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**Original article: Evolution of female colors in birds: the role of female cost of reproduction and paternal care**

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*Author contribution:* A.F., A.G. and C.D. designed the study; A.F. collected the data with help from D.G; A.F. analysed the data; A.F. wrote the first draft with several inputs from A.G., D.G. and C.D.

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*Abstract*

Female ornamentation is frequently observed in animal species and is sometimes found as more evolutionary labile than male ornamentation. A complex array of factors may explain its presence and variation. Here we assessed the role of female cost of reproduction and paternal care. Both factors have been pinpointed as important by theoretical studies but have not been investigated yet in details at the interspecific level. We worked on 133 species of North temperate Passeriformes bird species for which both the clutch volume – here taken as the proxy of female cost of reproduction - and amount of paternal care are relatively well known. Using spectrometry, we measured the whole-body colored plumage patches and quantified three metrics corresponding to brightness (i.e. achromatic component), color chromaticity (i.e. intensity), and color volume (i.e. diversity). We found a strong association between male and female color metrics. Controlling for this association, we found additional small but detectable effects of both cost of reproduction and paternal care. First, females of species with more paternal care were slightly brighter. Second, the interaction between the level of paternal care and egg volume was correlated with female color intensity: females with more paternal care were more chromatic, with this association mostly present when their investment in reproduction was low. Together these results suggest that female cost of reproduction and paternal care are part of the multiple factors explaining variation of female coloration, besides the strong covariation between male and female coloration.

*Keywords:* Sexual selection – female ornaments – paternal care – reproductive costs – avian visual space – social selection – comparative analyses

## Introduction

Males in many animal species display conspicuous ornaments and armaments and a large body of evolutionary research has aimed to understand the factors at the origin of this variation (Andersson, 1994). Females in many animal species also display conspicuous traits and in the past twenty years, research focusing on the evolution and variation in female ornaments has increased (Amundsen, 2000; Harrison & Poe, 2012; Nordeide *et al.*, 2013; Odom *et al.*, 2014; Dale *et al.*, 2015; Riebel *et al.*, 2019; Doutrelant *et al.*, 2020).

Owing to the paradigm that inter- and intra-sexual selection is typically stronger on males (Bateman, 1948; Janicke *et al.*, 2016; but see Hoquet, 2020), female ornamentation was historically considered as a genetic by-product of male ornamentation with natural selection (e.g. predation) leading to more cryptic phenotypes in females. Nowadays, there is a general agreement that natural, sexual and social selection also impact female ornamentation, and that studies need to understand how these complex arrays of forces interact and explain the observed variability (Kraaijeveld *et al.*, 2007; Clutton-Brock, 2009; Tobias *et al.*, 2012; Hare & Simmons, 2019; Cooney *et al.*, 2022; Doutrelant *et al.*, 2020).

Comparative studies have been a powerful tool to investigate the multiple drivers of female ornamentation. Overall most of the comparative studies focused on the selective forces driving the evolution of sexual dichromatism, which expresses the effect of sexual and natural selection acting on both sexes (Johnson *et al.*, 2013; Dunn *et al.*, 2015; Shultz & Burns, 2017). These studies clearly outlined three factors explaining the evolution of female ornamentation: predation, female competition, and selection acting on males. Increase of predation risk, migration and intense sexual selection on males are usually associated with lower coloration in females compared to males (Martin & Badyaev, 1996; Dale *et al.*, 2015; Dunn *et al.*, 2015) whereas higher female competition

for access to reproduction in cooperative breeding species is associated with lower sexual dichromatism (Rubenstein & Lovette, 2009; Dale *et al.*, 2015). To go further in understanding the variation in female ornamentation at the interspecific level, it is important to keep focusing on female ornamentation and to test the effect of female-related forces - i.e. intensity of selective pressures and constraints specifically acting on females (Rosvall *et al.*, 2020; Cooney *et al.*, 2022; Doutrelant *et al.*, 2020).

Egg production, as a female-specific cost of reproduction is a factor expected by theoretical models to influence female ornamentation (Fitzpatrick *et al.*, 1995). While predation risk has been well-studied as a cost of reproduction limiting the evolution of female ornaments (e.g.; Martin & Badyaev, 1996; Soler & Moreno, 2012; Dunn *et al.*, 2015; Matysiokova *et al.*, 2017; Cain *et al.*, 2019), the consequences of investing more in the production of eggs remain overlooked by comparative studies. Theoretically, females paying higher reproductive costs are predicted to invest less in signaling (Chenoweth *et al.*, 2006). This trade-off was shown experimentally in blue tits where females forced to lay more eggs during one breeding season produced less developed color ornaments in the consecutive molt (Doutrelant *et al.*, 2012). At the interspecific level, this trade off was verified in the Hirundinidae family for a morphological trait, with female tail fork depth decreasing with increasing egg size (Hasegawa & Arai, 2017). In another study, females from tropical passerine species – typically associated with smaller clutch size than temperate species – were found to be more colorful (Dale *et al.*, 2015). But yearlong territoriality and lifelong pairs are also more widespread in tropical species, and may also explain the evolution of female coloration through intrasexual selection and male mate choice. Thus, whether variation in female reproductive costs constrains the evolution of female coloration still needs attention.

Paternal care is by contrast a factor supposed to influence two female-related forces promoting

the evolution of female ornaments. Theoretical models predict the more time a male invests in parental care, the choosier he is expected to be (Kokko & Johnstone, 2002), enabling the evolution of female ornaments through intersexual selection. In addition, paternal care can also be indirectly related to the evolution of female ornaments through intrasexual selection if females compete for access to paternal care (Lyu *et al.*, 2017). At the interspecific level, the effect of paternal care has been rarely tested specifically, with mixed results across studies. Absence of paternal care was related to species with duller female upper part coloration in one study (Dale *et al.* 2015). In another study, paternal care was more widespread in more colorful monochromatic species, but with no change in female brightness and color (Dunn *et al.*, 2015). Last, male participation to nest-building was associated with more intense female coloration (estimated by human eye) in a comparative analysis on 178 Western Palearctic passerines (Soler *et al.*, 2019). In these three studies, paternal care was estimated as a binary index (presence/absence) while paternal investment can vary both within the stages of reproduction and across bird species. Thus, a necessary step to help clarifying the role of paternal investment in reproduction on the evolution of female ornament is to quantify variation in male investment across different stages of paternal care (from incubation to fledgling). Finally, it is important to estimate the effect of the interaction between costs of reproduction and paternal care, because the cost of female reproduction may reduce the expected expression of female coloration in species with high paternal care.

Here, we carried out phylogenetic comparative analyses to test whether interspecific variation in paternal care interacts with female reproductive costs to explain some of the variation in female coloration. We controlled for male coloration to account for genetic correlation between males and females. Excluding female coloration from the models is a common approach when working on the evolution of male ornamentation. Using this approach assumes that all coloration is

potentially adaptive, which seems unrealistic for both sexes (Price, 1996). Here, we chose a conservative perspective, and we studied female coloration while controlling for male coloration. Yet, for the sake of comparison with the literature, we presented the results of analyses that excluded male coloration in ESM and discussed both results.

We worked on passerine bird species from the temperate Northern hemisphere. The amount of paternal care during different stages of reproduction (incubation, chick rearing and post fledgling) is better described, thus more quantifiable for these species than for non-temperate ones. Likewise, information on female reproductive costs - egg size and volume - is also better described in temperate species, with temperate species also presenting more variability in reproductive costs compared to tropical ones. We measured the whole-body plumage of females and males with a spectrometer. Bird eye physiology allows many species of birds to see ultra-violet and to discriminate colors differently from human (Vorobyev, 2003). We therefore used avian visual perception models so that our color metrics reflect coloration as perceived by birds in their avian color space (Stoddard & Prum, 2008; Renoult *et al.*, 2017). We predicted that paternal care should enhance female conspicuous plumage coloration and female reproductive costs should constrain it, with possible interactions between these two factors (Fitzpatrick *et al.* 1995; Kokko and Johnstone 2002, Chenoweth *et al.* 2006).

## **Material & Methods**

We studied 133 Northern temperate passerine species (complete list in Table S1) for which we had enough information on paternal care and cost of reproduction. Because evolutionary lability in female color traits was historically detected in Icteridaes and Thraupidaes (Icteridaes: Irwin, 1994;



Thraupidae: Burns, 1998), we included species belonging to 17 families phylogenetically close to Icteridae and Thraupidae (Fig. S1). All selected species breed on the mainland to avoid some confounding effects of insularity syndrome (Doutrelant *et al.*, 2016).

### **Response variables - Color analyses**

We measured with a spectrophotometer (details in ESM) well preserved stuffed specimens of adults with breeding plumage. These specimens belong to the collections at the National Museum of Natural History in Paris and were selected by AF and DG. Spectrometry is a precise and objective method that is strongly recommended when the human visual system differs from that of the natural signal receivers (Odeen *et al.*, 2011). Previous analyses have shown that spectrometric estimates of plumage coloration are similar for well-preserved specimens and freshly collected specimens (Doucet & Hill, 2009). To estimate coloration across the whole body in both males and females we measured the same twenty-one topographical zones on each specimen (Fig. S2).

We selected one male (except for one species for which two males were selected) and one female from each species/subspecies, focusing on the best-preserved birds (see details in ESM and Table S1), a method which is similar to the common practice in recent comparative analyses of working on ‘typical’ specimens from bookplates or photos (Rubenstein and Lovette 2009; Dale *et al.* 2015; Negro *et al.* 2018; Soler *et al.* 2019, Merwin *et al.* 2020, Delhey *et al.* 2021), while gaining more precision, specifically by assessing ultraviolet part of coloration and integrating avian vision instead of human vision.

We analyzed the spectral data using the R (R Core Team, 2022) package *pavo* (Maia *et al.*, 2019).

We used both equal illuminance across wavelengths and the blue tit visual system (Stoddard &

Prum, 2008) to reconstruct how colors would be perceived by birds and more specifically by conspecifics.

For each male and female of each species, we quantified three coloration metrics to encompass different aspects of coloration (Renoult *et al.*, 2017): (i) mean brightness as an achromatic metric of coloration, (ii) mean chromaticity as an index of the intensity of coloration, and (iii) color volume as an index of the diversity of colors (see details in ESM and, Table S2 for correlation between these metrics). Male and female color volumes were log transformed to fit a normal distribution. The values of the coloration metrics were standardized to have a mean of zero and a variance of one.

#### **Explanatory variables.**

Values for life-history traits were determined using the literature (Cramp & Simmons, 2009; Rodewald, 2015).

Egg production. We used clutch volume ( $\text{mm}^3$ ; egg volume\*clutch size) to estimate reproductive costs associated with female initial investment in reproduction (referred as “egg production”) (Watson *et al.*, 2015). This allowed us to account for both egg production strategies: large clutch sizes or large eggs. We only used mean clutch size when median clutch size (a more common statistic) was not available. Egg volume ( $\text{mm}^3$ ) was calculated using Hoyt’s formula (Hoyt, 1979): egg volume =  $0.509 * (\text{egg length}) * (\text{egg width})^2$ . Since we used closely related songbird species, we assumed there was no bias due to the potential asymmetry in egg shape (Hoyt, 1979).

Paternal care. In songbirds, male investment can vary continuously from a lack of paternal care to equal share of duties with females. In some species, male’s contribution relates only to post-fledgling care whereas in other species, males also share incubation duty with females. To account

for this variation of investment in parental care, we characterized paternal care during three main reproductive stages: incubation, chick rearing (i.e., brooding and feeding), and post-fledgling.

We used the method developed by Webb et al. (2010) to quantify the relative male contribution during each stage ( $P_{x \text{ male}}$  in (1)) and then to define the relative male contribution to total parental care ( $P_{T \text{ male}}$  in (2)).

$$P_{X \text{ male}} = \frac{\sum \text{male contribution at stage "X"}}{\sum \text{male contribution at stage "X"} + \sum \text{female contribution at stage "X"}} \quad (1)$$

$$P_{T \text{ male}} = \frac{P_{I \text{ male}} * t_I + P_{R \text{ male}} * t_R + P_{F \text{ male}} * t_F}{t_T} \quad (2)$$

$P_{T \text{ male}}$ ,  $P_{I \text{ male}}$ ,  $P_{R \text{ male}}$ , and  $P_{F \text{ male}}$  in (2) refer to the relative contribution made by males to (T) total parental care, (I) incubation, (R) chick rearing, and (F) post-fledging, respectively. The variables  $t_T$ ,  $t_I$ ,  $t_R$ , and  $t_F$  refer to the duration (in days) of these same periods, where  $t_T = t_I + t_R + t_F$  (see ESM for details).

We based our scoring on quantitative estimates of contributions when available in (Webb *et al.*, 2010). Otherwise, we estimated them as followed: when only descriptions were provided, we applied a standardized scoring procedure based on the use of adverbs and other qualifiers (rarely, often, female-only, etc.; details in Table S3). Median activity duration was used when mean activity duration was not available. When possible, we employed information corresponding to the subspecies selected for plumage measurement; otherwise, we used information corresponding to main subspecies. AF assigned scores. To control for bias in assigning scores, the list of species with adverbs and qualifiers used in the literature was provided to all co-authors who were asked

to assign a score to each species based on the qualifiers. There was a high correlation among co-authors in the way of assigning scores ( $>0.82$ ). The scoring performed by AF was kept for analyses.

For all species in the dataset, the total female contribution to parental care was equal to or higher than the total male contribution. There were no species with male-only parental care; we thus avoided rare cases of reverse sexual selection, which have already received significant attention (Edward & Chapman, 2011).

**Controlled covariates.** Our analyses also included additional factors likely to affect the evolution of female coloration. Controlled covariates corresponding to life-history traits were determined using the literature (Cramp & Simmons, 2009; Rodewald, 2015).

Male coloration: genetic correlation and constraints on male coloration is predicted to affect female coloration. We used a conservative approach and included male coloration (corresponding color metric) as a covariable in our analysis to quantify this correlation.

Nest characteristics: nest height and openness were related to color evolution (Soler & Moreno, 2012) by increasing vulnerability to predation during nest attendance. We used an index of nest characteristics, combining nest openness and nest height, to control its effect on female coloration in our analysis. We assigned a score from 0 to 2 to both nest position and openness, for each species (details in Table S4). We then summed the two scores to an overall score ranging from 0 to 4, with 0 characterizing the lowest level of vulnerability and 4 the highest level of vulnerability of nest characteristics.

Female body size: Since female body size can influence egg production (Bennett & Owens, 2002) as well as plumage coloration (Dale *et al.*, 2015; Cooney *et al.*, 2022), we also included in our

analyses mean female body mass for each species and log transformed the values to fit a normal distribution.

Migration: migratory behavior has also been shown to affect color evolution (Friedman *et al.*, 2009; Dale *et al.*, 2015; Dunn *et al.*, 2015; Delhey *et al.*, 2021; Cooney *et al.*, 2022). Three levels were defined for this variable: strictly resident, partially migrant and strictly migrant.

Breeding period duration (in days): Breeding period duration was also added as a covariable because it may influence reproductive investment and thus plumage coloration (Bokony & Liker, 2005). It was calculated by multiplying the amount of time needed to produce a single brood by the mean number of broods per breeding season. This value was log transformed to fit a normal distribution.

### **Phylogenetic comparative methods**

We carried out phylogenetic generalized least squares (PGLS) (Grafen, 1989) using the R packages *phytools* (Revell, 2018) and *phylolm* (Ho & Ane, 2014). PGLS analyses make it possible to run a model and estimate the phylogenetic signal in the model residuals at the same time (Revell, 2010). To account for potential phylogenetic relationships among the species in our dataset (Felsenstein, 1985), we extracted 500 random phylogenetic trees (available file “phylogenies.tre” in dryad repository) with Hackett backbones from the birdtree.org website (Jetz *et al.*, 2012) using the R package *ape* (Paradis *et al.*, 2018).

For each of the three color metrics, we ran a linear model including our two predictors of interest (paternal care and egg production), allowing their interaction, and the five covariates defined above. All the predictors and covariates tested in our analysis are presented in Figure 1 and their values were similarly standardized. We tested for multicollinearity among them using the R

package *yhat* (Nimon *et al.*, 2013). Apart from a strong correlation between female body mass and egg production ( $r=0.683$ ), multicollinearity was low ( $r<0.07$ ).

For each color metric set as the variable to explain, we ran PGLS analyses on the models using each of the 500 phylogenetic trees and simultaneously estimated Pagel's lambda for tree (Table 1). To include uncertainty (Paradis, 2012; Garamszegi & Mundry, 2014) within the songbird phylogeny, we used a model-averaging procedure (Garamszegi & Mundry, 2014) that was based on the AIC weights associated with each tree and calculated the estimate values and 95% confidence intervals for all the predictors in the models accounting for phylogenetic uncertainty (Garamszegi & Mundry, 2014) based on 500 phylogenetic trees.

## Results

The three female color metrics were strongly associated (all estimates  $\sim 0.7$ ) with their corresponding male color metrics (Figure 1, Table 1). More colored females were found in species with more colored males.

Female brightness and female chromaticity were slightly correlated to paternal care (brightness: 0.14 [0.03; 0.26] 95% CI, chromaticity: 0.13 [0.002; 0.26] 95% CI) independently of egg production (Figure 1a, Figure 2, Table 1). Species with more paternal care had brighter females and higher female chromaticity. The interaction between paternal care and egg production was in addition marginally associated with female chromaticity ( $-0.14 [-0.26; -0.02]$  95% CI), Figure 1b, Table 1). At low egg production, female chromaticity increased when paternal care increased. When paternal care was relatively high, female chromaticity decreased when egg production increased (Figure 3). We found no effect of paternal care or egg production on female color volume (Figure 1c, Table 1).

Among the covariates, only migratory behavior was correlated with chromaticity. Females from strictly resident species had less intense coloration than partially migrant and migrant species (-0.43 [-0.83; -0.03] 95% CI) (Figure 1 and Table 1).

## Discussion

This study aimed at determining whether female cost of reproduction and paternal care explained part of the evolution of female ornaments. The results suggest modest but detectable male-independent associations between these two factors and two proxies of female coloration. Female brightness slightly covaries with paternal care, and female intensity of coloration (chromaticity) is associated with paternal care and the interaction between the two factors. In addition, our results confirm strong coevolution between male and female coloration, which represents a major source of variation for the coloration of both sexes.

In two former very large-scale comparative analyses, presence/absence of paternal care during nestling stage tested in association with other proxies of male sexual or natural selection, was associated with female coloration, once positively and once negatively (Dale *et al.*, 2015; Dunn *et al.*, 2015). In one smaller scale comparative analysis, the presence/absence of paternal care during incubation was in addition positively associated with female coloration (Soler *et al.* 2019). Our analysis, also conducted at a small scale but using a continuous index of paternal care, encompassing incubation to post-fledging care, suggests that interspecific variation in time invested by males in parental care is associated to both female brightness and female chromaticity.

In the Northern temperate passerine birds included in our study, paternal care is slightly positively related to female brightness (Figure 2). A positive association may result from the action of two non-exclusive forces: through male mate choice as males are predicted to be choosier when they invest more in paternal behaviors (Kokko & Johnstone, 2002), and through intra-sexual

competition where females compete to access paternal care (Tobias *et al.*, 2012; Cain, 2014). For female chromaticity, our study suggests in addition a small but detectable role of female investment in egg production. In species with low egg production, the chromaticity of female coloration increases with paternal care, but in species with the highest male investment, the chromaticity of female coloration decreases when investment in egg production increases (Figure 3). This interaction suggests a threshold beyond which the cost of reproduction in females could no longer favor the positive coevolution of female coloration and male investment in parental care. The colors of ornaments, i.e. their chromaticity, are often costly to produce (McGraw, 2006), and a trade-off between female investment in offspring and female investment in costly ornaments is predicted to limit the evolution of female coloration at some point (Fitzpatrick *et al.*, 1995; Chenoweth *et al.*, 2006). This trade-off can even lead female traits to become non-functional (Nordeide *et al.*, 2013). Nonetheless, most of the species included in our study have some form of paternal care, and only few species have large egg production, (Figure 3). Therefore, to confirm the detected trade-off between investing in eggs or color intensity, future comparative analyses may include more species with low or no paternal care and high level of female investment in eggs.

We found no association between female brightness and egg production. This suggests that the production of achromatic ornamentation may be less costly and thus less constrained by the cost of egg production than color intensity. In an experiment in blue tits, an increase in reproductive costs in females changed the chromatic component (hue) of the blue crown but did not affect brightness of the same patch (Doutrelant *et al.*, 2012). Experiments aimed at relating the effect of reproductive costs on both achromatic and chromatic components of coloration are needed to confirm this suggestion.



Color volume was not associated with any of our tested variables. Color volume relates to the diversity of coloration (Stoddard & Prum, 2008), and it is sometimes thought that greater volume indicates more diverse mechanisms of color production. The fact that paternal care and female investment in reproduction does not affect this diversity of coloration in females when controlling for male coloration may suggest diversity of coloration in females is not under strong intra- and intersexual selection in females and its evolution may be related to other selective forces. To date, comparative analyses found an association between color volume and sex, documenting higher diversity of colors in males than females (Delhey, 2015; Shultz & Burns, 2017), and males from sexually dichromatic species to be more colorful than males from less dichromatic species (Cooney *et al.*, 2022). Additionally, they found for each sex an association between color volume or colorfulness and type of habitats (Shultz & Burns, 2017; Cooney *et al.*, 2022), or between color volume and the number of sympatric species from the same family (Doutrelant *et al.*, 2016). Thus, habitat selection and interspecific competition may be the main factors associated with the evolution of color volume, with stronger selection in males than females.

For our three proxies of coloration, male coloration was the factor explaining most of the variation in female coloration. This result was also found in several former comparative studies (e.g. Dale *et al.* 2015; e.g. Delhey 2015; Shultz and Burns 2017; Cooney *et al.* 2019). This strong phenotypic correlation is potentially in favor of the prevailing role of genetic correlation (Lande, 1980) i.e. shared genetic architecture, in the level of expression of color traits in females. For instance, the coloration of the red bill of zebra finches is strongly correlated between fathers and daughters (Price, 1996). However, phenotypic correlation may also be the result of other color-correlated factors such as shared diets (Amundsen *et al.*, 2006) as well as shared natural, social, and sexual selective pressures acting on both sexes (Shultz & Burns, 2017). It could also be the

result of divergent types of selection in males and females that select for similar ornamentation in both sexes, for instance social selection for females and sexual selection for males (Tobias *et al.*, 2012). So the part of variance explained by the phenotypic correlation in our models can also overestimate the importance of genetic correlation. Female coloration may be driven by female-specific selective pressure even in species sharing similar colors, with different forces leading to similar colorations (Amundsen *et al.*, 2006; Enbody *et al.*, 2017).

By including male coloration in our analyses, we have statistically “corrected” for correlated plumage similarities between sexes and the effect of genetic correlation, but we have also drastically reduced our ability to detect the real importance of selective pressures. When removing male corresponding color metric from our models (See Table S5), we found that estimates for egg production were much bigger in relation to female brightness (0.435 [0.063;0.806] 95% CI), suggesting we potentially underestimated the effect of female investment on female coloration. Estimate values remained similar for paternal care and the interaction between paternal care and egg production (See Table S5). So female reproductive costs may drive the evolution of female coloration (constraining chromaticity and favoring brightness) as a higher level than what we find with our conservative approach including male coloration in the statistical model. Yet, we think it is better to retain the conclusion of the model controlling for male coloration, to include the acknowledged effect of genetic correlation.

We assumed that species showing higher values of brightness and chromaticity could be seen as more ornamented/conspicuous. This is reasonable for conspicuous carotenoid and structural colors (red, blue, yellow, blue, violet), but works poorly for dark to black ornaments (Marcondes & Brumfield, 2019). If males produce black ornaments and females not, female brightness and chromaticity will be higher than male brightness and chromaticity but in fact female would appear

duller. But only three species of our data set correspond to males with large amount of black coloration (using a method adapted from (Osorio *et al.*, 2004) that defines black as a coloration that produces less than 0.05 percentage reflectance of the white standard at each photoreceptors), so it unlikely affected our results.

Regarding ecological factors included as covariate in our study, we found a correlation between migratory behavior and intensity of coloration. In accordance with previous work (Dale *et al.*, 2015; Dunn *et al.*, 2015), females from strictly resident species were less likely to have intense colors (chromaticity metric). Unlike Cooney et al (2022), we did not find a correlation between migratory behavior and female color volume, which may be a consequence of our dataset, restricted to species breeding in northern temperate areas. We did not find any correlation between female color metrics and nest characteristics. Different studies had found that birds breeding in higher and more open nests have less conspicuous females (Martin & Badyaev, 1996; Soler & Moreno, 2012), but other recent studies failed to find a correlation between predation risk or nest openness and plumage conspicuousness (Matysiokova *et al.*, 2017; Cain *et al.*, 2019; Simpson *et al.*, 2020). This lack of consistency among studies can be explained by the difficulty to build adequate metrics to estimate predation risk. It can also be related to variation in the quantification of coloration (human vision, color from bookplates, spectrometry) or to the decision of treating males and females together or separately.

To conclude, our work confirms the strong covariation between male and female coloration. In addition, it reveals a moderate association between paternal care and female coloration when female costs are reduced, either with lower cost of egg production, or lower cost of producing female ornament. These costs are likely important to consider and should be incorporated when testing other potential factors that drives the evolution of female ornamentation (such as female

territoriality). Paternal care is associated with both female brightness and chromaticity showing the importance of considering this factor in further analyses. More generally, this study shows the importance of testing factors related to female-specific forces of selection and costs, to understand and determine the array of factors leading to the evolution of female ornaments.

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## Table and Figure legends

**Table 1:** Estimated values from the PGLS analyses. Variables are sorted in the same order as in Figure 1. 95% confidence intervals (displayed in brackets) include phylogenetic uncertainty. Estimates with confidence intervals not overlapping zero are represented in bold (except for Pagel's Lambda values).

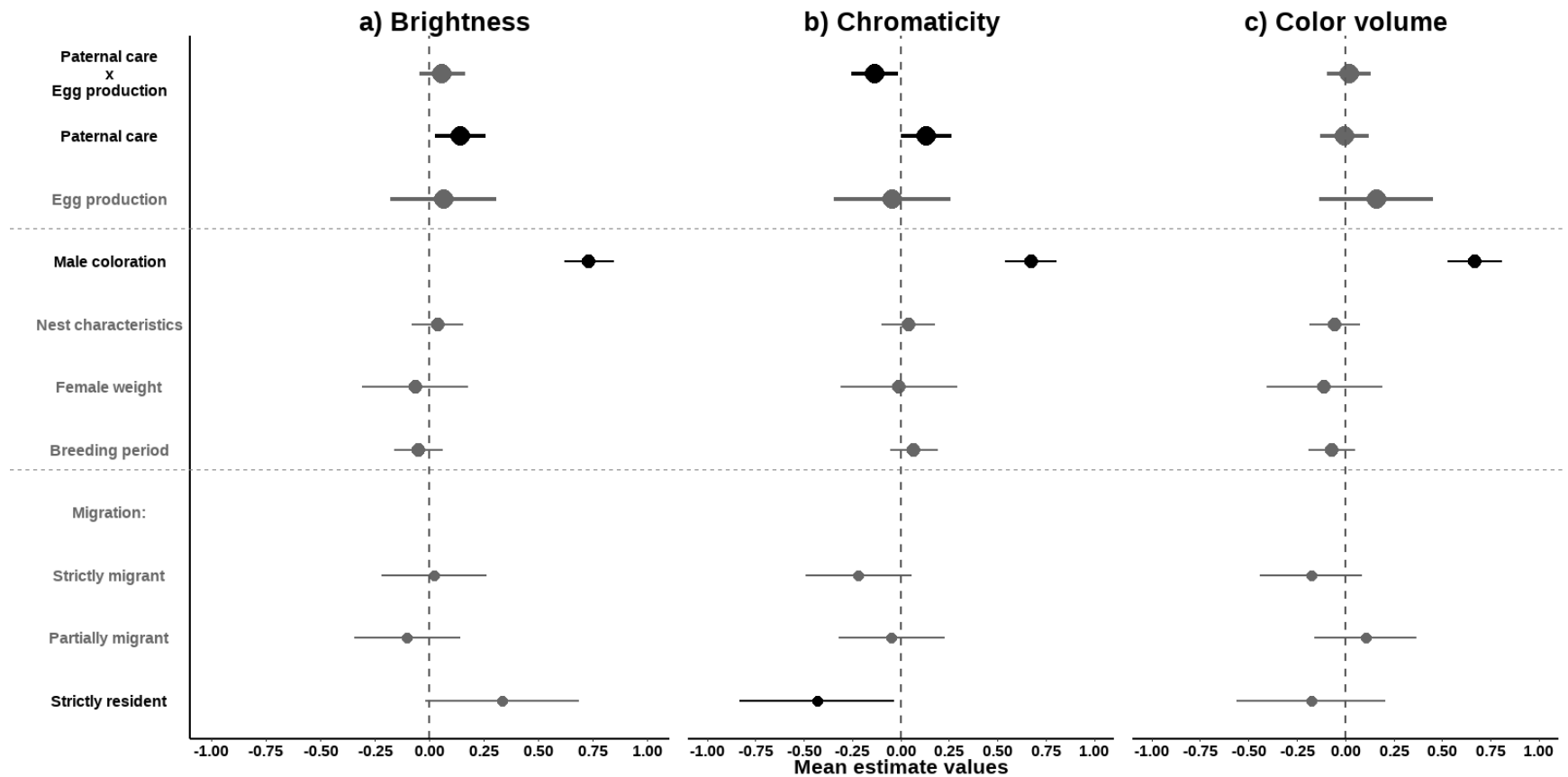
**Figure 1:** Forest plots for a) brightness, b) chromaticity, and c) color volume in females, representing the mean estimates and their confidence intervals obtained by model averaging (see ESM). Mean estimates integrated control for phylogenies (PGLS analyses) for b) and c). Confidence intervals included phylogenetic uncertainty with 95% confidence intervals. “Male coloration” refers to the corresponding coloration metric. Larger circles were used to emphasize the main proxies of interest in our studies (smaller circles for other tested covariates). Estimates associated with confidence intervals not overlapping zero are displayed in black along with corresponding covariate (on the left). Estimates associated with confidence intervals overlapping zero are in grey along with the corresponding covariate.

**Figure 2:** Relationship between paternal care and mean female plumage brightness. The black crosses are the raw values for each species, the best-fit line is dashed with grey area representing the 95% confidence intervals. We also tested the represented relationship excluding the four outliers (low paternal care values), and we obtained equivalent trend (0.10 [95% CI: -0.02;0.23]).

**Figure 3:** Depiction of the two-way interaction between paternal care and egg production and its effect on interspecific variation in mean female plumage chromaticity. The equation includes estimates for paternal care, egg production and their interaction. The black stars are the raw values for each species.

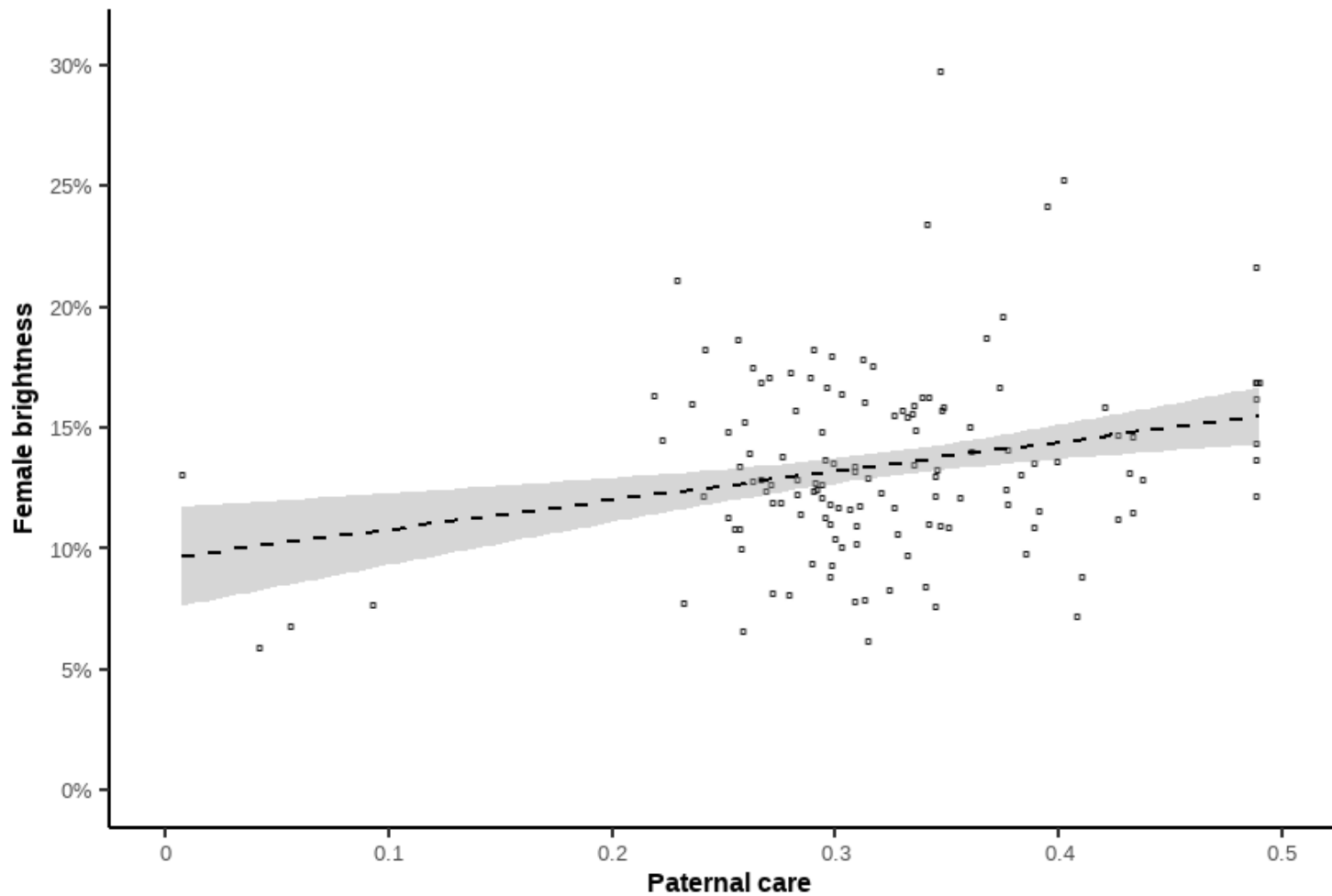
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Estimates with confidence intervals			
Variable	Brightness	Chromaticity	Color volume
Paternal care	<b>0.143 [0.028;0.258]</b>	<b>0.132 [0.002;0.262]</b>	-0.004 [-0.132;0.123]
Egg production	0.066 [-0.178;0.309]	-0.004 [-0.347;0.259]	0.159 [-0.133;0.452]
Egg production x Paternal care	0.059 [-0.045;0.164]	<b>-0.135 [-0.255;-0.015]</b>	0.019 [-0.096;0.133]
Male coloration	<b>0.733 [0.618;0.848]</b>	<b>0.672 [0.541;0.803]</b>	<b>0.670 [0.530;0.810]</b>
Nest characteristics	0.038 [-0.079;0.155]	0.040 [-0.098;0.177]	-0.055 [-0.186;0.076]
Female weight (log)	-0.065 [-0.310;0.180]	-0.009 [-0.312;0.294]	-0.108 [-0.406;0.190]
Breeding period (log)	-0.049 [-0.160;0.063]	0.068 [-0.055;0.191]	-0.069 [-0.188;0.050]
Migration			
Strictly migrant	0.021 [-0.220;0.262]	-0.217 [-0.490;0.056]	-0.176 [-0.562;0.207]
Partially migrant	-0.101 [-0.342;0.140]	-0.047 [-0.320;0.226]	0.104 [-0.160;0.369]
Strictly resident	0.334 [-0.019;0.687]	<b>-0.431 [-0.831;-0.031]</b>	-0.177 [-0.562;0.207]
Pagel's Lambda	$1.10^{-6}$ [ $1.10^{-6}$ ; $1.10^{-6}$ ]	0.355 [0.351 ;0.358]	0.444 [0.440 ;0.448]

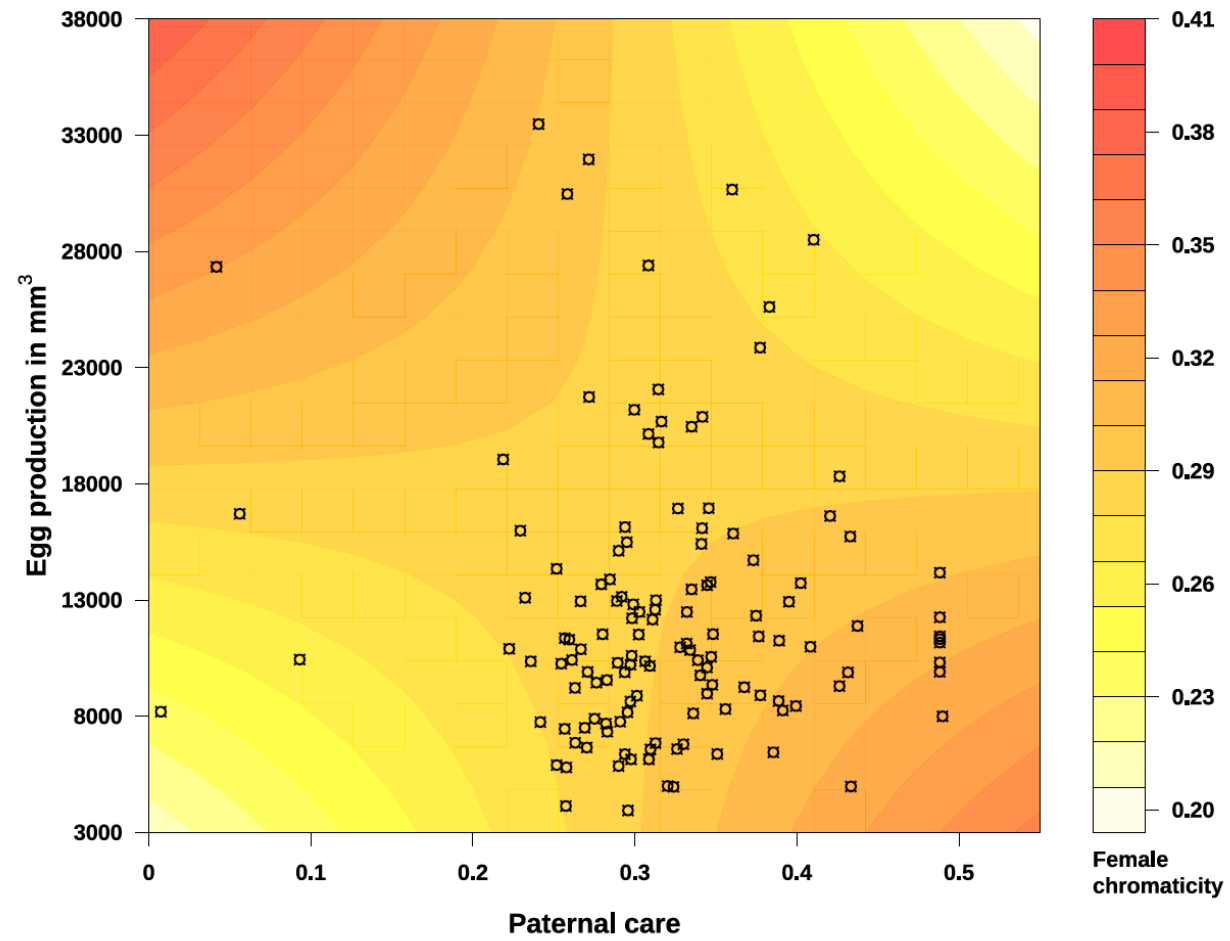


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