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David López-Idiáquez, Céline Teplitsky, Amélie Fargevieille, Maria del Rey Granado, Raphaëlle Mercier Gauthier, Christophe de Franceschi, Anne Charmantier, Claire Doutrelant, Denis Réale

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HAL Authorization

1 **Sex-dependent integration of ornamentation, personality, morphology,**  
2 **and life history**

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32 Abbreviated title:

33 Sex-dependent integration in the blue tit

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35 Abstract:

36 Phenotypic integration can be defined as the patterns and strength of the covariances between  
37 traits in an organism. The pace of life syndrome (POLS) hypothesis provides a testable case of  
38 phenotypic integration as it predicts that traits that mediate the trade-off between current and  
39 future reproduction should have coevolved with the slow-fast life-history continuum and may  
40 thus covary across individuals of a population. Although the POLS hypothesis has received  
41 increasing attention over the last decade, there is a need for investigating whether POLS are sex-  
42 specific and whether ornamental traits can be included within the POLS framework. We used  
43 nine years of data to describe the integration patterns of ornamental coloration, personality,  
44 morphology, and life history in blue tits (*Cyanistes caeruleus*) and whether they differed  
45 between males and females. With that aim, we fitted multivariate mixed models separating the  
46 among- from the within-individual covariances. We found that the overall integration between  
47 the studied traits was weak, but our results suggested some sex-specific covariances at the  
48 among- and within-individual levels. Finally, using structural equation models (SEM), we tested  
49 for the presence of trait modules (i.e. covariances between traits involved in the same biological  
50 function) within each sex. SEMs suggested the presence of a morphological module but no  
51 modules for coloration or behavioral traits. Also, results obtained from the SEM did not support  
52 the POLS hypothesis. Overall, this work highlights the importance of considering sex when  
53 studying phenotypic integration and the relevance of SEM to test POLS hypothesis.

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## 62 INTRODUCTION

63 Phenotypic integration can be defined as the patterns and strength of the covariance between traits in a  
64 single organism and its causes have puzzled evolutionary and developmental biologists for decades.  
65 The most studied mechanisms behind phenotypic integration are pleiotropic effects and trade-offs  
66 caused by allocation issues of limited resources (Ketterson et al. 2009; Laskowski et al. 2021).  
67 Modularity is a specific case of phenotypic integration and represents covariances between traits  
68 involved in the same biological function (Cheverud 1982; Klingenberg 2008). Modules can occur  
69 because traits that are simultaneously subject to directional selection evolve strong genetic correlations  
70 that hinder their independent evolution and illustrate past selection pressures favoring trait  
71 combinations (Roff 1996; Pavlicev et al. 2011). Modules can also exist because shared genes or  
72 developmental processes affect them and lead to their association at the phenotypic level (Wagner and  
73 Altenberg 1996).

74

75 At the phenotypic level, trait integration occurs at different hierarchical levels (e.g. among-individuals,  
76 within-individuals or among-years), depending on the mechanisms leading to the association between  
77 traits. Among-individuals, trait correlations can be the product of early life conditions including  
78 parental effects, ontogenetic feedback loops or differences in the environments experienced during life  
79 (e.g. predation vs no-predation), independently of whether these traits covary at the genetic level  
80 (Klingenberg 2014; Hämäläinen et al. 2018). For instance, experimental studies have shown that early-  
81 life stress strengthens the among-individual correlations between morphological and physiological  
82 traits (Merrill and Grindstaff 2018). Within-individuals and among-years, combined plasticity of traits  
83 throughout an individual's lifetime in response to changing environmental conditions or state-  
84 dependent feedback loops may lead to correlations between them (Dingemanse and Wolf 2010; Sih et  
85 al. 2015). Besides, at the among-year level, trait associations can also be explained by the selective  
86 appearance/disappearance of individuals with particular trait combinations.

87

88 The pace of life syndrome (POLS) hypothesis has been proposed as an evolutionary cause responsible  
89 for the evolution of trait integration. It originally predicted that integration between behavior and  
90 physiology was driven by their coevolution with life history (Ricklefs and Wikelski 2002; Réale et al.  
91 2010). More recent updates of the POLS hypothesis, however, have extended the definition to *any*

92 *trait* that mediates the trade-off between current and future reproduction (Montiglio et al. 2018). The  
93 presence of POLS has been explored in a wide array of species; still, it is unclear whether they can be  
94 generalized to all the species and traits or even to all the individuals within a population (Dammhahn  
95 et al. 2018; Montiglio et al. 2018; Royauté et al. 2018; Van De Walle et al. 2023).

96

97 Sex remains an overlooked factor within the POLS framework and the presence of sex-specific POLS  
98 is still poorly documented (Hämäläinen et al. 2018; Immonen et al. 2018). Yet, different POLS could  
99 be predicted between sexes given that males and females experience different selection pressures,  
100 show different life-history strategies and, thus, they might maximize fitness through different trait  
101 combinations (Hämäläinen et al. 2018; Immonen et al. 2018). It is important to consider that sex-  
102 specific POLS could be constrained by cross-sex genetic correlations. However, unless the cross-sex  
103 genetic correlation is perfect, sex-specific POLS will end up arising if males and females face different  
104 selection pressures. Aggressiveness, for example, could be more integrated with life-history or  
105 physiological traits in male than female POLS as it is expected to have stronger positive effects on  
106 male fitness in species where male competition for mates is high (Smith and Blumstein 2008). To date,  
107 the empirical evidence for sex-specific POLS is limited to a handful of studies conducted in captivity  
108 showing sex-specific associations of behavior with metabolic rate (Moschilla et al. 2019) and  
109 immunity (Monceau et al. 2017).

110

111 Another gap of knowledge within the POLS framework lies in the traits traditionally analyzed as part  
112 of a syndrome. Specifically, there is a lack of research on whether social and secondary sexual traits  
113 are components of POLS (Ricklefs and Wikelski 2002; Réale et al. 2010; Dammhahn et al. 2018, but  
114 see McGlothlin et al. 2005; Sowersby et al. 2022). Still, ornaments are important mediators of the  
115 trade-off between current and future reproduction or survival (Kokko et al. 2006; Robinson et al.  
116 2006). For instance, it has been shown that an increased investment in secondary sexual traits  
117 decreases male fecundity in houbara bustards (Preston et al. 2011) and male survival in crickets (Hunt  
118 et al. 2004).

119

120 Avian ornamental colors play a prominent signaling role in intra- and inter-sexual contexts (Hill and  
121 McGraw 2006), as colors are linked to life history (Tuttle 2003), survival (Acker et al. 2015), behavior

122 (López-Idiáquez et al. 2018) or physiology (Martinez-Padilla et al. 2010). Plumage coloration is  
123 produced by the deposition of pigments such as melanin or carotenoids, the interaction of feather  
124 structure and light or a combination of both, and it is renewed at least once a year during molt (Hill  
125 and McGraw 2006). Depending on the production mechanisms, color associations with other traits can  
126 have genetic, early-life and/or developmental bases. For instance, melanin-based colorations can have  
127 a strong genetic basis, and thus their association with other traits often has a genetic origin (Ducrest et  
128 al. 2008). For carotenoid-based or structural colors, which are often linked to individual condition  
129 (Doutrelant et al. 2012; White 2020), the correlations with other traits may arise through state-  
130 dependent feedback loops (Sih et al. 2015). For example, larger individuals with higher energetic  
131 needs, may be more aggressive and win contests over limited resources such as food (Wilson et al.  
132 2013) which in turn may allow them to produce enhanced costly signals reinforcing their dominance  
133 (Vitousek et al. 2014). Alternatively, negative associations could also be expected, for instance, if the  
134 cost of being aggressive or providing enhanced parental care impacts the resources available to invest  
135 in ornamentation. Still, genetic/early-life and developmental effects are not mutually exclusive and co-  
136 occur thus ornamental colors, life-history, physiology, and behavior can covary both among and  
137 within individuals. In addition, we can also expect among-year covariances between coloration and  
138 other traits if there is a selective appearance/disappearance of individuals with particular trait  
139 combinations or if current environmental conditions affect simultaneously coloration and other traits  
140 in a similar way across individuals. Interestingly, the strength and direction of the associations at each  
141 hierarchical level can differ (Nicolaus et al. 2016). For instance, the covariance between great tit's  
142 (*Parus major*) tie size and exploration is negative at the among-individual level but positive within-  
143 individuals (Nicolaus et al. 2016). Therefore, exploring the covariance patterns of multiple traits at  
144 different hierarchical levels is important to clarify the mechanisms behind their covariances and  
145 constitutes an important step towards deepening our understanding of the evolution of integrated  
146 phenotypes and of the signaling role of ornamental colors. So far, however, little evidence exists on  
147 trait covariances at multiple hierarchical levels, and those that have considered them usually focus on  
148 few traits (Nicolaus et al. 2016; Moiron et al. 2019; Gaona- Gordillo et al. 2023).

149

150 Here, using nine years of data, we first explored whether the covariance patterns between structural  
151 (crown UV chroma and brightness) and carotenoid-based coloration (breast yellow chroma and

152 brightness), morphology (tarsus and wing length, and size-dependent body mass), behavior (handling  
153 aggression and exploratory behavior) and life history (clutch size and number of fledglings), differ  
154 between male and female blue tits (*Cyanistes caeruleus*). Specifically, we decomposed the phenotypic  
155 covariances into the among-individual, within-individual, and among-year levels. Then, using  
156 structural equation models we tested for the occurrence of modules. We assumed that traits within  
157 each category (i.e. morphology, coloration, behavior or life-history) are involved in the same function,  
158 predicting that they covary among individuals forming modules. For example, tarsus length, wing  
159 length, and body mass should be subject to common physical constraints affecting a bird shape and size  
160 and should show positive covariances. Additionally, we may find among-individual associations  
161 between traits of different categories. For instance, given that color can signal aggressiveness or  
162 dominance (Hill and McGraw 2006; Blount and McGraw 2008; Svensson and Wong 2011; Umbers  
163 2013), we expected associations between color and behavior that will be stronger in males than in  
164 females. Besides, we additionally expected among-individual covariations between ornamental colors  
165 and clutch size and number of fledglings since coloration can signal parental investment (Midamegbe  
166 et al. 2013). Within-individuals and among-years, annual changes in resource availability and  
167 individual state may lead to positive or negative correlations between traits, with no predictions on  
168 whether the sexes should differ for these associations. We expected that most covariances between  
169 traits would show a similar sign across levels, although they may vary in strength. However, some  
170 covariances between traits, such as between behavior and color may differ at the among- and within-  
171 individual levels (Nicolaus et al. 2016).

172

## 173 **METHODS**

### 174 Study area and general procedures

175 We based our study on data collected between 2011 and 2019 in three Mediterranean populations (D-  
176 Muro, E-Muro and E-Pirio) equipped with nest boxes and located in Northwest Corsica (Charmantier  
177 et al. 2016). We captured blue tits up to twice per season, once right before or during nest construction  
178 (March – April) and a second time during breeding (May – June) when chicks were 10-15 days old. At  
179 each capture and after measuring its handling aggression (see below), we ringed each bird with a  
180 uniquely numbered metal ring provided by the *Centre de Recherches sur la Biologie des Populations*

181 *d'Oiseaux*. Besides, we collected six blue feathers from the crown and eight yellow feathers from the  
182 breast. Following a standardized protocol, we assessed their coloration in the lab using a UV-vis  
183 spectrophotometer and deuterium-halogen light source covering UV and visible coloration (Doutrelant  
184 et al. 2008; Fargevieille et al. 2017). Specifically, for the crown coloration we computed UV chroma  
185 and mean brightness and for the breast coloration yellow chroma and mean brightness using AVICOL  
186 or the R package *pavo* (Gomez 2006; Maia et al. 2019, see SM-1 for further information). We also  
187 measured tarsus length (to the nearest hundredth), wing length (to the nearest tenth), and body mass  
188 (to the nearest tenth). All individuals were also aged (one year-old vs.  $\geq$ two years-old) based on their  
189 wing covert's coloration (Svensson 1992). Finally, we measured clutch size and number of fledglings  
190 during the weekly nest-box visits during the laying period (Charmantier et al. 2016).

191

#### 192 Handling aggression score

193 From 2011 to 2019, we measured handling aggression during nest construction and breeding periods  
194 within two minutes after each capture before any other manipulation (including ringing). We scored  
195 handling aggression by holding the bird with one hand, always in the same position, and pointing the  
196 forefinger of the other hand at a spot about two-three centimeters in front of the bird's beak, noting if  
197 the bird struck at the finger, and the position of the tail and the wings. Then after two seconds in this  
198 position, the observer moved the forefinger towards the bird and recorded its reaction. The score  
199 ranged from zero (no reaction) to three (the bird strikes the handler's fingers and spreads its wings and  
200 tail) with seven different levels (for further details see Dubuc-Messier et al. 2017 and SM-2).

201

#### 202 Exploratory Behavior

203 We measured exploratory behavior between 2011 and 2018, during the nest construction period, by  
204 introducing each bird into a novel-environment apparatus based on the model of Mutzel et al. (2013)  
205 and filming its behavior for five minutes. The cage used for this test was enclosed in a larger chamber  
206 so that the bird saw nothing outside the box, had limited sound coming from outside, and was exposed  
207 to controlled lighting conditions (see Figure S1 in Dubuc-Messier et al. 2017). Before the test, we  
208 placed the bird for two minutes in a closed chamber on the side of the novel environment apparatus  
209 and connected to it by a sliding door. From the videos, we extracted the average speed of an individual  
210 (cm/s) during each trial using the software EthoVision XT (version 9). We used this measure as a

211 proxy of exploratory behavior in the analyses. A previous study in our population has shown a strong  
212 correlation between individual speed in the novel environment apparatus and the number of large  
213 flights during the test (Dubuc-Messier et al. 2017), a measure typically used to describe the  
214 exploratory behavior in other studies (Dingemanse et al. 2002; Mutzel et al. 2013).

215

## 216 Statistical analyses

### 217 *Sex-dependent covariances and integration patterns of coloration*

218

219 We analyzed whether the among- and within-individual covariances between color, behavior,  
220 morphology, and life-history differed between males and females using multivariate mixed models in  
221 a Bayesian framework. Specifically, we fitted two models, one in which the among- and within-  
222 individual (co)variance matrices were constrained to be equal in each sex and a second one in which  
223 we allowed these (co)variance matrices to differ between males and females (fitting a sex by  
224 individual identity interaction). The models were ran in R (v. 4.0.4; R Core Team 2021) using the  
225 package *MCMCglmm* (v. 2.32; Hadfield 2010).

226

227 In both models, the dependent variables were crown UV chroma and brightness, breast yellow chroma  
228 and brightness, handling aggression, exploratory behavior, clutch size, number of fledglings, wing  
229 length, mass, and tarsus length. Specifically for tarsus length, we used the mean value of the tarsus  
230 measurements for a single individual, as in blue tits tarsus length is fixed after 15 days. We  
231 standardized all variables to a mean of zero and a standard deviation of one, so that the covariance  
232 patterns were not driven by a subset of traits on a larger scale. As explanatory variables, we included  
233 age (one-year-old vs.  $\geq 2$ -year-old individuals), capture period (nest construction vs. breeding),  
234 population and sex. The random effects were year and individual identity for all the traits, and  
235 observer identity for handling aggression. We ran the models for 9000000 iterations, with a thinning  
236 of 7500, and a burning of 500000, to achieve autocorrelation values of less than 0.1 and an effective  
237 sample size of at least 1000. We used inverse Wishart priors with variances equal to phenotypic  
238 variance (here one due to standardization) divided by the number of random effects (reflecting a null  
239 hypothesis of variance being equally distributed among effects) and covariances of zero. The degree of  
240 belief was equal to the number of traits (11). As we used only one measure of tarsus length per

241 individual, we fixed the within-individual variance of this trait to a low value (0.0001). We selected  
 242 the best model using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). To compare  
 243 the strength of the association between traits we transformed all covariances to correlations. Finally,  
 244 we computed trait repeatability (Table 1) corrected for age, population and study period using the  
 245 package *rptR* (v.0.9.22; Stoffel et al. 2017).

246

### 247 *Modularity in the blue tit's phenotype*

248 We used structural equation modeling (SEM), to test for the hypotheses formulated in the introduction  
 249 about the association between traits at the among-, within-individual, and among-year levels. This  
 250 statistical approach allows evaluating multiple models testing a priori hypotheses on the association  
 251 between traits (Royauté et al. 2015; Frauendorf et al. 2021). Models were run using the (co)variance  
 252 matrices provided by the multivariate mixed models. Traits differ in the number of individuals and  
 253 measures (Table 1); thus, we chose to be conservative and to use the minimum number of individuals  
 254 for which we have data on one trait as a parameter to describe sample size in the SEMs (i.e., 565  
 255 females, 556 males, and 1121 individuals for the among-year covariance matrix).

256

257 Table 1: Number of observations and individuals (in parenthesis below: N) and trait repeatability with  
 258 95% CI (in brackets below; Rep) for each trait in males (M) and females (F). As tarsus length is fixed  
 259 after the initial growth period, we did not compute its repeatability (see methods).

		<b>Crown brightness</b>	<b>Crown UV chroma</b>	<b>Breast brightness</b>	<b>Breast yellow chroma</b>	<b>Wing length</b>	<b>Tarsus length</b>
<b>M</b>	N	2119 (993)	2119 (993)	2123 (995)	2123 (995)	2100 (983)	2113 (979)
	Rep.	0.235 [0.188, 0.289]	0.334 [0.282, 0.378]	0.309 [0.258, 0.363]	0.224 [0.171, 0.227]	0.571 [0.531, 0.613]	-
<b>F</b>	N	2243 (1071)	2243 (1071)	2262 (1072)	2262 (1072)	2202 (1060)	2243 (1054)
	Rep.	0.240 [0.188, 0.294]	0.380 [0.330, 0.434]	0.366 [0.312, 0.417]	0.207 [0.145, 0.261]	0.580 [0.539, 0.618]	-
		<b>Mass</b>	<b>Handling aggression</b>	<b>Clutch size</b>	<b>Number of fledglings</b>	<b>Exploratory behavior</b>	
<b>M</b>	N	2077 (970)	2065 (981)	1285 (824)	1266 (813)	693 (556)	
	Rep.	0.559 [0.514, 0.603]	0.245 [0.193, 0.302]	0.147 [0.066, 0.231]	0.090 [0.013, 0.178]	0.375 [0.235, 0.510]	
<b>F</b>	N	2220 (1063)	2191 (1044)	1382 (888)	1362 (874)	713 (565)	
	Rep.	0.344 [0.293, 0.392]	0.361 [0.308, 0.412]	0.453 [0.388, 0.519]	0.179 [0.102, 0.256]	0.375 [0.242, 0.510]	

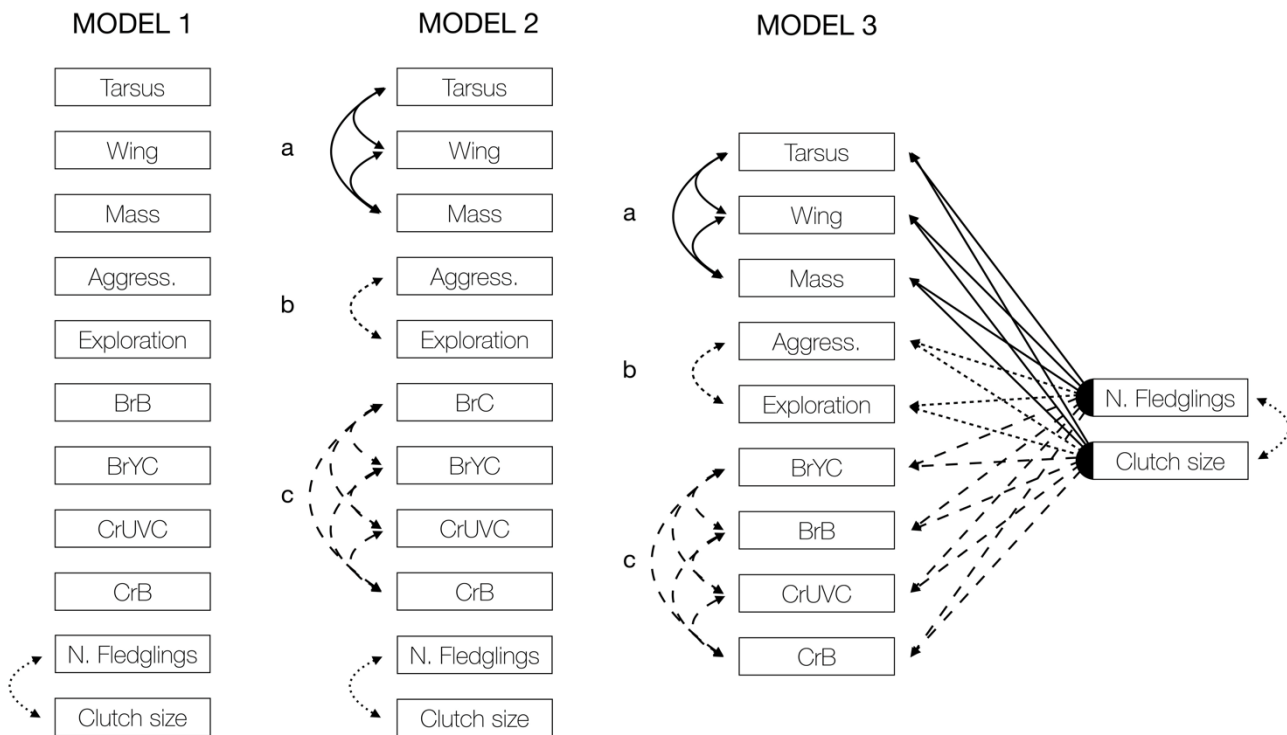
260

261 Based on the definition proposed in the introduction, we expect that traits belonging to the same  
262 module show covariances of similar signs among individuals, but also within individuals and among  
263 years, as they may jointly respond to seasonal changes in the environmental conditions of expression.  
264 Among-year covariance between two traits can arise because of plasticity in response to  
265 environmental changes shared by all the birds and/or selective disappearance of individuals with  
266 particular trait combinations. Covariances at the within-individual level reflect covarying plasticity of  
267 traits in response to environmental changes specific to individuals. Covariances between traits at the  
268 different levels are also expected to include potential combined measurement errors on the two traits  
269 (Brommer 2013). However, we expect these errors to range between 0 and 10% of the measure, and  
270 the chance that the same handler manipulates the same birds over several years is low.

271

272 For each level of analysis, we aimed to test the existence of modules (morphology, behavior, color  
273 and life history). In our models, clutch size and number of fledglings always covaried, as one depends  
274 on the other (Fig. 1). To avoid multiplying the tests and the risk of type I errors we decided not to test  
275 all possible models. We started by building a reference model where we specified independence of all  
276 the traits except life-history traits (model 1). This model was compared to a series of models, where  
277 we assumed the presence of modules of traits based on their type, but that life-history was  
278 independent of all the traits (Fig.1, model 2). We tested all the modules combinations: three modules  
279 (morphological, behavioral and coloration module; [Fig. 1, model 2abc]), two modules  
280 (morphological and behavioral [2ab], morphological and coloration [2ac] and behavioral and  
281 coloration [2bc]) or only a morphological [2a], behavioral [2b] or coloration module [2c]. In addition,  
282 we also compared the models mentioned above with a set of models that assumed covariances  
283 between the morphological, behavioral and coloration traits with life-history (Fig. 1, model set 3),  
284 where clutch size and fledging success are estimates of the pace of life. We tested whether all the  
285 traits covaried within their type and with life-history (Fig.1, model 3), only two trait types did  
286 (morphological and behavioral [Fig.1, model 3ab], morphological and coloration [3ac] and behavioral  
287 and coloration [3bc]) or only the morphological [3a], behavioral [3b], or coloration traits [3c]  
288 covaried with clutch size and number of fledglings. We compared these models with their Akaike  
289 Information Criterion (AIC), and we selected the “best” model as the most parsimonious (i.e. model  
290 with the lowest number of parameters) among all the models within a  $\Delta AIC < 5$ . Models of within-

291 individual covariance excluded tarsus length because there was no variation within individuals for this  
 292 trait. We ran the SEMs using the R package *Laavan* v. 0.6-11 (Rosseel 2012).



293 Figure 1: Hypothetical models with different structures of covariance matrices between the focal  
 294 traits in Corsican blue tits. BrYC stands for breast yellow chroma, BrB for breast brightness,  
 295 CrUVC for crown UV chroma, CrB for crown brightness, aggress. for handling aggression and  
 296 exploration for exploratory behavior. Letters and arrows in models 2 and 3 indicate the different  
 297 modules (a: morphology, b: behavior and c: color), so that in the main text e.g. “model [2ab]”  
 298 means that modules are considered for morphology and behavior but color traits are supposed  
 299 independent.

300

## 301 RESULTS

### 302 *Sex-dependent covariances and integration patterns of coloration*

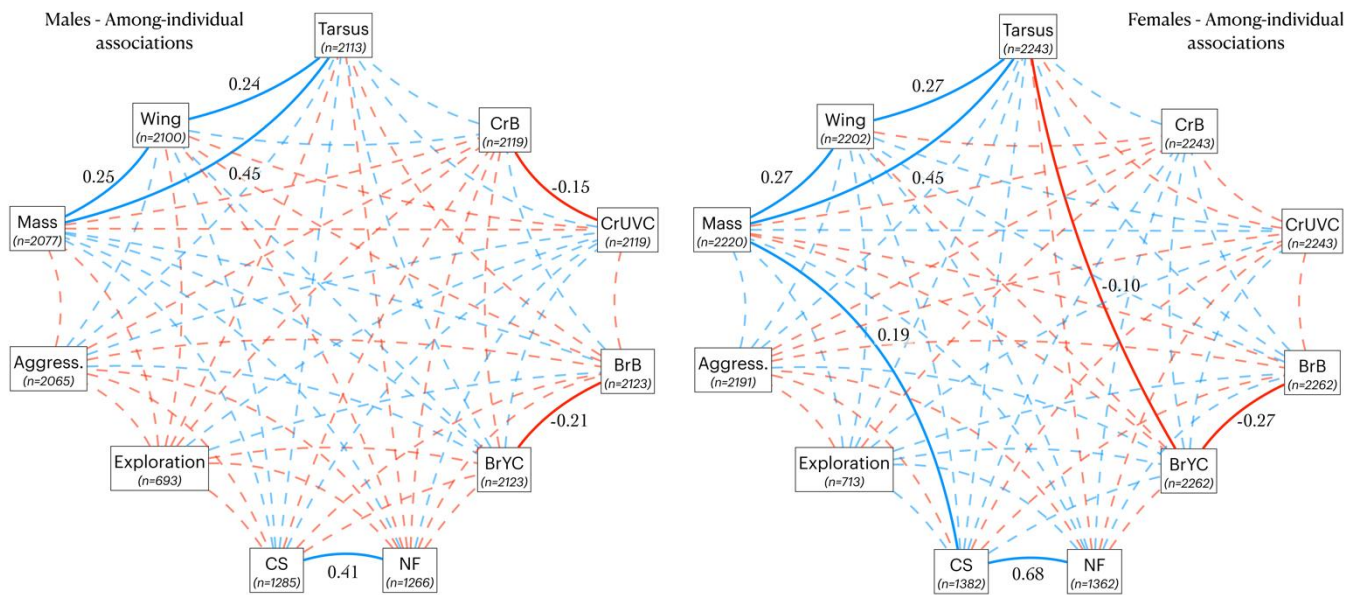
303

304 Our results show that the model including sex-dependent (co)variance matrices had a much smaller  
 305 DIC (49839.8, see SM-3 Table 1 for further information on the model fixed effects) than the model in  
 306 which the covariances were equal for males and females (51460.8;  $\Delta$ DIC: 1621.0). We thus present  
 307 analyses for the model with the covariance matrices for the two sexes separated.

308

309 At the among-individual level, we found positive covariances within the morphological and life-  
 310 history traits in both sexes. In addition, in males our results showed negative covariances between the  
 311 crown UV chroma and crown brightness and between the breast yellow chroma and breast brightness.  
 312 The average strength of the correlations among males was  $|0.09|$  (range: -0.21 – 0.45; Table 2 SM-4).

313 In females, breast yellow chroma was negatively correlated with breast brightness and tarsus length.  
 314 Besides color, we also found a positive among-individual covariance between clutch size and body  
 315 mass (Fig. 2, Table 1 SM-4). The average strength of correlations among females was  $|0.08|$  (range: -  
 316 0.27 - 0.68; Table 2 SM-4).



317 Figure 2: Among-individual covariances of the 11 focal traits in male and female blue tits. Solid  
 318 lines denote the covariances with 95% credible interval not overlapping with zero. Blue lines  
 319 represent positive and red lines negative covariances. CrB stands for crown brightness, CrUVC for  
 320 crown UV chroma, BrB for breast brightness, BrYC for breast yellow chroma, CS for clutch size,  
 321 NF for number of fledglings, aggress. for handling aggression and exploration for exploratory  
 322 behavior. The value close to the solid lines denotes the correlation between the two traits. n is the  
 323 number of observations.

324

325 At the within-individual level, in males, there was a positive covariance between body mass and wing  
 326 length, and between clutch size and number of fledglings. In addition, we found negative covariances  
 327 between the crown UV chroma and crown brightness and between breast yellow chroma and breast  
 328 brightness. Crown and breast brightness covaried positively between them. Finally, crown brightness  
 329 covaried positively with exploratory behavior and number of fledglings with wing length (Fig. 3,  
 330 Table 1 SM-5). The average strength of the correlations within males was  $|0.08|$  (range: -0.36 - 0.56;  
 331 Table 2 SM-5). In females, clutch size covaried positively with number of fledglings, and crown  
 332 brightness with crown UV chroma and with breast brightness. Finally, breast yellow chroma showed a  
 333 negative covariance with breast brightness (Fig. 3, Table 1 SM-5). The average strength of the  
 334 correlations was  $|0.06|$  (range: -0.37 - 0.51; Table 2 SM-5).

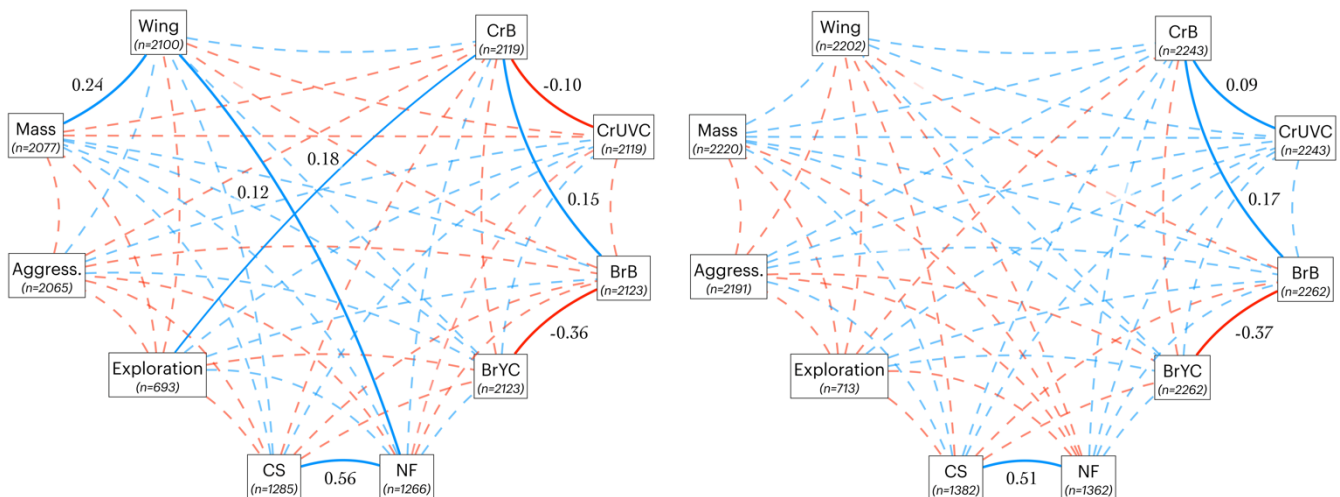
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Males - Within-individual associations

Females - Within-individual associations



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Figure 3: Within-individual covariances between the ten focal traits in males and females. Solid lines denote the covariances with 95% credible interval not overlapping with zero. Blue lines represent positive and red lines negative covariances. CrB stands for crown brightness, CrUVC for crown UV chroma, BrB for breast brightness, BrYC for breast yellow chroma, CS for clutch size, NF for number of fledglings, aggress. for handling aggression and exploration for exploratory behavior. The value close to the solid lines denotes the correlation between the two traits. n is the number of observations. Tarsus length within-individual variance was fixed to 0.0001 (see methods).

347 ***Modularity in the blue tit's phenotype***

348 Among-individual associations

349 Among males, model 2a and model 2ab showed the lowest AIC values ( $\Delta AIC < 5$ , Table 2). From  
350 these, we selected model 2a as the most parsimonious (Fig. 4, SM-6 Table 1). All the other models  
351 showed  $\Delta AIC > 11.6$  (Table 2-A). Among females, model 2a and 2ab also showed the lowest AIC  
352 values ( $\Delta AIC < 5$ , Table 2), and we selected model 2a as the most parsimonious (Table 2-B, Fig. 4,  
353 SM-6 Table 2). All the other models showed  $\Delta AIC > 9.1$ .

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361 Table 2. Structural equation models of among-male (A) and among-female (B) between-trait  
 362 covariances in Corsican blue tits ranked based on their Akaike Information Criterion (AIC). In bold,  
 363 the most parsimonious model with a  $\Delta\text{AIC} < 5$ . Models are described in Figure 1.

364 A: Among-males

Model	Description	N param	AIC	$\Delta\text{AIC}$
<b>2a</b>	<b>One morphological module, no link with life-history</b>	<b>15</b>	<b>17331.1</b>	
2ab	One morphological and one behavioral module no link with life-history	16	17334.0	1.9
2ac	One morphological and one coloration module no link with life-history	21	17343.4	11.3
3a	One morphological module linked to life-history	21	17353.7	11.6
2	Three modules, no link life-history	22	17345.2	13.1
3ab	One morphological and one behavioral module linked with life-history	22	17353.5	21.4
1	Morphology, behavior, and coloration are independent	12	17367.4	35.3
2b	One behavioral module, no link with life-history	13	17369.2	37.1
3ac	One morphological and one coloration module linked with life-history	35	17370.6	38.5
3b	One behavioral module linked to life-history	17	17377.2	45.1
2c	One coloration module, no link with life-history	18	17378.7	46.6
3	Three modules linked to life-history	40	17380.5	48.4
2bc	One behavioral and one coloration module no link with life-history	19	17380.5	48.4
3c	One coloration module linked to life-history	26	17394.3	62.2
3bc	One behavioral and one coloration module linked with life-history	31	17404.1	72.0

365 B: Among-females

Model	Description	N param	AIC	$\Delta\text{AIC}$
<b>2a</b>	<b>One morphological module, no link with life-history</b>	<b>15</b>	<b>17600.4</b>	
2ab	One morphological and one behavioral module no link with life-history	16	17602.4	2.0
3a	One morphological module linked to life-history	21	17609.5	9.1
2ac	One morphological and one coloration module no link with life-history	21	17611.8	11.4
2	Three modules, no link life-history	22	17613.8	13.4
3ab	One morphological and one behavioral module linked with life-history	22	17618.2	17.8
3ac	One morphological and one coloration module linked with life-history	35	17636.1	35.7
1	Morphology, behavior, and coloration are independent	12	17637.0	36.6
2b	One behavioral module, no link with life-history	13	17639.0	38.6
3	Three modules linked to life-history	40	17644.9	44.5
3b	One behavioral module linked to life-history	17	17645.7	45.3
2c	One coloration module, no link with life-history	18	17648.4	48.0
2bc	One behavioral and one coloration module no link with life-history	19	17650.4	50.0
3c	One coloration module linked to life-history	26	17663.7	63.3
3bc	One behavioral and one coloration module linked with life-history	31	17672.5	72.1

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367 Within-individual associations

368 Within males, model 2, model 2ac, model 2bc and model 2c showed the lowest AIC values ( $\Delta\text{AIC} <$   
 369 5). Model 2c was selected as the most parsimonious (Table 3-A, Fig. 4, SM-6 Table 3) and all other  
 370 models showed  $\Delta\text{AIC} > 7.0$ . Within females, model 2c, model 2ac, model 2bc and model 2 showed

371 the lowest AICs ( $\Delta AIC < 5$ , Table 3-B). Model 2c was selected as the most parsimonious model (Fig.  
 372 4, SM-6 Table 4). All the other models showed  $\Delta AIC > 14.4$ .  
 373  
 374 Table 3. Structural equation models of within-male (A) and within-female (B) between-trait  
 375 covariances in Corsican blue tits ranked based on their Akaike Information Criterion (AIC). In bold,  
 376 the most parsimonious model with a  $\Delta AIC < 5$ . Models are described in Figure 1.

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A: Within-males

Model	Description	N param	AIC	$\Delta AIC$
2	Three modules, no link life-history	19	15699.0	
2ac	One morphological and one coloration module no link with life-history	18	15699.9	0.9
2bc	One behavioral and one coloration module no link with life-history	18	15700.2	1.2
<b>2c</b>	<b>One coloration module, no link with life-history</b>	<b>17</b>	<b>15701.1</b>	<b>2.1</b>
3bc	One behavioral and one coloration module linked with life-history	30	15703.6	4.6
3	Three modules linked to life-history	35	15706.0	7.0
3b	One behavioral module linked to life-history	16	15709.1	10.1
3ab	One morphological and one behavioral module linked with life-history	13	15720.2	12.6
3c	One coloration module linked to life-history	25	15716.8	17.8
3ac	One morphological and one coloration module linked with life-history	30	15719.5	20.5
2ab	One morphological and one behavioral module no link with life-history	13	15720.2	21.2
2a	One morphological module, no link with life-history	12	15721.0	22.0
2b	One behavioral module, no link with life-history	12	15721.4	22.4
1	Morphology, behavior, and coloration are independent	11	15722.3	23.3
3a	One morphological module linked to life-history	16	15725.0	26.0

379 B: Within-females

Model	Description	N param	AIC	$\Delta AIC$
<b>2c</b>	<b>One coloration module, no link with life-history</b>	<b>17</b>	<b>15972.5</b>	
2ac	One morphological and one coloration module no link with life-history	18	15974.3	1.8
2bc	One behavioral and one coloration module no link with life-history	18	15974.4	1.9
2	Three modules, no link life-history	19	15976.2	3.7
3c	One coloration module linked to life-history	25	15986.9	14.4
1	Morphology, behavior, and coloration are independent	11	15993.8	21.3
3bc	One behavioral and one coloration module linked with life-history	30	15994.0	21.5
3ac	One morphological and one coloration module linked with life-history	30	15995.2	22.7
2a	One morphological module, no link with life-history	12	15995.6	23.1
2b	One behavioral module, no link with life-history	12	15995.7	23.2
2ab	One morphological and one behavioral module no link with life-history	13	15997.5	25.0
3b	One behavioral module linked to life-history	16	16001.0	28.5
3a	One morphological module linked to life-history	16	16002.2	29.7
3	Three modules linked to life-history	35	16002.5	30.0
3ab	One morphological and one behavioral module linked with life-history	13	16009.5	71.5

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382 Among-year associations

383 Among years, model 3c and model 3bc showed the lowest AICs ( $\Delta AIC > 5$ ). Model 3c was retained as  
 384 the most parsimonious (Table 4, Fig. 4, SM-6 Table 5). We found positive covariances between  
 385 coloration traits except for the association between breast brightness and breast yellow chroma,  
 386 although the 95% CI always included zero (Table 1 SM-7). Also, while breast yellow chroma, and  
 387 crown UV chroma were positively associated with clutch size, the association with breast and crown  
 388 brightness was negative. For number of fledglings, there was a positive association with crown UV  
 389 chroma and a negative association with breast and crown brightness and breast yellow chroma. Still,  
 390 the 95% C.I. always included zero and the average strength of the correlations was weak ( $|0.13|$ ; Table  
 391 1 SM-7).

392

393 Table 4. Structural equation models of among-year, between-trait covariances in Corsican blue tits,  
 394 ranked based on their Akaike Information Criterion (AIC). In bold, the most parsimonious model with  
 395 a  $\Delta AIC < 5$ . CS stands for clutch size and NF for number of fledglings. Models are described in Figure  
 396 1.

397

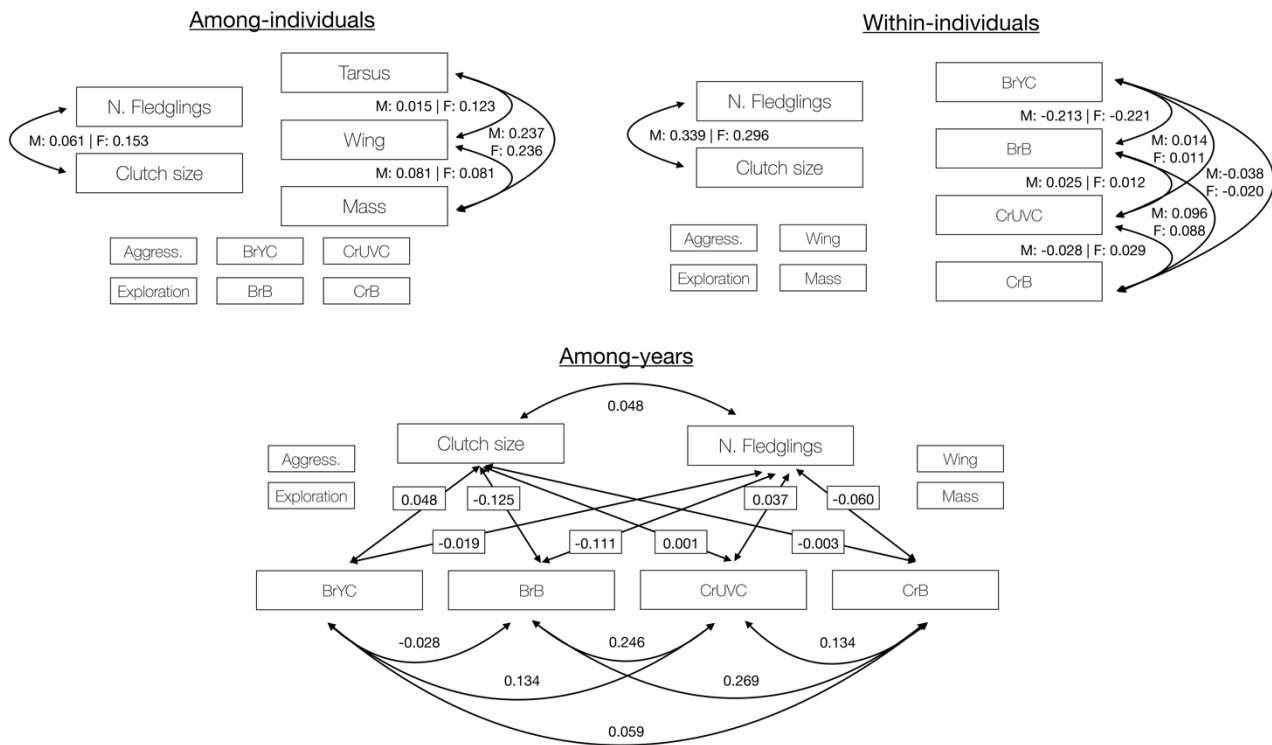
Model	Description	N param	AIC	$\Delta AIC$
<b>3c</b>	<b>One coloration module linked to life-history</b>	<b>26</b>	<b>34801.6</b>	
3bc	One behavioral and one coloration module linked with life-history	31	34806.3	4.6
3ac	One morphological and one coloration module linked with life-history	35	34810.3	8.7
3	Three modules linked to life-history	40	34815.0	13.4
2c	One coloration module, no link with life-history	18	34827.4	25.8
2bc	One behavioral and one coloration module no link with life-history	19	34829.2	27.6
2ac	One morphological and one coloration module no link with life-history	21	34829.4	27.7
2	Three modules, no link life-history	22	34831.2	29.6
1	Morphology, behavior, and coloration are independent	12	35004.3	202.7
2b	One behavioral module, no link with life-history	13	35006.1	204.5
2a	One morphological module, no link with life-history	15	35006.3	204.7
2ab	One morphological and one behavioral module no link with life-history	16	35008.1	206.5
3b	One behavioral module linked to life-history	17	35009.3	207.7
3a	One morphological module linked to life-history	21	35013.6	212.0
3ab	One morphological and one behavioral module linked with life-history	26	35018.8	217.2

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402 Figure 4: Schematic representation of the most parsimonious structural equation models.  
 403 Arrows represent covariances between traits and numbers their strength. M, represents the  
 404 values for males and F for females. CrB stands for crown brightness, CrUVC for crown UV  
 405 chroma, BrB for breast brightness, BrYC for breast yellow chroma, aggress. for handling  
 406 aggression, and exploration for exploratory behavior.

407

## 408 DISCUSSION

409 The multivariate mixed models run on a multi-trait dataset collected in the field across nine years  
 410 revealed a weak integration of the 11 studied traits but suggested some sex-specific covariances at the  
 411 among- and within-individual levels. Both sexes showed consistent weak to moderate positive  
 412 correlations among morphological traits and between two life-history traits, indicating the presence of  
 413 morphological (i.e. body size) and life-history modules. Structural equation models, however, showed  
 414 no evidence in support of the existence of a behavioral or a coloration module. In these models, the  
 415 covariances between traits were weak and the model assuming the existence of three modules  
 416 associated with life-history never showed an AIC lower than another more parsimonious model. Our  
 417 results, thus, show some phenotypic integration in morphology and life-history, but do not provide  
 418 strong support for the POLS hypothesis at the within population level.

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## 422 **Integration at the among-individual level**

423

424 The positive covariance between morphological traits at the among-individual level denotes the classic  
425 allometric associations between traits linked to body size (Roff 1996; Delahaie et al. 2017) that  
426 probably arises because morphological traits share the developmental precursors regulating their  
427 expression (West-Eberhard 2003; Klingenberg 2008). In males and females, the correlation patterns  
428 were similar in strength and direction, and were in line with two previous studies in birds showing  
429 among-individual correlations between tarsus length, wing length and body mass ranging between  
430 0.20 and 0.54 (Araya-Ajoy et al. 2019; Moiron et al. 2019). Compared to other phenotypic  
431 correlations of morphological traits available for vertebrates (average: 0.49, range: -0.02, 0.99; Conner  
432 et al. 2014), the strength of our correlations is moderate, probably because the traits we studied are  
433 more labile than other traits typically studied in this context (e.g. skeletal measures). Specifically, the  
434 among-individual integration of the morphological traits we report probably has a genetic basis as it  
435 has been shown that these traits are correlated at the genetic level in these blue tit populations (range:  
436 0.36-0.51; Delahaie et al. 2017), suggesting that morphology responds as an evolutionary unit.

437 We found weak integration for color traits, but some covariances between specific traits seem to exist,  
438 and potentially reveal some trade-offs and constraints. Breast brightness was negatively associated  
439 with breast yellow chroma in both sexes. While brightness is the product of the structure of the  
440 feather, yellow chroma is generated by carotenoid deposition in the feather (Shawkey and Hill 2005;  
441 Isaksson et al. 2008). Thus, an increased carotenoid concentration can mechanically limit the  
442 brightness arising from the feather structure, leading to a negative association between them  
443 (Andersson and Prager 2006). Regarding crown coloration, we found a negative among-individual  
444 association between brightness and UV chroma in males but not in females. Crown UV chroma and  
445 brightness result from the interaction of the feather structure and light (Prum et al. 1999; Hegyi et al.  
446 2018). The negative association between these two traits can be explained because some structural  
447 features of the feathers that increase brightness are negatively correlated to characteristics enhancing  
448 UV chroma (Hegyi et al. 2018). The lack of a significant association in females could arise because  
449 male and female blue tits differ in the macrostructure of their feathers, and thus females might face  
450 different structural constraints than males (Hegyi et al. 2018). Still, although the association differed in

451 significance in males and females, it was weak in both sexes (SM 3 – Table 2), suggesting that the  
452 association between crown UV chroma and brightness may not have strong biological implications.  
453

454 According to the POLS hypothesis, we predicted a positive association among individuals between  
455 handling aggression, exploratory behavior, and life history. The weak correlation values found  
456 between these traits, however, did not validate this hypothesis. The presence of among-individual  
457 associations among behavioral traits (i.e. behavioral syndromes) and their link with reproduction has  
458 been reported in different species, but their presence is not general (Royauté et al. 2018). This  
459 disparity of results on behavioral syndromes can be driven by factors such as age (Class and Brommer  
460 2015) or environmental conditions (Dingemanse et al. 2007). For example, in three-spined  
461 sticklebacks (*Gasterosteus aculeatus*) a behavioral syndrome only appears in individuals inhabiting  
462 large ponds with predators and not in those living in small ponds with no predators (Dingemanse et al.  
463 2007). Analyzing together three blue tit populations may mask within-population correlations, if these  
464 correlations differ across them. We think however that this is unlikely as previous work has found that  
465 P and G matrices between life-history and morphological traits are not different among these same  
466 populations (Delahaie et al. 2017). It remains possible that behavioral syndromes in these blue tit  
467 populations may only be detectable under specific environments or may be hardly detectable (Van De  
468 Walle et al. 2023).

469

470 Finally, we found weak integration across trait modules that was limited to a few traits in females. We  
471 found a negative association between breast yellow chroma and tarsus length and a positive  
472 association between mass and clutch size. Given the moderate heritability of breast yellow chroma  
473 (Charmantier et al. 2017; López-Idiáquez et al. 2022), we speculate that the association between breast  
474 yellow chroma and tarsus length can be the product of early-life effects. This would be in line with  
475 previous research showing that the environment experienced during early life, e.g. stress or diet, can  
476 drive the strength of the associations between morphological, behavioral or physiological traits (Han  
477 and Dingemanse 2015; Merrill and Grindstaff 2018). However, the specific mechanism explaining the  
478 association between tarsus length and breast yellow chroma remains to be elucidated. The covariance  
479 between clutch size and mass is in line with previous evidence showing that females in better  
480 condition lay larger clutches (Slagsvold and Lifjeld 1990; Karell et al. 2008). The lack of association

481 in males is probably due to clutch size being a female-specific trait (Slagsvold and Lifjeld 1990; Auld  
482 and Charmantier 2011, Table 1).

483

484 Overall, the lack of significant covariances between trait types at the among-individual level, also in  
485 line with the SEM, does not support the presence of a POLS in our system. This is in appearance  
486 contradicting results from Dubuc-Messier et al. (2017), who found different paces of life across these  
487 three populations, based on differences between trait averages (but note that their study did not  
488 investigate covariances among trait). However, this discrepancy agrees with a recent study using data  
489 from 17 species showing that while life-histories are structured by a slow-fast continuum at the  
490 between species level, they are not detectable at the within population level (Van De Walle et al. 2023;  
491 see also Royauté et al. 2018). This could arise from a power issue to detect smaller patterns, but it  
492 could also arise from ecological mechanisms: stochastic environmental events, such as variations in  
493 mortality or resource availability, or between individual differences in resource acquisition abilities  
494 which can constrain our ability to detect trade-offs between traits.

495

#### 496 **Integration among years and within individuals**

497

498 Among years, we found positive and negative covariances between the studied traits (SM-7 Table 1).  
499 The positive covariances between colors probably are product of the inter-annual changes in the  
500 environmental quality. Due to the condition dependence of these color traits (Doutrelant et al. 2012;  
501 White 2020), benign environmental conditions likely enhance the expression of both the crown and  
502 breast colorations, while the opposite is true under harsh environments (Doutrelant et al. 2012; López-  
503 Idiáquez et al. 2022). Still, although, these correlations were not weak (range: 0.14-0.42, SM-7 Table  
504 1), their 95% credible interval always included zero as the other among year correlations we report,  
505 probably because of the limited number of years included.

506

507 Within individuals, the best model assumed one coloration module with no link with clutch size (Table  
508 2). It is worth mentioning, however, that there were other less parsimonious SEM within the  $\Delta AIC < 5$   
509 threshold, supporting the presence of a morphological and/or behavioral module in addition to the  
510 coloration one. In both sexes, breast brightness was positively associated with crown brightness

511 probably because of their shared production basis (i.e. feather structure) and thereby the changes in the  
512 environmental conditions have similar effects on both traits. Besides, as for the among individuals  
513 analysis, we found a negative covariance between breast brightness and yellow chroma within males  
514 and females that probably arises because increased chroma limits brightness (see above; Andersson  
515 and Prager 2006). Also, we found that while crown brightness is positively associated with crown UV  
516 chroma in females, this association is negative in males. We are unaware of the mechanisms  
517 explaining this divergence but perhaps it arises due to the different macrostructure of the blue crown  
518 feathers in males and females (Hegyi et al. 2018). Alternatively, and non-exclusively, males could face  
519 a stronger trade-off between crown brightness and UV chroma due to their brighter and more  
520 chromatic crowns.

521

522 In males, we also found a positive within-individual correlation between mass and wing length,  
523 meaning that in years when males are heavier, they also have longer wings. This association aligns  
524 with our results at the among-individual level and suggests that wing length is a condition-dependent  
525 trait. Besides, we found positive associations between exploratory behavior and crown brightness in  
526 males. This shows that changes in behavior are coupled with the level of expression of the ornamental  
527 coloration. A possible mechanism to explain this association is that by becoming more explorative  
528 blue tits may be able to gain more resources allowing them to develop brighter feathers, but this idea  
529 should be confirmed experimentally.

530

531 Our results showed several within individual covariances that often were positive, suggesting that the  
532 combined plasticity between traits probably arises through annual variation in resource  
533 acquisition/availability. By contrast, the negative within-individual covariances between the color  
534 components probably root on the structural trade-offs constraining their expression. Finally, our results  
535 showed that trait integration was slightly stronger in males than in females. This difference may be  
536 caused by the enhanced competition rates among males, for instance due to intra-sexual selection  
537 (Schlicht and Kempenaers 2013; García-Navas et al. 2014) that may generate a higher variability in  
538 resource acquisition between years in males than in females.

539

540

## 541 **Implications in the context of signaling**

542 The evidence available on the role of ornamental colorations as signals of personality has mostly  
543 focused on melanin-based traits (Nicolaus et al. 2016; López-Idiáquez et al. 2018; Thys et al. 2020)  
544 and whether carotenoid or structural colors signal personality remains poorly known (Blount and  
545 McGraw 2008; Green et al. 2022). Our results of a positive association between male crown  
546 brightness and exploration at the within individual level suggest that crown coloration could inform  
547 about personality in males. This trait has been described to work as a badge of status (Alonso-Alvarez  
548 et al. 2004; Rémy et al. 2010, but see Korsten et al. 2007), so perhaps it could provide information  
549 about exploratory behavior in an intrasexual competition context. Although significant, the association  
550 was weak, thus, is important to bear in mind that this information is probably associated with high  
551 uncertainty. For the carotenoid-based coloration, we found no associations with behavior perhaps  
552 because this type of color is more involved in signaling other characteristics such as parasite resistance  
553 (del Cerro et al. 2009) or oxidative status (Pérez-Rodríguez 2009; Weaver et al. 2018). Besides, our  
554 results show weak integration between the two-colored ornaments, as only breast and crown  
555 brightness covaried at the within-individual level. This seems to align with the idea that the multiple  
556 ornamental traits exhibited by an individual convey different information (e.g. multiple message  
557 hypothesis; Candolin 2003), probably due to the different production constraints of each color,  
558 something that should be experimentally confirmed.

559

## 560 **Conclusion**

561 In this study we have shown that the covariance patterns between morphology, coloration, behavior,  
562 and life history are weak, but that slightly differ in male and female blue tits at the among- and within-  
563 individual levels. This highlights the importance of considering sex and the different hierarchical  
564 levels at which the traits might covary to fully understand how phenotypes are integrated.  
565 Furthermore, the absence of a strong covariance between the studied traits does not validate the POLS  
566 hypothesis within Corsican blue-tit populations.

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591

## 592 **Data availability**

593 Analyses reported in this article can be reproduced using data provided by López-Idiáquez et al.  
594 (2023)

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