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Variability, heritability and condition-dependence of the multidimensional male colour phenotype in a passerine bird

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Elaborate ornamental traits are commonly assumed to be honest signals of individual quality, owing to the presumed costs involved in their production and/or maintenance. Such traits are often highly variable, possibly because of condition-dependence and/or high underlying genetic variation, and it has been suggested that their expression should be more sensitive to condition and/or more heritable than non-ornamental traits. Many bird species display colourful plumage with multiple distinct patches of different developmental origins, forming complex colour phenotypes. Despite this complexity, colourful ornaments are often studied in isolation, without comparison to suitable non-ornamental controls. Based on plumage reflectance data collected over 8 years, we assessed the signalling potential of the multidimensional male colour phenotype in a tropical bird: the purple-crowned fairy-wren *Malurus coronatus*. Specifically, we tested the predictions that the expression of putative ornamental colours (purple and black – the breeding colours – and blue) is (1) more variable, (2) more heritable and (3) more condition-dependent compared to year-round non-ornamental colours (buff-white and brown). Our results show that ornamental colours exhibit greater levels of variability, and some chromatic components of purple and blue colouration appear slightly heritable ($h^2 = 0.19–0.30$). However, contrary to predictions of heightened condition-dependence in ornaments, only brightness of the buff-white and brown colouration increased with male body condition, although brightness of the purple colouration was related to male age as expected. Despite partial support for predictions, the lack of consistent patterns illustrates the complexity of visual signals and highlights the need to study colour phenotypes in their entirety.

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INTRODUCTION

Many animals use elaborate or conspicuous traits as signals of individual quality to choose mates and/or assess rivals (Darwin 1871). Such ornamental traits may reliably convey information about signallers' quality if trait production and/or maintenance entail substantial costs (Hamilton and Zuk 1982; Cotton et al. 2004; Andersson 2006; but see Prum 2010). Birds have frequently been used as model systems to investigate the evolution of conspicuous traits, as many species display ornamental colours in both males and females (Dale et al. 2015), which can sometimes be sexually dimorphic (Owens and Hartley 1998; Dunn et al. 2001). Yet, despite the fact that many species display complex phenotypes, including multiple distinct colour patches or patterns, the study of adaptive functions of colourful ornaments is often performed on single traits (Cotton et al. 2004). Moreover, studies using non-ornamental 'controls' (i.e. less elaborate, non-signalling traits) are scarce (Cotton et al. 2004; Gosden and Chenoweth 2011; but see Kemp and Rutowski 2007; Peters et al. 2008; Tibbetts 2010). In order to fully understand why colourful ornaments evolve and how they may serve as quality indicators, it is crucial to use an integrated approach by considering the complete colour phenotype and include suitable non-ornamental controls. Quantifying and comparing colour expression across different colours can be challenging, but recent methodological advances informed by the perceptual ability of birds (i.e. the broad implementation of psychophysical models of avian colour vision; Vorobyev et al. 1998; Renoult et al. 2017; Lind et al. 2017) allow us to do so in a robust way.

Ornamental colours used for signalling are often assumed to have specific characteristics that make them suitable for their role. Specifically, ornaments are expected to be: variable (Delhey and Peters 2008), honest signals of quality (Cotton et al. 2004) and/or heritable (Pomiankowski and Møller 1995). Variability is essential to facilitate discrimination between individuals if ornamental colours are used to select mates that are more attractive or of higher quality, or to gauge the competitiveness of potential rivals (Guilford and Dawkins 1991). Indeed, comparative analyses of colour variability across diverse colours in a large sample of birds demonstrated that more conspicuous colours show greater variability (Delhey et al. 2017) and this seems to follow the general pattern across ornaments (Pomiankowski and Møller 1995).

On the other hand, whether colours are honest indicators of individual quality remains a contentious issue (Cotton et al. 2004). Ornamental colours are implicitly assumed to be costlier and more strongly correlated with individual condition than non-ornamental colours, and such heightened condition-dependence would result from their being subject to stronger sexual selection, leading to

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greater exaggeration and higher sensitivity to condition (Rowe and Houle 1996; Cotton et al. 2004; Bonduriansky and Rowe 2005). Yet, this may not necessarily be the case: as ornamental traits undergo exaggeration due to intensifying sexual selection, their expression may become more or less sensitive to condition, or remain unchanged, depending on the precise form of the relationship between trait magnitude and cost (Johnstone et al. 2009).

Alternatively, if ornamental traits are not indicative of underlying qualities but simply reflect attractiveness to mates (Prum 2010), the main benefit derived by them would be to produce attractive offspring and this requires heritable variation. To what extent ornaments are heritable remains unclear. So far empirical work on ornament heritability has been equivocal (Pomiankowski and Møller 1995; Merilä and Sheldon 1999; Tibbetts 2010; Charmantier et al. 2017). Heritability is the ratio of additive genetic variance to total phenotypic variance, which includes environmental effects (Merilä and Sheldon 1999), and so consequently high levels of additive genetic variance may not necessarily result in high heritability if levels of environmental variance are also high (Price and Schluter 1991). In addition, directional selection on ornament expression may lead to the erosion of genetic variation further affecting heritability (Pomiankowski and Møller 1995). If an ornamental trait is indicative of 'good genes', we may expect its expression to be highly heritable; conversely, the trait could be an effective signal of the environmental conditions experienced by the individual, and therefore be subject to strong environmental effects and show low heritability. The balance of these processes may vary among traits, with their ornamental function (or lack thereof), and particularly with the mechanisms of colour production in the case of colour traits.

Bird plumage colours are produced by two main mechanisms that often interact to create the observable diversity of feather colours: the deposition of pigments (e.g. melanins and carotenoids), and the interaction of light with feather nanostructures (i.e. structural colouration; Shawkey and D'Alba 2017). The mechanistic separation of pigmentary and structural colours is not clear-cut, as both pigmentary and structural colours require microstructures and pigments respectively, to produce their colours (Shawkey and D'Alba 2017), yet is useful because it captures the main mechanism behind the colour. The main pigment in birds, melanin, which generates hues ranging from black to grey and brown to rufous, is endogenously synthesised (McGraw 2006). Hence, the expression of melanin-based colours is generally thought to be strongly genetically determined (Roulin and Ducrest 2013) and weakly sensitive to individual condition or quality (Badyaev and Hill 2000; Hill 2006; McGraw 2006), although support for this second assumption is mixed (Hill and Brawner 1998; McGraw et al. 2002; Meunier et al. 2011; Guindre-Parker and Love 2014). Indeed, a recent review (Roulin 2016) highlights a multiplicity of mechanisms through which melanin-based colours can be associated with individual quality and condition: from direct condition-dependence due to limiting resources to pleiotropic effects. This uncertainty highlights the need for a broader base of empirical evidence.

Similar to melanin-based colours, the highly ordered nanostructures composed of keratin and air, responsible for non-iridescent UV, violet and blue colours, are also endogenously produced and need to be assembled and arranged in three-dimensional arrays during feather development (Prum 2006). Whether structural colouration is costly to produce and/or related to individual quality appears, however, to vary among studies (Keyser and Hill 2000; McGraw et al. 2002; Prum 2006; Peters et al. 2011). While a recent meta-analysis summarising the available evidence indicates that structural colours can reflect individual quality, especially body condition and parasite resistance (White 2020), there have been no formal attempts to compare structural colours with those of a more pigmentary nature. To date, only a few studies have simultaneously studied multiple plumage patches of different developmental origins within a same species (Hadfield et al. 2007; Hegyi et al. 2007; Charmantier et al. 2017). Given the differences in the optical and developmental mechanisms underlying structural and melanin-based colouration, we may expect ornaments of both types to differ in their information content and heritability.

Here we aim to compare the variability, heritability and condition-dependence of male ornamental vs. non-ornamental colours using multiple colour traits within the same species: the purple-crowned fairy-wren *Malurus coronatus*. This tropical species breeds cooperatively (Kingma et al. 2010) year-round but with a peak in breeding activity during the wet season (December-March), and – in some years – a smaller peak in the late dry season (August–September) (Hall and Peters 2009; Peters et al. 2013). Males moult into a breeding plumage before the breeding season (July–September; Fan et al. 2017), replacing their dull brown non-breeding head plumage with a purple crown surrounding a black central patch and nape (Fig. 1). Adult males display black cheeks (ear coverts) year-round, but also replace cheek feathers when they moult into breeding plumage (pers. obs.). The presence (vs. absence), as well as the extent (only 16% of first-year males have complete breeding plumage) of male breeding colouration, signal male competitive ability (Fan et al. 2017, 2018). Other plumage patches do not change noticeably in colouration over the year, including the blue tail and the rest of the plumage that is mainly brown above (back and wings) and buff-white below (throat, breast and belly; Rowley and Russell 1997; Delhey et al. 2013; Fig. 1).

Thus, in this species, males display multiple coloured plumage patches, produced through different mechanisms and with variable signalling potential. Possible ornamental colours include the purple (structural and melanin-based) and black (melanin-based) breeding colouration (Fan et al. 2019), and the blue (structural) tail colouration (Fig. 1). Both are sexually dichromatic: the purple and black colours are not present in females, and the blue tail is less conspicuous and less blue in females and juveniles. In contrast, the rest of the plumage, which includes buff-white and brown (melanin-based) patches, is much less conspicuous and displayed year-round by both sexes at all ages (Delhey et al. 2013; Fig. 1); therefore, these patches are considered as non-ornamental colours. Here we use 8 years of reflectance measurements, together with psychophysical models of avian colour vision (Vorobyev et al. 1998) to compare the chromatic (colour) and achromatic (brightness) components of each patch colour in a way that reflects the perceptual ability of the intended receivers (conspecifics). We predict that putative ornamental colours of wild male purple-crowned fairy-wrens will have higher (1) variability and (2) heritability, as well as (3) stronger associations with indicators of individual quality and environmental conditions than non-ornamental colours.

MATERIALS AND METHODS

Field methods

We studied a population of *Malurus coronatus coronatus* at the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in northwest Australia (17°31′S, 126°6′E) from July 2005 to November 2017. From July 2005 to March 2011, every week we conducted population censuses to document group size and social status of each uniquely colour-banded male. Breeding activity was intensively monitored (see Kingma et al. 2009; Hidalgo Aranzamendi et al. 2016) and all nestlings banded and assigned an accurate hatch date. Birds captured as adults at the start of the study were classified as 'age unknown' with a minimum age based on the presence/absence of offspring (of known age) or the completeness of the breeding plumage. From October 2011 to November 2017, biannual population censuses were conducted in October–November and May–June instead (see Hidalgo Aranzamendi et al. 2016; Fan et al. 2017). All new unbanded

birds (fledglings, subordinates or immigrants) were banded, aged by age-specific development of appearance and behavioural cues (tail length, begging behaviour, plumage colour and bill colour). Parentage of all local birds was determined using six or nine microsatellite loci (see Kingma et al. 2009; Hidalgo Aranzamendi et al. 2016).

From 2005 to 2009 and from 2015 to 2017, we measured plumage reflectance of all birds that were captured using mist-nets, with repeated measures across or within years for some individuals (see 'Colour analysis' section below). We also measured tarsus length (a measure of body size) and body mass – together indicative of body condition at the time of colour measurement (see 'Statistical analyses' section below). Tarsus length could also be an indicator of male quality in *M. coronatus* as it correlates with song frequency (pitch) in male advertising songs (Hall et al. 2013).

We also quantified two environmental variables: territory quality and rainfall. Territory quality was estimated based on *Pandanus* cover surveys (Hidalgo Aranzamendi et al. 2016) as *M. coronatus coronatus* is highly dependent on *Pandanus* (wherein 51% of daytime is spent and 95% of nests are built; Kingma et al. 2011) and cover varies considerably within the population. Surveys were conducted annually between 2005 and 2008, and once in 2013, 2015 and 2017; for in-between sampling seasons data were interpolated at even increments or decrements. Most territories remain stable year-round, and any occasional changes in boundaries (territory shifts, splits or new establishments) were recorded throughout the study. Daily records of rainfall were obtained from a weather station at the study site (Mornington Wildlife Sanctuary) from October 2004 to December 2017 (Australian Bureau of Meteorology weather station 002076). A summary of the sampling regime for the different variables can be found in Table S1.

Colour analysis

From 2005 to 2009 (throughout the year) and from 2015 to 2017 (in October–November only), 195 different males were captured using mist-nets (357 captures in total) and their plumage reflectance measured (45% had repeated measures, across or within years, mostly 1–2 years apart). Reflectance measurements were collected using an AvaSpec-2048 spectrometer connected to an AvaLight-XE xenon pulsed light source via a bifurcated fibre optic cable fitted at the end with a cylindrical probe to standardise measuring distance and exclude ambient light. For each male we collected five reflectance spectra of five plumage patches – at predefined and standardised spots – at a perpendicular probe angle: (1) purple crown (for males in partial or complete breeding plumage; note that only purple feathers were measured when in partial breeding plumage), (2) black cheek, (3) buff-white throat, (4) brown back and (5) blue tail (Fig. 1). Reflectance spectra between 300 and 700 nm (the visual sensitivity range of birds; Cuthill 2006) were calculated relative to a WS-2 white standard using the software AVASOFT 7.5 (Fig. 2a, b). All spectrometry equipment was manufactured by Avantes (Apeldoorn, Netherlands). We also visually scored the extent of breeding plumage of each male on a scale between 0 and 100% (0–100% purple; see Fan et al. 2017, 2018).

To quantify chromatic variation, we used psychophysical models of avian colour vision (Vorobyev et al. 1998) following the formulas described in Cassey et al. (2008) as implemented by Delhey et al. (2015) in the R statistical environment. Visual models require knowledge of the visual sensitivity functions of the cones used in avian colour vision, their relative abundance in the retina and the spectrum of illuminating light. Colour vision in birds is mediated by four types of single cone sensitive to very short (*VS*), short (*S*), medium (*M*) and long (*L*) wavelengths of light (Vorobyev et al. 1998). Variation in visual sensitivity between species is

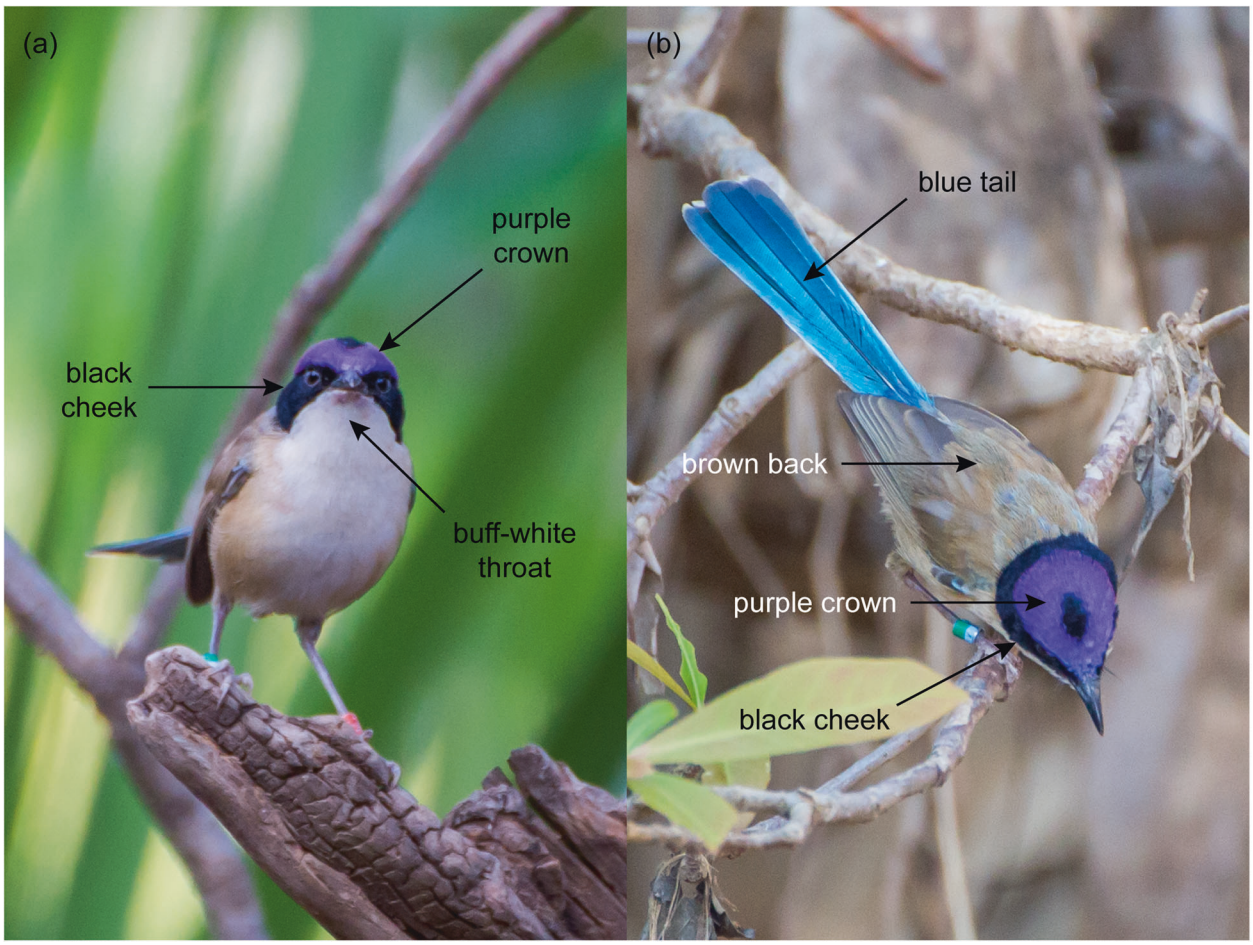

Fig. 1 Breeding plumage in male purple-crowned fairy-wrens. Photographs show a male in purple-and-black breeding plumage viewed (**a**) from the front and (**b**) from above. Arrows indicate the five plumage patches whose reflectance was measured in this study: purple crown (**a**, **b**), blue tail (**b**), buff-white throat (**a**), brown back (**b**) and black cheek (**a**, **b**). Photos: L. Lermusiaux.

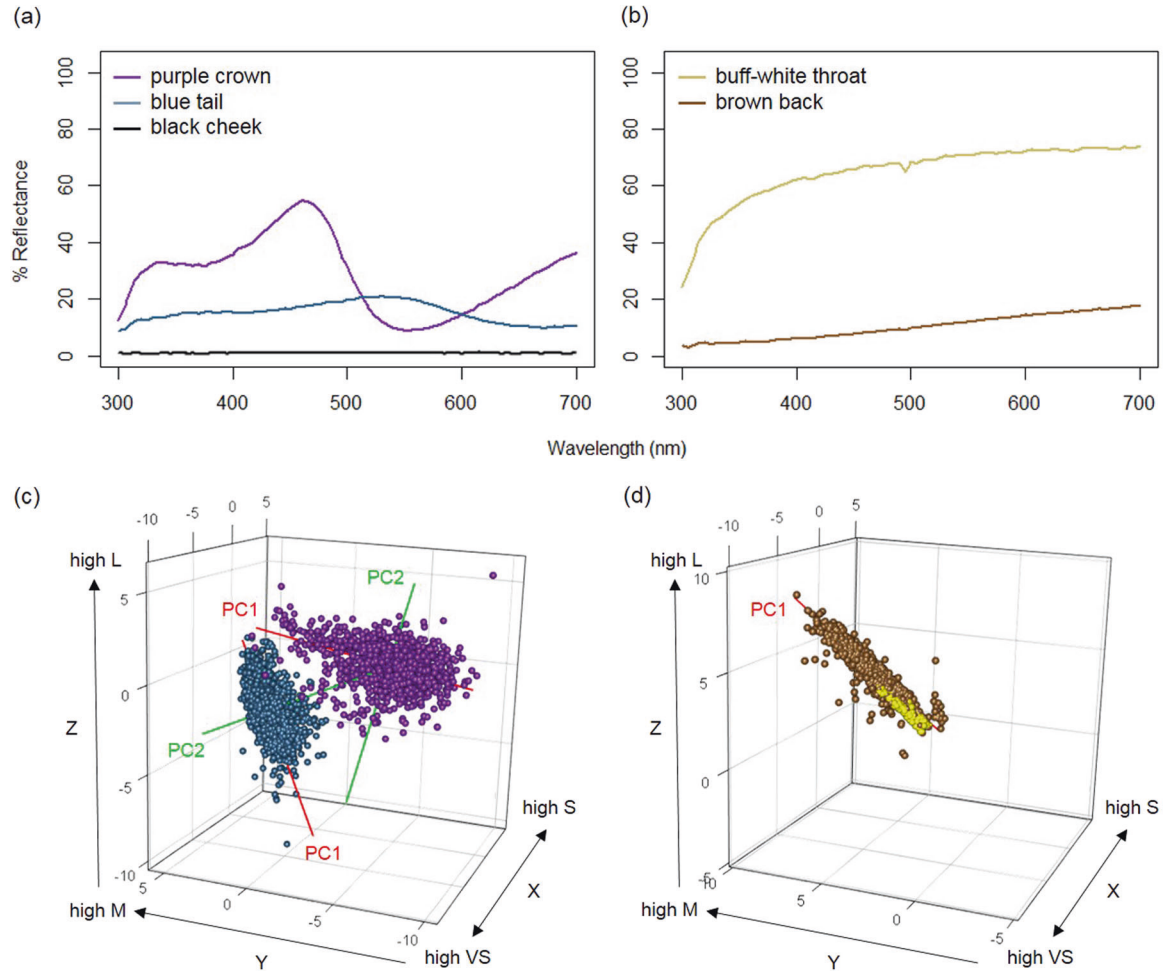

Fig. 2 Plumage reflectance spectra measured in male purple-crowned fairy-wrens and represented in their visual space. Shown are examples of reflectance spectrum measured in a male in breeding plumage for (**a**) the purple crown, black cheek and blue tail colouration, and (**b**) the buff-white throat and brown back colouration. Chromatic variability of each patch (except the black cheek) computed in the avian visual space is represented for (**c**) the purple crown and blue tail colouration, and (**d**) the buff-white throat (in yellow) and brown back colouration. PCs explaining ≥95% of chromatic variation for each colour are depicted, in red for PC1 axes and in green for PC2 axes; PC1 axes are very similar for the buff-white and brown colouration and therefore indistinguishable in (**d**). The *X*-axis represents stimulation of the *VS* cone relative to the *S* cone, higher values of the *Y*-axis represents higher stimulation of the *M* cone relative to *VS* and *S* cones, while the *Z*-axis represents higher relative stimulation of the *L* cone compared with the other three (units = jnd).

mainly restricted to the *VS* and *S* cones and birds can be generally classified in two groups: ultraviolet-sensitive (U-type) and violet-sensitive (V-type) species; and U-type species have *VS* cones with peak sensitivity shifted towards shorter wavelengths (Hart and Hunt 2007). As *M. coronatus* is a V-type species (Ödeen et al. 2012), we used the associated visual sensitivity function obtained from Endler and Mielke (2005). We used average cone proportions for the 22 species described in Hart (2001) (0.38:0.69:1.14:1.00 for *VS*:*S*:*M*:*L*, respectively) and combined these with behavioural estimates of the noise-to signal-ratio or Weber fraction for the *L* cone (0.1; Vorobyev et al. 1998; Lind et al. 2014; Olsson et al. 2017) using formula (10) in Vorobyev et al. (1998) to obtain the noise-to-signal ratios for each other cone type ($v_{VS} = 0.162$, $v_S = 0.120$, $v_M = 0.094$, $v_L = 0.1$). Cone proportions vary substantially between species but not consistently between different visual systems (Delhey et al. 2013) and given the lack of data for close relatives of fairy-wrens we decided to use the overall average. We used the spectrum of standard daylight (D65, open habitats) as illuminant (Vorobyev et al. 1998).

Visual models yield a set of quantum catches for the four types of single cone (i.e. how much each cone type is stimulated by a specific combination of reflectance spectrum and irradiance) that can be transformed into three coordinates x, y, z defining the position of each spectrum in the avian visual space (Fig. 2c, d). This visual space takes the shape of a tetrahedron where each apex represents the sole stimulation of one cone type (Endler and Mielke 2005). Using the formulas in Cassey et al. (2008), distances between points in visual space are measured in 'just noticeable differences' (jnd), whereby distances >1 jnd are considered to be discriminable by birds. We computed chromatic variability of all colours except black that contains very little discriminable chromatic variation.

For each patch colour (except black), we then performed a Principal Component Analysis (PCA, using the function 'princomp' in the R package "stats" (R Core Team 2017)) on the three xyz coordinates using a covariance matrix (Table S2). The computed principal component (PC) scores (also measured in jnd) can be used as independent chromatic variables (Fig. 2c, d). PCs that explain low amounts (<10%) of chromatic variability with a range <4 jnd are less likely to carry meaningful biological information. For this reason, purple PC3, blue PC3, buff-white PC2 and PC3, and brown PC2 and PC3 (Table S2), were excluded from further analysis.

Similarly, we computed achromatic variability (i.e. 'brightness' or luminance variation) as described by Delhey et al. (2015) for all plumage patches. We used a Weber fraction of 0.2, following Olsson et al. (2017). For each spectrum, the computed brightness value was noted L (lightness, in jnd).

As multiple (≤5) measurements were taken per plumage patch per capture, we averaged the values for each colorimetric variable (PC1, PC2 and L; differences between measurements were small and mostly below the discrimination threshold; see Appendix S1). We used these average PC

and L values in the statistical analyses below ($n_{purple} = 233$; $n_{black} = 248$; $n_{blue} = 350$; $n_{buff\text{-}white} = 208$; $n_{brown} = 349$).

Statistical analyses

For each colour, we first analysed (A) the degree of chromatic and achromatic variability. Then, we (B) determined whether the PCs and L correlated with any intrinsic or environmental factors, therefore testing for condition-dependence, and (C) used this information to estimate additive genetic effects and individual heritability of PCs and L using a detailed pedigree of our study population. All analyses were done in R 3.4.0 (R Core Team 2017).

Chromatic and achromatic variability of plumage reflectance. We tested whether the ornamental colours display a higher degree of variability compared to non-ornamental colours. To assess chromatic variability, for each patch colour (except black) we computed the distance between each reflectance spectrum and the centroid (i.e. the joint average of the xyz coordinates) of that colour in the bird visual space (Delhey and Peters 2008). To assess achromatic variability, for each patch colour we computed the distance to the average L value of that colour. Then, to test differences among patch colours in both chromatic and achromatic variability, we built two linear mixed models (LMMs), using the function 'lmer' in the package "lme4" (Bates et al. 2015), as well as the package "lmerTest" (Kuznetsova et al. 2015) to obtain *P*-values for the fitted models, with distance to the centroid and average L value as the respective response variables (both *log*-transformed to ensure normal distribution of residuals), patch colour as a fixed effect and individual identity as random effect. Using Tukey's Honest Significant Difference test, we performed post hoc comparisons between patch colours. In addition, we examined differences between ornamental vs. non-ornamental colours by running similar models as above but including 'colour type' (ornamental or non-ornamental) as a fixed effect instead.

Intrinsic and environmental correlates of plumage reflectance. The analyses described below were performed on the biologically meaningful colorimetric variable of each patch colour (PC1, PC2 and L for purple and blue; PC1 and L for buff-white and brown; L for black). Each colorimetric variable was fitted as the response variable in separate linear mixed models. As above, LMMs were built using the function 'lmer' and packages "lme4" and "lmerTest". To control for potential false positives due to multiple testing, we used the Benjamini–Hochberg procedure to decrease the false discovery rate (Benjamini and Hochberg 1995). Because our hypotheses state that ornamental colours should differ from non-ornamental colours, we divided the examined variables into two groups: (1) purple PC1, PC2, L, blue PC1, PC2, L and black L (i.e. 7 tests in total), and (2) buff-white PC1 and L, and brown PC1 and L (i.e. 4 tests in total). The false discovery rate was set at 0.05.

In each LMM, we fitted age, social status (subordinate or dominant), body condition, group size and territory quality as fixed effects. Values of body condition were obtained by extracting the residuals of a linear regression of body mass (at capture) against tarsus length and time of the day (hourly; controlled for because body mass varies throughout the day, generally being lowest at dawn and highest at dusk, particularly in relation to foraging intensity and energy expenditure; Kendeigh et al. 1969; Bednekoff and Houston 1994). We also re-ran these models fitting, instead of residuals, body mass and tarsus length as predictors in the same model. This revealed similar patterns as using residuals and confirmed that the effects of body condition as detected by using residuals are due to variation in body mass rather than tarsus length (see Table S11).

To determine whether population-level plumage reflectance depended on rainfall, we also included the cumulative rainfall over the past year (from November of the preceding calendar year to October) as a fixed effect and the same period was used in all models for consistency. We used rainfall across this broad period of time mainly because it has been previously shown to affect the timing of pre-breeding moult at the population level, whereas other time periods did not have such strong effects (Fan et al. 2017). In addition, we note that even though annual moult and pre-breeding moult happen at different time intervals, the entire plumage in fairy-wrens can be partially 'refreshed' by adventitious moulting across the year (Lantz and Karubian 2016; McQueen et al. 2021; pers. obs.) and thus conditions during this period could affect its expression. Finally, we focused on rainfall rather than temperature because rainfall is clearly associated with breeding onset and food availability in this species (Hidalgo-Aranzamendi et al. 2019), while temperature is not, which might be due to the fact that temperature variation is more predictable in our monsoonal tropical study site (although daily fluctuations can be marked; Hidalgo-Aranzamendi et al. 2019).

For LMMs associated with purple reflectance, we also included the extent of breeding plumage (0–100% purple) of each male to control for potential variation in males in partial breeding plumage due to the presence of brown feathers (all colorimetric variables associated with purple were indeed positively correlated with breeding plumage completeness; Table S4). Although different plumage patches have different moult schedules (see Appendix S2a), for consistency we also included the extent of breeding plumage (as a proxy for moulting stage) in the LMMs associated with the other plumage patches. Additionally, for LMMs associated with purple and black reflectance, we included the time interval since pre-breeding moult completion to account for potential within-year variation in colour due to fading, soiling and/or abrasion (Delhey et al. 2010). Since exact moult date was not known for all individuals, we first tested whether the average population-level moult date had an effect, and then using a more restricted dataset tested the effect of individual moult date variation. As including or excluding this variable made no significant difference, we only report the results for models excluding it (see Appendix S2b). The lack of colour fading in purple-crowned fairy-wrens is consistent with results in two other species in the genus (Lantz and Karubian 2016; McQueen et al. 2021).

Bird identity and year (1st July = start of year) were included as random intercepts to account for non-independence in the data. This analysis was first restricted to birds whose age was accurately known ($n = 81$–152 for the different patch colours), but as age did not affect any chromatic or achromatic variables (except for buff-white PC1, but the variations with age were below the discrimination threshold; Tables S4-S8; see Appendix S2c), it was repeated using two age classes, "1" and "2 + ", with all birds of unknown age but known to be at least 2 years old included in the "2 + " class (total sample size $n = 169$–235 for the different plumage patches). All continuous explanatory variables were mean-centred.

Heritability. To estimate heritability of each colorimetric variable, we built animal models using the genetic pedigree information available for our population (Wilson et al. 2010; Fig. S1). Because we needed to control for potential non-genetic sources of variation, we based our animal models on results from section (B). We used the pedigree data to transform the LMMs detailed above into animal models, using a Bayesian framework as implemented by the function 'MCMCglmm' within the R package "MCMCglmm" (Hadfield 2010). However, we only kept the fixed effects that were both statistically significant ($P < 0.05$) and biologically important, i.e. when the variation of the colorimetric variable across the range of realistic values of the fixed effect (e.g. from 9 to 13 g for body mass) was larger than 1 jnd. This approach allowed us to use simpler models with larger sample sizes (because we did not have data for all covariates across all individuals). As a result, most models contained no additional fixed effects, while models for blue, buff-white and brown L contained body condition, and models for purple PC1, purple PC2 and black L contained % purple. Random effects included bird identity (to account for repeated measurements on some individuals, i.e. permanent environmental variance), pedigree data (to estimate the additive genetic variance) and year. We ran between 2,005,000 and 27,005,000 iterations per model, from which we discarded the initial 5000 (burn-in period). Each chain was sampled so that the effective sample size was 1000 (i.e. at an interval between 2000 and 27,000 iterations according to the total number of iterations). The total number of iterations was chosen to ensure low autocorrelation among thinned samples. Fixed effect priors were normally distributed and centred on zero with large variances. Different relatively un-informative prior settings were used for the residuals and random effects; the detailed structure of each model is summarised in Table S14. Posterior means and 95% credible intervals (CI) were estimated across the thinned samples for heritabilities (i.e. additive genetic variance to total phenotypic variance ratios), as well as for analogous variance ratios attributable to other random effects (permanent environmental effects, annual effects and residuals) for comparison; annual effects are of particular interest as they may reflect large-scale environmental effects. Since heritability estimates (and CI) are constrained to be positive, we assessed their statistical significance by comparing models without and with the pedigree using the deviance information criterion (DIC) which is the MCMCglmm equivalent of the Akaike information criterion (for models excluding the pedigree: number of iterations = 305,000–405,000, burn-in period = 5000, effective sample size = 1000).

Table 1. Chromatic and achromatic variability of ornamental vs. non-ornamental colours in male *M. coronatus*.

	Chromatic variability			Achromatic variability		
Fixed effects	***β***	**SE**	***t***	***β***	**SE**	***t***
Intercept	−0.70	0.04	−19.74***	−0.78	0.05	−14.19***
Type[a]	**0.85**	**0.05**	**17.56*** **	**0.64**	**0.07**	**9.35*** **
Random effects (σ^2)						
Bird ID	0.01			0.02		
Residual	0.67			1.59		
Marginal / conditional R^2	0.21 / 0.22			0.06 / 0.07		

Shown are results from linear mixed models examining the effects of the type of colour (reference: [a]non-ornamental) on chromatic variability (calculated as the *log*-transformed distance to the colour centroid in the bird visual space; black excluded; $n = 1147$) and achromatic variability (calculated as the *log*-transformed distance to the colour average brightness; $n = 1396$). Level of significance: ***$P < 0.001$ (in bold).

In addition, we ran the exact same animal models using ASReml-R (which uses the frequentist 'restricted maximum likelihood' estimation method; Butler 2009), by running the function 'asreml' from the package "asreml", in order to check the robustness of the results obtained using MCMCglmm. Random effects were tested for significance using likelihood ratio tests of models with and without each effect, assuming a chi-squared distribution with 1 d.f. Finally, given that variation between individuals in body condition can have a genetic basis and body condition can in turn affect the expression of colours, accounting for the effects of body condition while estimating heritability may underestimate it. Thus, for those models that included body condition as fixed effect we re-ran the animal models using MCMCglmm without this covariate and re-computed heritability.

RESULTS

Chromatic variability

Male purple breeding colouration is characterised by a multi-peaked spectrum, as observed to a lesser extent for the blue tail colouration (Fig. 2a). For both colours, the PCA indicates a complex pattern of chromatic variation with two main principal components: purple PC1 (range of 13 jnd) and purple PC2 (range of 10 jnd) explain 76 and 20% of variation respectively, while blue PC1 (range of 12 jnd) and blue PC2 (range of 5 jnd) explain 81 and 18% of variation respectively (Fig. 2c and Table S2). Component loadings indicate that, compared to purple PC1 and PC2, blue PC1 and PC2 are oriented differently in the visual space, i.e. they stimulate the bird vision cones differently (Fig. 2c and Table S2). Higher values of purple PC1 are associated with spectra with higher reflectance in the shorter wavelengths (UV, blue) relative to longer wavelengths (green, red), and higher values of purple PC2 with spectra with higher red reflectance relative to shorter wavelengths (green) and simultaneously higher blue reflectance relative to UV, i.e. overall more purple spectra (Fig. S2). In contrast, higher values of blue PC1 correspond to spectra with lower red reflectance relative to shorter wavelengths (UV, blue and green), and higher values of blue PC2 to spectra with higher reflectance in the UV, blue and red ranges relative to green and yellow reflectance (Fig. S3).

Both buff-white throat and brown back colouration are characterised by a spectrum with no peak (Fig. 2b). In both cases, chromatic variation happens along one principal component axis explaining ≥97% of variation (Fig. 2d and Table S2). Visualisation of the spectra in the bird visual space shows that chromatic variation of the brown colouration encompasses chromatic variation of the buff-white colouration, but exhibits greater variation in one direction (range of 4 jnd and 10 jnd for buff-white PC1 and brown PC1 respectively; Fig. 2d). In line with this, the loadings of PC1 are very similar for both colours (Table S2), and higher values of PC1 are associated with higher UV reflectance and lower red reflectance (Fig. S4).

Comparison of chromatic variability among the four colours shows that variability significantly decreases as follows: purple (mean ± SE = 1.58 ± 0.08 jnd) > blue (0.97 ± 0.06 jnd) > brown (0.68 ± 0.04 jnd) > buff-white (0.30 ± 0.02 jnd) (Table S3). Additionally, the ornamental colours (purple and blue) display higher chromatic variability compared to the non-ornamental colours (buff-white and brown; ornamental vs. non-ornamental = 1.16 ± 0.02 jnd vs. 0.50 ± 0.02 jnd; Table 1).

Achromatic (brightness) variability

Purple, blue, buff-white and brown L show variations in the population close to 10 jnd. In contrast, black L shows a substantially larger variation of 40 jnd. Comparison of achromatic variability among the five colours shows that variability decreases as follows: black (mean ± SE = 2.51 ± 0.25 jnd) > blue (0.62 ± 0.06 jnd) ≈ purple (0.50 ± 0.04 jnd) ≈ buff-white (0.49 ± 0.06 jnd) ≈ brown (0.44 ± 0.04 jnd) (Table S3). Additionally, the ornamental colours (purple, black and blue) display higher achromatic variability compared to the non-ornamental colours (buff-white and brown; ornamental vs. non-ornamental = 0.87 ± 0.06 jnd vs. 0.46 ± 0.02 jnd; Table 1).

Intrinsic and environmental correlates of plumage reflectance

No aspects of chromatic variation of the purple crown, blue tail, buff-white throat and brown back colouration show biologically meaningful association with any of the investigated intrinsic and environmental variables, namely age class (1- vs. ≥2-year-old), social status (subordinate vs. dominant), body condition, group size, territory quality and rainfall accumulated over the previous year (Fig. 3, Tables 2 and S4–S8; but see results on large-scale annual effects below). Some correlations were detected for a few chromatic variables, but only two remained statistically significant after running the false discovery rate (FDR) procedure – between buff-white PC1 and age class, as well as territory quality – and the associated biological effects are all small (i.e. the transition from first-year to older males, and the range of variation in territory quality do not correlate with chromatic differences that can be easily discriminated by receivers (<1 jnd); Fig. 3 and Tables S4–S8 and S10). The random effect 'year' explains up to 16% of the phenotypic variance of purple and blue PC1 and PC2, while it explains 35 and 44% of the phenotypic variance of buff-white PC1 and brown PC1 respectively (Table S9), indicating substantially larger annual variations in the non-ornamental colours (in agreement with our results from the animal models below; Table S16 and Fig. 5).

In contrast, achromatic brightness (L) of the different patch colours is related to age and/or body condition (Table 2). Purple L

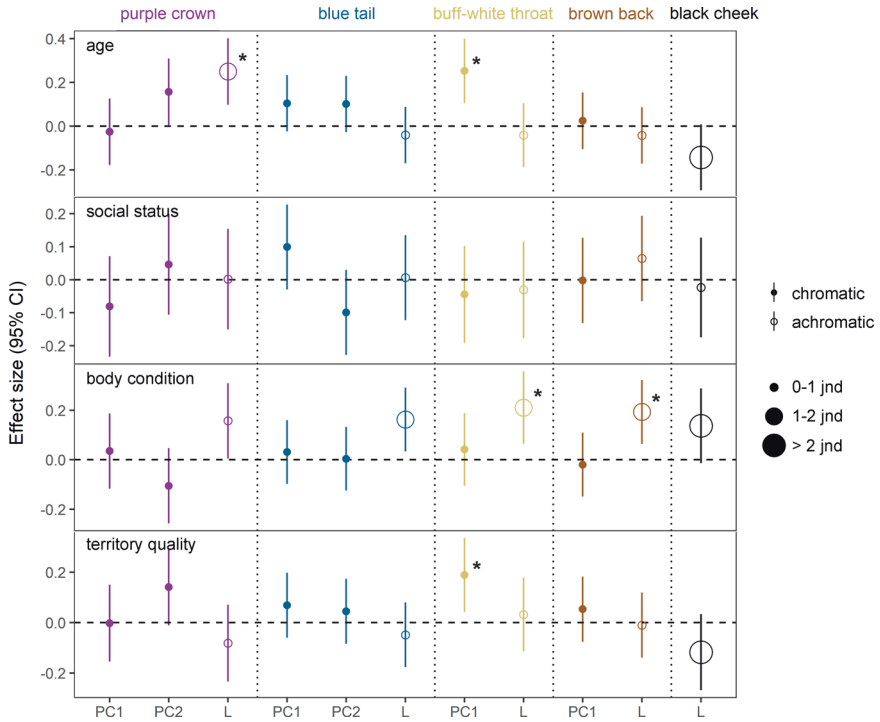

Fig. 3 Effect size estimates of correlations between age class (1- vs. 2+-year-old), social status (subordinate vs. dominant), body condition and territory quality and the chromatic (PC1, PC2) and achromatic (L) components of the colour phenotype of male purple-crowned fairy-wrens. Circle area depicts whether variation in PCs and L across the range of realistic values of the predictors is between 0 and 1 jnd (i.e. not discriminable by conspecifics), between 1 and 2 jnd, or larger than 2 jnd, and error bars the 95% confidence intervals. Asterisks depict significant correlations after FDR procedure.

is positively correlated with age, with 2-year-old and older males producing brighter crowns than 1-year-old males (Fig. 3 and Table S4). This difference is quite small (~1 jnd), but the effect remains statistically significant after FDR procedure (Table S10). Conversely, black L shows a negative trend with age, with 2-year-old and older males producing darker cheeks than 1-year-old males; this difference is large but marginally non-significant and does not remain after FDR procedure (Fig. 3 and Tables S8 and S10). In addition, the brightness of all colours exhibits a positive association with body condition (marginally non-significant for black; Fig. 3 and Tables S4–S8): males in better condition display a brighter plumage overall. While these differences are large for the black colouration, they are much smaller and only discriminable between individuals with the lowest and highest values of body condition for other colours (just below the discrimination threshold for purple; Fig. 3 and Tables S4–S8). However, only the associations with the non-ornamental colours (buff-white and brown L) remain statistically significant after FDR procedure (Tables 2 and S10). For all colours, the 'year' effect explains between 15 and 28% of the phenotypic variance of L (Table S9), indicating moderate annual variation in overall plumage brightness (also in line with our results from the animal models below; Table S16 and Fig. 5).

Heritability of plumage reflectance

Purple PC2, blue PC1 and blue PC2 show moderate to substantial heritability estimates (MCMCglmm: h^2 (ΔDIC) = 0.22 (3.92), 0.30 (14.13), 0.19 (11.66), respectively; ASReml-R: h^2 (P) = 0.27 (0.14), 0.37 (<0.001), 0.27 (<0.001), respectively; Fig. 4 and Table S15), with moderate to substantial estimates of additive genetic variance for purple PC2 and blue PC1 (V_A = 0.18 and 0.55 respectively; Table S15). In contrast, the heritability estimates of all other chromatic and achromatic variables are rather low (<0.12, except for purple L with h^2 = 0.19 (P = 0.14) when using ASReml-R; Fig. 4. and Table S15). We note however that the credible intervals (and standard errors) for some estimates are very broad (Fig. 4 and Table S15); it is therefore difficult to make confident inferences about their exact values. Additionally, for all colour components the MCMCglmm model including the additive genetic effects has a lower DIC value (i.e. a better fit) than that excluding it, although the magnitude of difference varies among colour components (ΔDIC > 10 for blue PC1 and blue PC2 only; Table S15). Estimates of heritability are not affected by the inclusion of the fixed effect body condition (Table S17).

Comparison of the proportions of total phenotypic variance explained by the different random effects indicates that colour components exhibiting moderate to high heritability tend to show low to moderate annual variation (the random effect 'year' explains up to 21% of the phenotypic variance of purple PC2, blue PC1 and blue PC2; Table S16 and Fig. 5). In contrast, weakly heritable colour components generally display substantial annual variation ('year' explains 22–43% of variance of all other colour components except purple PC1 (5%); Table S16 and Fig. 5). More particularly, the chromatic components of non-ornamental colours (i.e. buff-white PC1 and brown PC1) exhibit significantly larger annual variation than the chromatic components of ornamental colours (i.e. purple PC1 and PC2, and blue PC1 and PC2; Table S16 and Fig. 5).

DISCUSSION

In this study, we examined the variability, heritability and condition-dependence of the multidimensional colour phenotype of wild male *M. coronatus*, which consists of both ornamental and non-ornamental colours. As expected, ornamental colours appeared to display (1) greater levels of variability, and there was some evidence for (2) higher levels of heritability for some of them. However, there was (3) limited support for heightened

Table 2. A summary of results indicating which plumage patch components are associated with indicators of individual quality and environmental conditions.

Intrinsic and environmental variables	Purple			Blue			Buff-white		Brown		Black
	PC1	PC2	L	PC1	PC2	L	PC1	L	PC1	L	L
Age (1- vs. 2 + -year-old)	NS	NS	+***	NS	NS	NS	NS	NS	NS	NS	NS
Social status (subordinate vs. dominant)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Body condition	NS	NS	NS	NS	NS	NS	NS	+**	NS	+**	NS
Group size	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Territory quality	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Rainfall	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% purple	+***	+***	NS	NS	NS	NS	NS	NS	NS	NS	−***

Full results are found in Tables S4–S10. Depicted are the direction of the association (positive or negative) and the level of significance after FDR procedure (***$P < 0.001$, **$P < 0.01$, NS: $P > 0.05$).

condition-dependence of ornamental colours compared to non-ornamental colours. Specifically, seasonal male purple breeding colouration appeared to show high phenotypic variation, with partial heritable components, as well as some association with age, but no link with condition.

Variability

Ornamental traits subject to directional selection often show high variability (but see Evans and Barnard 1995; Reinhold 2011), an important feature that can inform about differences in quality among signallers. Strong directional selection should, however, rapidly deplete the underlying genetic variation and lead to reduced phenotypic variability (Taylor and Williams 1982; Merilä and Sheldon 1999). Contrasting with this notion, our data provide support for greater levels of variability in the putative ornamental colours of male *M. coronatus* compared to the non-ornamental colours: the purple and blue plumage displayed higher chromatic variability, while the black plumage showed higher achromatic variability than any other colour (Table S3 and Fig. 2). This is in line with the findings of Delhey et al. (2017) which, based on more than 100 plumage colours across 55 bird species, demonstrated that more conspicuous colours display greater chromatic variability. Furthermore, the purple and blue colouration are both unusually complex, with two axes of chromatic variation (Fig. 2), contrasting with most plumage colours that generally show a single axis of chromatic variation (Endler et al. 2005; Delhey et al. 2010, 2013, 2015). Therefore, as highly variable, complex traits, both the purple and blue plumage, and perhaps to a lesser extent the black plumage, have a strong potential to inform on various aspects of the signaller's quality and may be considered as prime candidates for being elaborate, successful signals in male *M. coronatus*.

Heritability

Some chromatic components of the ornamental seasonal purple crown and sexually dichromatic blue tail colouration (purple PC2 and blue PC1) exhibited greater levels of additive genetic variance (Table S15) and were also more heritable than any other colour components, even though heritabilities were not particularly high ($h^2 = 0.19$–0.30; Figs. 4 and 5). In addition, our estimates of heritability may be overestimated because we could not separate the effects of common rearing environment (nest sharing) from true genetic effects. Moreover, it is also worth mentioning that in the case of the purple colour, only the second chromatic axis of variation (PC2) showed some level of heritability and this axis accounted only for 20% of the chromatic variation in this plumage patch.

Earlier quantitative genetic research has reported variable levels of heritability of bird plumage colours, notably depending on their developmental mechanism. Previous studies supported a tight genetic control and high heritability of melanin-based colouration ($h^2 = 0.53$–1.0) based on endogenous production of melanin, although these studies focused mostly on polymorphic species (Roulin and Ducrest 2013; Kappers et al. 2018; Dobson et al. 2019). In addition, chromatic components of carotenoid-based coloration (i.e. yellow, orange and red plumages based on pigments acquired through the diet; McGraw 2006) have been found to exhibit low to moderate heritability ($h^2 = 0.06$–0.29), while achromatic brightness appears mostly not heritable (Hadfield et al. 2006; Evans and Sheldon 2012; Charmantier et al. 2017). On the other hand, structural colouration generally shows low heritability based on studies of blue colours in blue tits ($h^2 = 0.12$ and 0.05 for the crown and primary coverts respectively; $h^2 = 0.01$–0.12 for the tail; Hadfield et al. 2007; Class et al. 2019), but this seems to vary between sexes and subspecies (in another study: $h^2 = 0.06$–0.23 for chromatic and achromatic components of the crown; Charmantier et al. 2017).

Heritability of plumage colours also appears to vary with underlying mechanisms of colour production in our study. However, although some of our estimates of additive genetic variance and heritability showed relatively large uncertainty, our results seem to disagree with previous findings: in male *M. coronatus*, structural colours (i.e. blue and to a lesser extent purple) showed higher heritable variation than melanin-based colours (i.e. black and brown) that were weakly heritable ($h^2 = 0.06$–0.11; Figs. 4 and 5). Taken together, those data suggest that our understanding of the genetic basis of the different types of plumage colouration is still incomplete, and more particularly highlight the need for further quantitative genetic analyses of feather structural colouration. Additionally, further work is required to determine more specifically the nature of the genetic aspects that may be signalled by the purple and blue colouration, and how they may influence male fitness, particularly in terms of reproductive benefits.

Condition-dependence

Although all ornamental colours showed greater levels of variability and some components appeared more heritable compared to non-ornamental colours, there was no clear indication of stronger condition-dependence: only the brightness of the buff-white and brown plumage was correlated with male body condition, while none of the other colours were related to condition (Fig. 3). Males in better body condition display brighter buff-white and brown patches than those in poorer condition, and the strength of this effect was similar for both colours (although only discriminable between individuals in very different condition; Fig. 3). Meta-analytical evidence suggests that in general melanin-based colours can be associated with indicators of quality such as

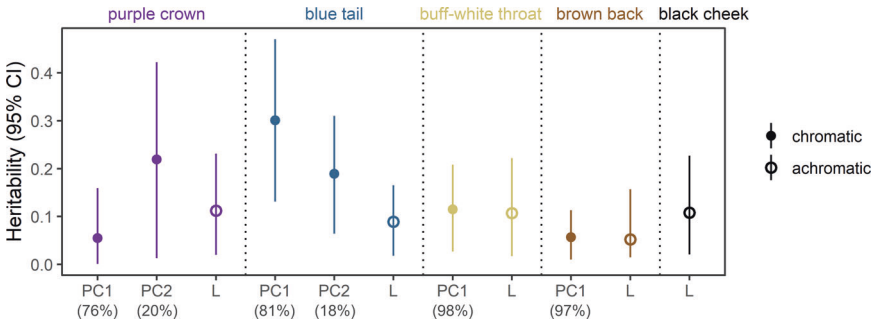

Fig. 4 Heritability of chromatic (PC1, PC2) and achromatic (L) components of colour variation in five plumage patches of male purple-crowned fairy-wrens (posterior mean values obtained using MCMCglmm). PC2 of the purple crown colouration and PC1 and PC2 of the blue tail colouration show moderate to substantial heritability. Error bars depict the 95% credible intervals. Also indicated (in brackets) is the proportion of chromatic variation explained by each PC for each patch colour. Purple: higher PC1 = higher UV/blue reflectance relative to green/red, higher PC2 = higher red reflectance relative to green and higher blue reflectance relative to UV, i.e. more purple overall; blue: higher PC1 = lower red reflectance relative to UV, blue and green, higher PC2 = higher UV, blue and red reflectance relative to green/yellow; buff-white and brown: higher PC1 = higher UV and lower red reflectance.

condition (Guindre-Parker and Love 2014), although most of the evidence comes from putative ornamental traits. Puzzlingly, our results suggest that putative non-ornamental traits can also show condition-dependent expression.

A similar positive association between individual condition and brightness of melanin-based patches was previously reported in several passerine species, and linked to changes in feather microstructure (barbule density and barb thickness) rather than melanin content (density of melanin granules; D'Alba et al. 2014). Possibly, in male *M. coronatus*, body condition also influences the growth of feather microstructure in buff-white and brown patches (both melanin-based), affecting their brightness in a similar way. Alternatively, melanin deposition in these patches may be lower in males in better body condition, thereby increasing patch brightness (McGraw et al. 2005). Analyses of overall feather structure (including both pigmentary and structural components) would help verify and potentially disentangle these two hypotheses. The lack of condition-dependence of the structural ornamental colours in our study species (purple and blue) stands in contrast with a recent meta-analysis that revealed overall positive effects of condition on the expression of structural colours (White 2020), but fits with experimental work on a different species of fairy-wren. In the closely-related superb fairy-wren (*Malurus cyaneus*), experimental testosterone implants forced males to moult earlier in the year when in poorer body condition and under challenging environmental conditions, yet this did not affect the expression of UV/blue plumage colours (McQueen et al. 2021).

Nevertheless, we must interpret the lack of condition-dependence with caution since in this population body condition does not seem to be associated with other indicators of quality such as survival, reproductive success or acquisition of a breeding position (Roast et al. 2020). Moreover, we used only one, relatively crude, estimate of body condition based on body mass taken at the time of colour measurement, when males were possibly at different stages of moult (during the pre- or post-breeding moult, or in between). As the moulting process may entail substantial energetic costs (Lindström et al. 1993), this might have impacted our estimates of body condition. Nonetheless, within-year repeatability of male body mass appears to be high in our study ($R = 0.53–0.90$, $P < 0.001$ to $P < 0.01$, for four different years; Table S18; see Appendix S2d), suggesting that this trait shows significant consistency and that our estimates of body condition are thus relatively robust to short-term temporal variation.

Our study identified no environmental variable that affected colour expression. However, decomposition of the total phenotypic variance of all colour components across years showed significant variation between years, particularly for the chromatic components of buff-white and brown colours (Fig. 5). This suggests that some environmental factors other than those measured in our study (i.e. annual precipitation and habitat quality) may affect the expression of these colours. Such an annual effect may be driven by large-scale environmental variations (Garant et al. 2004; Masello et al. 2008; Evans and Sheldon 2012) during the period of moult, such as wet spells and drought. The non-ornamental patches are moulted around April-May (after the wet season), which differs from the moult schedules of ornamental colours, peaking around September–October (at the end of the dry season) for the purple and black patches, and occurring year-round for the blue tail (Schodde 1982; Rowley and Russell 1997; Fan et al. 2017; unpublished data). During the wet season, birds at our study site may experience extreme climatic events, including very hot days (>40 °C) and extreme levels of rainfall (>48 mm a day), whose frequency and intensity vary among years (e.g. from 2006 to 2018, within the January-March period were recorded 1–49 days above 40 °C –max. 44.8 °C– and 0–6 days of heavy rainfall –max. 151 mm), while such events (almost) never occur during the dry season (Hidalgo Aranzamendi 2017; unpublished data). Therefore, the moult of the non-ornamental colours takes place after a period characterised by generally more fluctuating weather conditions from 1 year to another, possibly accounting for the larger annual variations.

Although there was no evidence for a link between ornamental colouration and condition, the brightness of the purple breeding colouration appeared to increase with male age, again in disagreement with meta-analytical data that indicate no overall association between age and structural colours (White 2020). That 2-year-old and older males produce brighter purple crowns compared to first-year males, may represent an age-dependent investment in signals, where the production of costly traits is delayed until older ages to indicate higher viability at that point (Kokko 1997). Alternatively, this may represent delayed plumage maturation, whereby younger males display a less elaborate version of the ornament to minimise aggressions by older birds (Hawkins et al. 2012). Age may function as a signal of (genetic) quality since an older age necessarily indicates the ability of an individual to survive up to that age at least (Trivers 1972; Manning 1985). Honest signalling should favour an increase in the level of sexual advertisement over time and therefore preferences for older males (Brooks and Kemp 2001; Proulx et al. 2002). Although the average difference in brightness between first-year males and older males is relatively small (~1 jnd; Fig. 3), age-dependence of the purple breeding colouration could reflect honest signalling of male quality in *M. coronatus*. Moreover, as first-year males develop a less complete breeding plumage (only half-complete on average) than older males (Fan et al. 2017, 2018), they may invest less in the elaboration of their relatively limited purple patch.

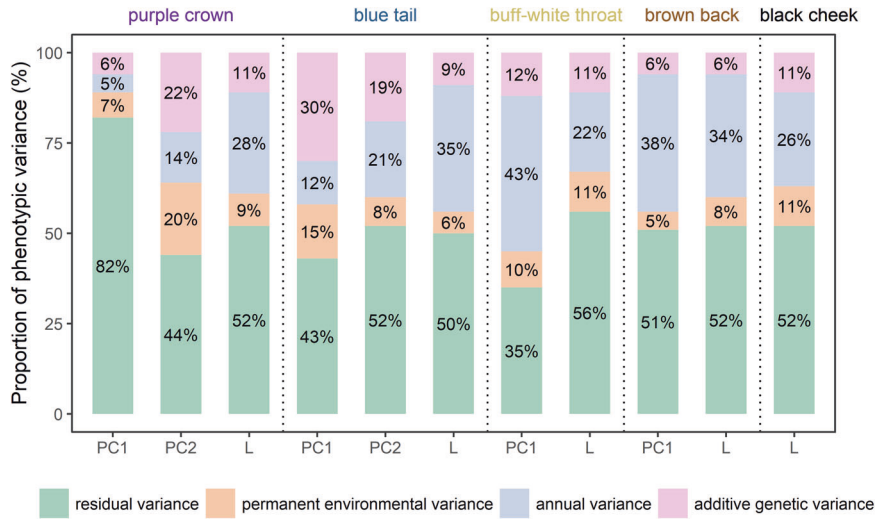

Fig. 5 Proportion of total phenotypic variance explained by random effects (stacked) for the chromatic (PC1, PC2) and achromatic (L) components of the colour phenotype (obtained using MCMCglmm). Annual variation in colouration generally appears substantial, especially for weakly heritable colour components, accounting for a larger proportion of chromatic variation in non-ornamental colours compared to ornamental colours.

CONCLUSION

Overall, we found limited support for the hypothesis that ornamental colours are more strongly correlated with individual condition than non-ornamental colours. Nonetheless, ornamental colours showed somewhat higher heritability than melanin-based colours. Specifically, the main ornamental colour, i.e. the purple breeding colouration, appeared to be highly variable, partly heritable and related to male age, therefore showing some potential to act as a signal of male quality or attractiveness. The apparent lack of condition-dependence may however reflect the absence of major physiological costs involved in its production or maintenance. Through the integrated assessment and comparison of multiple ornamental and non-ornamental colours, our study demonstrates that ornamental traits may not follow a consistent pattern, therefore challenging the existing theories regarding their evolution, and calling for more studies using an integrated approach. This will help to provide a more complete picture of why and how complex animal signals might evolve.

Data archiving

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1zcrjdfsb.

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Declarations (Ethics)

COMPETING INTERESTS

The authors declare no competing interests.

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