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

Amélie Fargevielle, Arnaud Grégoire, Doris Gomez, Claire Doutrelant

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1 *Abstract*

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

19

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

22 Introduction

23 Males in many animal species display conspicuous ornaments and armaments and a large body
24 of evolutionary research has aimed to understand the factors at the origin of this variation
25 (Andersson, 1994). Females in many animal species also display conspicuous traits and in the past
26 twenty years, research focusing on the evolution and variation in female ornaments has increased
27 (Amundsen, 2000; Harrison & Poe, 2012; Nordeide *et al.*, 2013; Odom *et al.*, 2014; Dale *et al.*,
28 2015; Riebel *et al.*, 2019; Doutrelant *et al.*, 2020).

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

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

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

51 Egg production, as a female-specific cost of reproduction is a factor expected by theoretical
52 models to influence female ornamentation (Fitzpatrick *et al.*, 1995). While predation risk has been
53 well-studied as a cost of reproduction limiting the evolution of female ornaments (e.g.; Martin &
54 Badyaev, 1996; Soler & Moreno, 2012; Dunn *et al.*, 2015; Matysiokova *et al.*, 2017; Cain *et al.*,
55 2019), the consequences of investing more in the production of eggs remain overlooked by
56 comparative studies. Theoretically, females paying higher reproductive costs are predicted to
57 invest less in signaling (Chenoweth *et al.*, 2006). This trade-off was shown experimentally in blue
58 tits where females forced to lay more eggs during one breeding season produced less developed
59 color ornaments in the consecutive molt (Doutrelant *et al.*, 2012). At the interspecific level, this
60 trade off was verified in the Hirundinidae family for a morphological trait, with female tail fork
61 depth decreasing with increasing egg size (Hasegawa & Arai, 2017). In another study, females
62 from tropical passerine species – typically associated with smaller clutch size than temperate
63 species – were found to be more colorful (Dale *et al.*, 2015). But yearlong territoriality and lifelong
64 pairs are also more widespread in tropical species, and may also explain the evolution of female
65 coloration through intrasexual selection and male mate choice. Thus, whether variation in female
66 reproductive costs constrains the evolution of female coloration still needs attention.

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

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

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

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

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

108

109

110 **Material & Methods**

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

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

117 **Response variables - Color analyses**

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

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

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

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

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

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

145 **Explanatory variables.**

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

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

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

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

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

$$163 \quad P_{X \text{ male}} = \frac{\sum \text{male contribution at stage "X"}}{\sum \text{male contribution at stage "X"} + \sum \text{female contribution at stage "X"}} \quad (1)$$

$$164 \quad P_{T \text{ male}} = \frac{P_{I \text{ male}} * t_I + P_{R \text{ male}} * t_R + P_{F \text{ male}} * t_F}{t_T} \quad (2)$$

165
 166
 167
 168 $P_{T \text{ male}}$, $P_{I \text{ male}}$, $P_{R \text{ male}}$, and $P_{F \text{ male}}$ in (2) refer to the relative contribution made by males to (T) total
 169 parental care, (I) incubation, (R) chick rearing, and (F) post-fledging, respectively. The variables
 170 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
 171 for details).

172 We based our scoring on quantitative estimates of contributions when available in (Webb *et al.*,
 173 2010). Otherwise, we estimated them as followed: when only descriptions were provided, we
 174 applied a standardized scoring procedure based on the use of adverbs and other qualifiers (rarely,
 175 often, female-only, etc.; details in Table S3). Median activity duration was used when mean
 176 activity duration was not available. When possible, we employed information corresponding to the
 177 subspecies selected for plumage measurement; otherwise, we used information corresponding to
 178 main subspecies. AF assigned scores. To control for bias in assigning scores, the list of species
 179 with adverbs and qualifiers used in the literature was provided to all co-authors who were asked

180 to assign a score to each species based on the qualifiers. There was a high correlation among co-
181 authors in the way of assigning scores (>0.82). The scoring performed by AF was kept for analyses.
182 For all species in the dataset, the total female contribution to parental care was equal to or higher
183 than the total male contribution. There were no species with male-only parental care; we thus
184 avoided rare cases of reverse sexual selection, which have already received significant attention
185 (Edward & Chapman, 2011).

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

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

192 *Nest characteristics:* nest height and openness were related to color evolution (Soler & Moreno,
193 2012) by increasing vulnerability to predation during nest attendance. We used an index of nest
194 characteristics, combining nest openness and nest height, to control its effect on female coloration
195 in our analysis. We assigned a score from 0 to 2 to both nest position and openness, for each species
196 (details in Table S4). We then summed the two scores to an overall score ranging from 0 to 4, with
197 0 characterizing the lowest level of vulnerability and 4 the highest level of vulnerability of nest
198 characteristics.

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

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

203 Migration: migratory behavior has also been shown to affect color evolution (Friedman *et al.*,
204 2009; Dale *et al.*, 2015; Dunn *et al.*, 2015; Delhey *et al.*, 2021; Cooney *et al.*, 2022). Three levels
205 were defined for this variable: strictly resident, partially migrant and strictly migrant.

206 Breeding period duration (in days): Breeding period duration was also added as a covariable
207 because it may influence reproductive investment and thus plumage coloration (Bokony & Liker,
208 2005). It was calculated by multiplying the amount of time needed to produce a single brood by
209 the mean number of broods per breeding season. This value was log transformed to fit a normal
210 distribution.

211 **Phylogenetic comparative methods**

212 We carried out phylogenetic generalized least squares (PGLS) (Grafen, 1989) using the R
213 packages *phytools* (Revell, 2018) and *phylolm* (Ho & Ane, 2014). PGLS analyses make it possible
214 to run a model and estimate the phylogenetic signal in the model residuals at the same time (Revell,
215 2010). To account for potential phylogenetic relationships among the species in our dataset
216 (Felsenstein, 1985), we extracted 500 random phylogenetic trees (available file “phylogenies.tre”
217 in dryad repository) with Hackett backbones from the birdtree.org website (Jetz *et al.*, 2012) using
218 the R package *ape* (Paradis *et al.*, 2018).

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

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

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

232

233 **Results**

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

237 Female brightness and female chromaticity were slightly correlated to paternal care (brightness:
238 0.14 [0.03; 0.26] 95% CI, chromaticity: 0.13 [0.002; 0.26] 95% CI) independently of egg
239 production (Figure 1a, Figure 2, Table 1). Species with more paternal care had brighter females
240 and higher female chromaticity. The interaction between paternal care and egg production was in
241 addition marginally associated with female chromaticity (-0.14 [-0.26 ; -0.02] 95% CI), Figure 1b,
242 Table 1). At low egg production, female chromaticity increased when paternal care increased.
243 When paternal care was relatively high, female chromaticity decreased when egg production
244 increased (Figure 3). We found no effect of paternal care or egg production on female color volume
245 (Figure 1c, Table 1).

246 Among the covariates, only migratory behavior was correlated with chromaticity. Females from
247 strictly resident species had less intense coloration than partially migrant and migrant species (-
248 0.43 [-0.83; -0.03] 95% CI) (Figure 1 and Table 1).

249 **Discussion**

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

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

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

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

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

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

306 For our three proxies of coloration, male coloration was the factor explaining most of the
307 variation in female coloration. This result was also found in several former comparative studies
308 (e.g. Dale *et al.* 2015; e.g. Delhey 2015; Shultz and Burns 2017; Cooney *et al.* 2019). This strong
309 phenotypic correlation is potentially in favor of the prevailing role of genetic correlation (Lande,
310 1980) i.e. shared genetic architecture, in the level of expression of color traits in females. For
311 instance, the coloration of the red bill of zebra finches is strongly correlated between fathers and
312 daughters (Price, 1996). However, phenotypic correlation may also be the result of other color-
313 correlated factors such as shared diets (Amundsen *et al.*, 2006) as well as shared natural, social,
314 and sexual selective pressures acting on both sexes (Shultz & Burns, 2017). It could also be the

315 result of divergent types of selection in males and females that select for similar ornamentation in
316 both sexes, for instance social selection for females and sexual selection for males (Tobias *et al.*,
317 2012). So the part of variance explained by the phenotypic correlation in our models can also
318 overestimate the importance of genetic correlation. Female coloration may be driven by female-
319 specific selective pressure even in species sharing similar colors, with different forces leading to
320 similar colorations (Amundsen *et al.*, 2006; Enbody *et al.*, 2017).

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

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

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

342 Regarding ecological factors included as covariate in our study, we found a correlation between
343 migratory behavior and intensity of coloration. In accordance with previous work (Dale *et al.*,
344 2015; Dunn *et al.*, 2015), females from strictly resident species were less likely to have intense
345 colors (chromaticity metric). Unlike Cooney et al (2022), we did not find a correlation between
346 migratory behavior and female color volume, which may be a consequence of our dataset,
347 restricted to species breeding in northern temperate areas. We did not find any correlation between
348 female color metrics and nest characteristics. Different studies had found that birds breeding in
349 higher and more open nests have less conspicuous females (Martin & Badyaev, 1996; Soler &
350 Moreno, 2012), but other recent studies failed to find a correlation between predation risk or nest
351 openness and plumage conspicuousness (Matysiokova *et al.*, 2017; Cain *et al.*, 2019; Simpson *et*
352 *al.*, 2020). This lack of consistency among studies can be explained by the difficulty to build
353 adequate metrics to estimate predation risk. It can also be related to variation in the quantification
354 of coloration (human vision, color from bookplates, spectrometry) or to the decision of treating
355 males and females together or separately.

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

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

365

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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.

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).

Estimates with confidence intervals			
Variable	Brightness	Chromaticity	Color volume
Paternal care	0.143 [0.028;0.258]	0.132 [0.002;0.262]	-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]	-0.135 [-0.255;-0.015]	0.019 [-0.096;0.133]
Male coloration	0.733 [0.618;0.848]	0.672 [0.541;0.803]	0.670 [0.530;0.810]
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]	-0.431 [-0.831;-0.031]	-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]

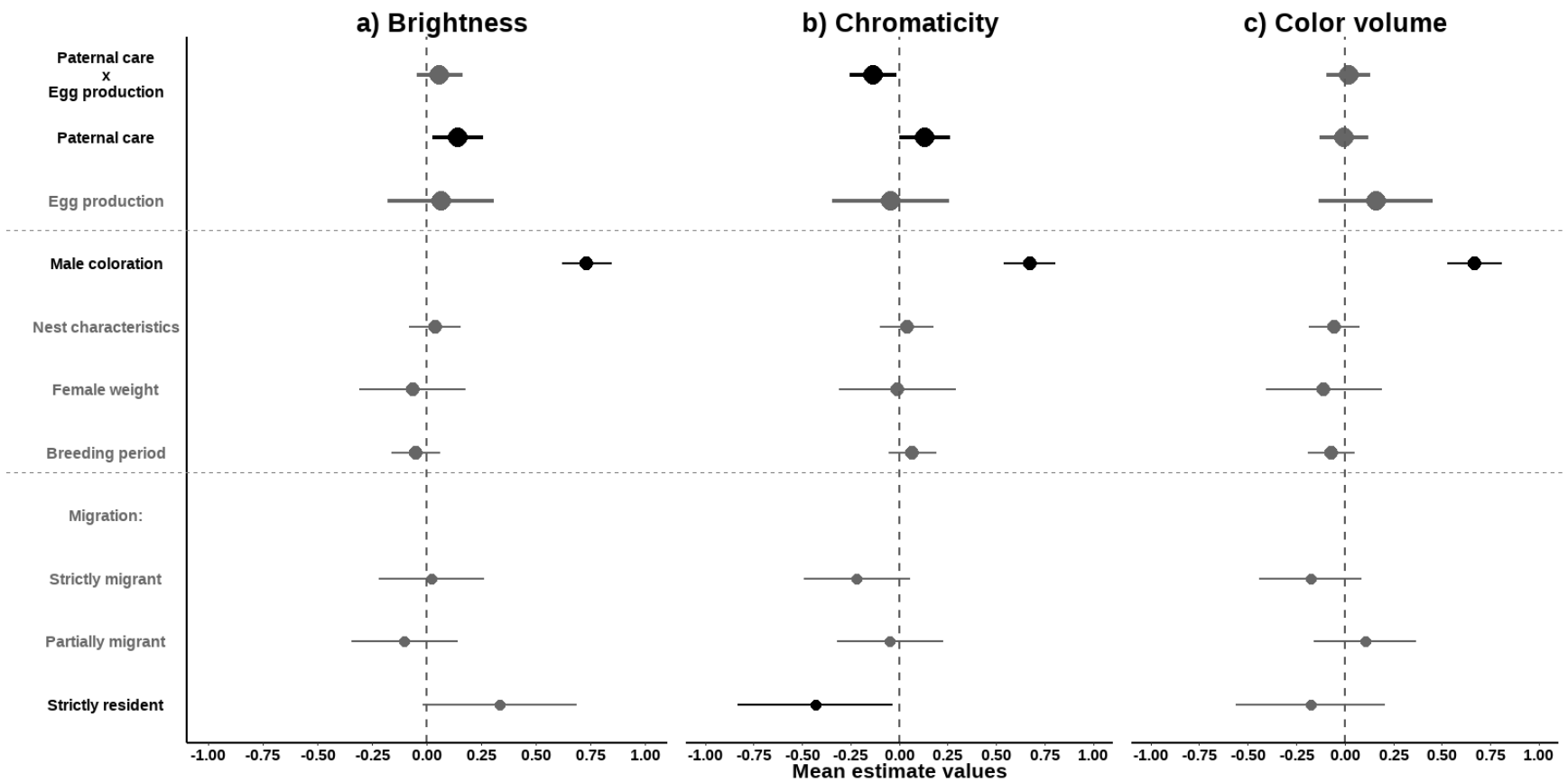


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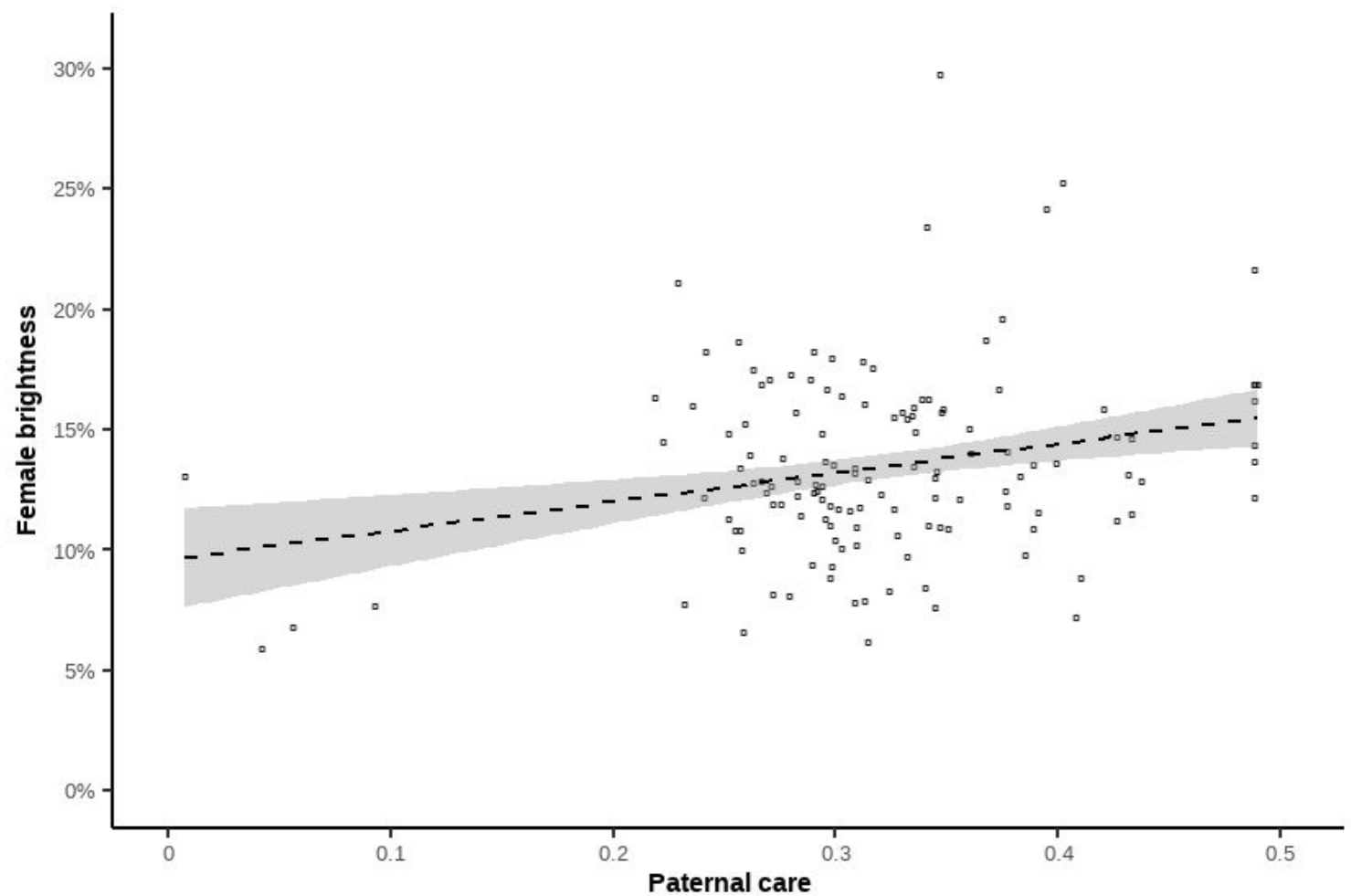


Figure 2: Relationship between paternal care and mean female plumage brightness. The black crosses are the raw values for each species, the best-fit line is dashed with grey area representing the 95% confidence intervals. We also tested the represented relationship excluding the four outliers (low paternal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

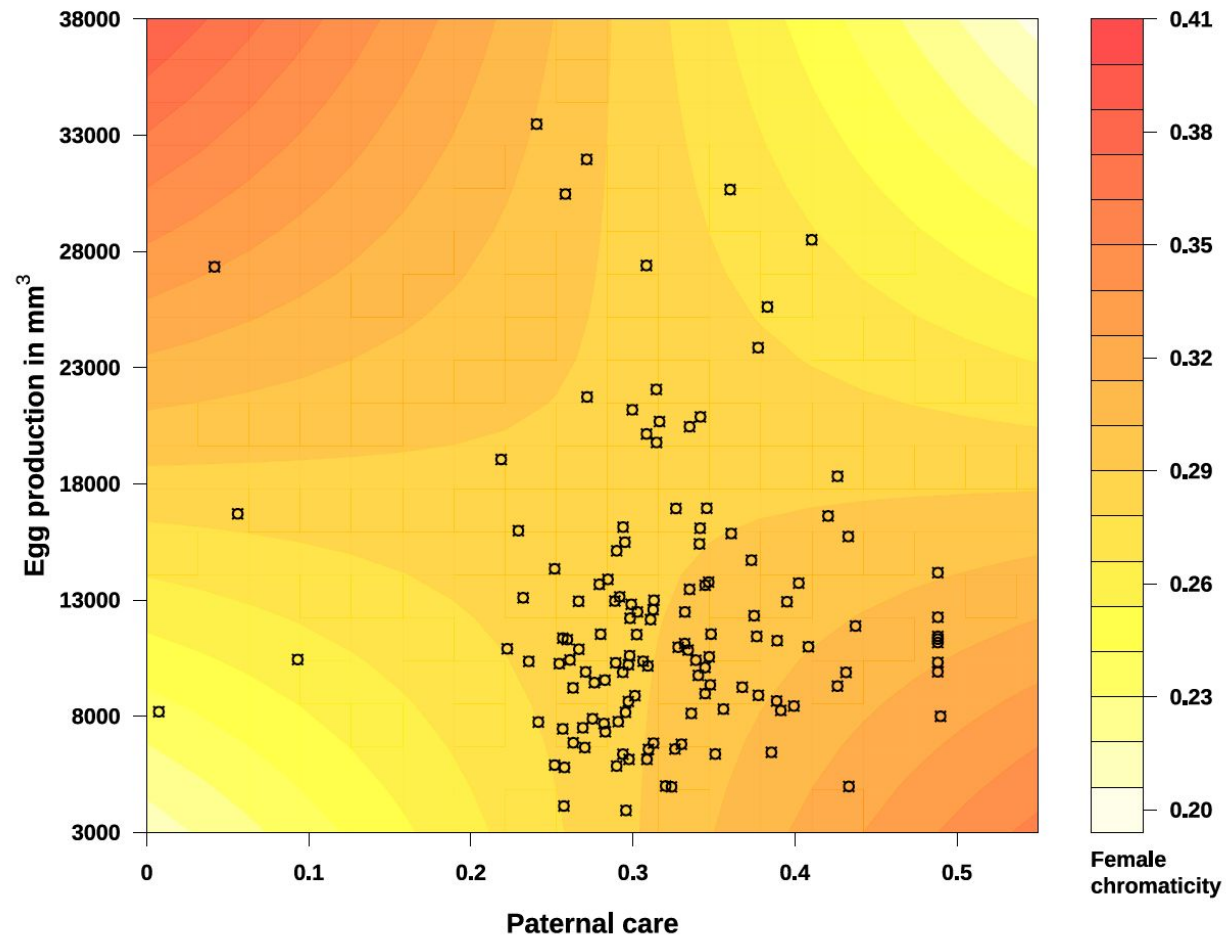


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Supplementary information

Table S1: Bird species/subspecies/families included in the analyses. The scientific names are those used by birdtree.org. The collection point is where the bird was collected (nearest town/city (state), country; the list of country abbreviations is at the bottom of the table). The number of measurements is the total number of color measurements carried out by spectrometry on the bird, where *3 indicates that the measurements were replicated three times to test repeatability. (1) Two male specimens of *Myadestes townsendi* were used; measurements were carried out on the second specimen in zones that were stained on the first specimen (except for the stain on its abdomen, the first specimen was in better condition than the second specimen).

Scientific name	Family	Male			Female		
		Collection point	Voucher number	Number of measurements	Collection point	Voucher number	Number of measurements
<i>Agelaius phoeniceus</i>	Icteridae	Auburn (NY), USA	1921-140	38	Rochester (NY), USA	1938-360	38
<i>Aimophila ruficeps</i>	Passerellidae	Dulzura (CA), USA	NA	33	Dulzura (CA), USA	NA	33
<i>Amphispiza bilineata deserticola</i>	Passerellidae	Tucson (AZ), USA	1949-417	28	El Rosario, MX	1956-1109	28*3
<i>Quiscalus mexicanus</i>	Icteridae	Chimalapa, MX	1953-656	23	Tlatizapan, MX	1937-443	23
<i>Anthus pratensis pratensis</i>	Motacillidae	Plougasnou, FR	1960-2798	36	Plougasnou, FR	1960-2818	36
<i>Anthus spinoletta spinoletta</i>	Motacillidae	Urdos, FR	1979-25	27	Saint-Jean-de-Luz, FR	1979-19	27
<i>Xanthocephalus xanthocephalus</i>	Icteridae	Silver Lake (MI), USA	1962-3448	25	Bixby(MO), USA	1955-376	25*3
<i>Bombycilla garrulous garrulous</i>	Bombycillidae	Uppsala, SE	1928-1890	28*3	Uppsala, SE	1928-1891	28
<i>Miliaria calandra</i>	Emberizidae	Pons, FR	1933-223	37	Jonzac, FR	1933-224	37
<i>Cardinalis cardinalis coccineus</i>	Cardinalidae	MX	1999-2482	27	Chimalapa, MX		27
<i>Carduelis cannabina cannabina</i>	Fringillidae	Lion-sur-Mer, FR	1965-2876	38	Le Puy-Notre Dame, FR	1978-270	38
<i>Carduelis carduelis carduelis</i>	Fringillidae	Eure-et-Loir, FR	1933-658	35	Andeville, FR	1960-1580	35*3
<i>Carduelis chloris chloris</i>	Fringillidae	Plougasnou, FR	1960-1583	27*3	Remomeix, FR	1960-76	27
<i>Carduelis flammae flammae</i>	Fringillidae	Armentières-en-Brie, FR	1977-56	43	Le Mage, FR	1977-51	43

<i>Carduelis pinus</i>	Fringillidae	Auburn (NY), USA	1921-189	39	Auburn (NY), USA	1922-18	39
<i>Carduelis psaltria</i>	Fringillidae	Dulzura (CA), USA	2001-1148	25	Dulzura (CA), USA	2001-1147	25
<i>Carduelis spinus</i>	Fringillidae	Vannes, FR	1973-506	39	Remomeix, FR	1960-75	39
<i>Carduelis tristis</i>	Fringillidae	Auburn (NY), USA	1962-3445	24*3	Kamouraska (QC), CA	1921-133	24
<i>Carpodacus mexicanus</i>	Fringillidae	Dulzura (CA), USA	1879-2771	37	La Paz, MX	2003-1580	37
<i>Carpodacus purpureus purpureus</i>	Fringillidae	Ithaca (NY), USA	1953-338	37	Ithaca (NY), USA	1953-339	37
<i>Catharus guttatus</i>	Turdidae	Reading (NY), USA	2002-42	27	Jackson County (MI), USA	1939-7	27
<i>Catharus ustulatus</i>	Turdidae	Los Angeles (CA), USA	1956-1047	26	Long Beach (CA), USA	1955-268	26
<i>Emberiza citrinella</i>	Emberizidae	Plougasnou, FR	1960-2470	42	Noisiel, FR	1962-4110	42
<i>Certhia familiaris macrodactyla</i>	Certhiidae	Saint-Cassin, FR	1993-215	39	Lucéram, FR	2008-678	39
<i>Certhia brachydactyla megarhynchos</i>	Certhiidae	Le Puy-Notre Dame, FR	1979-228	38	Le Puy-Notre Dame, FR	1979-229	38
<i>Cinclus cinclus</i>	Cinclidae	Condat-sur-Vienne, FR	1956-754	28	Solignac, FR	1948-519	28
<i>Cistothorus palustris palustris</i>	Troglodytidae	Auburn (NY), USA	1921-164	34	Cayuga (ON), CA	1921-165	34
<i>Coccothraustes coccothraustes coccothraustes</i>	Fringillidae	Southwestern FR	1990-575	32	Tencin, FR	2008-723	32
<i>Dendroica coronata auduboni</i>	Parulidae	Pasadena (CA), USA	1955-302	33	El Monte (CA), USA	1955-304	33
<i>Dendroica petechia castaneiceps</i>	Parulidae	La Paz, MX	1932-110	28*3	La Paz, MX	1932-111	28
<i>Dumetella carolinensis</i>	Mimidae	Ixtacomitan, MX	1951-800	23	Ixtacomitan, MX	1951-803	23*3
<i>Luscinia luscinia</i>	Muscicapidae	Amani Forest, TZ	1967-675	23	Joinville-le-Pont, FR	1989-246	23
<i>Emberiza cia cia</i>	Emberizidae	Aussois, FR	1969-1103	37	Urdos, FR	1978-170	37
<i>Emberiza cirius</i>	Emberizidae	Trois-Monts, FR	1965-2767	42	Le Puy-Notre Dame, FR	1978-180	42

<i>Sitta canadensis</i>	Sittidae	Cayuga (OR), USA	1921-171	29	New Haven (CT), USA	1972-1646	29
<i>Emberiza hortulana</i>	Emberizidae	Cellule, FR	1947-67	34	Fronsac, FR	1997-518	34
<i>Emberiza leucocephalos</i>	Emberizidae	Baïkal Lake, RU	1960-1440	42	Zaisan-Nor, KZ	2009-982	42
<i>Emberiza schoeniclus schoeniclus</i>	Emberizidae	Saint-Jean-du-Doigt, FR	1960-2450	42	Tonneins, FR	1987-496	42
<i>Erithacus rubecula</i>	Muscicapidae	Saix, FR	1978-878	28	Morsang-sur-Orge, FR	2013-69	28
<i>Icterus bullockii</i>	Icteridae	(CA), USA	2002-1430	30*3	Dulzura (CA), USA	2002-1429	30
<i>Spizella arborea</i>	Passerellidae	Auburn (NY), USA	1921-137	35	Rochester (NY), USA	1999-1956	35
<i>Ficedula albicollis albicollis</i>	Muscicapidae	Laconie, GR	1979-985	29	Laconie, GR	1979-991	29
<i>Ficedula hypoleuca hypoleuca</i>	Muscicapidae	Bouillé-Loretz, FR	1978-785	27	Chaponost, FR	1978-768	27
<i>Ficedula parva parva</i>	Muscicapidae	Teheran, IR	1969-2330	24	Teheran, IR	1957-875	24
<i>Fringilla coelebs coelebs</i>	Fringillidae	Brunoy, FR	1995-34	31	Plougasnou, FR	1960-1501	31
<i>Fringilla montifringilla</i>	Fringillidae	Le Crotoy, FR	1997-1452	36	Plougasnou, FR	1960-2570	36
<i>Icterus spurius</i>	Icteridae	Ixtacomitan, MX	1951-963	29	Ixtacomitan, MX	1951-969	29*3
<i>Coccothraustes vespertinus vespertinus</i>	Fringillidae	Watkins Glen (NY), USA	1953-342	27	Lewis County (NY), USA	1953-343	27
<i>Hylocichla mustelina</i>	Turdidae	Yaxchilan, MX	1975-910	28	Yaxchilan, MX	1975-915	28
<i>Sitta carolinensis</i>	Sittidae	Auburn (NY), USA	1921-100	34	Auburn (NY), USA	1921-169	34
<i>Euphagus cyanocephalus</i>	Icteridae	El Monte (CA), USA	1955-379	22	Whittier (CA), USA	1956-1121	22
<i>Icterus galbula</i>	Icteridae	Motzorongo, MX	1940-648	29	Comitan, MX	1939-1177	29
<i>Icterus parisorum</i>	Icestrida	El Triunfo, MX	1930-19	33*3	El Triunfo, MX	1930-20	33
<i>Spizella pusilla</i>	Passerellidae	Reading (NY), USA	1999-137	29	Wheatland (WY), USA	1886-87	29
<i>Zoothera naevia meruloides</i>	Turdidae	Nicasio (CA), USA	1921-161	30*3	Pasadena (CA), USA	1955-263	30
<i>Junco hyemalis aikeni</i>	Passerellidae	Newcastle (WY), USA	1939-50	25	Newcastle (WY), USA	1939-51	25*3

<i>Loxia curvirostra curvirostra</i>	Fringillidae	Jurques, FR	1965-2824	37	Pierre-de-Bresse, FR	1899-670	37
<i>Anthus trivialis trivialis</i>	Motacillidae	Remomeix, FR	1947-81	36	Trois-Monts, FR	1965-2519	36
<i>Luscinia megarhynchos megarhynchos</i>	Muscicapidae	Saint-Jean-de-Luz, FR	1978-932	22	Wissous, FR	1967-1735	22
<i>Luscinia svecica cyaneola</i>	Muscicapidae	Nancy, FR	1972-1279	29*3	Ansauville, FR	1929-1752	29
<i>Melospiza georgiana</i>	Passerellidae	Reading (NY), USA	1999-1860	40	Reading (NY), USA	1999-1861	40
<i>Melospiza lincolni lincolni</i>	Passerellidae	Chippewa (OH), USA	1939-56	45	Fleming (OH), USA	1939-59	45
<i>Melospiza melodia</i>	Passerellidae	Dulzura (CA), USA	1999-1873	40	Dulzura (CA), USA	1999-1871	40
<i>Mimus polyglottos leucopterus</i>	Mimidae	MX	1933-306	25	Los Angeles (CA), USA	1956-1050	25
<i>Monticola saxatilis</i>	Muscicapidae	Tizi n'Taka, MA	1963-495	39	Mwaktau, KE	1969-1320	39
<i>Monticola solitarius solitarius</i>	Muscicapidae	Nice, FR	1960-2231	34*3	Marseille, FR	1960-1234	34
<i>Motacilla alba alba</i>	Motacillidae	Hendaye, FR	1978-123	29	Ranville, FR	1965-2434	29
<i>Motacilla cinerea</i>	Motacillidae	Rennes-les-Bains, FR	1978-110	29	Saint-Jean-du-Doigt, FR	1978-108	29
<i>Icterus cucullatus igneus</i>	Icteridae	Yucatan, MX	2002-1378	29	Mérida, MX	2002-1387	29*3
<i>Oenanthe hispanica hispanica</i>	Muscicapidae	Douar Zaara, TN	1978-488	26*3	Redeyef, TN	1986-253	26
<i>Muscicapa striata striata</i>	Muscicapidae	Ahetze, FR	1987-8	27	Trois-Monts, FR	1965-1959	27
<i>Myadestes townsendi (1)</i>	Turdidae	Paradise (AZ), USA Silver City (NM), USA	1939-8 2000-2088	25	Cochise County (NV), USA	1939-9	25
<i>Chondestes grammacus</i>	Passerellidae	Dulzura (CA), USA	1955-329	36	Pasadena (CA), USA	1999-1974	36
<i>Oenanthe isabellina</i>	Muscicapidae	Ito, TD	1966-2280	26	100 km north of Rosso, MR	1954-106	26
<i>Oenanthe oenanthe oenanthe</i>	Muscicapidae	Remomeix, FR	1960-60	34	Biarritz, FR	1989-218	34*3

<i>Geothlypis trichas</i>	Parulidae	Auburn (NY), USA	1921-123	30	Auburn (NY), USA	1921-124	30
<i>Sitta europaea caesia</i>	Sittidae	Saumur, FR	1978-1525	27	Mouliherne, FR	1978-1547	27*3
<i>Passer montanus montanus</i>	Passeridae	Chamigny, FR	1988-583	32*3	Saint-Jean-de-Luz, FR	1978-156	32
<i>Passerculus sandwichensis princeps</i>	Passerellidae	South Duxbury (MA), USA	1886-77	38	South Duxbury (MA), USA	1886-76	38
<i>Motacilla flava flava</i>	Motacillidae	Saint-Jean-de-Luz, FR	1979-76	26	Remomeix, FR	1960-450	26
<i>Passerella iliaca</i>	Passerellidae	Auburn (NY), USA	1921-192	36	Reading (NY), USA	1999-1901	36
<i>Passerina amoena</i>	Cardinalidae	Santa Barbara (CA), USA	1955-356	28	(CA), USA	1999-2622	28
<i>Passerina caerulea</i>	Cardinalidae	MX	1999-2591	41	MX	1999-2592	41
<i>Passerina ciris</i>	Cardinalidae	Naha, MX	1975-801	27*3	Naha, MX	1975-803	27
<i>Passerina cyanea</i>	Cardinalidae	Cayuga (TX), USA	1921-134	24	Auburn (NY), USA	1921-135	24
<i>Passerina versicolor</i>	Cardinalidae	Ixmiquilpan, MX	1940-604	26	Ixmiquilpan, MX	1940-601	26
<i>Petronia petronia</i>	Passeridae	Tataouine, TN	1997-479	37	Tunis, TN	2008-711	37
<i>Pheucticus ludovicianus</i>	Cardinalidae	Cayuga (TX), USA	1921-788	37	Naha, MX	1975-787	37
<i>Pheucticus melanocephalus</i>	Cardinalidae	(CO), USA	1999-2477	37	(CO), USA	1999-2479	37
<i>Phoenicurus ochruros gibraltariensis</i>	Muscicapidae	Lorraine, FR	1976-1301	26	Le Puy-Notre Dame, FR	1978-911	26
<i>Phoenicurus phoenicurus phoenicurus</i>	Muscicapidae	Trois-Monts, FR	1965-2208	28	Lagny-sur-Marne, FR	1951-367	28
<i>Pipilo maculatus megaloyx</i>	Passerellidae	Dulzura (CA), USA	1999-2273	27	Dulzura (CA), USA	1999-2275	27*3
<i>Piranga flava hepatica</i>	Cardinalidae	La Parada, MX	1999-2894	25*3	Oaxaca, MX	1999-2896	25
<i>Piranga olivacea</i>	Cardinalidae	Ann Arbor (MI), USA	1939-42	23*3	Lorne Park (ON), CA	1891-738	23
<i>Piranga rubra</i>	Cardinalidae	Tepic, MX	1901-458	25	Tepic, MX	1901-457	25*3
<i>Anthus campestris campestris</i>	Motacillidae	Manonville, FR	1965-2527	30	FR	1933-2196	30
<i>Prunella collaris collaris</i>	Prunellidae	CH	1972-1350	32	Isgoun Ouagouns, MA	1963-62	32

<i>Prunella modularis modularis</i>	Prunellidae	Trois-Monts, FR	1965-2412	32	Trois-Monts, FR	1965-2422	32
<i>Pipilo crissalis</i>	Passerellidae	Pasadena (CA), USA	1955-360	24	Pasadena (CA), USA	1955-362	24
<i>Pyrrhula pyrrhula pyrrhula</i>	Fringillidae	Ahetze, FR	1988-585	26*3	Ahetze, FR	1981-881	26
<i>Turdus iliacus iliacus</i>	Turdidae	Ahetze, FR	1982-956	30	Argenton l'Eglise, FR	1970-1052	30
<i>Quiscalus quiscula aeneus</i>	Icteridae	Webster (TX), USA	1939-66	23	Auburn (NY), USA	1921-141	23
<i>Poocetes gramineus</i>	Passerellidae	Rochester (NY), USA	1999-1980	38	Rochester (NY), USA	1999-1978	38
<i>Regulus ignicapilla ignicapilla</i>	Regulidae	Saint-Pern, FR	1975-1703	33	Saumur, FR	1978-1283	33
<i>Regulus regulus regulus</i>	Regulidae	Remomeix, FR	1949-34	32	Magny-les-Hameaux, FR	1985-231	32
<i>Salpinctes obsoletus</i>	Troglodytidae	Tehuantepec, MX	1996-1122	32	Dulzura (CA), USA	1996-1123	32
<i>Saxicola rubetra</i>	Muscicapidae	Remomeix, FR	1949-499	40	Solignac, FR	1960-2101	40
<i>Saxicola torquatus rubicola</i>	Muscicapidae	Meuvaines, FR	1965-2227	39	Meuvaines, FR	1965-2233	39
<i>Seiurus noveboracensis</i>	Parulidae	Auburn (NY), USA	1921-177	28	Rochester (NY), USA	2001-1869	28*3
<i>Serinus serinus</i>	Fringillidae	Saumur, FR	1978-135	38	Plougasnou, FR	1960-2590	38
<i>Setophaga ruticilla</i>	Parulidae	Ixtacomitan, MX	1951-834	26	Ixtacomitan, MX	1951-836	26*3
<i>Sialia currucoides</i>	Turdidae	Basset (VA), USA	1955-269	25*3	Coachella (CA), USA	1955-270	25
<i>Sialia mexicana</i>	Turdidae	Dulzura (CA), USA	2000-2068	27	Dulzura (CA), USA	2000-2067	27*3
<i>Sialia sialis fulva</i>	Turdidae	Comitan, MX	1951-92	28	Comitan, MX	1951-97	28
<i>Regulus calendula calendula</i>	Regulidae	Kern River (CA), USA	1956-1045	28	Pasadena (CA), USA	1955-295	28*3
<i>Erythropygia galactotes galactotes</i>	Muscicapidae	Rabat, MA	1970-574	29	Berkane, MA	1963-53	29
<i>Calamospiza melanocorys</i>	Passerellidae	Colorado Springs (CO), USA	1930-23	39	Chihuahua, MX	1930-24	39
<i>Motacilla citreola</i>	Motacillidae	Irkoutsk, RU	1898-790	27*3	Petchora Valley, RU	1905-36	27

<i>Sturnella neglecta</i>	Icteridae	Summer Lake (OR), USA	1962-3450	43	Garnsey (OR), USA	1955-374	43
<i>Thryomanes bewickii</i>	Troglodytidae	Santa Rita Mountains (AZ), USA	1886-36	26	Santa Rita Mountains (AZ), USA	1886-35	26
<i>Toxostoma rufum</i>	Mimidae	Ithaca (NY), USA	1953-332	28	Fort Benning (GA), USA	1975-1679	28*3
<i>Troglodytes troglodytes troglodytes</i>	Troglodytidae	Plougasnou, FR	1970-2300	34	Morlaix, FR	1970-2302	34
<i>Oreoscoptes montanus</i>	Mimidae	Menifee (CA), USA	1927-1872	31	Cajon Wash (CA), USA	1927-1893	31
<i>Turdus merula merula</i>	Turdidae	Île-de-France, FR	1990-569	27	Paris, FR	2000-978	27
<i>Turdus migratorius</i>	Turdidae	Cayuga (TX), USA	2001-2398	29	Rochester (NY), USA	1921-103	29
<i>Turdus philomelos philomelos</i>	Turdidae	Bourron-Marlotte, FR	1985-80	30	Biarritz, FR	1985-242	30
<i>Turdus pilaris</i>	Turdidae	Le Puy-Notre Dame, FR	1978-1489	32	Orly, FR	1984-489	32*3
<i>Turdus torquatus torquatus</i>	Turdidae	Pyrénées-Atlantiques, FR	1988-580	31	Saint-Jean-du-Doigt, FR	1960-2230	31
<i>Turdus viscivorus viscivorus</i>	Turdidae	Aussois, FR	1969-1034	32	Aussois, FR	1969-1035	32
<i>Vermivora celata sordida</i>	Parulidae	Pasadena (CA), USA	1955-300	26	CA	1955-301	26
<i>Passer domesticus domesticus</i>	Passeridae	Signy-Signets, FR	1976-1507	37	Trois-Monts, FR	1976-2967	37
<i>Zonotrichia albicollis</i>	Passerellidae	Reading (NY), USA	1999-1907	35	CA	1999-1906	35
<i>Zonotrichia leucophrys gambeli</i>	Passerellidae	Pasadena (CA), USA	1955-348	30*3	Santa Barbara (CA), USA	1955-349	30

CA=Canada; CH=Switzerland; FR=France; GR=Greece; IR=Iran; KE=Kenya; KZ=Kazakhstan; MA=Morocco; MR=Mauritania; MX=Mexico; RU=Russia; SE=Sweden; TD=Chad; TN=Tunisia; TZ=Tanzania; USA=United States of America.

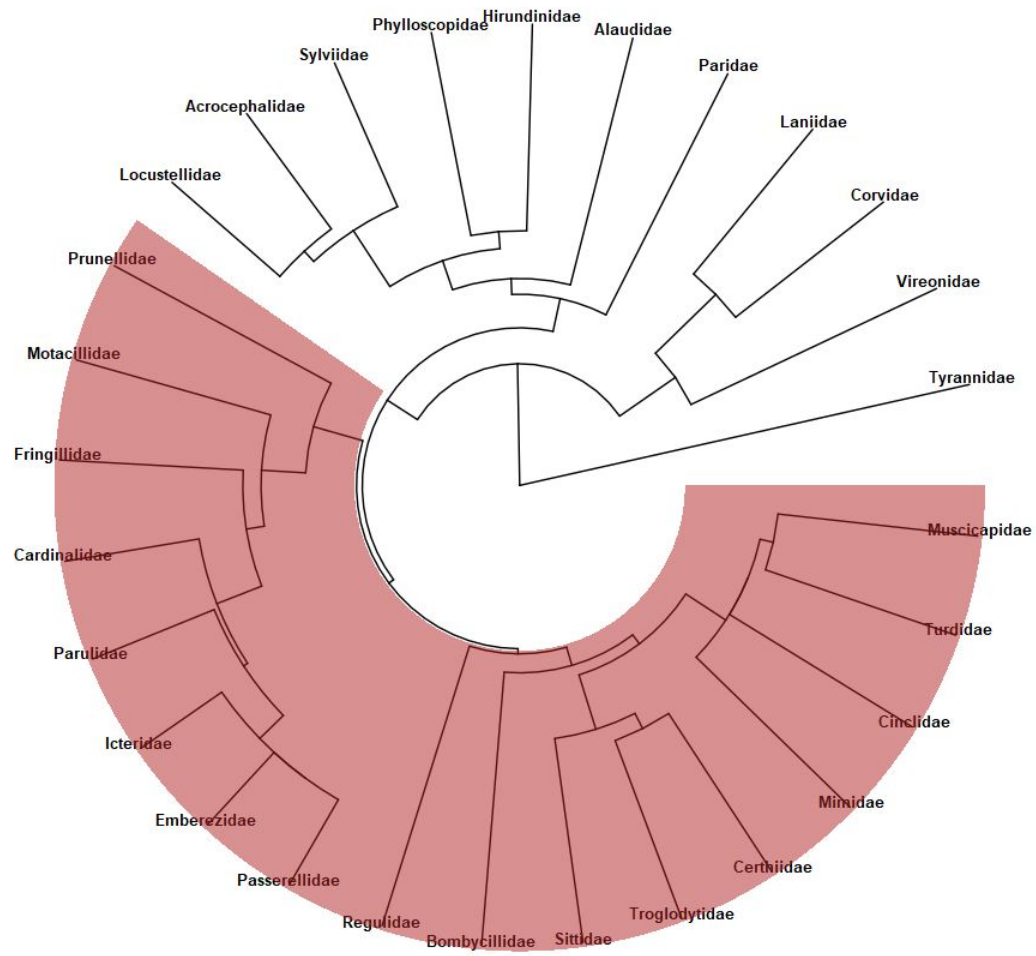


Figure S1. Phylogenetic tree representing the major families of Passerines from the Northern Hemisphere. Highlighted families correspond to the 17 families included in the analyses and show they are more closely related to each other than to the other families represented on the tree. The species of tanagers included in our analyses were formerly identified as “Thraupidae” but are now included in the sister-family of Cardinalidae. Therefore, we did not include “Thraupidae” in the phylogenetic tree.

1/ Specimen collection

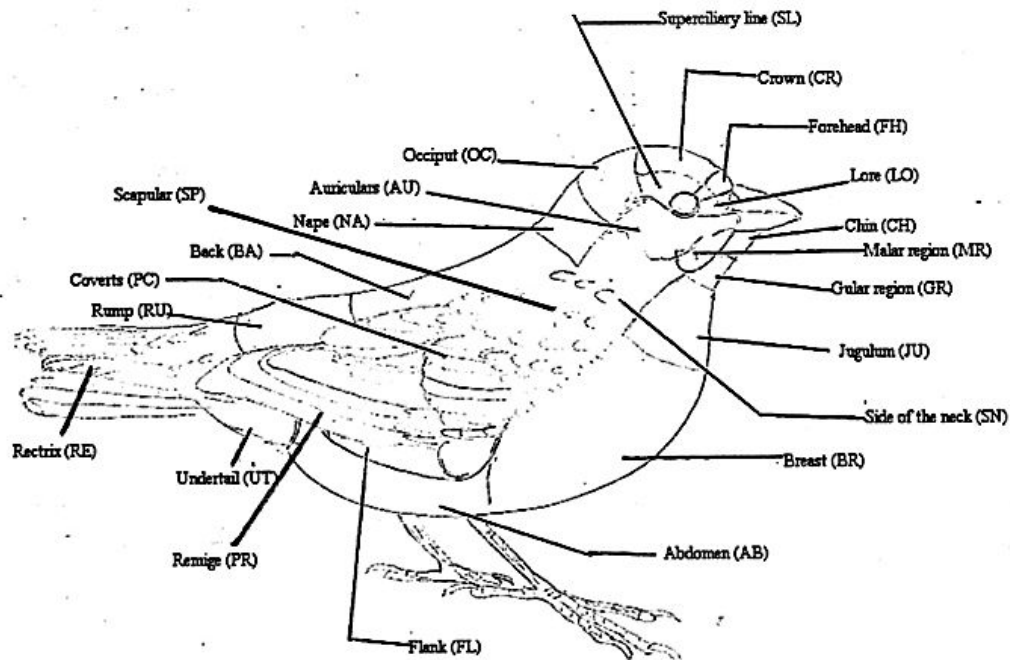
We only selected specimens for which sex, adult status, subspecies, and collection area were specified. If the collection area but not the subspecies was specified, we looked in the Handbook of the Birds of the World (Del Hoyo *et al.*, 2004) to see if we could identify the subspecies; we did not use specimens for which there was any taxonomic doubt because of subspecies sympatry. When possible, we selected males and females from the same locality (details in Table S6). When this was impossible, we selected males and females of the same subspecies coming from locations as close together as possible.

1 **2/ Coloration measurement**

2 **Spectrometry:** A single person (AF) performed all the spectrometric measurements, using a Jaz
3 spectrometer (Ocean Optics, Dunedin FL, USA) with a Jaz light source covering a spectral range of 300
4 nm to 700 nm and a 200 μ m optical probe (FCR-7UV200-2-45-ME, Avantes, Apledoorn, NL) whose
5 tip contained a 45° quartz window, which guaranteed a constant distance between the light and the
6 sample and highly repeatable measurements. Reflectance was calculated in relative terms, via
7 comparison with a black and a white reference (WS1, Ocean Optics, Dunedin FL, USA).

8 Before measuring the whole plumage, we first characterized zone coloration for each bird (see Figure
9 S2). When a bird had distinct color patches or a patch was composed of different colors (up to four) in
10 any of the 21 zones, we measured each color. Although the preliminary assessment of distinct patches
11 or colors was carried out with the naked eye (and thus affected by human visual bias), we double-
12 checked the assessment by examining the spectrometric spectra (Gomez & Thery, 2004; Stoddard &
13 Prum, 2008; Doutrelant *et al.*, 2016). Ultimately, number of measurements ranged from 22 to 45
14 depending on the species (details in Table S1); the mean number of measurements per bird was 33.
15 Within species, measurements number was the same for both sexes, even if one sex displayed fewer
16 colors (Shultz & Burns, 2017). For some specimens we repeated all measurements three times to test
17 measurement repeatability (details in Table S1).

18 For specimens in which we tested repeatability, we calculated the mean spectra per patch after
19 controlling for concordance in spectral shape among the replicates.



20

21 **Figure S2:** Topography of a house sparrow (*Passer domesticus*). In this study, we started characterizing coloration in 22
 22 zones (abbreviations for zone names in brackets). The lore zone (LO) was initially included but then later removed
 23 because it was poorly preserved in a large number of specimens. Consequently, only 21 zones were used in the final
 24 analyses.

25

26 **Visual model:** colors are points in the avian tetrahedron color space, and plumage is a cloud of points.
27 The center of the color space is where all the cones receive equal stimulation, and a color is thus
28 perceived as achromatic (Maia *et al.*, 2019). A color is perceived as more intense or vivid as its distance
29 from the center of the color space increases. Mean plumage brightness was the mean relative reflectance
30 over the entire spectral range (300 nm to 700 nm) and corresponded to the number of photons caught by
31 double cones (Stoddard & Prum, 2008). We calculated mean plumage chromaticity based on the mean
32 distance from the center of the color space. We calculated color volume as the convex hull that included
33 all the points in a plumage cloud. Different colors differentially stimulate the four cones responsible for
34 color detection, which leads to point dispersal and increased color volume (Renoult *et al.*, 2017). Hence,
35 color volume expresses color diversity in bird plumage. We also calculated the mean distance between
36 all color pairs (Stoddard & Prum, 2008) as a metric of mean within-plumage contrast. This mean distance
37 was highly correlated with color volume (see Table S2), so we omitted it from later analyses.

38

39

40

Table S2: Pearson correlation coefficients for coloration metrics. Coefficients for female coloration metrics are in bold, and coefficients for male coloration metrics are in italics. * indicates a p-value of less than 0.05, and *** a p-value of less than 0.001.

	Brightness	Chromaticity	Color volume	Contrast
Brightness		-0.17*	-0.06	-0.08
Chromaticity	<i>0.02</i>		0.40***	0.41***
Color volume	<i>-0.15</i>	<i>0.33***</i>		0.77**
Contrast	<i>-0.04</i>	<i>0.39***</i>	<i>0.80***</i>	

3/ Life history traits

Table S3: Scoring of descriptive contributions of males and females to parental care

Activity description	Male score	Female score	Comments
Female only	0	1	
Both	1	1	
Female mostly/mainly/primarily/Greater by female	0.5	1	
Male occasionally/rarely helps/may help	0.2	1	
Male mostly/mainly/primarily/ Greater by males	1	0.5	
Only male if female starts 2nd brood	1	1	Female is still invested in reproduction even if it is a 2nd brood
Both, male does more when female broods	1	1	Female is still highly invested
Male involvement varies	0.5	1	
Mainly male at first	1	1	“at first” means female is invested in brooding hatchlings
Some males observed covering eggs for considerable periods	0.2	1	Few males, little information on male incubation duration
Female more than male	0.7	1	
Female leaves first	1	0.5	Post-fledging period
Male may cover eggs briefly	0.2	1	
Male observed incubating	0.5	1	
Male provides more supplies	1	0.7	
One observation of male feeding	0.1	1	
Male with small harem; male if fledgling in territory	0.1	1	Very rare situation

Miscellaneous

"Several weeks" was estimated to be 21 days.

When information on activity or duration was missing for a species, we used the median value for the whole data set.

Table S4: Scoring nest characteristic (from lowest to highest vulnerability)

Ecological factor	Description	Score	Comment
Nest position	Tree	0	> 2 m
	Shrub	1	50 cm–2 m
	Ground	2	< 50 cm
Nest openness	Closed, located in hole	0	
	Partially open, well concealed	1	
	Open	2	

4/ Phylogenetic analyses.

Table S5: Estimated values from the PGLS analyses when excluding corresponding male coloration from the models. Variables are sorted in the same order as in Figure 1 (excluding male coloration). 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).

Variable	Estimates with confidence intervals		
	Brightness	Chromaticity	Color volume
Paternal care	0.165 [0.008;0.323]	0.112 [-0.051;0.275]	-0.133 [-0.294;0.027]
Egg production	0.435 [0.063;0.806]	-0.225 [-0.621;0.170]	-0.001 [-0.381;0.379]
Egg production x Paternal care	0.079 [-0.064;0.222]	-0.165 [-0.311;0.019]	0.039 [-0.106;0.185]
Nest characteristics	0.111 [-0.054;0.277]	0.227 [0.051;0.403]	0.020 [-0.149;0.189]
Female weight (log)	-0.575 [-0.960;-0.189]	-0.011[-0.432;0.409]	-0.027 [-0.423;0.370]
Breeding period (log)	-0.099 [-0.247;0.049]	0.040 [-0.114;0.194]	-0.134 [-0.286;0.018]
Migration			
Strictly migrant	0.014 [-0.310;0.339]	-0.365 [-0.694;-0.036]	-0.166 [-0.497;0.165]
Partially migrant	-0.245 [-0.570;0.080]	-0.116 [-0.446;0.213]	0.323 [-0.008;0.653]
Strictly resident	0.492 [0.012;0.972]	-0.155 [-0.661;0.351]	-0.180 [-0.672;0.312]
Pagel's lambda	0.573 [0.570 ;0.575]	0.747 [0.744 ;0.749]	0.587 [0.584 ;0.589]

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

Authors: Amélie Fargevieille (ORCID 0000-0003-0934-3563)[§], Arnaud Grégoire (ORCID 0000-0001-6103-355X)[§], Doris Gomez (ORCID 0000-0002-9144-3426)[§], Claire Doutrelant (ORCID: 0000-0003-1893-3960)[§]

Author institutional affiliations: [§]CEFE-CNRS UMR 5175, Université de Montpellier, Campus du CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France

Corresponding author contact details: Amélie Fargevieille, CEFE-CNRS UMR5175, Campus du CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5; France. afargevieille@gmail.com

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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