. & Peters, A. 2013. Increased conspicuousness can explain the match between visual sensitivities and blue plumage colours in fairy-wrens. *Proc. Biol. Sci.* **280**: 20121771.

Driskell, A.C., Norman, J.A., Pruett-Jones, S., Mangall, E., Sonsthagen, S. & Christidis, L. 2011. A multigene phylogeny examining evolutionary and ecological relationships in the Australo-papuan wrens of the subfamily Malurinae (Aves). *Mol. Phylogenet. Evol.* **60**: 480–485.

Eaton, M.D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *Proc. Natl. Acad. Sci. USA* **102**: 10942–10946.

Emlen, D.J., Corley Lavine, L. & Ewen-Campen, B. 2007. On the origin and evolutionary diversification of beetle horns. *Proc. Natl. Acad. Sci. USA* **104**: 8661–8668.

Endler, J.A. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**: 315–352.

Endler, J.A. & Basolo, A.L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* **13**: 415–420.

Endler, J.A. & Mielke, P.W. 2005. Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* **86**: 405–431.

Figuerola, J. & Green, A.J. 2000. The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.* **14**: 701–710.

Friedman, N.R., Hofmann, C.M., Kondo, B. & Omland, K.E. 2009. Correlated evolution of migration and sexual

dichromatism in the New World Orioles (Icterus). *Evolution* **63**: 3269–3274.

Friedman, N.R., Kiere, L.M. & Omland, K.E. 2011. Convergent gains of red carotenoid-based coloration in the New World blackbirds. *Auk* **126**: 678–687.

Goldstein, G., Flory, K.R., Browne, B.A., Majid, S., Ichida, J.M., & B.E.H, Jr. 2004. Bacterial degradation of black and white feathers. *Auk* **121**: 656–659.

Gomez, D. & Théry, M. 2007. Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a Neotropical rainforest bird community. *Am. Nat.* **169**: S42–S61.

Hamilton, T.H. 1961. On the functions and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. *Am. Nat.* **95**: 121–123.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.

Hart, N.S. & Hunt, D.M. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *Am. Nat.* **169**: S7–S26.

Hauser, F.E., van Hazel, I. & Chang, B.S.W. 2014. Spectral tuning in vertebrate short wavelength-sensitive 1 (SWS1) visual pigments: can wavelength sensitivity be inferred from sequence data? *J. Exp. Zool. B Mol. Dev. Evol.* **322**: 529–539.

Higgins, P.J., Peter, J.M., Steele, W.K. Price, G.D., Myers, C.M., Al-Dabbagh, K.Y., Matthew, J.S. *et al.* 2001. *Handbook of Australian, New Zealand, & Antarctic Birds, Volume 5: Tyrant-flycatchers to Chats*. Oxford University Press, Melbourne, Australia.

Hofmann, C.M., Cronin, T.W. & Omland, K.E. 2008. Evolution of sexual dichromatism. 1. convergent losses of elaborate female coloration in New World orioles (*Icterus* spp.). *Auk* **125**: 778–789.

Irwin, R.E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. *Am. Nat.* **144**: 890–907.

Johnson, A.E., Jordan Price, J. & Pruett-Jones, S. 2013. Different modes of evolution in males and females generate dichromatism in fairy-wrens (Maluridae). *Ecol. Evol.* **3**: 3030–3046.

Joseph, L., Edwards, S.V. & McLean, A.J. 2013. The Maluridae: inferring avian biology and evolutionary history from DNA sequences. *Emu* **113**: 195–207.

Karubian, J. 2013. Female ornamentation in Malurus fairy-wrens: a hidden evolutionary gem for understanding female perspectives on social and sexual selection. *Emu* **113**: 248–258.

Kimball, R.T. & Ligon, J.D. 1999. Evolution of avian plumage dichromatism from a proximate perspective. *Am. Nat.* **154**: 182–193.

Klaczko, J., Ingram, T. & Losos, J. 2015. Genitals evolve faster than other traits in Anolis lizards. *J. Zool.* **295**: 44–48.

Kunte, K. 2008. Mimetic butterflies support Wallace's model of sexual dimorphism. *Proc. Biol. Sci.* **275**: 1617–1624.

Lee, J.Y., Joseph, L. & Edwards, S.V. 2012. A species tree for the Australo-Papuan Fairy-wrens and allies (Aves: Maluridae). *Syst. Biol.* **61**: 253–271.

Lind, O. & Delhey, K. 2015. Visual modelling suggests a weak relationship between the evolution of ultraviolet vision and plumage colouration in birds. *J. Evol. Biol.* **28**: 715–722.

Lindsay, W.R., Webster, M.S. & Schwabl, H. 2011. Sexually selected male plumage color is testosterone dependent in a tropical passerine bird, the Red-backed Fairy-wren (*Malurus melanocephalus*). *PLoS One* **6**: e26067.

Liu, L. 2008. BEST: Bayesian estimation of species trees under the coalescent model. *Bioinformatics* **24**: 2542–2543.

Liu, L. & Pearl, D.K. 2007. Species trees from gene trees: reconstructing Bayesian posterior distributions of a species phylogeny using estimated gene tree distributions. *Syst. Biol.* **56**: 504–514.

Maddison, W.P. & Maddison, D.R.. 2011. Mesquite: a modular system for evolutionary analysis. version 2.75, http://mesquiteproject.org

Maia, R., Rubenstein, D.R. & Shawkey, M.D. 2013a. Key ornamental innovations facilitate diversification in an avian radiation. *Proc. Natl. Acad. Sci. USA* **110**: 10687–10692.

Maia, R., Eliason, C.M., Bitton, P.-P., Doucet, S.M. & Shawkey, M.D. 2013b. pavo : an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* **4**: 906–913.

Martin, M.D. & Mendelson, T.C. 2014. Changes in sexual signals are greater than changes in ecological traits in a dichromatic group of fishes. *Evolution* **68**: 3618–3628.

McLennan, D.A. & Brooks, D.R. 1993. The phylogenetic component of cooperative breeding in perching birds: a commentary. *Am. Nat.* **141**: 790–795.

Montgomerie, R. 2006. Analyzing colors. In: *Bird Coloration Vol. I: Mechanisms and Measurements* (G.E. Hill & K.J. McGraw, eds), pp. 90–147. Harvard University Press, Cambridge, MA.

Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenby-Cohen, K.A. & Howell, M.J. 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proc. R. Soc. Lond. B.* **255**: 223–229.

Murphy, T.G., Hernandez-Mucino, D., Osorio-Beristain, M., Montgomerie, R. & Omland, K.E. 2009. Carotenoid-based signaling by females in the tropical streak-backed oriole. *Behav. Ecol.* **20**: 1000–1006.

Ödeen, A. & Håstad, O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol. Biol. Evol.* **20**: 855–861.

Ödeen, A. & Håstad, O. 2010. Pollinating birds differ in spectral sensitivity. *J. Comp. Physiol A. Neuroethol. Sens. Neural. Behav. Physiol.* **196**: 91–96.

Ödeen, A., Håstad, O. & Alstrom, P. 2011. Evolution of ultraviolet vision in the largest avian radiation – the passerines. *BMC Evol. Biol.* **11**: 313.

Ödeen, A., Pruett-Jones, S., Driskell, A.C., Armenta, J.K. & Håstad, O. 2012. Multiple shifts between violet and ultraviolet vision in a family of passerine birds with associated changes in plumage coloration. *Proc. Biol. Sci.* **279**: 1269–1276.

O'Meara, B.C. & Beaulieu, J.M. 2014. Modelling stabilizing selection: the attraction of Ornstein-Uhlenbeck models. In: *Modern Comparative Methods and Their Application in Evolutionary Biology* (L.Z. Garamszegi, ed), pp. 381–393. Springer, New York, NY.

Peters, A. 2007. Testosterone treatment of female Superb Fairy-wrens *Malurus cyaneus* induces a male-like prenuptial moult, but no coloured plumage. *Ibis (Lond. 1859)* **149**: 121–127.

Peters, A., Astheimer, L.B., Boland, C.R.J. & Cockburn, A. 2000. Testosterone is involved in acquisition and maintenance of

sexually selected male plumage in superb fairy-wrens, Malurus cyaneus. *Behav. Ecol. Sociobiol.* **47**: 438–445.
Price, J.J. & Eaton, M.D. 2014. Reconstructing the evolution of sexual dichromatism: current color diversity does not reflect past rates of male and female change. *Evolution* **68**: 2026–2037.
Price, J.J. & Whalen, L.M. 2009. Plumage evolution in the oropendolas and caciques: different divergence rates in polygynous and monogamous taxa. *Evolution* **63**: 2985–2998.
Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.
Schodde, R. 1982. *The Fairy-wrens: A Monograph of the Maluridae*. Lansdowne Editions, Melbourne, Australia.
Seddon, N., Botero, C.A., Tobias, J.A., Dunn, P.O., Macgregor, H.E.A., Rubenstein, D.R. *et al.* 2013. Sexual selection accelerates signal evolution during speciation in birds. *Proc. Biol. Sci.* **280**: 20131065.
Seehausen, O., Terai, Y., Magalhaes, I.S., Carleton, K.L., Mrosso, H.D.J., Miyagi, R. *et al.* 2008. Speciation through sensory drive in cichlid fish. *Nature* **455**: 620–626.
Stoddard, M.C. & Prum, R.O. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. *Am. Nat.* **171**: 755–776.
Stutchbury, B.J.M. & Morton, E.S. 2001. *Behavioral Ecology of Tropical Birds*. Academic Press, San Diego, USA.
Trail, P.W. 1990. Why should lek-breeders be monomorphic? *Evolution* **44**: 1837–1852.
Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C. 1998. Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A.* **183**: 621–633.
West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**: 155–183.
Whittingham, L.A., Kirkconnell, A. & Ratcliffe, L.M. 1992. Differences in song and sexual dimorphism between Cuban and North American Red-winged Blackbirds (*Agelaius phoeniceus*). *Auk* **109**: 928–933.
Wilkie, S.E., Robinson, P.R., Cronin, T.W., Poopalasundaram, S., Bowmaker, J.K. & Hunt, D.M. 2000. Spectral tuning of avian violet- and ultraviolet-sensitive visual pigments. *Biochemistry* **39**: 7895–7901.

Supporting information

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

Figure S1 Principle components analysis (PCA) loadings obtained from an analysis of all reflectance data collected.

Figure S2 Ancestral state reconstructions for selective regimes used in OU model fitting, performed in Mesquite (Maddison & Maddison, 2011).

Figure S3 Posterior distributions of the evolutionary rate parameter for BM models, comparing rates for males at left to females at right.

Figure S4 Posterior distributions of the evolutionary rate parameter for OU models, comparing rates for males at left to females at right.

Figure S5 (a) Sexual dichromatism compared across breast patches for Maluridae. (b) Net sexual dichromatism, which is calculated as the sum of dichromatism scores across all patches.

Figure S6 Sexual dichromatism compared across breast patches for Maluridae.

Appendix S1 ANWC specimen numbers.

Appendix S2 Equations for color metrics.

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