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Original Article

Which plumage patches provide information about condition and success in a female fairy-wren?

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Recent evidence suggests that female ornaments can commonly act as signals. However, how signaling functions might be affected by the tendency for reduced ornament elaboration in relation to males is less well-understood. We address this in mutually ornamented purple-crowned fairy-wrens. We investigated putatively ornamental (tail, ear coverts, crown) and non-ornamental (throat, back) plumage patches in females and compared our findings to previous studies in males. Both sexes have brown backs, buff-white throats, and turquoise-blue tails (bluer in males), while ear coverts are rufous in females and black in males. Both sexes also have a seasonal crown (slate-gray in females, black-and-purple in males). Dominant (breeder) females expressed more complete and grayer (more ornamented) crowns, although variation in coloration should not be discriminable by individuals. Unexpectedly, subordinates showed more colorful (saturated) rufous ear coverts, which should be discriminable. Condition-dependence was only evident for crown completeness (% slate-gray cover). Females with more reddish-brown backs were more reproductively successful. Variation in plumage characteristics did not explain differential allocation by mates or chances of gaining dominance. Our outcomes were not entirely consistent with findings in males. The most notable disparity was for the crown, a signal used in male-male competition that in females seems to be expressed as an incomplete version of the male crown that is not associated with fitness benefits. Our study shows that in a species, multiple traits can vary in their information content and that female ornaments can sometimes be less informative than in males, even those that are produced seasonally.

Key words: **badges of status, genetic correlations, *Malurus coronatus*, mutual ornamentation, partial ornamentation, seasonal breeding plumage.**

INTRODUCTION

Exaggerated phenotypic traits that look like decorations are broadly known as ornaments. These traits are known to act as signals for attracting mates of the opposite sex or for deterring rivals, and commonly advertise the bearers' quality (Andersson 1994; Johnstone 1995). However, in females, ornaments were once largely assumed to be non-functional by-products of selection on male ornaments resulting from cross-sex genetic correlations (i.e., the intersex genetic correlation hypothesis; Lande 1980). This assumption was based on the observation that female ornaments are often expressed as less elaborate, sometimes very much reduced, versions of male ornaments (Amundsen 2000a, b). Although female ornaments indeed at times have no discernible function (e.g., Prum 2017; Clark and Rankin 2020), research over the past two decades suggests that they can often act as signals under direct selection (reviewed in Hare and Simmons 2019; Doutrelant et al. 2020; Nolazco et al. 2022).

Females are usually assumed to be more constrained than males to produce elaborate ornaments. Unlike males, females mostly increase fitness by investing directly in offspring rather than by securing multiple matings (Trivers 1972; Clutton-Brock 2007, 2009; Doutrelant et al. 2020). Moreover, it is often assumed that female ornamentation and fecundity trade-off against each other (Fitzpatrick et al. 1995, Chenoweth et al. 2006, but see Mobley et

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al. 2018), which provides an explanation for why ornaments are not only less common in females, but also often reduced in elaboration in comparison to males. Natural selection should resolve this conflict with reproduction by reducing or breaking cross-sex genetic correlations (Chenoweth et al. 2006; Swiek and Langkilde 2013; Kraaijeveld 2014; Sedláček et al. 2014). Indeed, comparative studies suggest rapid evolutionary changes in ornamentation can occur independently in one sex or another (e.g., Burns 1998; Wiens 1999; Ord and Stuart-Fox 2006; Hofmann et al. 2008). Although this may result in the absence of female ornamentation, apparently it often results in lower ornament expression than in males (Fitzpatrick et al. 1995; Cuervo and Møller 2000; Chenoweth et al. 2006; Hare and Simmons 2019).

Empirical studies suggest that female ornaments can widely serve to attract mates and as "badges of status" that indicate competitive ability to monopolize superior mates or other limited resources for reproduction (LeBas 2006; Tobias et al. 2012; Hare and Simmons 2019). These are labeled as sexually selected when the targets are mates or socially selected when competition is over resources that ultimately increase reproductive success (sensu Shuker and Kvarnemo 2021). Ornamental traits can fulfill such roles in many systems under certain conditions. First, in monogamous and polyandrous mating systems relative to polygynous systems, the availability of male mates decreases, and females are expected to compete for access to limited and superior males. Therefore, female ornaments are more likely to evolve under sexual selection (e.g., via male mate choice) in polyandrous and monogamous species than in polygynous species (Fitzpatrick et al. 1995; Dale et al. 2015; Fitzpatrick and Servedio 2017, 2018). Second, male care may also favor the evolution of female ornaments. This can occur if males invest more in parental care when mated with highly ornamented females (Lyu et al. 2017) or if male care alleviates costs in females (e.g., exposure to predators, energy allocation) that trade-off with ornament investment (Fitzpatrick et al. 1995). For example, in the polyandrous sex-role reversed species, female-biased ornamentation can be explained by stronger sexual selection acting on females and the predominance of male-biased or male-only postzygotic care (e.g., LeBas et al. 2003; Schamel et al. 2004; Mobley et al. 2018). Likewise, in cooperative breeders, which are characterized by high reproductive skew among females and alloparental care (Clutton-Brock et al. 2010; Raihani and Clutton-Brock 2010), the incidence of female ornamentation is particularly high (Rubenstein and Lovette 2009; Karubian 2013).

Irrespective of their specific function, female ornaments can act as honest signals of quality (reviewed in Hare and Simmons 2019; Doutrelant et al. 2020; Hernández et al. 2021). Honest signaling is important because communicating reliable information of condition or quality (here: interchangeable terms indicating superior individuals in the population), at least on average, makes these traits evolutionarily stable (Johnstone and Grafen 1993). Thus, signalers and receivers benefit from communicating reliable messages and responding to them accordingly, rather than cheating or ignoring them (Searcy and Nowicki 2005). However, females sometimes express ornaments that are so reduced in comparison to males that production cost in itself would not be expected to ensure honest signaling and avoid cheating. In such cases, alternative costs associated with ornament expression may be involved to ensure honesty; for example, if ornament expression is intrinsically linked to physiological processes that cannot be faked (Emlen et al. 2012; Hill and Johnson 2012; Weaver et al. 2017). Alternatively or additionally, ornaments may be associated with higher predation risk (Martin and Badyaev 1996; Soler and Moreno 2012), social agonistic interactions (Tibbets and Dale 2004; Tarvin et al. 2016), or sexual harassment (Hosken et al. 2016). Ultimately, the total cost of producing and/or bearing an ornament should ensure honest signaling so that only individuals of superior quality or condition display the most enhanced ornaments (Zahavi 1975, 1977; Andersson 1994).

Although it is no longer under debate that female ornaments can be under direct selection and can act as honest signals, it is less well-understood whether large variation in elaboration among female ornaments has implications for their signaling functions. For instance, ornament conspicuousness can involve costs that displace ornamental traits from their natural selection optimum (Pomiankowski and Iwasa 1998) but may also increase their efficiency at communicating their signaling messages to conspecifics (Tazzyman et al. 2014). To get a better understanding how variability of female ornament expression affects signaling functions, it is necessary to evaluate multiple traits that vary in elaboration within the same species. Mutually ornamented species expressing multiple ornaments are ideal study systems for this purpose. To understand how such ornaments vary in their information content and signaling potential, here we investigate female plumage traits in purple-crowned fairy-wrens (*Malurus coronatus*), a species with multiple ornaments that range from slightly to markedly sexually dimorphic (Nolazco et al. 2020).

Purple-crowned fairy-wrens are cooperative breeders with unusually low extra-pair paternity among fairy-wrens (~4% of offspring; Kingma et al. 2009, 2013), two characteristics that favor the evolution of female ornamentation (Fitzpatrick et al. 1995; Dale et al. 2015; Fitzpatrick and Servedio 2017). The main ornament is the seasonal crown plumage, that is conspicuously purple-and-black in males (a combination of structural and melanin-based coloration), but slate-gray (mostly melanin-based) in females (Fan et al. 2019; Nolazco et al. 2020). Seasonal plumages are extremely rare in passerines (~4% of species; McQueen et al. 2019) and, as far as we are aware, their signaling functions have been investigated only in males (e.g., red fodies: Estep et al. 2006), including a number of other fairy-wren species (Peters et al. 2013). Contrary to other fairy-wrens, in purple-crowned fairy-wren males, producing the breeding plumage earlier in the season does not seem to provide any fitness advantage in terms of reproductive success, social status gains or survival (Fan et al. 2017) and this is similar in females (Nolazco et al. 2020). However, in males, crown plumage completeness (% cover by purple/black plumage) predicts dominance acquisition and elicits aggressive male-male interactions (Fan et al. 2018). Additionally, males with more chromatic crowns (more purple) achieved greater reproductive success (Fan 2018). Other non-seasonal ornamental plumage traits, such as the coloration of the blue tail (turquoise in females) and black ear coverts (rufous in females), showed no clear evidence for a role in sexual or social contexts in males (Fan 2018). The potential signaling functions of homologous seasonal and non-seasonal ornamental colors in females are unknown.

We investigate associations between five plumage patches of variable elaboration (conspicuousness) and condition- and fitness-related parameters in female purple-crowned fairy-wrens. We also test for links with differential allocation (offspring provisioning by male partners) and likelihood of dominance acquisition. Because traits may covary with condition and fitness without serving signaling functions (e.g., due to pleiotropic effects, Roulin 2016), we also include non-ornamental traits as controls and use metrics that estimate if fairy-wrens can perceive variation in coloration for

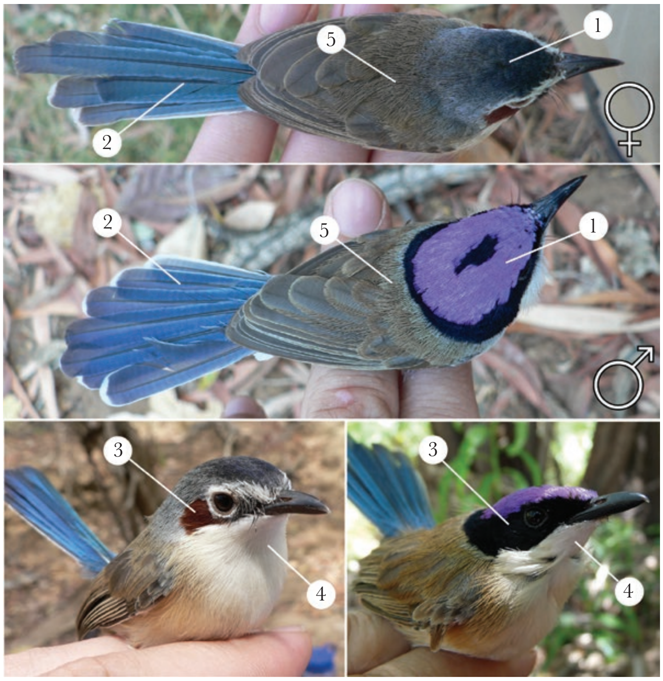

Figure 1
Photos of female and male purple-crowned fairy-wrens taken at the study site showing the five plumage patches investigated (females: this study, males: Fan et al. 2021). (1) Crown: a seasonal breeding plumage that differs between sexes, with the brown crown plumage replaced by slate-gray feathers (higher in eumelanin) in females and purple-and-black feathers (high in eumelanin overlain by nanostructure) in males; (2) tail: colorful year-round in both sexes, more greenish-blue in females, deep blue in males; (3) ear coverts: rufous (pheomelanin-based) in females and black (eumelanin-based) in males; (4) throat: buff-white and (5) back: brown, in both sexes.

each plumage patch investigated. Traits include the putatively ornamental sexually dimorphic 1) seasonal crown, 2) ear coverts and 3) tail, and putatively non-ornamental traits, 4) white throat and 5) brown body coloration, which are similar between the sexes (Figure 1). We expect to obtain detectable or stronger associations with fitness-related parameters for ornamental than non-ornamental traits. As ornaments are generally assumed to act as signals under stronger directional selection, we also predict heightened condition dependence for ornaments (Cotton et al. 2004; but see Johnstone et al. 2009). We discuss our results in the context of previous findings on purple-crowned fairy-wren males, and consider which traits are likely to act as sexual or social signals.

METHODS

Study species

Purple-crowned fairy-wrens (hereafter PCFWs) are cooperative breeding passerines endemic to northern Australia. They form social groups that live in year-round territories associated with riparian vegetation dominated by River Pandanus *Pandanus aquaticus* (Kingma et al. 2011a). Groups are composed of a dominant pair, which are the only birds that breed, and male and female subordinates, who generally help raising the offspring and protect the territory. Subordinates are usually offspring from the dominant pair that can stay for years in the natal territory before dispersal but can also be individuals unrelated to one or both dominants (Kingma et al. 2011b). Both sexes have brown backs, buff-white throats, and turquoise-blue tails that cock upwards and "wag" from side to side, while females differ from adult males in their rufous, instead of black, ear coverts. Immatures of both sexes have rufous ear coverts. In addition, each year, adult PCFWs molt into a seasonal crown plumage (breeding plumage) generally between July and September (Peters et al. 2013; Nolazco et al. 2020), anticipating the peak breeding period (December–March). However, they can reproduce at any time of the year when conditions are favorable (Hidalgo Aranzamendi et al. 2019). The period of a molt cycle (hereafter, molt year) is defined from 1 July of a given year, after which the first birds start molting into the breeding plumage, to 30 June of the subsequent calendar year, when most birds have completed their post-breeding molt into non-breeding plumage (Nolazco et al. 2020). The breeding plumage clearly differs between sexes as the brown crown plumage (non-breeding plumage) is replaced by purple-and-black feathers in males and by slate-gray feathers that contrast with the cream-white eye-ring and eyebrow in females (Figure 1).

Study site and data collection

The study site is located within the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary, a protected area in the Kimberley Region of Western Australia (17°31′S, 126°6′E). Specifically, we studied birds along the Annie Creek and an adjacent section of the Adcock River. PCFW territories are linearly arranged along riparian vegetation dominated by Pandanus. We conducted nest monitoring and nestling banding, adult captures (by mist netting), sampling, and population censuses year-round from 2005 to 2010, and biannually from 2015 to 2017 in October-November and May-June (details in Hidalgo Aranzamendi et al. 2016; Fan et al. 2017).

During captures, we marked nestlings and unbanded adult birds with colored bands for individual identification, measured body mass (g) using a spring-loaded Pesola scale, and tarsus length (mm) using a caliper to the nearest 0.1 mm. We used average tarsus length as an indicator of body size (Senar and Pascual 1997) after correcting for observer (i.e., predicted values of a model including observer identity as a random intercept). We collected blood samples for parentage analyses (details in Kingma et al. 2009, 2013). We also collected reflectance measurements from five plumage patches (seasonal crown, tail, ear coverts, throat, and back), and scored breeding plumage as a percentage of slate-gray plumage covering the crown (Supplementary Figure S1). All reflectance data of birds only included adult individuals that were either subordinates or dominants (i.e., those who reached independence: ≥ 90 days old; Hidalgo Aranzamendi et al. 2019). We also collected 350 measurements of reflectance for the natural background at the study site between 2005 and 2010, taken from bark, leaf litter and soil (details in Delhey et al. 2013). These elements of mostly brown tones are predominant in the natural backgrounds at the study site.

During weekly censuses, we documented group size and social status of each color-banded female (dominance determined by duetting; Hall and Peters 2008, 2009), followed individuals' movements, and determined postfledging survival. We also monitored nests to obtain information on number of breeding attempts per molt year (only including nests in which females laid eggs), clutch size as number of eggs per clutch, hatching and fledging success per nest (proportion of eggs that hatched and proportion of nestlings that fledged, respectively), and provisioning rates. To calculate provisioning rates, we conducted one to five (mode = 2) nestling feeding observations per nest of generally 1 h each (standardized as feeds per hour^{-1}/offspring^{-1}/nest^{-1}) from years 2006 to 2009 and 2016 to 2017 (more details on provisioning observations are provided in Kingma et al. 2010; Teunissen et al. 2020a).

Color analysis

All analyses were performed using R (version 3.6.3; Core Team 2020). To summarize plumage coloration, we first obtained reflectance measurements of 182 females, with some of them (67) being measured more than once in a year or across multiple years (details in Supplementary Table S1). Reflectance was measured using a portable AvaSpec-2048 spectrometer connected to an AvaLight-XE xenon pulsed light source through a bifurcated fiber optics cable probe (Avantes, Netherlands). The end of the probe was cylindrical to standardize measuring distance and exclude ambient light. Plumage measurements were taken up to five times on predetermined and standardized spots at each plumage area (slate-gray crown, turquoise-blue tail, rufous ear coverts, buff-white throat, and brown back; Figure 1). For the crown, we only used reflectance data that was measured on those individuals expressing a complete or near-complete breeding plumage over fully molted plumage areas (i.e., ≥ 80% slate-gray crown score; see Supplementary Figure S1). Maximum gray crown score achieved in a season (hereafter, plumage completeness) was determined when birds had completed their molt into breeding plumage—between 15th October and 1st March (Nolazco et al. 2020). Reflectance was computed every 5 nm for wavelengths (WL) within the visible range of birds (300–700 nm; Cuthill 2006) using a WS-2 white standard as a reference and the software AVASOFT 7.5 (Avantes, Netherlands).

We synthetized these reflectance data into chromatic and achromatic variation per plumage patch and natural background using psychophysical models of avian color vision (Vorobyev et al. 1998). Using models of avian color vision allows us to quantify color variation as close as currently possible to the perceptual world of the intended receivers (conspecifics in our case). Importantly, we can estimate to what extent any of the detected effects are associated with levels of ornamental variation that can be perceived by the birds, thus providing clues on their biological relevance.

We used the equations described in Cassey et al. (2008) and implemented by Delhey et al. (2015) in R. These models are based on the spectral sensitivity of cones to light, which depends on the type of photoreceptors (cones), their relative abundance in the retina, and the spectrum of ambient illuminating light. Birds possess four types of single cones 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 mostly restricted to the VS and S single cones, and birds can be classified in two groups: ultraviolet-sensitive (U-type) and violet-sensitive (V-type). The U-type species possess VS single cones with greater peak sensitivity toward shorter wavelengths (Hart and Hunt 2007). Given that PCFWs are V-type (Ödeen et al. 2012), we used average visual sensitivities functions for this type obtained from Appendix A in Endler and Mielke (2005). To obtain the noise-to-signal ratios for each single cone type ($\nu VS = 0.162$, $\nu S = 0.120$, $\nu M = 0.094$, $\nu L = 0.1$), we used the equation 10 in Vorobyev et al. (1998) with average cone proportions from Hart (2001) (0.38:0.69:1.14:1.00 for VS:S:M:L, respectively) and a Weber fraction of 0.1 for the L cone (Olsson et al. 2018). We used the spectrum of standard daylight in open habitats (D65) as ambient illuminant (Vorobyev et al. 1998), the same that was used to study ornaments in PCFW males at the study site (Fan et al. 2021). We chose this illuminant as, despite PCFWs inhabit riparian vegetation, their territories were predominantly exposed to direct sunlight with a very sparse canopy (when present). Considering that birds can also use shaded areas at a microhabitat scale, an alternative illuminant would be “woodland shade” (Endler 1993), but our reflectance parameters from avian vision models were strongly correlated between both illuminants (all cases: $r \sim 0.99$, $P < 0.001$). This is consistent with previous studies showing that using different illuminants leads to almost identical results (Delhey and Peters 2008; Stoddard and Prum 2008; Delhey et al. 2013).

Implementing these models yields for each reflectance spectrum a set of cone quantum catches, the degree of stimulation of each cone by a specific combination of reflectance spectrum and irradiance. Cone quantum catches were transformed into a set of three chromatic coordinates (xyz) which define the position of each spectrum in the avian chromatic visual space. This visual space takes the shape of a tetrahedron where each apex represents the sole stimulation of a single cone type (Endler and Mielke 2005). Using the equation in Cassey et al. (2008), distances between points in visual space are expressed in “just noticeable differences” (jnd), whereby distances > 1 jnd are considered to be discriminable by PCFWs. Achromatic variability (i.e., lightness or luminance variation) was computed as described by Delhey et al. (2015). This was based on the stimulation of the double cone which in birds is the most likely photoreceptor capturing achromatic variation (Cuthill 2006). For the double cone, we used a Weber fraction of 0.2, following Olsson et al. (2018). This achromatic variable was defined as Lightness (DL), with higher values (in jnd) representing lighter (brighter) plumage patches and background. Since multiple reflectance measurements were taken per plumage patch per capture, we averaged the resulting values.

We also used models of avian color vision to estimate how birds perceive the contrast between trait coloration and their environment as an objective way to measure conspicuousness (Delhey et al. 2013). We consider that both chromatic and achromatic contrast are important indicators of overall conspicuousness since not only PCFWs possess color vision, but also birds of prey, the main predators of adult PCFWs, as well as nest predators such as varanid lizards and snakes (Teunissen et al. 2020a, b) are also likely to perceive color (Simões et al. 2016; Osorio 2019). To compare the contrast between the different plumage patches and the natural background, we computed Euclidean distances using overall averages for xyz coordinates and DL per plumage patch and background following Delhey et al. (2013). These Euclidean distances for chromatic $((x_{patch} - x_{background})^2 + (y_{patch} - y_{background})^2 + (z_{patch} - z_{background})^2)^{1/2})$ and achromatic information $((DL_{patch} - DL_{background})^2)^{1/2})$ are also interpreted in jnd. Since avian predators such as birds of prey also possess V-type vision as PCFWs, the contrast between plumage coloration and the natural background should be similarly detectable by such predators (Delhey et al. 2013), which are likely the main predators of adult PCFWs (Teunissen et al. 2020a, b).

To summarize chromatic variability, we performed a Principal Component Analysis (PCA) on the xyz coordinates using a covariance matrix. This allowed us to obtain a single chromatic variable from xyz coordinates, the first principal component (PC1) score, that was also expressed in jnd. To standardize PC scores across plumage patches, we changed their sign when needed so that higher values always indicate reflectance spectra richer in short wavelengths. These can be interpreted differently for each plumage patch/color.

Gray crowns, turquoise-blue tails, and buff-white throats richer in shortwave reflectance are grayer (less brown), deeper blue (less green), and whiter (less buff), respectively. Ear coverts (rufous) and backs (brown) richer in longwave reflectance are more reddish. For each plumage patch, we used PC scores and lightness (DL) values in the statistical analyses below as our chromatic and achromatic variables, respectively. Adjusted repeatability along with 95% confidence intervals based on parametric bootstrapping (Nakagawa and Schielzeth 2010) were calculated for each of these parameters. We included significant fixed effects from models investigating influential factors for reflectance parameters (section *Age-, status- and condition dependence*; see below).

Statistical models

To test several associations involving the multiple plumage patches, we built additive linear mixed models (LMM), generalized linear mixed models, and generalized linear models. First, we tested whether these traits vary according to age, social status, or individual condition. Second, we assessed how those traits correlate with several fitness-related parameters. Third, we tested whether males show greater parental effort by investing more in offspring when mated to more attractive females, those that show the most elaborate or conspicuous plumage (i.e., the differential allocation hypothesis; Burley 1986; Sheldon 2000). Last, we tested whether variation in plumage patches among subordinates is linked to the likelihood of gaining a dominant position.

For mixed models, we used the package “lme4” (Bates et al. 2015). For LMMs, we used the “lmerTest” package to derive *P*-values of fixed effects with the Satterthwaite approximation for degrees of freedom (Kuznetsova et al. 2017). We adjusted the *P*-values using the false discovery rate (FDR) Benjamini–Hochberg procedure (Benjamini and Hochberg 1995) set at 0.05 to control for potential type I errors (false positives) due to multiple testing. We divided our traits parameters into two families for FDR *P*-value adjustments: 1) ornamental traits comprising crown completeness, PC1 and DL, tail PC1 and DL, and ear coverts PC1 and DL (i.e., seven tests), and 2) non-ornamental throat PC1 and DL, and back PC1 and DL (i.e., four tests). We scaled and centered all numeric predictors (following Schielzeth 2010). By default, we always include *individual ID* (identity) as a random effect in models, except in exceptional cases in which there was a paucity of replicates (i.e., one to two *individuals* with more than one observation). To evaluate potential multicollinearity between predictors, we calculated variance inflation factors (VIFs) using the “car” package (Fox and Weisberg 2019). In none of our models, the predictors showed potential multicollinearity issues (VIFs < 4; James et al. 2013). Sample sizes varied between models since these incorporate different predictors or response variables for which data was not always available to the same extent.

Age-, status- and condition dependence

To determine whether age, social status and individual condition were associated with plumage characteristics of females, we built linear regression models with seasonal breeding *plumage completeness*, and *PC1 scores* and *lightness DL* for all plumage patches as response variables. Our predictors of interest were *age* (in months), *social status* (subordinate, dominant), *body mass* and *territory quality* (estimates of condition). *Age* was estimated for individuals that were first captured as nestlings or fledglings. *Territory quality* was measured as the relative coverage of Pandanus (following Kingma et al. 2011a; Roast et al. 2019). Greater Pandanus coverage is strongly associated with PCFWs spatial distribution and larger cooperative groups (Kingma et al. 2011a), lower nest failure rates (Hidalgo Aranzamendi 2017), and is preferred by “divorced” females settling on a new territory (Hidalgo Aranzamendi et al. 2016). *Tarsus length* was incorporated as a covariate to control for the effect of body size on body mass so that the latter can be interpreted as an indicator of body condition (Senar and Pascual 1997; Green 2001). To control for other effects on plumage coloration, we also included *group size* as conflicting energetic costs of parental investment can be reduced in larger groups (load lightening; Kingma et al. 2010; Hall et al. 2013). For *group size* we only included birds that have reached independence as they are the ones capable of contributing to offspring care (adults ≥ 90 days; Hidalgo Aranzamendi et al. 2019). *Plumage wear* was also included but only for the seasonal crown plumage as number of days from the date the reflectance data was taken to mid-October (15th), when birds have completed their molt into their breeding plumage (Nolazco et al. 2020) as this may affect the quality of the coloration. Random effects were *individual ID* and *molt year* to control for variation on plumage coloration attributed to the identity of birds and vagaries in environmental conditions among years. To determine whether the effects of our variables of interests resulted in discriminable differences in plumage coloration by PCFWs, we rescaled the coefficients. Then, for each variable of interest, we multiplied their rescaled coefficient by their range of variation which provides a range of predicted values in terms of jnd for *PC1 scores* and *lightness DL*. Values larger than 1 jnd were considered indicative of discriminable differences.

Fitness

To determine whether fitness metrics were associated with plumage characteristics of females, we built linear and generalized linear models with fitness-related parameters as response variables and *seasonal breeding plumage completeness, PC1 scores* and *lightness DL* of the different plumage patches as our predictors of interest. Fitness-related parameters included: dominant *females' feeding rate* (linear regression model), number of *breeding attempts* and *clutch size* (both Poisson models), *hatching* and *fledging success* (both binomial models with proportions: successes/failures), *recruitment success* (binomial model with binary response: yes/no, indicating whether females produced at least one offspring that survived till independence per molt year), and *annual survival* (binomial model with binary response: yes/no, indicating whether females survived to the end of the molt year). Hereafter, we included in the same model only plumage patches with the same number of observations (tail, ear coverts, and back; crown and throat each in separate models). Sample sizes became too small if data for all plumage patches were incorporated in the same models, leading to overparametrization, convergence problems, power reduction, and potentially misleading point estimates and errors. To control for confounding effects on the response variables, we included *breeding experience* (except for the survival analysis), *territory quality* and *group size* as covariates. *Breeding experience* to control for effects on reproductive performance as days since becoming dominant was strongly correlated with age ($r = 0.89$, $P < 0.001$, $n = 79$), so we did not incorporate age as an additional covariate. We did not incorporate age in survival analyses as age has no effect on adult survival in our population (Roast et al. 2020). *Territory quality* was considered a proximal indicator of favorable environmental conditions based on associative patterns of spatial aggregation that are associated with higher fitness (Kingma et al. 2011a; Hidalgo Aranzamendi 2017). Load lightening of parental effort in larger *groups* is also known to have positive effects on fitness (Nolazco et al. 2020). To control for additional confounding effects on reflectance parameters, we also included covariates that we found had significant effects on specific plumage patches' completeness (crown) and coloration (from models on section "Age-, status- and condition dependence"). Random effects were *observer ID* (only for the feeding rate model), *individual ID*, and *molt year* (except for survival analyses since molt year did not explain any of the variation across survival models). We excluded data of pairs formed by siblings or parent–offspring (i.e., incestuous; 12 pairs) from models including reproductive parameters, due to negative effects on reproductive performance (e.g., >30% lower hatching success; Kingma et al. 2013). For all models involving annual data, we only included individuals that were already dominants at the beginning of the molt year, and that manage to survive that entire year (except for survival models), and that did not change territories within the molt year.

Differential allocation

To determine whether male care varies in relation to plumage characteristics of female mates, we built linear models with dominant *male feeding rate* hour^{-1}/offspring^{-1}/nest^{-1} as response variable and dominant female *seasonal breeding plumage completeness*, *PC1 scores* and *lightness DL* of the different plumage patches as our predictors of interest. To control for confounding effects on the response variables, we included *breeding experience*, *territory quality* and *group size* as covariates (same criteria as applied for dominant females' own maternal feeding rates in the section above). To control for additional confounding effects, we also included other covariates whenever these had significant effects on specific traits (crown completeness, coloration) according to previous models. Random effects were *observer ID*, *individual ID* and *molt year*. We excluded data from incestuous pairs.

Dominance acquisition

To determine whether dominance acquisition was associated with plumage characteristics of females, we built binomial regression models with the occurrence of *dominance acquisition* success as a binary response variable (yes/no), indicating whether a subordinate gained a dominant position by the end of the molt year. Our predictors of interest were seasonal breeding *plumage completeness*, and *PC1 scores* and *lightness DL* for this and all other plumage patches. In this model, we only included individuals that were subordinates at the beginning of the molt year. To control for additional confounding effects, we also included covariates that we found had significant effects on specific plumage patches' completeness (crown) and coloration. Covariates such as territory quality, group size and age were not always included since they had no significant effects on dominance acquisition based on previous studies of this species in either sex (Fan et al. 2017; Nolazco et al. 2020). *Molt year* was excluded as a random effect when it did not explain any of the variance, in order to avoid overparametrization since these models have relatively small sample sizes. *Individual ID* was not included in any of these models due to the paucity of replicates. We only included in the models individuals that were already born at the beginning of the molt year, that manage to survive that entire year, and excluded cases in which dominance acquisition resulted from incestuous pairing.

RESULTS

Descriptive analyses of reflectance parameters

Achromatic (*lightness DL*) and chromatic (*PC* scores) parameters showed variation greater than 1 jnd across all plumage patches, suggesting that PCFWs can recognize variation in lightness and coloration among conspecific females (Supplementary Figures S2 and S3). The first principal component (*PC1*) of PCAs explained more than 87% of the chromatic variation across traits (Supplementary Table S2), therefore, we only used *PC1* scores to summarize chromatic variation, with higher values indicating coloration relatively richer in shorter wavelengths. Achromatic and chromatic variation were weakly to moderately correlated among traits ($r = 0.21$–0.69; Supplementary Table S3), so birds tend to express and maintain similar coloration patterns throughout their plumage. The only exception was the tail that showed no significant chromatic correlations with the ear coverts, throat or back. Repeatability was highly variable across plumage patches (*lightness DL* range: 0.02–0.61, *PC1* scores: 0.06–0.61; complete results in Supplementary Table S1). The highest values were obtained for the crown lightness and tail color ($R_{\text{lightness(crown)}} = 0.61[\text{CI} = 0.37–0.84]$, $R_{\text{PC1 scores(tail)}} = 0.61$ [0.49–0.72]), indicating moderately consistent individual color over the study period.

The plumage patches that showed the lowest chromatic contrast with natural background (i.e., least conspicuous) were the throat, back, and seasonal slate-gray crown. Females with purer white throats and grayer (less brown, relatively richer in shortwave reflectance, i.e., higher eumelanin) crowns contrasted more with the natural background. The back was the most cryptic against the background, with no discriminable changes in contrast across the range of chromatic plumage variation. Conversely, chromatic contrast was higher for the tail and ear coverts (i.e., more conspicuous), being highest for the tail. Females with bluer tails and more rufous (i.e., higher pheomelanin) ear coverts contrasted more with the natural background. The achromatic contrast was highest for the ear coverts that were overall darker than the natural background, followed by the crown. Most traits were on average darker than the background except for the throat, which was also the least conspicuous plumage patch in terms of achromatic contrast (Table 1, Supplementary Tables S4 and S5).

Associations with age, status, and individual condition

Dominants showed a more complete and grayer (less brown, richer in shortwave reflectance) seasonal crown than subordinates ($\beta_{\text{dominant}} = 1.97$, $t = 4.80$, $P < 0.001$, $n = 90$ and $\beta_{\text{dominant}} = 0.99$, $t = 2.35$, $P = 0.02$, $n = 42$, respectively). However, the mean difference in crown coloration between dominant and subordinate, even though statistically significant, should not be discriminable (<1 jnd). Dominants also showed browner/less rufous (richer in shortwave reflectance) ear coverts than subordinates ($\beta_{\text{dominant}} = 1.30$, $t = 3.06$, $P = 0.003$, $n = 113$), variation that should be visually discriminable by conspecifics (>1 jnd). Moreover, individuals in better body condition (mass corrected by size) expressed more complete seasonal crowns independently of their social status ($\beta_{\text{mass}} = 1.12$, $t = 7.40$, $P < 0.001$, $n = 90$). No other plumage patches showed evidence for condition-, age- or status dependence after FDR *P*-value adjustments (Figure 2, Supplementary Table S6; detailed summary of estimated parameters in Supplementary Tables S7–S10).

Fitness

Among dominant (breeder) females, those with more reddish-brown backs (richer in longwave reflectance) achieved greater annual reproductive success ($\beta_{\text{PC1 scores}} = -0.35$, $z = -2.50$, $P = 0.01$, $n = 84$). No other plumage patches showed associations with any indicator of reproductive effort, productivity, or annual survival (Figure 3, Supplementary Table S6; detailed summary of estimated parameters in Supplementary Tables S11–S26).

Differential allocation

Males did not adjust offspring provisioning in relation to any aspect of their mate's appearance: there was no effect of completeness of the seasonal crown plumage, or any color parameter (achromatic or achromatic variability) for this or any other plumage patch investigated (Supplementary Table S6; detailed summary of estimated parameters in Supplementary Tables S27–S30).

Dominance acquisition

No plumage patches, including completeness or coloration of the seasonal plumage, explained variability in the probability of gaining a dominant position (Supplementary Table S6, detailed summary of estimated parameters in Supplementary Tables S31–S34).

DISCUSSION

Female ornaments can act as signals (Hare and Simons 2019; Doutrelant et al. 2020), but this might not always be the case (e.g., Prum 2017; Clark and Rankin 2020). Understanding how ornaments work in mutually ornamented species can provide insights into the similarities and differences in ornament evolution between the sexes. In purple-crowned fairy-wrens, we found that dominant females produced a more complete and grayer seasonal crown plumage and less rufous ear coverts compared to subordinate females. Evidence for condition dependence was only found for the seasonal crown plumage completeness (% covered by slate-gray feathers). Among dominant females, those with more reddish-brown backs (a putatively non-ornamental trait) achieved higher reproductive success. Our findings are puzzling and incongruent with our predictions as variation in coloration of a non-ornamental trait was associated with fitness, while we found no evidence in support of ornamental traits having associations with fitness. Moreover, our results showed some similarities and inconsistencies with previous studies in conspecific males (Fan 2018; Fan et al. 2018, 2021), mainly due to the lack of clear associations to suggest that female ornamentation plays a role in social or sexual contexts.

The crown, a seasonal ornament that is less elaborate in females

Seasonal changes in plumage from cryptic to conspicuous colors correlate with sexual selection, lower predation risk and seasonality (Andersson 1983; Butcher and Rohwer 1989; McQueen et al. 2019). Studies in males generally support that elaborate seasonally breeding plumages are indicative of individual quality (Pryke and Andersson 2005; Estep et al. 2006; Hudson and Wilcoxen 2018) and may evolve under directional selection by mate choice or male-male competition (Dunn and Cockburn 1999; Pryke and Andersson 2005; Webster et al. 2008; Prager and Andersson 2009; Maia et al. 2012). Similarly, studies in PCFW males, suggest a role of the seasonal crown in male–male competition (Fan et al. 2018), with more ornamented individuals (i.e., more complete and colorful crowns) achieving higher reproductive success (Fan 2018). In contrast, our results do not support a similar adaptive function in PCFW females. Basically, the crown patch was not associated with increased reproductive success, and we found no evidence for a role in competition over social status positions or support for the differential allocation hypothesis.

Although the seasonal slate-gray crown of PCFW females differs qualitatively from males, it does seem to be an incomplete version of the male ornament. In males with an incomplete breeding plumage, the non-purple-and-black feathers can also look slate-gray, presumably due to the deposition of eumelanin (Supplementary Figure S4). This suggests that the purple crown in PCFW males is a seasonal ornament in which pigment deposition can be (partly) decoupled from production of nanostructures in the feathers. Such decoupling has been indicated for other fairy-wrens by experimental studies showing that androgen treatment in females induces a partial expression of ornamental male-like plumages (Peters 2007; Lindsay et al. 2016; Boersma et al. 2020). Sex-specific regulatory mechanisms may prevent females from exhibiting male ornaments in their full extent, thus potentially avoiding the costs of expressing a conspicuous trait.

Table 1

Conspicuousness of the five investigated plumage patches. Shown is mean contrast (SE) between plumage coloration and the natural background, measured as Euclidean distances for averaged chromatic coordinates (xyz) and achromatic *lightness* (*DL*). Signs indicate the direction of associations between coloration and background contrast (chromatic: positive sign indicates that contrast increases when plumages are richer in shortwave reflectance, negative sign when these are richer in longwave reflectance; achromatic: positive indicates that contrast increases when plumages are lighter, negative when these are darker). Significant associations in bold ($P \leq 0.05$; full summary in Supplementary Table S5). For all plumage patches, the range in contrast to background is discriminable by conspecifics (except for chromatic variation in back color which is < 1 jnd).

Chromatic					Achromatic				
Crown	Tail	Ear coverts	Throat	Back	Crown	Tail	Ear coverts	Throat	Back
2.99 (0.09)	**6.35** (0.06)	**−3.78** (0.08)	**2.85** (0.03)	+0.96 (0.05)	**−6.95** (0.11)	**−4.89** (0.08)	**−8.14** (0.12)	**2.39** (0.07)	**−4.83** (0.08)

Crown reflectance was measured for slate-gray breeding plumage state (non-breeding crown plumage is similar to the back). All other plumage patches do not change color throughout the year. Contrasts in bold are discriminable by conspecifics (> 1 jnd).

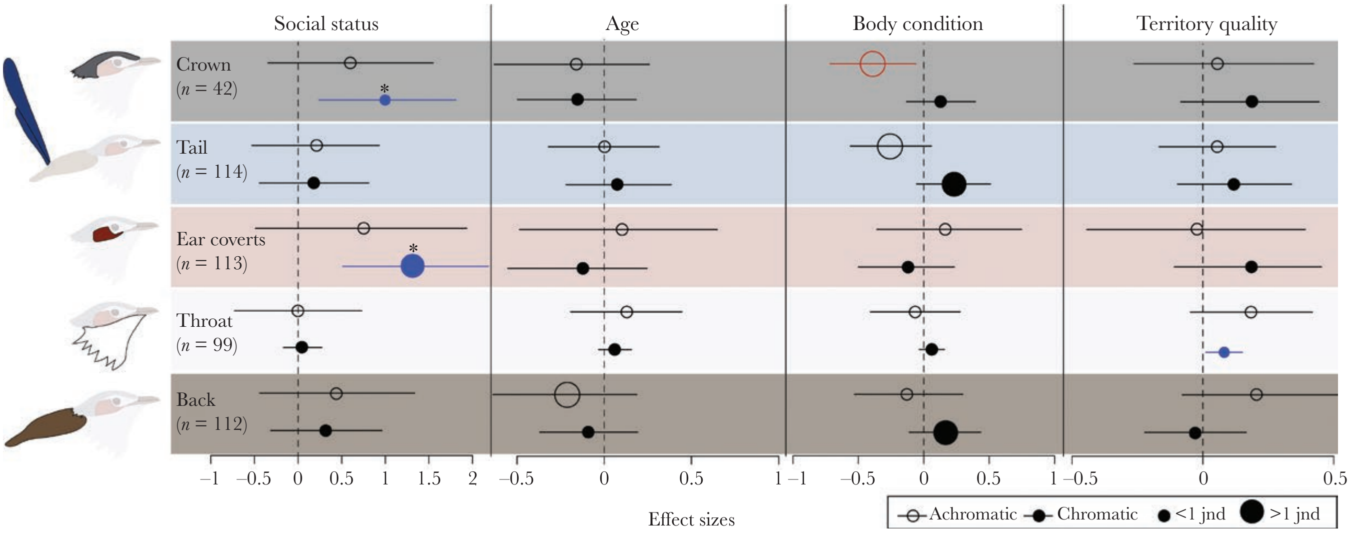

Figure 2
Dominant females show crowns and ear coverts richer in shortwave reflectance than subordinates (i.e., grayer or more ornamented crowns, but less rufous or less ornamented ear coverts). Shown are associations between color parameters (chromatic and achromatic variation) of multiple plumage patches and: social status (dominant vs. subordinate [reference level]), age (in months), body condition (body mass corrected by size; tarsus length as covariate) and territory quality (index of relative abundance of River Pandanus). Significant associations based on 95% confidence limits are depicted in blue (positive) and red (negative), with those that remained significant after the FDR correction for multiple testing indicated by an asterisk. Achromatic and chromatic variation from plumage reflectance data are represented by *lightness* (*DL*) and *PC1* scores (indicative of richness in shortwave reflectance), respectively (details in *Methods*). Larger circles indicate cases in which variation in *DL* and *PC1* scores across the range of realistic values of the predictors should be discriminable by conspecifics (>1 jnd; just noticeable differences). "Subordinate" is the reference level for social status (i.e., positive values indicate greater trait values in dominants). Crown reflectance was measured for slate-gray breeding plumage state. All other plumage patches do not change color throughout the year.

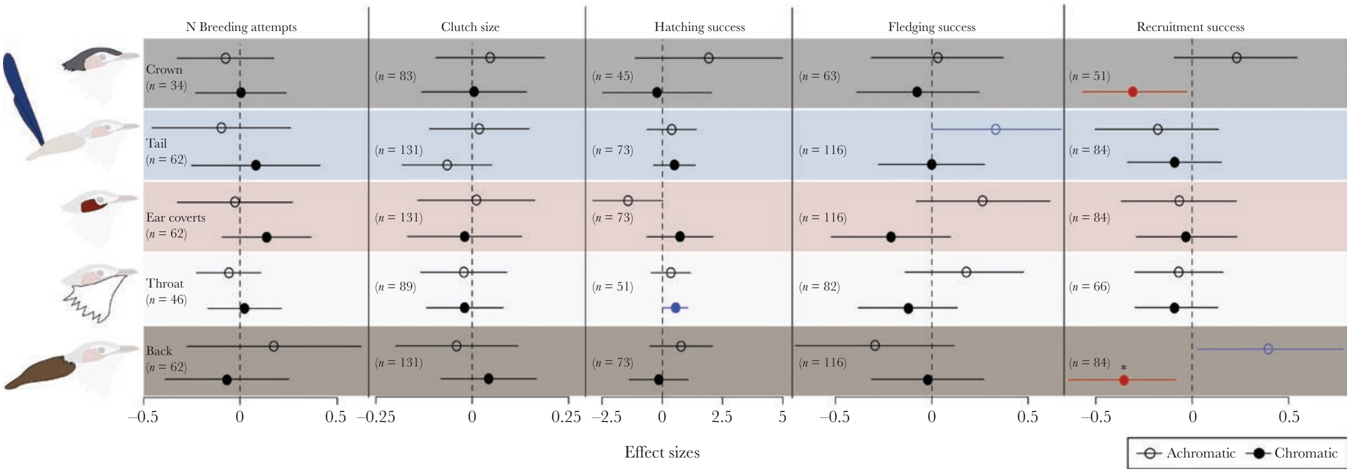

Figure 3
Dominant females with more reddish-brown backs (higher pheomelanin content) achieved higher annual reproductive success (i.e., recruitment success). Shown are associations between color parameters (chromatic and achromatic variation) of multiple plumage patches and: number of breeding attempts per molt year, clutch size (number of eggs per clutch), hatching and fledging success per nest (proportion of eggs that hatched and nestlings that fledged, respectively), and recruitment success per molt year (at least one offspring ≥ 90 days old produced). Significant associations based on 95% confidence limits are depicted in blue (positive) and red (negative), with those that remained significant after the FDR correction for multiple testing indicated by an asterisk. Achromatic and chromatic variation from plumage reflectance data are represented by *lightness* (*DL*) and *PC1* scores (indicative of richness in shortwave reflectance), respectively (details in *Methods*). Crown reflectance was measured for slate-gray breeding plumage state. All other plumage patches do not change color throughout the year.

However, we also found that dominant females expressed more complete crowns than subordinates. A possibility, likely to be undetected by our analyses, is that the full expression of the seasonal crown of females may act as a signal used by dominants to deter subordinate females within the social group from becoming or attempting to become dominant (i.e., reduce competition within the social group). By not expressing a fully developed ornament, subordinate individuals may avoid the social cost of aggressive interactions with dominants, which fits within the framework of the status signaling hypothesis (sensu Lyon and Montgomerie

1986). Studies in other species support this hypothesis in females by showing that individuals exhibit delayed plumage maturation for traits that elicit more aggressive responses by conspecifics (tree swallows: Coady and Dawson 2013, Eurasian kestrels: Vergara et al. 2013). Testing for the possibility that seasonal plumage in PCFW females act similarly as a signal of status within social groups may require an experimental approach such as manipulating ornament expression.

The tail, a conspicuous ornament among fairy-wrens

Bird tails play an aerodynamic function during flight (Hedenström 2002), but deviations from their apparent naturally selected optimum (size, shape, and/or color) are common and generally attributed to sexual selection (e.g., Winquist and Lemon 1994). Supporting evidence in females is scarce, with studies suggesting sexual selection acting in both sexes (Siefferman and Hill 2005) or only in one, generally males (Murphy 2007). Among female fairy-wrens, tails are the most common colorful ornament (Rowley and Russell 1997), ranging from very cryptic to strongly male-like colored, presenting an interesting model system to study signaling functions (Karubian et al. 2009; Karubian 2013). Indeed, we found that, regardless whether PCFW females were in non-breeding or breeding plumage, the tail was the most contrasting plumage trait in terms of chromatic attributes, and that those females with more male-like tails (bluer) were also more conspicuous against the natural background. While such a colorful tail may attract predators, this might be less likely during incubation as the nest structure conceals it (Supplementary Figure S5). Thus, a potential lower reproductive conflict than for other plumage traits provides a plausible explanation for why colorful tails are the most common female ornament among fairy-wrens.

Although we did not find associations to support the possibility of signaling functions for female tails, females with male-like colorful tails (bluer) tended to have higher chances of gaining a dominant position and greater fledging success (Supplementary Table S6). In PCFW males, those producing lighter tails show better body condition (Fan et al. 2021) and have higher chances of gaining dominance, but the latter effect was negligible (Fan 2018). Overall, findings in both sexes are still inconclusive and may require experimental testing to understand the evolution of the conspicuous tail.

The ear coverts, a sexually dimorphic plumage patch

Conspicuous or contrasting patches of facial feathers are common in birds and have been attributed to sexual and social selection (Delhey 2020; Kenyon and Martin 2022). In PCFW females, ear coverts are most conspicuous in terms of achromatic contrast, and second in terms of chromatic contrast. However, we found at best limited evidence that the rufous ear coverts of PCFW females act as a sexual or social signal (similar to previous findings for black ear coverts of conspecific males; Fan 2018).

Within breeding females, chromatic or achromatic (lightness) variation of ear coverts was not associated with measures of fitness or differential allocation by males. Likewise, in subordinate females, variation in (a)chromatic coloration of ear coverts was not associated with chances of gaining a dominant position. However, we found that subordinate females produced more rufous ear coverts (higher pheomelanin content) than dominants (browner) and that such differences should be discriminable by conspecifics (>1 jnd). A possible explanation is that females may reduce the amount of pheomelanin or deposit eumelanin in ear coverts to favor crypsis when becoming dominants (breeders) as the face is an area that can be visually exposed while on the nest (Supplementary Figure S5) and more rufous ear coverts are more conspicuous against the natural background. However, ear coverts are not particularly large, so whether the reduction in conspicuousness in breeding females is meaningful would have to be assessed experimentally. An alternative explanation for reduced pheomelanin/increased eumelanin deposition in the ear coverts in dominant breeders has a similar function to increased completeness and grayness (increased eumelanin deposition) of crown plumage: to signal/reinforce dominant social status.

Ear coverts in PCFWs become sexually dichromatic with age, as they are rufous in all juveniles but become black in males; however, within sexes, there is no evidence for age-related discriminable variation in coloration among adults (males: Fan et al. 2021, females: this study). A possibility is thus that the sexually distinctive coloration of ear coverts may serve as a year-round visual cue for recognition of males that may pose a threat for dominants in social or sexual contexts (e.g., Sætre and Slagsvold 1992; Slagsvold 1993; Vos 1994; Xu et al. 2014).

Throats and backs, inconspicuous non-ornamental traits

Plain dark upperparts and whitish light underparts are common in animals and generally considered cryptic traits favored by natural selection. Claimed functions include countershading to provide concealment for predators and prey, UV protection, and thermoregulation (Rowland 2009). In particular, the back is often inconspicuous, resembling natural background colors, and not often used during displays (Delhey 2020). Accordingly, we found that in PCFW females, the buff-white throat and brown backs were the most inconspicuous plumage areas against natural backgrounds.

However, we found that females with more reddish-brown backs (higher rufous pheomelanin content) achieved higher annual reproductive success but no evidence for condition-dependence. In contrast, in PCFW males, individuals in better condition show lighter plumage overall (Fan et al. 2021), but no fitness-related associations were detected for back coloration (Fan 2018). There is considerable evidence suggesting that melanin-based plumage can be condition-dependent (Guindre-Parker and Love 2014), but this may occur due to pleiotropic effects that are poorly understood (Roulin 2016). For instance, it has been hypothesized that pheomelanin synthesis has evolved as a mechanism to remove toxic excess of cysteine which may have an impact on condition (Ito et al. 2011). Condition can also affect the structure of feathers, and therefore, overall plumage reflectance parameters (D'Alba et al. 2014). For non-ornamental traits that are not expected to be under sexual or social selection but rather selection for crypsis alone, correlations with fitness may arise in females through an indirect correlation with higher quality or condition resulting in higher fecundity or better reproductive outcomes (e.g., Bonduriansky and Rowe 2005). This may explain the association between back coloration and fitness in PCFW females, and although we did not find evidence for condition dependence, unlike males, it is possible that we have overlooked aspects of condition that were not measured or that require manipulation.

CONCLUSION

Our study suggests that ornaments in females can differ in their information content from that in male conspecifics. Moreover, the signaling functions of reduced male-like ornaments in females may be harder to detect, or potentially be absent. Nevertheless, examples of functional signaling traits in males but not females of mutually ornamented species are rare in the literature. Indeed, previous studies suggest that ornaments can also act in females as sexual or social signals in other species of fairy-wrens (e.g., white-shouldered fairy-wrens: Enbody et al. 2018, 2022, Boersma et al. 2020; lovely fairy-wrens: Leitão et al. 2019, 2021). And overall, across mutually ornamented birds, it seems that ornaments in males and females are equally informative, and that female ornaments widely function in a similar manner as male ornaments (meta-analysis: Nolazco et al. 2022). It is therefore surprising that the seasonal breeding plumage of female purple-crowned fairy-wrens does not appear to function in this way, and all evidence is consistent with it being a less informative version of the male trait. In this regard, it would be interesting to investigate genetic cross-sex correlations and/or shared mechanistic pathways between sexes that might be responsible for its seasonal expression in females. More broadly, further research should be conducted to investigate multiple traits in both sexes in other mutually ornamented species to bring us a more detailed and unbiased perspective of how ornamentation evolves.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online

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DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Nolazco et al. (2022).

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