

Female ornamentation in *Malurus* fairy-wrens: a hidden evolutionary gem for understanding female perspectives on social and sexual selection

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Abstract. Phylogeny, ecological environment, social organisation, and mating system are expected to affect degree of female ornamentation, either directly or indirectly, but our understanding of how female ornaments respond to these forces remains incomplete. This article evaluates the evolutionary history and adaptive significance of three putative ornaments – plumage colouration, bill colouration and tail-length – in female fairy-wrens. Despite considerable research on these traits in male fairy-wrens, they have yet to be studied in any detail in females. Phylogeographic analyses in combination with life-history data suggest that female plumage colouration and bill colouration are under active selection, independent of that experienced by males. Social organisation and mating system, as mediated by ecological environment, may shape degree of ornamentation in these traits among females. In contrast, tail-length appears to be driven directly by natural ecological selection imposed by environmental conditions, leading to parallel trait evolution among the sexes within each species. More refined comparative and population-level investigations of adaptive consequences and proximate mechanisms are future research priorities. The study of female fairy-wrens holds great promise to advance our collective understanding of how the ecological environment interacts with sexual selection and social competition to shape ornament evolution in complex social organisms.

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Introduction

A satisfactory understanding of the evolution of sexual differences depends upon understanding sexual selection and ornamentation in both males and females (Clutton-Brock 2007). However, there has been a pronounced bias towards the study of males in the field, beginning with the original formulation of the theory of sexual selection. Darwin (1871) first argued that males compete for access to females (the ‘limiting’ sex) and that this competition for mates drives the evolution of male ornamentation. This perspective was entrenched by seminal papers by Bateman (1948) and Trivers (1972), and thousands of subsequent studies have provided generally robust support for Darwin’s theory of sexual selection as it relates to males (Andersson 1994; Clutton-Brock 2007). In contrast, the factors that shape the evolution and maintenance of female ornamentation have remained elusive. For this reason, a better understanding of female ornamentation has emerged as a core goal of the contemporary research agenda of behavioural ecology (e.g. Amundsen 2000; Forsgren *et al.* 2004; Heinsohn *et al.* 2005; Rosvall 2011; Rubenstein 2012a, 2012b; Tobias *et al.* 2012).

Three main explanations currently exist for ornamentation in females (Tobias *et al.* 2012). Although each has received some support, none has enjoyed the widespread acceptance of sexual selection in males. The first is that females may exhibit ornamentation as a result of genetic correlations between the sexes; in this scenario, female ornamentation is selectively neutral or

costly. This genetic correlation model has solid theoretical support (Lande 1980, 1987) and some empirical support (e.g. Cuervo *et al.* 1996) but it is unlikely to provide a universal explanation for female ornamentation (Tobias *et al.* 2012). This is self-evident in cases where female ornamentation is distinctive from that of males in terms of colour and pattern. Rapid evolutionary transitions between ornamented and unornamented females in several groups of birds is also at odds with the idea that these traits are selectively neutral (Irwin 1994; Burns 1998; Hofmann *et al.* 2008).

The two remaining explanations propose that female ornamentation is adaptive because it affects access to mates (i.e. sexual selection) or to ecological resources that increase reproductive output or survival (i.e. natural selection). It has been challenging to delineate between these two putatively non-overlapping adaptive explanations for female ornamentation (i.e. sexual v. natural selection), in part because traditional models of sexual selection, geared towards males, may be inappropriate for females (Rosvall 2011). For example, whereas most models of sexual selection assume that males seek to maximise their number of mates, we expect females to focus more on mate-quality. Similarly, when female mate-choice is influenced or determined by access to resources, it may not be possible to distinguish where competition for mates ends and competition for resources begins. Additional work suggests that female ornamentation should not be as pronounced as male ornamentation because females would do

better to invest directly in fecundity rather than indirectly in offspring quality by a direct investment in costly ornaments (Kokko and Johnstone 2002; Chenoweth *et al.* 2006). Issues such as these have proved vexing and have spurred calls to modify (e.g. Rosvall 2011), or even abandon altogether (e.g. Roughgarden *et al.* 2006), the current theory of sexual selection.

For this, and other, reasons, there have been several calls recently to study ornamentation within a broader evolutionary ecology framework (Hunt *et al.* 2009; Cornwallis and Uller 2010; Robinson *et al.* 2012; Rubenstein 2012a), which has the benefit of shifting the focus away from distinguishing between sexual selection and natural selection as discrete categories of selection. In particular, attention to: (1) social interactions beyond those restricted to mate-choice and sexual selection, (2) the relationship between ecological conditions, social organisation and mating system and (3) phylogenetic context, may provide additional insights into the evolution and adaptive significance of female ornamentation. To accommodate this broader perspective, sexual selection can be treated as a subset of social selection or competition among conspecifics for any type of resources, such as mates (including mate-choice), food and reproductive opportunities (West-Eberhard 1979, 1983). Social selection is useful when applied to female ornamentation because it shifts the focus away from competition for mates *v.* resources as dichotomous, alternative end-points towards the reality that female ornamentation, social interactions (both sexual and non-sexual) and fitness may interact in potentially complex ways (Lyon and Montgomery 2012; Tobias *et al.* 2012).

Together with social interactions, ecological environment is also likely to have an important role in shaping female plumage ornamentation. Ecological environment may act directly on expression of sexual or social signals by constraints associated with diet, transmission or predation risk (e.g. Hill 1992; Marchetti 1993; Burns 1998; Baldassarre *et al.* 2013). Ecological environment may also affect female ornamentation by indirect effects on social selection pressures. This is because temporal and spatial distribution of resources shape social organisation and mating system (Emlen and Oring 1977), which may influence the type and degree of intraspecific competition over access to mates or resources (Rubenstein and Lovette 2009). These intraspecific social interactions are mediated by, and shape, the evolution of signals and ornaments (Rubenstein 2012a, 2012b). In addition to the effects of social and ecological environment, and the interaction between them, a complete understanding of female ornamentation also depends on documenting phylogenetic context and evolutionary history using a comparative approach (e.g. Irwin 1994; Burns 1998; Hofmann *et al.* 2008).

Over the past few decades, *Malurus* fairy-wrens have emerged as a model system for understanding sexual selection, social dominance and ornamentation in males (e.g. Brooker *et al.* 1990; Pruett-Jones and Lewis 1990; Mulder and MacGrath 1993; Webster *et al.* 1995, 2004, 2008; Dunn and Cockburn 1999; Peters *et al.* 2001; Karubian 2002; Peters 2002; Tarvin *et al.* 2005; Rowe and Pruett-Jones 2006, 2013; Cockburn *et al.* 2008a, 2008b; Kingma *et al.* 2009; Lindsay *et al.* 2009, 2011; Baldassarre *et al.* 2013; Peters *et al.* 2013). As has been the case in many taxa, females have largely been relegated to a supporting role for understanding male ornamentation, only occasionally serving a focal point of research (but see Double and Cockburn 2000; Peters

2007; Hall and Peters 2008; Varian-Ramos *et al.* 2012). This represents a serious gap in our knowledge, but also an opportunity to use fairy-wrens as a vehicle to advance our broader understanding of the ways in which sexual selection, social competition and signal evolution interact in socially complex organisms. *Malurus* fairy-wrens offer a particularly rich palette of variation for inquiries into the evolution and adaptive significance of female ornamentation (Fig. 1). Fairy-wrens are socially complex, occur across a wide range of ecological environments, exhibit considerable variation in degree of female ornamentation both within and between species, and robust phylogenies exist for the group. This article provides an overview of variation in ornaments among female fairy-wrens in relation to phylogenetic, ecological and life-history factors, and proposes directions for future research that are likely to illuminate the adaptive significance and evolutionary history of female ornamentation among fairy-wrens and other socially complex organisms.

Methods

Study system

The genus *Malurus* consists of 11 small, insectivorous species found from southern Tasmania to northern New Guinea (Rowley and Russell 1997; Joseph *et al.* 2013). This represents a latitudinal range of $\sim 43^\circ$, a longitudinal range of $\sim 40^\circ$, and an elevational range from 0 to 2300 m above sea level. Fairy-wrens inhabit desert, shrublands, temperate forest and woodland, monsoonal savanna and grassland, rainforest and anthropogenic habitats, all of which exhibit substantial differences in their vegetation structure and in seasonal and annual averages and variances in temperature and rainfall. Fairy-wrens also exhibit substantial variation in social organisation and mating system (for reviews see Rowley and Russell 1997; Magraf and Cockburn 2013; Peters *et al.* 2013; Rowe and Pruett-Jones 2013). Males and females typically form long-term socially monogamous pair bonds and the breeding pair can be joined by one or more auxiliary helpers, which are usually young that delay dispersal and assist their parents with subsequent reproductive efforts (i.e. cooperative breeding). Typically, males remain on their natal territories as helpers, whereas females often disperse before their first potential breeding season. However, there are species in which both males and females may help, there is wide variation within and between species in the incidence of helping behaviour, and helpers are not always offspring from a previous year. Fairy-wrens also exhibit sexual promiscuity; despite socially monogamous pair bonds, both males and females engage in extra-pair copulations (EPC) that result in extra-pair paternity (EPP). However, as with cooperative breeding, there is much variation within and between species and populations in rates of EPP.

Based on studies of male fairy-wrens (as well as males and females of other taxa), there are *a priori* reasons to expect that plumage, bill colouration and tail-length may serve as ornaments in female fairy-wrens. For the purposes of this article, an ornament is defined as a phenotypic trait that signals information about individual quality during interactions with conspecifics. The extent of breeding plumage and the timing when breeding plumage is expressed both within a season (i.e. timing of moult) and among seasons (i.e. delayed plumage maturation) may act as signals in male fairy-wrens and predict access to mates and

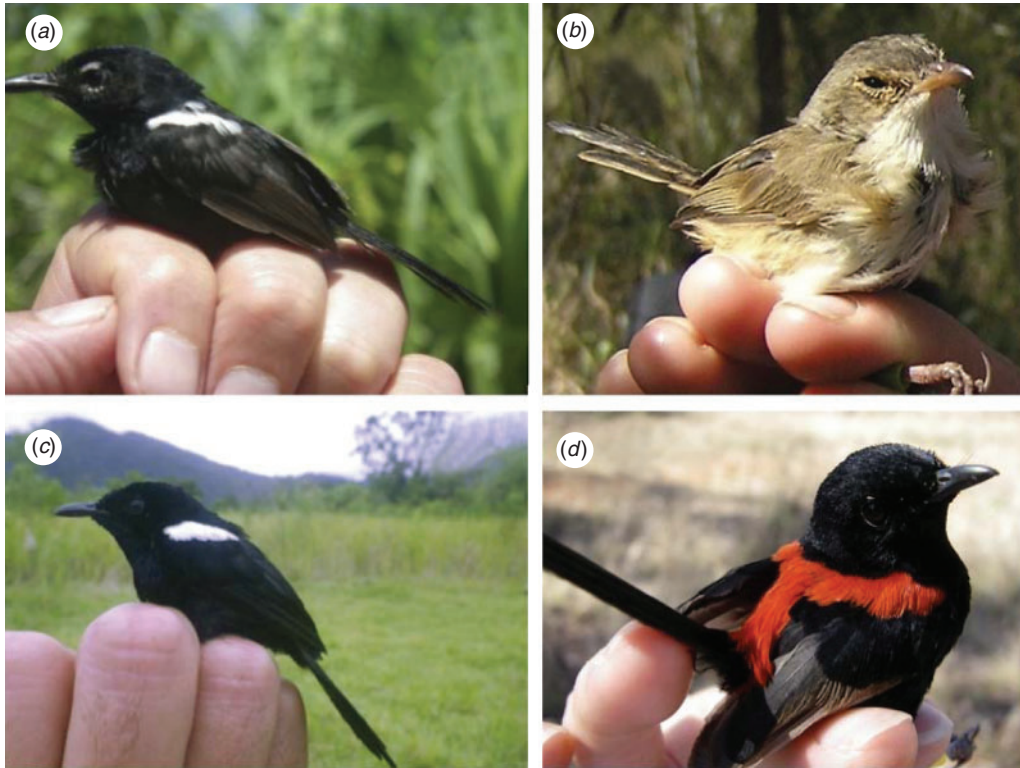


Fig. 1. Female fairy-wrens exhibit considerable interspecific variation in two putative social signals, plumage ornamentation and bill colouration. The female White-shouldered Fairy-wren (*M. alboscapulatus moretoni*) (a) is covered in breeding plumage and its bill is black, whereas the female Red-backed Fairy-wren (*M. melanocephalus melanocephalus*) (b) has no obvious plumage ornamentation and a pink bill. As is the case for nearly all species in the genus, male White-shouldered Fairy-wrens (c) and Red-backed Fairy-wrens (d) are highly ornamented in both traits. Females may also exhibit considerable intraspecific variation; for example, females subspecies *M. a. lorentzi* of White-shouldered Fairy-wrens (not shown) are qualitatively similar to female Red-backed Fairy-wrens (b). Patterns of expression among these sister species, and within the genus as a whole, are consistent with the idea that social or sexual interactions, as mediated by the ecological environment, play a central role in shaping ornamentation in female fairy-wrens.

intrasexual social dominance (Mulder and MacGrath 1993; Dunn and Cockburn 1999; Karubian 2002; Karubian *et al.* 2008; Webster *et al.* 2008; Peters *et al.* 2013). Bill colouration is also used by male fairy-wrens to convey information about status or condition (Karubian 2008; Karubian *et al.* 2011). Finally, it has been proposed that fairy-wren tails may serve as ornaments because they are long, frequently conspicuously coloured or patterned, and held over the head at a conspicuous angle (Rowley and Russell 1997 and references therein); in at least one species, tail-length of males is correlated with social dominance (Karubian *et al.* 2009).

I quantified plumage colouration, bill colouration and tail-length in male and female fairy-wrens for subsequent phylogenetic and statistical analyses using colour plates, species descriptions, and morphological measurements provided by Rowley and Russell (1997). There are several shortcomings associated with this approach. Most notably, using colour plates rather than live specimens makes it possible that biologically relevant variation was overlooked, either because of contextual use of signals that is not evident from plates or because of differences between human and avian visual systems. The coarse nature of the colouration

data collected using this approach led me to apply a three-level scoring scheme (i.e. high, medium, and low; see below), which is likely to be overly simplistic given the continuous nature of the traits in this study; more refined measures, including photospectrometric measures of colouration (e.g. Delhey *et al.* 2013), assessment of specific plumage patches, and attention to the proximate basis of colouration (e.g. melanin *v.* structural) would provide useful, and potentially different, results from those presented here. It is also important to note that the three characters analysed here form only a subset of the suite of signals available to females, including vocalisations, displays and other traits that are less conspicuous to the human eye or imagination, and it is not clear whether these focal traits function as signals in all, or even most, species of fairy-wren. For these reasons, this study should be considered an initial effort to describe broad patterns in the genus, based on information that was tractable to collect without direct access to field or museum data.

To quantify the extent of plumage ornamentation, I qualitatively scored the presence of coloured plumage that differed from neutral shades of brown, beige or grey-white on each of five main sections of the body (head, back, tail, belly and chest). No

intermediate scores were assigned; if coloured plumage occurred on any portion of a given section of the body, the entire section was considered to be coloured (e.g. head was scored as coloured based on coloured lores of female Splendid (*M. splendens*), Superb (*M. cyaneus*), Variegated (*M. lamberti*), Blue-breasted (*M. pulcherrimus*) and Red-winged (*M. elegans*) Fairy-wrens and chestnut ear-patches of female Purple-crowned Fairy-wrens (*M. coronatus*); and back scored as coloured based on rufous scapulars of Red-winged Fairy-wrens). I used this approach to place species into one of three plumage ornamentation categories: high (brightly coloured plumage on three or more sections of the body), moderate (brightly coloured plumage on two sections of the body), and low (exhibiting coloured plumage on one or no sections of the body). Though simplistic, this approach provided an unambiguous method of characterising degree of plumage ornamentation with only one borderline case: female Superb Fairy-wrens, in which a very light wash of colour on the tail was classified as neutral, leading to the species being classed as 'low' rather than 'moderate' (modifying the categorisation of this species between low and moderate did not change the qualitative results presented below).

Based on earlier findings that black bill colouration is associated with social dominance and mate-choice (Karubian 2008; Karubian *et al.* 2011), I identified two categories of bill ornamentation: black and light (the latter ranging from pink to orange to brown, depending on the species). Both black and light bills, as characterised here, may serve as social signals (e.g. Murphy *et al.* 2009a). There is extensive variation between species of *Malurus* in the colouration of light bills; the extent of variation within species is poorly known. Also, because the bill is vascularised, individuals have the ability to modify its colour relatively quickly, in some cases hours, by moving pigments through the blood (e.g. Rosen and Tarvin 2006; Rosenthal *et al.* 2012). This could allow individuals of species with light bills to convey information about status or condition on a fine temporal scale (e.g. Rosenthal *et al.* 2012).

For tail-length, I used morphological measures to establish three arbitrary character states for length within each sex: long (>10% of the genus average for the ratio of tail-length to tarsal-length), moderate (within 10% of the genus average) and short (<10% of the genus average). It is worth emphasising that, although long tails in fairy-wrens are conspicuous, it may be that shorter tails are the more elaborated state in at least some species (Swaddle *et al.* 2000; Karubian *et al.* 2009). Thus, it is not clear whether short or long tails would correspond to a high ornamentation ranking. There was no relationship between tarsal-length and latitude for all species combined (Spearman rank correlation $\rho = -0.20$, $P = 0.53$).

I conducted phylogenetic analyses by mapping character states onto Driskell *et al.*'s (2011) maximum likelihood phylogeny of *Malurus*; I excluded the Broad-billed Fairy-wren (*Chenorhampus grayi*, formerly *Malurus grayi*) from my analyses because of recent consensus that it be removed from the genus *Malurus* (Driskell *et al.* 2011; Lee *et al.* 2012; Joseph *et al.* 2013). I then used the parsimony method in the program Mesquite (Maddison and Maddison 2011) to reconstruct ancestral character states and identify evolutionary transitions between character states (use of the likelihood method returned identical results). It is important to emphasise again that this approach assesses

evolutionary transitions in the degree of ornamentation not the type of ornamentation. I assessed the distribution of character states in a geographically explicit context by correlating trait value with the midpoint of latitude for each species range, calculated by averaging the northernmost and southernmost points of the distribution of each species.

For polytypic species (there are 30 recognised subspecies in the genus *Malurus*; Rowley and Russell 1997), I calculated species-level character scores by independently scoring the values of each putative ornament for each subspecies, and then averaging these scores and rounding to the nearest character state. Inclusion of subspecies in the analyses does not change qualitative results in terms of pattern description and latitudinal trends, and weakens phylogenetic analyses because an arbitrary and greatly reduced number of subspecies are included in Driskell *et al.*'s (2011) phylogeny of *Malurus*. For this reason, analyses are restricted to the level of species. This procedure masks the fact that two species, the White-shouldered Fairy-wren (*M. alboscapulatus*) and Variegated Fairy-wren, exhibit considerable variation in female plumage ornamentation at the subspecies level (Schodde 1982; Rowley and Russell 1997). The White-shouldered Fairy-wren (Fig. 1) has six recognised subspecies (Rowley and Russell 1997) that are distinguished by distribution and female plumage, which can range from fully ornamental, to pied, to almost completely dull. The Variegated Fairy-wren has four subspecies (Rowley and Russell 1997) that range from low to moderate or heavy female ornamentation.

Results

Degree of ornamentation in plumage colouration, bill colouration and relative tail-length expressed by female fairy-wrens is similar to or reduced relative to that of breeding plumaged male conspecifics. Of the 11 species of *Malurus*, female plumage ornamentation is classed as high in 3 species, moderate in 5 and low in 3, whereas plumage ornamentation of males is classed as high in 10 species and moderate in 1. Females of five species have black bills and the remaining six species have light bills. In contrast, breeding plumaged males of all species of *Malurus* have black bills. The ratio of tail-length to tarsal-length ranges from 2.42 in female Emperor Fairy-wrens (*M. cyanocephalus*) to 3.15 in female Blue-breasted Fairy-wrens (mean \pm s.d. for genus = 2.77 ± 0.31). Male fairy-wrens exhibit a similar range of variation in tail-length (range = 2.21–3.17; mean \pm s.d. = 2.70 ± 0.38). At first glance, these patterns of expression appear inconsistent with strong selection on these characters in females and suggest instead that patterns of plumage variation among females may result from genetic correlations of varying strength with males, genetic drift or both.

Phylogeographic analyses provide an alternative perspective (Fig. 2). Character-state reconstruction indicates that four transitions in the degree of female plumage ornamentation have occurred within *Malurus*, a high number given that there are only 11 species in the genus. In contrast, only one evolutionary transition in degree of plumage ornamentation is indicated for males. Similarly, there is high evolutionary lability of bill colouration among females, with multiple ($n = 4$) transitions between light and black bills, but males exhibit no evolutionary transitions throughout the entire phylogeny. In contrast to plumage and bill

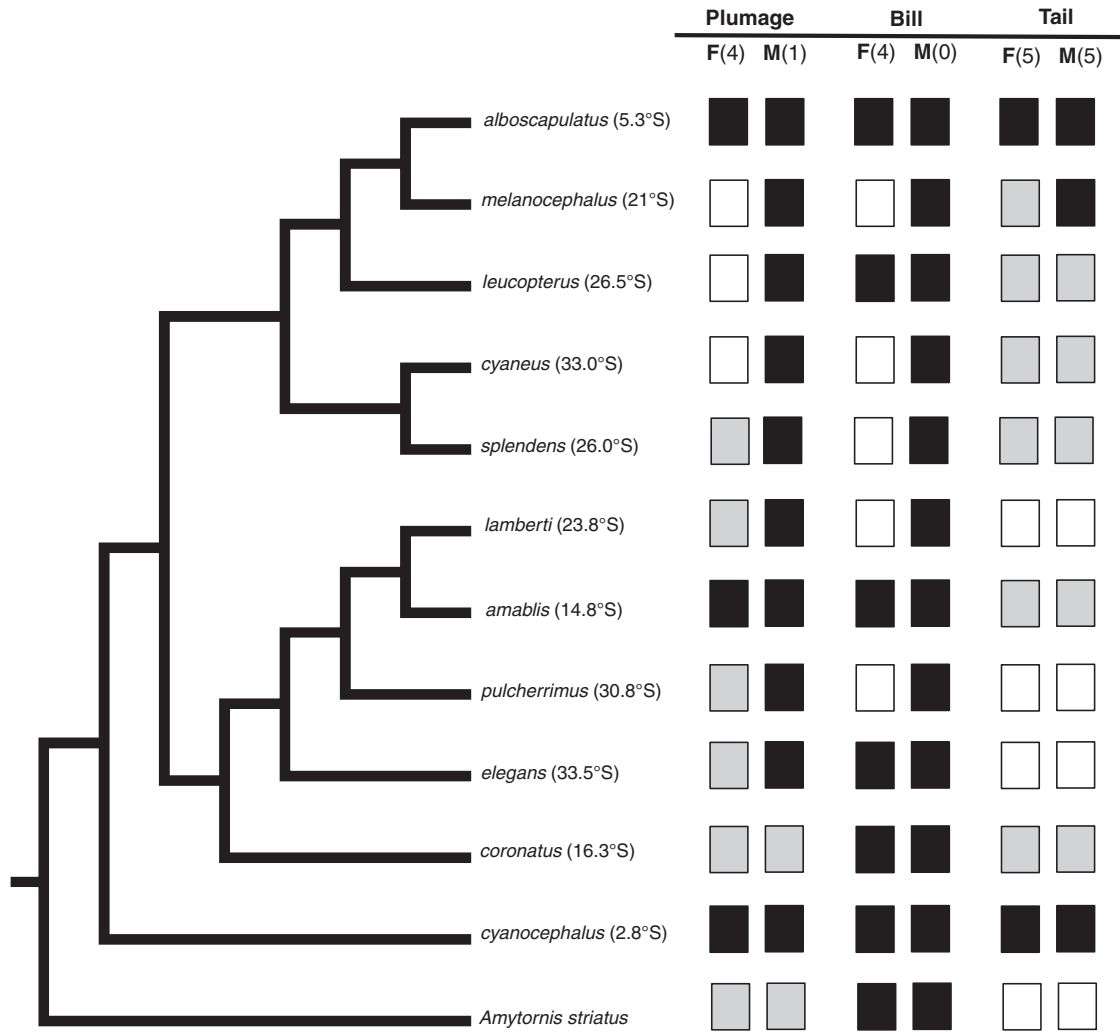


Fig. 2. Plumage colouration, bill colouration and tail-length in female fairy-wrens exhibit substantial evolutionary lability. Evolution of tail-length is concordant between the sexes, whereas plumage and bill colouration follow distinctive evolutionary trajectories in males and females. This suggests that patterns of plumage and bill colouration in female fairy-wrens cannot be explained by phylogenetic inertia or genetic correlations with males, and that alternative selective scenarios are likely to apply. Character states for degree of ornamentation exhibited in each trait (black, high ornamentation; grey, moderate; white, low; see Methods) are provided for males (M) and females (F) of each terminal taxon of *Malurus* in the phylogeny of Driskell *et al.* (2011), and for the outgroup (Striated Grasswren, *Amytornis striatus*). The number of evolutionary transitions estimated from character reconstruction is indicated in parentheses for each sex under each trait. Figures in parentheses for each species in the phylogeny are the midpoint latitude of the species range.

colouration, the sexes exhibit parallel evolutionary trajectories for relative tail-length, with five transitions between tail-length states in both females and males; the sole outlier in this pattern is the Red-backed Fairy-wren (*M. melanocephalus*), in which tail-length has evolved to be shorter in males than in females (Swaddle *et al.* 2000).

The degree of female plumage ornamentation increases as the distribution of species approaches the Equator (Spearman rank correlation $\rho = 0.66, P = 0.027$). There is also a significant trend for fairy-wren species closer to the Equator to have black bills (logistic regression between mean latitude and bill-score (i.e. light or black); $\chi^2 = 4.87, P = 0.027$). There exists a loose association between female plumage ornamentation score and bill coloura-

tion, in that black bill colouration is exhibited by all three species with heavily ornamented females and two species with moderately ornamented females. These patterns are driven by tropical species; the mean latitude for high plumage ornamentation in females is 7.6°S, whereas that for medium plumage ornamentation is 26.1°S and for low ornamentation 26.7°S. This suggests that females of tropical fairy-wren species, which are among the most distantly related species in the genus, have converged upon the highest degrees of plumage and bill ornamentation in the genus. The lack of meaningful variation among males in these traits using the methods employed here precludes parallel analyses for males. In contrast to plumage and bill colouration, relative tail-length in both males and females decreases in parallel

as the ranges of species approach the Equator (females: slope = -0.02 , $R^2 = 0.52$, $P = 0.012$; males: slope = -0.02 , $R^2 = 0.37$, $P = 0.046$).

Discussion

Female fairy-wrens exhibit substantial interspecific variation in the degree of plumage and bill ornamentation. Phylogeographic analyses demonstrate that, for these traits, evolutionary transitions between character states among females are common and degree of ornamentation increases as the ranges of species approach the Equator. Male fairy-wrens, in contrast, tend to be highly ornamented in general, most likely as a result of strong sexual selection associated with high rates of sexual promiscuity in the genus (Peters *et al.* 2013; Rowe and Pruett-Jones 2013). As a consequence, male fairy-wrens exhibit few evolutionary transitions and no geographical trend in degree of plumage or bill ornamentation. These findings – high evolutionary lability independent of males and in concert with a geographical trend – suggest that genetic correlations with males, genetic drift or both cannot suitably explain observed patterns of ornamentation among female fairy-wrens. Instead, it appears that plumage and bill colouration in female fairy-wrens evolved under active selection pressures that shift along a latitudinal gradient. Female tail-length is also highly labile evolutionarily and covaries with latitude, but differs in that males and females share very similar evolutionary and geographical patterns of expression, suggesting alternative selective scenarios on tail-length *v.* plumage and bill colouration.

The geographical distribution of female ornamentation in the genus *Malurus* is consistent with convergent selection processes acting upon fairly distantly related species that inhabit similar ecological conditions (i.e. homoplasy). Female plumage and bill colouration increase, and tail-length decreases, as species approach the Equator. Ecological environment may act directly on these traits by ecological selection (e.g. selective pressure imposed by ecological environment factors such as diet, signal transmission, predation risk, etc.), or indirectly by effects on social organisation and mating system, which in turn affect social and sexual selection pressures and trait values. For tail-length, the fact that males and females within each species appear to have evolved in parallel suggests that ecological selection may be more important than social selection driving observed patterns in this trait (see also Baldassarre *et al.* 2013). This hypothesis, which requires additional testing, posits that shared environmental conditions may directly select for similar tail morphology among the sexes of the same species, which may in turn affect factors such as flight efficiency or foraging constraints (e.g. Mumme 2002). Alternatively, it may be that production of ornamented plumage carries physiological costs, and highly ornamented females respond to this energetic burden by producing shorter, and presumably less costly, tails (Swaddle *et al.* 2000), though this hypothesis does not explain why a similar pattern is not observed in males.

In the case of plumage and bill colouration, there are reasons to be sceptical about the proposition that ecological selection *per se* is directly driving this relationship. First, if plumage or bill colouration were directly shaped by ecological context, we would expect at least some congruence between conspecific males and

females in patterns of expression (as with tail-length). Yet this is not the case: males are nearly uniformly highly ornamented whereas we find broad variation among females. Alternatively, certain selection pressures may affect females but not males, and to the degree that these pressures vary with latitude, they might yield the observed latitudinal patterns of female ornamentation. For example, plumage in female tanagers (Thraupidae) is likely to have evolved in response to differential predation pressures associated with nesting behaviour (e.g. open *v.* closed cups; Burns 1998), so if type of nest varied in relation to latitude in fairy-wrens (i.e. open nests in the temperate zone and closed nests in the tropics), this could potentially produce the observed pattern of ornamentation. However, all female fairy-wrens construct similar covered domes for nesting (Rowley and Russell 1997). It is also possible that predation pressure may vary along a latitudinal gradient, with increased predation risk away from the Equator selecting for reduced ornamentation among temperate zone species, but at present there is no support for this proposition, and no other obvious ecological factors that are associated with latitude that would affect females, but not males.

Second, there is biologically meaningful variation in the ecological environment experienced by different species of fairy-wren at the same latitude (Rowley and Russell 1997; see also Odeen *et al.* 2012). Latitude does not account for longitudinal and altitudinal variation, which can significantly alter ecological environment. For example, the two species of *Malurus* in Papua New Guinea have similar mean latitudes but inhabit distinctive habitats: tropical lowland forest for the Emperor Fairy-wren and open grasslands for the White-shouldered Fairy-wren. These species, which both have highly ornamented females, experience dramatically different vegetation structure, lighting conditions and predator and prey communities, making it unlikely that the ecological conditions *per se* are driving convergence towards a shared optimum value for female plumage or bill colouration. However, among species of fairy-wrens with more temperate distributions (among which there is no pronounced trend between ornamentation and latitude), ecological environment *per se* could potentially play a more prominent role in constraining and shaping patterns of ornamentation (e.g. Marchetti 1993). For example, the midpoints of the ranges of the White-winged (*M. leucopterus*), Splendid, Variegated and Red-backed Fairy-wrens all fall within 5° of each other, yet these species occupy distinct habitats within a broad longitudinal band of nearly 40° that includes desert, shrubland, open forest and grassland. Additional research using niche modelling and other approaches to assess more accurately the relationship between ecological conditions and ornamentation in these species would be desirable.

Alternatively, ecological environment may indirectly affect social selection pressures experienced by females and hence expression of ornamentation. African starlings provide one example of this proposed chain of causality: environmental conditions influence whether certain species breed cooperatively or not, females of cooperatively breeding species exhibit higher reproductive skew than females of pair-breeding species, and this increased skew is associated with more pronounced female ornamentation among the cooperatively breeding species (Rubenstein and Lovette 2009; see also Dey *et al.* 2012). As another example, the distribution of resources in time and space affects the frequency and intensity of dominance interactions,

which in turn are expected to serve as proximate selective pressures on ornament development (Bro-Jørgensen 2010). At the population level, ecological conditions may affect parameters such as the density of breeding individuals in time and space, thereby affecting the opportunity for sexual promiscuity and hence the strength and direction of mate-choice processes and sexual signals in both sexes (Stutchbury and Morton 1995).

In the case of fairy-wrens, average annual rainfall increases and seasonality decreases as one moves northward through Australia and into New Guinea (Rowley and Russell 1997). More rain and less seasonality, in turn, are associated with extended breeding seasons and even year-round breeding in the tropics (Rowley and Russell 1997). This axis of environmentally mediated variation in breeding behaviour may have several consequences for life history, social organisation and mating system that might in turn affect female ornamentation. In particular, species living in tropical regions are expected to exhibit greater survival rates (Martin 1995, 1996; Mauck *et al.* 1999), year-round territorial defence (Auer *et al.* 2007), greater male parental investment (Ashmole 1963; Martin *et al.* 2000) and, perhaps, reduced sexual promiscuity (Stutchbury and Morton 2001; Griffith *et al.* 2002; Macedo *et al.* 2008) relative to their temperate counterparts. Environmental conditions are also likely to affect dispersal behaviour and, as a consequence, operational sex-ratio and group composition in cooperatively breeding fairy-wrens (Kingma *et al.* 2009, 2010; Jetz and Rubenstein 2011; Rubenstein 2012b). These factors should all affect social selection for female ornamentation, either through competition for access to ecological resources, mates or reproductive opportunities (Tobias *et al.* 2012).

Questions for future research

In the rest of the article, I summarise some priority research questions related to female ornamentation in fairy-wrens, and discuss how these questions might be addressed at individual, population and interspecific levels. This effort is somewhat hindered by a lack of basic information on the social organisation and mating systems of the most ornamented species, especially those found in New Guinea. For this reason, some predictions below are based on the assumption that these species behave as typical tropical species (above; see also Stutchbury and Morton 2001), which may or may not turn out to be accurate. Indeed, descriptive natural history information on female life history and behaviour, along with more refined measures of female ornamentation, are fundamental research priorities that transcend all the specific questions outlined below. Similarly, a better understanding of how the ecological environment shapes female ornamentation, either directly (via constraints associated with ecological selection) or indirectly (via effects on social organisation and mating system), is a fundamental goal implicit in the research questions below.

Does female ornamentation affect competition for ecological resources?

Among tropical species, high survival rates may lead to increased competition for ecological resources and year-round territorial defence. Females of these species may contribute more directly to territorial defence than do their temperate zone coun-

terparts, and female ornamentation may play an important role in these aggressive interactions. Consistent with this idea, all three species of *Malurus* with high female plumage ornamentation and four of the five species with high bill ornamentation are likely to exhibit year-round territorial defence, whereas those with lower levels of ornamentation tend to form facultative flocks during the non-breeding season to varying degrees, depending on the seasonality of the habitat (Rowley and Russell 1997; see also Murphy *et al.* 2009b; Dey *et al.* 2012). Additional research is needed to determine whether increased female ornamentation is associated with aggression and social dominance at the population level. This could be tested by correlational (e.g. do more ornamented females hold higher quality territories, behave more aggressively, or exhibit dominance in naturally occurring interactions with conspecifics) or experimental approaches based on natural or manipulated variation in ornamentation (but see Hill 2011).

Does female ornamentation affect competition for reproductive opportunities?

When auxiliary helpers are female, operational sex-ratios may become skewed towards females or at least less skewed towards males. In such cases, competition to be the breeding female of the group may be intense and reproductive skew between females that obtain breeding positions and those that do not may be substantial. In these species, female ornaments that affect access to breeding opportunities by direct female contests are likely to be adaptive (Rubenstein and Lovette 2009). Female helpers have been recorded in at least six species of fairy-wren: White-winged, Blue-breasted, Splendid, Red-winged and Superb Fairy-wrens (Rowley and Russell 1997; Brouwer *et al.* 2011) and the Purple-crowned Fairy-wren (Kingma *et al.* 2010, 2011). Female helpers may occur in more species, especially poorly studied tropical species such as White-shouldered and Emperor Fairy-wrens. There is virtually no published information on behavioural interactions between females that determine social rank and ascension to the breeding position, and close observation of the social interactions that determine which female fills a naturally or experimentally created breeding vacancy are needed. More broadly, tests of this hypothesis would be similar to those proposed for access to ecological resources above, because in both cases social dominance in female–female social interactions is likely to be the primary mechanism by which ornaments serve an adaptive function. The difference occurs in the pay-off females receive for this dominance; access to food or territory in the one case *v.* access to breeding opportunity in the other.

Does female ornamentation affect male mate-choice?

Mutual mate-choice is thought to be most likely among socially, and sexually, monogamous species with obligate biparental care (Burley 1986; Kirkpatrick *et al.* 1990; Kraaijeveld *et al.* 2007), two characteristics often reported for tropical species (Ashmole 1963; Martin *et al.* 2000; Stutchbury and Morton 2001; Griffith *et al.* 2002; Macedo *et al.* 2008). Under these circumstances, females may compete for access to males (i.e. male mate-choice) in addition to males competing for access to females (i.e. female mate-choice). To the degree that this scenario applies in fairy-wrens, female ornamentation may signal female quality

and play a role in mate-attraction. However, males of tropical species appear to invest heavily in sperm production (Rowe and Pruett-Jones 2006), suggesting that rates of EPP are high in these species. Also, among Purple-crowned Fairy-wrens, the species with the lowest rate of EPP known to date (Kingma *et al.* 2009), females (as well as males) express a moderate degree of plumage ornamentation (rather than a high degree, as might be expected). Thus, the limited data available from tropical species provides mixed evidence for the hypothesis that female ornamentation affects male mate-choice in fairy-wrens.

Information on rates of EPP from tropical species with highly ornamented females would help with evaluating the relevance of mutual mate-choice as a driver of female ornamentation by comparative analyses. At the population level, information on prevalence of assortative mating and the degree to which female ornamentation accurately signals aspects of female quality that males value when selecting a mate (e.g. clutch-size, nestling provisioning, rates of nesting success or physiological condition) would be useful. Field- and aviary-based experiments could also shed light on this question. Manipulative experiments in which female plumage or bill colouration is experimentally adjusted could be used in concert with trials of male mate-choice in aviaries, or by following natural patterns of mate-choice in the field, to test the hypothesis that degree of ornamentation affects male choices.

What are the proximate mechanisms by which female ornaments are produced?

Testosterone (T) appears to drive the development of breeding plumage and dark bill colouration in male fairy-wrens (Peters *et al.* 2000, 2001; Peters 2002; Lindsay *et al.* 2009, 2011; Karubian *et al.* 2011) but the mechanisms underlying production of ornaments in females remains unclear. One possibility is that the mechanisms leading to elaboration of traits are conserved and present in females as well as males, such that a simple change (e.g. an increase or decrease in production of T in females) determines the degree of female ornamentation (Hau 2007). Alternatively, the mechanisms of signal elaboration may be evolutionarily labile, with different sensitivities to T and independently derived hormonal or non-hormonal mechanisms leading to ornamentation in females. Females of Superb Fairy-wrens (Peters 2007) and Red-backed Fairy-wrens (W. Lindsay, H. Schwabl and M. Webster, unpubl. data) produce at least some male-like ornamentation in response to T implants, consistent with the idea that T as a mechanism for trait elaboration is evolutionarily conserved. However, detailed studies of the hormonal mechanisms responsible for elaboration of traits in both sexes, and across closely related species that are monochromatic and dichromatic, are required to disentangle these possibilities. Doing so would have important consequences for our understanding of the evolutionary potential and constraint that hormonal mechanisms impose on reproductive phenotypes (McGlothlin *et al.* 2004; Hau 2007; Adkins-Regan 2008; Lessells 2008).

Concluding comments

This article organises, contextualises and describes basic patterns of female ornamentation in fairy-wrens in an evolutionary context. The findings here are consistent with the idea that ecological

environment shapes female ornamentation by indirect effects on social organisation and mating system. Additional study is likely to show that the forces governing female ornamentation are complex and vary across species and populations. For example, monsoonal areas of northern Australia and some portions of New Guinea exhibit marked seasonality despite the fact that these areas are in the tropics. Comparative work on the behavioural ecology of these tropical fairy-wrens in highly variable habitats may be particularly informative in linking seasonality, and its effects on mating and social systems, to female ornamentation. A case in point is the White-shouldered Fairy-wren, whose range extends from highly seasonal, monsoonal grasslands in southern New Guinea to areas in the highlands and other regions of New Guinea that experience little seasonal variation in temperature or rainfall relative to southern New Guinea (Schodde 1982, Rowley and Russell 1997). Populations of White-shouldered Fairy-wren inhabiting monsoonal grasslands exhibit low levels of ornamentation (similar to those found in females of its sister species from monsoonal Australia, the Red-backed Fairy-wren), whereas those in more aseasonal regions are either moderate or heavily ornamented (see Fig. 1). In at least one population with ornamented females in relatively aseasonal eastern New Guinea (*M. a. morotoni*), groups appear to defend year-round territories, to breed year-round, and may have female helpers that compete with each other for access for breeding opportunities within groups (J. Karubian, unpubl. data).

Although the White-shouldered Fairy-wren provides a particularly compelling case-study for testing the hypotheses and predictions presented above, it is likely that comparative and population-level studies in any of the fairy-wrens will uncover valuable information on the evolutionary history and adaptive significance of female ornamentation. Indeed, the patterns of ornamentation exhibited by female fairy-wrens, along with the rich variation within and between species in ecological environment and social organisation, suggest a host of intriguing adaptive scenarios for female ornamentation at the levels of population, subspecies, species and genus. As a new generation of studies uncovers these relationships, *Malurus* fairy-wrens are likely to provide insights into the evolutionary history, adaptive significance and proximate mechanisms underlying female ornamentation, with applicability for a broad range of social organisms.

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