

1 **Stable correlation structure among multiple plumage colour**

2 **traits: can they work as a single signal?**

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11 Running head: Stable correlation structure among sexual traits

12 The presence of multiple distinct ornamental traits in the same species is frequently explained  
13 by context-specificity and different information content. However, the expression of multiple  
14 ornaments is often correlated, and such traits may therefore function as a single, integrated  
15 signal. Delayed use of an integrated signal relative to production requires temporal stability in  
16 integration, which has seldom been examined. We used autumn and spring reflectance data  
17 from the breast, breast stripe and crown of great tits (*Parus major*) to assess the stability and  
18 mating implications of colour signal integration, as well as the repeatability of any integrated  
19 colour trait and its correlation with condition during moult. We found high levels of stability  
20 between seasons, years, sexes and ages in the correlation patterns of colour measures across  
21 the three plumage areas. The first principal component colour axis described joint variation of  
22 UV reflectance on the crown and the breast stripe, thereby representing an among-trait UV  
23 chroma axis. However, only breast yellow chroma showed condition-dependence, while  
24 temporally consistent and significant assortative mating was restricted to crown UV chroma.  
25 Our results therefore do not support the ideas that the overall UV chroma of the breast stripe  
26 and the crown is special in condition-dependence and repeatability, or it plays a specific role  
27 in mutual sexual selection as an integrated signal. Our results show that stable association  
28 between display traits is an existing phenomenon. They also indicate that even in the presence  
29 of correlated traits, functional trait integration among these requires further scrutiny.

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31 **ADDITIONAL KEYWORDS:** body condition – feather abrasion – moult – plumage colour –  
32 redundant signal – sexual selection.

## 33 INTRODUCTION

34 Research of sexually selected ornamental traits has always been at the forefront of  
35 evolutionary ecology studies (Darwin, 1871; Andersson, 1994; Hill & McGraw, 2006). With  
36 the exploration of an increasing number of different sexual traits, recent studies increasingly  
37 emphasize the variety of sexual signals and their different information content, even within a  
38 single species. This focus on signal variety is well illustrated by the recent introduction of the  
39 concept of within-species ornament diversity (Chen *et al.*, 2012). Regarding colour traits,  
40 classically used categories include pigment-based (Svensson & Wong, 2011) and structurally  
41 based ornaments (Srinivasarao, 1999). Both of these occur in bird feathers (Gray, 1996;  
42 Badyaev & Hill, 2003). On the other hand, some recent work indicated that many colours (in  
43 birds nearly all plumage colours) in fact combine pigment- and structurally based mechanisms  
44 (Rutowski *et al.*, 2005; Doucet *et al.*, 2006; Kuriyama *et al.*, 2006; Shawkey *et al.*, 2006;  
45 Wilts *et al.*, 2012), and highlighted similarities in information content among classical  
46 categories of colour (Blas *et al.*, 2006; Griffith, Parker & Olson, 2006). This indicates that  
47 seemingly distinct ornamental traits of the same species may not behave independently at the  
48 developmental and functional levels.

49 Multiple sexual traits may function in the same sexual selection process, either  
50 conveying different information or reinforcing each other (Møller & Pomiankowski, 1993;  
51 Johnstone, 1996), but they can also be used in different contexts (Pryke *et al.*, 2001; Dunn *et*  
52 *al.*, 2010). The concept of composite sexual signals emerged relatively early, but classical  
53 studies of this phenomenon examined the separate information content and role of multiple  
54 aspects of the same conspicuous trait (Badyaev *et al.*, 2001; Møller & Petrie, 2002). By  
55 contrast, if the same species apparently displays multiple traits indicating phenotypic quality,  
56 these may actually indicate one or few common aspects of quality (Badyaev, 2004; Martín &  
57 López, 2009). For example, multiple ornaments may depend on the overall physiological state

58 or body condition of the individual (Rowe & Houle, 1996) and thereby share some of their  
59 genetic and environmental background (Tomkins *et al.*, 2004). This raises the possibility that  
60 even perceptually distinct traits of different developmental origins, for example, patches of  
61 different pigmentary basis in the same plumage, may correlate in their expression and may  
62 even constitute a single integrated signal (Hebets & Papaj, 2005). A much more  
63 straightforward case is when multiple distinct traits of similar developmental origin convey  
64 similar information (Peters *et al.*, 2008). Functional integration among these may occur  
65 simply due to a shared sensory processing pathway, i.e. sensory exploitation (Partan &  
66 Marler, 2005), although this will not happen if the possibility to assess the individual traits is  
67 different or context-specific (Hebets & Papaj, 2005). In sum, multiple processes may cause  
68 developmental integration, functional integration, or both, among some components of a  
69 system of multiple display traits.

70         An increasing number of studies investigate multiple conspicuous traits in the same  
71 species (Candolin, 2003). Some studies have estimated among-trait correlations and treated  
72 multiple unrelated ornaments as separate signals (Reudink *et al.*, 2009), while others pooled  
73 correlated ornaments into a single trait (Merilä, Sheldon & Lindström, 1999) or examined  
74 them separately despite their interrelation (Guindre-Parker *et al.*, 2013). However, many  
75 authors do not even consider the possibility of relationships among multiple traits of different  
76 developmental origins. Therefore, there are only a handful of studies that suggested sexual  
77 selection on complexes of multiple distinct but nevertheless integrated ornaments. Examples  
78 for such integration include pairs of structurally based and melanin-based (Siefferman & Hill  
79 2003), depigmented white and melanin-based (Laczi *et al.*, 2011), and carotenoid- and  
80 melanin-based plumage colour traits (Hegyi *et al.*, 2008). Likewise, in general, investigations  
81 of possible adaptive mate choice for the parallel variation or occurrence of conspicuous

82 character states are still relatively rare (Møller *et al.*, 1998; McGlothlin *et al.*, 2005;  
83 Lancaster, Hipsley & Sinervo, 2009).

84         A fundamental but seldom examined question concerning signal integration is whether  
85 it is sufficiently consistent (among contexts) and stable (in time) to permit receivers to pay  
86 special attention to the signal complex rather than the univariate traits *per se*. Recent research  
87 puts particularly strong emphasis on fluctuating information content and fluctuating selection  
88 in multiple signal systems (Bro-Jørgensen, 2010). To the contrary, there are two cases in  
89 which the evolutionary persistence of sexual selection on an integrated signal as opposed to  
90 multiple independently processed signals requires stability in trait correlation structure and  
91 information content across seasons: when the signal complex is used in multiple seasons, and  
92 when the production and the use of the signal complex are temporally separated. Ornaments  
93 produced in a limited time window but maintained year-round are subject to seasonal wear  
94 and other damages (staining, chemical degradation etc.). For instance, feather abrasion  
95 contributes to the expression of various types of plumage signals (Delhey *et al.*, 2010) and it  
96 may therefore also affect correlations among them. Feather structures including melanins and  
97 carotenoids presumably reduce and increase, respectively, the susceptibility of feathers to  
98 abrasion (Bonser, 1995; Bleiweiss, 2004), so abrasion (and other processes) may differentially  
99 alter the coloration of such areas across seasons (Figuerola & Senar, 2005; Adamík &  
100 Vanáková, 2011). Many species replace their ornaments well before the main period of sexual  
101 displays, while others may use them year-round. If seasonal wear increases, reduces or  
102 reorganizes developmental integration among multiple ornaments, this will have implications  
103 for their functional integration. In the case of delayed ornament use relative to production,  
104 integration at production may be completely different or absent at use. In the case of  
105 prolonged use, integration may gradually change with time. This may in turn reduce or  
106 reverse the adaptive value of paying attention to the trait complex.

107           In addition, year-specific environmental conditions may exert major influences on  
108 sexual signal expression (Saino *et al.*, 2004; Scordato, Bontrager & Price, 2012; Molnár,  
109 Bajer & Török, 2012), and there may be different year-specific effects on different ornaments  
110 of the same species (Hegyi *et al.*, 2007a). This may cause among-year variation in the  
111 magnitude and pattern of integration among multiple ornamental traits. Sexual ornamentation  
112 often drastically changes with age and this may involve shifts in information content (Hegyi  
113 *et al.*, 2006; Grunst, Rotenberry & Grunst, 2014). With differential delayed maturation of  
114 different ornamental components (Hawkins, Hill & Mercadante, 2012) relationships among  
115 these components may also undergo an age-related change. Finally, the proximate  
116 determination of homologous sexual traits in males versus females is sometimes similar  
117 (Doutrelant *et al.*, 2012) but in other cases very different (Murphy & Pham, 2012), which may  
118 cause sex differences in signal interrelation. If the ornamentation of the two sexes is  
119 qualitatively similar, the degree of similarity in ornament integration between males and  
120 females is informative regarding the evolution of ornament integration and it is therefore  
121 relevant to the stability of integration. For example, integration may have evolved similarly or  
122 differently in the two sexes, and the evolution of integration may have preceded or followed  
123 the evolution of sexual dichromatism.

124           Here we use a long-term spectral dataset from great tits (*Parus major*) to examine the  
125 integration of plumage colouration and the above mentioned four aspects of signal  
126 consistency. Some components of the plumage ornamentation of great tits have been  
127 abundantly studied (see e.g. Fitze & Richner, 2002; Senar, Figuerola & Domènech, 2003;  
128 Jacot *et al.*, 2010; Romero-Diaz *et al.*, 2013). However, despite suggestions of similarity in  
129 information content among multiple traits (Galván, 2010), their correlation structure and  
130 especially the temporal stability of this correlation structure have not yet been explored (but  
131 see Hegyi *et al.*, 2008 for a partial attempt; see also Senar & Quesada, 2009). We analyze the

132 autumn and spring reflectance descriptors of birds caught in seven year-specific moult cycles  
133 (autumn or the following spring). This species has a single complete moult in summer  
134 (Gosler, 1993; see also Methods) and shows strong within-individual changes in plumage  
135 colour expression across seasons (Figuerola & Senar, 2005; Adamík & Vanáková, 2011), so it  
136 is ideal for testing the relative importance of moult and plumage abrasion for signal  
137 expression and integration. We assess reflectance variation and spectral integration among  
138 three ornamental plumage areas: the melanised breast stripe (Norris, 1993) and crown (Hegyi  
139 *et al.*, 2007b), and the carotenoid containing breast (Partali *et al.*, 1987). The reflectance of  
140 melanised traits has very scarcely been studied in great tits (this is the first study of breast  
141 stripe reflectance and the second study of crown reflectance), while studies of the yellow  
142 breast principally involved nestlings (reviewed in Hegyi *et al.*, 2007b). The role of these traits  
143 in signalling is unknown at present. The seasonal consistency of colour integration in this  
144 system would be important if some integrated component of reflectance had a role in mate  
145 choice (which occurs many months after moult) and would be especially important if the  
146 integrated component had a signalling role both within and outside the breeding season, as  
147 previously observed for breast stripe area in the same species (Norris, 1990; Lemel & Wallin,  
148 1993).

149         Here we first compare signal integration patterns between the sexes and between  
150 yearling and older birds. Second, we quantify changes in trait interrelation from autumn to  
151 spring due to abrasion. Third, we compare the structure of trait correlation matrices among  
152 years. Fourth, we define composite colour traits and test the within-individual repeatability of  
153 univariate and composite traits in the face of different combinations of moult and abrasion, as  
154 well as their relationship with body condition during moult. Finally, we assess assortative  
155 mating patterns (the degree of correlation in colour between pair members) to compare one  
156 potential indicator of sexual selection between single and composite plumage colour traits. If

157 univariate colour traits are developmentally integrated as an ancestral character state and  
158 functionally integrated throughout the year in both sexes, we predict similar colour trait  
159 interrelation patterns across sexes, ages, seasons and years. If the costly assessment of  
160 composite traits is adaptive, we also predict that the dominant composite colour axis will  
161 provide additional or more reliable information compared to the univariate traits, and  
162 accordingly show stronger or more consistent assortative mating than the univariate traits.

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## MATERIAL AND METHODS

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### FIELD METHODS

167 Great tit feather samples were collected in our nestbox plots near Szentendre, Hungary (Török  
168 & Tóth, 1999). The time span of our present data ranges from autumn 2006 to spring 2013.

169 For comparability, we consider seven pairs of seasons belonging to the same summer moult  
170 (e.g. autumn 2006 and spring 2007). Therefore, we have seven ‘moult years’ from 2006 to

171 2012 (hereafter, ‘year’). In the autumn and early winter (6 October to 28 January in this

172 dataset), great tits were caught using mist nets at two feeders baited with sunflower seed. In

173 spring (5 May to 26 June), parents feeding 8- to 10-day old nestlings were caught in the nest

174 box. All birds received numbered aluminium rings and their age (yearling or older) and sex

175 were determined based on wing covert contrast and breast stripe size respectively (Svensson,

176 1992). The category “yearling” refers to first-years (1Y) in autumn and second-years (2Y) in

177 spring. The plumage of both “yearling” categories was grown at the post-juvenile summer

178 moult. The category “older” refers to second-years (2Y) and after-second-years (2Y+) in

179 autumn and 2Y+ in spring, both of which have plumage grown at a post-breeding summer

180 moult. Body mass was measured using a Pesola spring balance (nearest 0.1g) and tarsus

181 length using callipers (nearest 0.1mm). Feather samples were collected from the black crown,



182 yellow breast and black breast stripe. We collected approximately ten feathers from each area,  
183 which is at the lower threshold of sample size to ensure reliable spectrometric results  
184 (Quesada & Senar, 2006). Ten feathers are a small proportion of the plumage in each area.  
185 The location of feather collection is hardly visible after sampling and the feathers are regrown  
186 in a few weeks (our pers. obs.). The total number of birds sampled was  $N = 425$  in autumn  
187 and  $N = 433$  in spring (sample sizes for autumn and spring respectively; 2006: 91+25; 2007:  
188 48+36; 2008: 49+94; 2009: 90+65, 2010: 59+41; 2011: 29+121; 2012: 59+51), and they were  
189 also  $N = 90$  recaptures ( $N = 21$  in autumn and  $N = 69$  in spring). In autumn, we also collected  
190 the two second outermost rectrices to estimate body condition during moult from the width of  
191 daily feather growth bars (see below). It is important to state here that, in line with some  
192 southern populations of the species (Svensson 1992), all or nearly all juvenile birds in our  
193 area replace their rectrices at the post-juvenile moult (see Supplementary Methods Part 1 for  
194 details). Yearling rectrices therefore reflect body condition at the post-juvenile moult when  
195 the rest of the plumage was grown, so they are comparable with the rectrices of older birds.  
196 Collected feathers were stored in envelopes in a dark and dry place until processing in the  
197 laboratory. Breast stripe area (Figuerola & Senar 2000) was measured in a subset of our birds  
198 but it was weakly correlated with plumage reflectance in our population and showed very  
199 weak assortative mating so it was omitted from our analysis to preserve sample size. We also  
200 did not measure the reflectance of another ornamental trait, the cheek patch (Ferns & Hinsley,  
201 2004) in this study. Inserting additional, possibly unknown ornamental traits could rearrange  
202 the results we report here, although this is still the most comprehensive study of great tit  
203 plumage reflectance we are aware of. Note that few birds are recaptured between seasons and  
204 years in our population (see above). (These were used to test repeatability, see below.) Our  
205 comparisons of seasons and years may therefore reflect the fact that we have partly different  
206 great tit individuals present in different seasons (residents in spring while residents plus

207 vagrants in autumn). However, absolute differences in average colour among seasons and  
208 years were removed from our data before analyses (see below), while any sampling-related  
209 differences in colour correlation structure make our results conservative.

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#### SPECTRAL MEASUREMENTS

212 Reflectance was measured with an Ocean Optics USB2000 spectrometer, using a bifurcated  
213 fibre-optic probe and Ocean Optics deuterium-tungsten-halogen light source DH2000. A  
214 black plastic tube was fixed on the probe to standardize measurement distance and exclude  
215 ambient light. The probe was held perpendicular to the sample. Feathers were placed on top  
216 of one another on a piece of black velvet. Three scans were taken for each set of feathers, with  
217 frequent calibration using a WS-1 white reflection standard (Ocean Optics Europe) and a  
218 black reference (no incoming light to the sensor) during the measurements. Reflectance  
219 curves were stored using OOIBase software (Ocean Optics Europe). The repeatability of  
220 spectral data acquisition in this system is high (intraclass correlation coefficient  $r_I = 0.761$  to  
221  $0.969$ ,  $N = 948$ , all  $P < 0.001$ ; Becker, 1984). Spectral data acquisition was done within a few  
222 years of feather collection. As feather samples were stored in a dry, cool and dark place and  
223 were not treated with any chemicals, the reflectance characteristics of our samples are  
224 unlikely to have substantially changed during the period between collection and  
225 measurements (Armenta, Dunn & Whittingham, 2008). Mean reflectance spectra for males  
226 and females of each plumage area are shown in Fig. 1.

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#### BODY CONDITION DURING MOULT

229 Body condition (i.e. nutritional condition) during moult was estimated from the growth rate of  
230 tail feathers, that is, ptilochronology (Grubb, 1995; see Hill & Montgomerie, 1994; Keyser &  
231 Hill, 1999; Hargitai, Hegyi & Török, 2012 for applications to plumage ornamentation). We

232 restricted these measurements to the autumn data to ensure that we measure the post-moult  
233 state of plumage colour, minimizing the confounding effect of differential abrasion. In  
234 addition, abrasion also hampers the readability of feather growth bars. The method adapted to  
235 the great tit by Senar *et al.* (2003) was used here (also see Hegyi *et al.*, 2007b, 2008). The  
236 total width of the first ten visible growth bars (light and dark) from the distal end of the  
237 feather was measured by calliper (nearest 0.1 mm), under intense direct illumination. Ten bars  
238 indicate body condition over ten days of moult, a long period relative to the total duration of  
239 moult. The left and right feathers of the same individual were measured separately in time,  
240 and measurer experience bias was avoided by alternating between the sides after every eight  
241 samples. The repeatability of growth rate between the two temporally separate measurements  
242 of an individual was high ( $r_I = 0.699 \pm 0.030SE$ ,  $N = 302$  in juveniles and  $r_I = 0.617 \pm$   
243  $0.067SE$ ,  $N = 87$  in older birds). The mean of the two sides was used as growth rate in the  
244 analyses, except for the case of damaged or missing feathers on one side. Overall 410 of the  
245 425 autumn birds could be measured for ptilochronology, 21 of these on one side of the tail  
246 only. The two sides did not differ systematically (paired  $t_{388} = 1.208$ ,  $P = 0.228$ ) so using one  
247 side does not cause bias.

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#### STATISTICAL ANALYSIS

250 We calculated two measures from the spectral data of each plumage area, using the ‘tit-  
251 visible’ range (320 to 700 nm) of the spectra (Hart *et al.*, 2000). The first measure was  
252 average reflectance (brightness,  $R_{320-700}$ ). The second was a measure of the dominant direction  
253 of changes in spectral shape in the respective plumage area: UV chroma ( $R_{320-400}/R_{320-700}$ ) for  
254 the crown and the breast stripe, and yellow chroma ( $R_{700}-R_{450}/R_{700}$ ) for the yellow breast.  
255 These spectral shape measures have previously been validated using principal components  
256 analyses (PCA) of raw spectral bands (Hegyi *et al.*, 2007b). Here we calculated derived

257 colour descriptors rather than using a PCA of raw spectral bands. A recent study showed that  
258 derived colour variables showed higher correspondence with other colour quantification  
259 methods (tristimulus variables, two avian visual models) than spectral band PCs (Evans *et al.*,  
260 2010). We refrained from calculating estimates of the avian visual stimulus (Vorobyev *et al.*,  
261 1998) because great tits use an extreme variety of light environments (from completely open  
262 sunlight to forest shade) and the light environment profoundly affects visual stimulus values,  
263 thereby making any one of them a misleading estimate of colour in our present case.  
264 Correlations between single light environment visual stimulus estimates and raw brightness  
265 and chroma of the given plumage area are extremely high (see Supplementary Methods Part 2  
266 for details; see also Delhey & Peters, 2008; Evans *et al.*, 2010).

267         The six colour variables (brightness and chroma for each plumage area) were first  
268 transformed to improve normality of the model residuals (breast stripe brightness log  
269 transformed, breast yellow chroma square transformed). Repeated measurements of a given  
270 colour variable were then averaged within individuals and the averaged values were compared  
271 between sexes, binary ages (yearling or older), years (2006 to 2012, see above) and seasons  
272 (autumn vs. spring) in separate general linear models for each colour variable, using all  
273 possible interactions (except the three-way interactions of age; General Linear Model module  
274 of Statistica 5.5). We used stepwise backward simplification with reintroduction of the  
275 removed terms to the final model one by one (Hegyí & Gáramszegi, 2011). The results are  
276 shown in Table 1. We then extracted standardized residuals (mean of zero, SD of 1) from the  
277 final models and used these residuals as area-level colour variables in the following analyses.  
278 Using residuals was necessary because different colour traits showed different among-group  
279 patterns (Table 1). Therefore, the pooled correlation matrix of raw, uncorrected colour traits  
280 does not represent the consistent within-group correlations we detected, and using this matrix  
281 to fit overall colour axes would accordingly produce nonsensical results. Residuals were also

282 necessary in the models of assortative mating and repeatability to exclude confounding factors  
283 such as year or age. Finally, we used residuals in the analysis of body condition to facilitate  
284 comparability with other parts of the paper.

285         We did not correct our spectral data for date within season. When doing a correction  
286 for capture date in the autumn data using second-order polynomials (Delhey *et al.*, 2010), we  
287 obtained very similar results to those presented below. We report the uncorrected data here  
288 because a similar date-correction in spring would remove a component of individual quality  
289 (breeding date) and would therefore confound our results with respect to the information  
290 content of coloration.

291         In the following steps, we compared the correlation matrices of the six standardized  
292 (i.e. standard residual) colour traits between sexes, ages, seasons and then years ( $N = 425$  in  
293 autumn and  $N = 433$  in spring, see details above under Field methods). Matrix comparisons  
294 were done using the common principal component (CPC) method developed by Flury (1988)  
295 as implemented in the program CPC (Phillips & Arnold, 1999). This method evaluates a  
296 hierarchy of models that represent different degrees of matrix similarity, looking for the  
297 number of dominant PC axes (first, first two, first three etc.) that are shared between two data  
298 sets. Very small degrees of similarity are termed an “unrelated structure”. Increasing  
299 similarity levels correspond to different numbers of common PCs ( $CPC_1$  to  $CPC_{k-2}$  where  $k$  is  
300 the number of input variables). The highest similarity levels are when all PCs are similar in  
301 direction (full CPC), direction and relative importance (matrix proportionality) or direction  
302 and absolute importance (matrix equality). The program calculates the Akaike Information  
303 Criterion (AIC) as a measure of the relative suitability of these different similarity scenarios  
304 (models) given the data. To choose the model best supported by our data, we looked for the  
305 simplest model within a difference of  $AIC = 2$  from the model with the lowest AIC. Note that  
306 this is not necessarily the model with the lowest AIC. This approach was used consistently

307 when comparing the colour trait correlation matrices of sexes, ages, autumn and spring, or the  
308 seven different years. Note that the PCA approach may miss information lying outside the  
309 orthogonal axis structure (i.e. among-trait contrasts in our case) but variation outside the axis  
310 structure is by definition responsible for a small percent of trait covariation. The PCA  
311 approach may also fail if receivers use multiple colour traits hierarchically, but we have no  
312 information to build trait hierarchies into our models.

313         The focus of the present work was on quantifying the correlation structure of colour  
314 among plumage areas of the same individuals. Different plumage areas of the same  
315 individual, belonging to the same sample, are in practice measured consecutively. Inadvertent  
316 fluctuations in measurement quality due to various factors (changing attention levels of  
317 measurers, light source drift etc.) necessarily cause autocorrelation among neighbouring  
318 measurements, and this autocorrelation may inflate correlations among plumage areas or  
319 create artefacts in the correlation matrix. To control for this, we re-measured the samples of  
320 100 randomly chosen breeding individuals (50 males and 50 females) from six different years  
321 so that plumage areas were measured separately and in different, completely randomized  
322 orders. In this sample, the effect of temporal autocorrelation on the correlations of spectral  
323 variables was completely eliminated. We then used CPC to compare the correlation structure  
324 in this randomized sample to that in the original measurement order in the same 100 samples.

325         Based on the results of the matrix comparisons, we then calculated the PCA of  
326 individual colour trait residuals using Varimax rotation in the Factor Analysis module of  
327 Statistica 5.5 (StatSoft, Inc.). To check the effect of mathematical interdependence, we also  
328 ran separate PCAs for brightness and chroma traits. The resulting PC scores (when handling  
329 all plumage traits together) were used in three further analyses. First, the within-individual  
330 repeatability of univariate colour trait residuals and the PCs was calculated. We had four  
331 different types of repeated measurements: from spring to the next spring ( $N = 41$ ; two

332 measurements separated by moult but involving similar degrees of plumage abrasion); from  
333 autumn to the next spring ( $N = 19$ ; two measurements separated by a period of plumage  
334 abrasion but no moult), between autumn and spring with a moult in between ( $N = 19$ ; both  
335 moult and abrasion), and between two autumns ( $N = 11$ ; moult but no abrasion). We have  
336 unfortunately too few within-season recaptures and therefore no information on within-season  
337 repeatability. Within-individual data were analyzed using general linear models with second  
338 measurement as the dependent variable, first measurement as a covariate, and repeat type as a  
339 factor, also including their interaction. Sexes were pooled due to the high similarity of their  
340 trait correlation matrices (see Results).

341         Second, relationships with body condition during moult (mean growth bar width) were  
342 estimated for univariate residual and composite colour traits in the autumn data. This analysis  
343 avoided repeated measures from the same individual ( $N = 268$  for males and  $N = 142$  for  
344 females). We calculated standard residual condition from a model with binary age, year and  
345 sex as factors (binary age  $F_{1,401} = 4.73$ ,  $P = 0.030$ ; year  $F_{6,401} = 10.48$ ,  $P < 0.001$ ; sex  $F_{1,401} =$   
346  $29.26$ ,  $P < 0.001$ ; year x sex interaction was non-significant and removed) and tested the  
347 residuals against the residual colour variables using Pearson correlations (age and sex  
348 differences in condition-dependence were always non-significant when tested in general  
349 linear models; age x condition  $F_{1,406} < 2.92$ ,  $P > 0.089$ ; sex x condition  $F_{1,406} < 2.43$ ,  $P >$   
350  $0.120$ ). Year comparisons were not done for condition-dependence because the statistical  
351 power to detect such patterns was low.

352         Finally, univariate colour trait residuals and PCs of members of breeding pairs with  
353 complete spectral data (only spring data,  $N = 175$ ) were used to estimate assortative mating as  
354 one possible measure of sexual selection (Pearson correlations, Basic Statistics module of  
355 Statistica 5.5). We also examined the among-year consistency of assortative mating by formal  
356 meta-analysis with a 'random effects model' that assumes heterogeneity in effect size among

357 samples (Lipsey & Wilson, 2001). Weighted mean effect sizes and their confidence intervals  
358 were calculated using Comprehensive Meta-Analysis Version 2 ([http://www.meta-](http://www.meta-analysis.com)  
359 [analysis.com](http://www.meta-analysis.com)).

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## 362 RESULTS

### 363 STABILITY OF COLOUR INTEGRATION

364 In the first step, we compared the correlation matrices of univariate colour trait residuals (i.e.  
365 group-standardized colour traits) between the sexes and age groups using CPC. This program  
366 uses an information theoretic approach to compare alternative models representing varying  
367 numbers of common PC axes (with the remaining, lower order axes being different). The CPC  
368 comparison of sexes (Table 2) indicated matrix proportionality, which implies that all PC axes  
369 have similar directions and similar relative importance. Concerning age, the first four PC axes  
370 of the colour correlation structure were shared between yearling and older birds (Table 2). We  
371 then assessed the effect of plumage abrasion on the integration of coloration by comparing the  
372 correlation matrices of autumn (little abrasion) and spring (substantial abrasion). The strict  
373 sense best model of this CPC comparison indicated that three PCs were shared between the  
374 seasons, although the model with one shared PC performed only slightly less well in  
375 suitability than the best model (Table 2). This ambiguous result occurred because the first  
376 three PCs of the two colour traits were the same in autumn versus spring but PC2 and PC3  
377 “changed places”, although differences in their explained variances were small (results not  
378 shown). Our final CPC comparisons focused on among-year differences in trait integration.  
379 The ratio of autumn data to spring data was drastically different among years, with the  
380 proportion of autumn data among all data of a given year ranging from 19% to 78% (see  
381 Methods). Therefore, an among-year comparison of data while pooling autumn and spring



382 would confuse year differences with between-season differences. Consequently, we assessed  
383 among-year variation in the correlation matrices separately for autumn and spring (Table 2).  
384 The results indicated that correlation patterns were consistent among years, with all PCs  
385 shared in both autumn and spring. Among-year means and confidence intervals of  
386 correlations for univariate trait pairs (from a random effect meta-analysis) can be seen in Fig.  
387 2 for the two seasons separately.

388 Finally, to examine possible measurement order effects, we compared in the 100  
389 samples with randomized measurement order the correlation structure of (residual) colour  
390 traits to that obtained in the same 100 samples with the original measurement protocol. This  
391 revealed a situation very close to matrix equality, i.e. nearly perfect matching (matrix equality  
392 AIC = 25.977; matrix proportionality AIC = 27.970; full CPC AIC = 28.112; all other models  
393 AIC > 30). Furthermore, using the original protocol, the sample of these 100 data yielded a  
394 similar correlation matrix to that in the whole sample ( $N = 858$  after eliminating within-  
395 individual repeats), again being close to matrix equality (matrix equality AIC = 10.174;  
396 matrix proportionality AIC = 12.127; all other models AIC > 17). The latter result shows that  
397 the small sample was representative of the whole dataset concerning its correlation structure.  
398 We can therefore conclude that the effect of temporal autocorrelation on our correlation  
399 matrices was negligible and our results on matrix stability are not measurement artifacts.

400

401

#### MAIN COLOUR AXES

402 The component loadings of the main PC axes for the pooled dataset (again using residual  
403 colour traits) are summarized in Table 3. The first PC linked two plumage areas, correlating  
404 positively with the UV chroma of both melanised regions (crown and breast stripe). The  
405 second PC described yellow breast coloration, correlating positively with yellow chroma and  
406 negatively with brightness. Finally, the third PC was positively related to the brightness of

407 both melanised plumage areas. The proportions of variance explained by the three PCs were  
408 very similar and together accounted for 61% of total variance. This PCA included the within-  
409 individual repeats for the sake of later repeatability testing. Using one data point per  
410 individual yielded almost quantitatively identical results (not shown here).

411 A separate PCA of brightness and chroma traits to avoid their mathematical  
412 interdependence also yielded the same plumage area associations. For both brightness and  
413 chroma, the crown and the breast stripe were joined and the breast was treated separately  
414 (Supplementary Table 2). This indicates that although PC2 in the pooled PCA (yellow  
415 brightness and yellow chroma) could possibly be affected by mathematical dependence and  
416 should be viewed as such, other PC axes are not affected by this issue. As PC2 can also be  
417 explained by a biological mechanism (lutein absorbance increases chroma and reduces  
418 brightness), we use the output of the pooled PCA in the following.

419

#### 420 REPEATABILITY AND CONDITION DURING MOULT

421 In the analysis of within-individual repeatability, there was no significant difference among  
422 repeat types in any residual colour trait or PC (four different combinations of abrasion and  
423 moult; repeat type x previous value  $F_{3,82} < 1.943$ ,  $P > 0.129$ ). Pearson correlations indicated  
424 that repeatability was relatively strong in breast yellow chroma and crown UV chroma, but  
425 generally low for the remaining individual traits (Table 4). PC1 had a marginally non-  
426 significant repeatability, while the other two PCs were very weakly repeatable.

427 The only colour traits (residuals or PCs) related to residual body condition during  
428 moult in the autumn data (Table 4) were breast yellow chroma and the corresponding PC  
429 (PC2). The UV chroma of the two melanized plumage areas showed little trace of condition-  
430 dependence. Colour PC1, an indicator of the parallel changes of these two UV chroma traits,  
431 was similarly independent of condition.

432

433

## MATING PATTERNS

434 Assortative mating for univariate colour trait residuals and colour PCs (spring data only) was

435 generally weak (Table 4). Crown UV chroma and overall UV chroma (PC1) showed the

436 strongest relationships. We also examined within-trait, among-year variation in assortative

437 mating estimates (Fig. 3). The weighted mean estimate significantly differed from zero,

438 indicating consistent positive assortative mating, for crown UV chroma but not for any other

439 individual or composite trait. Overall UV chroma (PC1) gave a combined assortative mating

440 estimate in between those of its two constituent traits. This was not significantly different

441 from zero.

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## DISCUSSION

445 Here we examined the stability of phenotypic integration in a system of multiple plumage

446 colour traits. For each of the three plumage areas we considered, we used overall brightness

447 and the single dominant direction of spectral shape variation. This ensured a representative

448 analysis of colour with a reasonable complexity. Of the three plumage areas considered here,

449 our PCAs revealed correlations in brightness and UV chroma between the melanised crown

450 and breast stripe, while the carotenoid containing breast plumage varied independently of the

451 other two areas. Among our PC axes, PC1 and PC3 likely reflect the structural regularity and

452 melanin content of the two melanised areas, while PC2 may mirror the carotenoid content of

453 breast feathers (Bleiweiss, 2004). Notably, a previous study of the same population detected

454 an axis of parallel variation between breast yellow chroma and crown UV chroma (Hegyí *et*

455 *al.*, 2008). Differences from the present findings may principally stem from the lack of breast

456 stripe reflectance from the previous study, and the different statistical method (spectral band

457 PCA). As the correlation structure we report here was statistically similar across seven years  
458 (see below), we consider our results robust and representative.

459         The great tit is qualitatively sexually monochromatic, with the basic outline of the  
460 ornament complex being the same in the two sexes, but the expression of especially melanin-  
461 based coloration clearly differing between males and females (Norris, 1993; Hegyi *et al.*,  
462 2007b). In our data, all colour variables except yellow chroma (see Evans *et al.*, 2010 for a  
463 different result) were sexually dichromatic before the calculation of residuals (Fig. 1). Our  
464 present analysis nevertheless indicated that the among-trait correlation structure of colour was  
465 very similar between males and females. The principal axes of colour variation agreed in both  
466 direction and relative importance, suggesting that the genetic or permanent environmental  
467 background of colour integration is similar in the two sexes (Price, 1996; Potti & Canal,  
468 2011). Likewise, yearling and older great tits are superficially similar but there are significant  
469 changes in some colour variables with age (Table 1). However, the correlation structure of  
470 colour was still similar between the two age groups.

471         Seasonal changes in colour integration may be attributable to two processes: moult and  
472 abrasion. Plumage colour traits may diverge in their expression and lose their correlated  
473 variation due to different condition-dependence or environmental effects during moult  
474 (McGraw *et al.*, 2002; Hill, Doucet & Buchholz, 2005; Hill, Hood & Huggins, 2009; Vágási  
475 *et al.*, 2012) or differential abrasion or fading of colour types (Bonser, 1995; Surmacki,  
476 Siefferman & Yuan, 2011), plumage regions (Delhey *et al.*, 2010) and even different parts of  
477 the same region (Pap *et al.*, 2007). We found that the first three colour axes were shared  
478 between autumn and spring, suggesting between-season stability in colour trait interrelation.  
479 Sexual ornaments are often used in both mate attraction in the breeding season and  
480 competitive contexts outside the breeding season (McGraw, 2004; Reudink *et al.*, 2009). Our  
481 results in great tits indicate that paying attention to the same overall aspect of plumage

482 ornamentation throughout the year could be a viable strategy for receivers, either males or  
483 females, in this population.

484 Finally, non-directional among-year variation attributable to environmental conditions  
485 is widespread among sexual ornaments (Møller, 1991; Jensen *et al.*, 2006; Evans & Sheldon  
486 2012; Molnár *et al.*, 2012), but among-year variation has rarely been studied for multiple  
487 ornaments simultaneously (Chaine & Lyon, 2008a). Different ornamental traits are often  
488 affected by different year-specific environmental factors (Hegyi *et al.*, 2007a), and this may in  
489 turn limit their utility as components of an integrated signal system. Despite drastic among-  
490 year variation in food availability and phenology in our study area (Török *et al.*, 2004; Hegyi,  
491 Nagy & Török, 2013), the correlation patterns of colour traits remained nearly identical across  
492 years. This stability existed despite the fact that the basic determinants of the different colour  
493 traits (effects of year, age, season and their interactions) were different. These results indicate  
494 robust integration between the brightness and the UV chroma traits of the two melanised,  
495 black plumage areas, while the carotenoid-containing breast plumage did not take part in this  
496 integration, perhaps due to its different developmental background. This partial colour  
497 integration in the plumage opens a possibility for great tits to use the parallel colour variation  
498 of the two melanised areas as a single sexual signal. Although this cannot be definitively  
499 assessed without experiments, we could nevertheless tentatively examine whether these  
500 potential composite signals (and particularly the UV chroma PC which is the dominant axis of  
501 colour trait covariation) could confer specific information on some aspects of individual  
502 quality, and whether they could specifically explain variation in assortative mating patterns  
503 when compared to the univariate colour traits of different plumage areas.

504 We first examined within-individual repeatability, which indicates whether a trait can  
505 signal stable aspects of individual quality (Tomkins *et al.*, 2004, Wilson & Nussey, 2010). We  
506 could not detect significant differences in repeatability between different combinations of

507 moult and abrasion, although the small sample sizes limited the power of this comparison.  
508 Overall repeatability was significant only for breast yellow chroma and crown UV chroma.  
509 Breast stripe UV chroma had a much smaller repeatability, likely due to looser feather  
510 structure and more frequent physical contact with hard surfaces like tree bark or hole  
511 entrance, leading to stronger abrasion and soiling than on the crown. For the composite of  
512 crown and stripe UV chroma (PC1), repeatability was very similar to the average of the two  
513 constituent traits. It therefore seems that considering the two areas together does not provide  
514 more reliable information to the receiver in this respect.

515         We also examined the relationship between body condition during moult and  
516 subsequent colour expression. Breast yellow chroma was the only trait for which this  
517 correlation was significant, likely due to a relationship between carotenoid availability and  
518 body condition during moult (Partali *et al.*, 1987). Note that despite its indicator value, yellow  
519 chroma was not subject to significant assortative mating in our population, in contrast to a  
520 previous study in Spain (Quesada & Senar, 2009). Melanin-based traits, on the other hand, do  
521 not depend so directly on nutritional limitations (but see Talloen, Van Dyck & Lens, 2004;  
522 Poston *et al.*, 2005; Bize *et al.*, 2006; Punzalan *et al.*, 2008). Indeed, crown and breast  
523 brightness, and their composite (PC3) were largely unrelated to condition during moult.  
524 Finally, the condition-dependence of structural plumage colour in birds is debated due to the  
525 lack of a clear mechanism (Prum, 2006). Although laboratory experiments suggest nutritional  
526 effects on structural colour, these effects largely concerned total reflectance (Siefferman &  
527 Hill, 2005a, 2007; Jacot *et al.*, 2010) and only rarely relative UV reflectance (Siefferman &  
528 Hill, 2005b; for condition-dependence in non-avian structural colours, see Kemp & Rutowski,  
529 2007; Lim & Li, 2007). In a recent study in blue tits (*Cyanistes caeruleus*) it was further  
530 suggested that experimental condition-dependence of structural colour may arise via stress  
531 and not body condition (Peters *et al.*, 2011). In our great tits, in agreement with this, neither

532 the UV chroma of black areas, nor the composite colour axis they formed (PC1) correlated  
533 with natural body condition during moult to any notable extent. It is important to stress that  
534 the UV reflectance of the crown likely has a different developmental mechanism in blue and  
535 great tits (involving different feather microstructures), and this mechanism is unknown in  
536 detail in both species. Therefore, comparisons must be made with caution.

537         In sum, despite the robust and stable interrelation between the UV chroma of the  
538 crown and the breast stripe in our population, we found no evidence that the “overall” UV  
539 chroma of black plumage areas was especially informative when compared to the individual  
540 ornaments. Crown and breast UV chroma belong to the same proximate determination  
541 pathway as well as the same sensory modality, which may in theory facilitate both  
542 developmental and functional integration between them (Hebets & Papaj, 2005). However, an  
543 ideal composite ornament should provide emergent or more reliable information than its  
544 constituent traits. In our case, the UV chroma of the two black plumage traits is likely  
545 produced by a similar mechanism and may therefore provide similar information. Moreover,  
546 breast stripe UV chroma seemed to convey less reliable information as judged from its weaker  
547 repeatability. In addition, both UV chroma traits were similarly uninformative with respect to  
548 body condition during moult. The composite trait, overall UV chroma was similar in  
549 condition-independence to its component traits, and its repeatability was halfway between  
550 those of the individual traits. Therefore, the two aspects of information content we examined  
551 here did not highlight the composite colour traits as particularly informative over the  
552 univariate traits. Other measures of information content (e.g. developmental stability, stress  
553 tolerance) may have given different results.

554         The sexual selection perspective reinforced our conclusion on information content that  
555 composite traits are “not special”. In the case of mutual sexual selection on ornamentation,  
556 specific attention to a composite trait by both sexes may be expected to produce stronger

557 assortative mating patterns for this trait than for its constituents. In our population, breast  
558 stripe UV chroma showed weaker mating patterns than crown UV chroma, possibly due to its  
559 poorer quality indicator value. Strength of the mating pattern for the composite trait (PC1)  
560 was again halfway between those of the two constituent traits, suggesting that great tits pay no  
561 special attention to the combined expression of the two traits, or that this attention is not  
562 mutual (i.e. involves only one sex). Therefore, despite the stable phenotypic integration  
563 between the two UV chroma traits in both sexes, we could not detect functional integration  
564 between them in terms of assortative mating. On the other hand, they supported previous  
565 results in this population on the importance of crown UV chroma in mutual sexual selection  
566 (Hegyi *et al.*, 2007b).

567         It is important to stress here that the information content and function of sexual signals  
568 often differs among populations (Baird, Fox & McCoy, 1997; Dale *et al.*, 1999; Hegyi, Török  
569 & Tóth, 2002; Møller *et al.*, 2006). Accordingly, other populations of the great tit may show  
570 different patterns of colour trait integration and may show functional integration between  
571 some of their colour traits. Moreover, testing other measures of sexual selection (mate choice  
572 during the winter, territorial competition in early spring) may have given different results,  
573 potentially indicating selection on composite traits, or on yellow chroma, the condition-  
574 dependent aspect of plumage colour in this population. Breeding dates do not correlate with  
575 either the univariate or the composite colour traits of males or females in our population  
576 (results not shown), which reinforces the notion that apparent assortative mating on crown  
577 UV chroma was not due to territory quality patterns, but tells little on sexual selection in this  
578 particular species. Further studies are needed on this topic, especially given the painful lack of  
579 evidence for sexual selection on great tit plumage colour in general.

580         The possible existence of functional sexual trait complexes is a largely unexplored  
581 area in sexual selection research (Hebets & Papaj, 2005). At least three different evolutionary



582 patterns are conceivable with respect to multiple coexisting sexual traits. The first is different  
583 information content or function, as discussed above. The second is temporally and spatially  
584 fluctuating selection on different traits, as emphasized by some recent reviews (Bussière *et*  
585 *al.*, 2008; Cornwallis & Uller, 2009; Bro-Jørgensen, 2010). Finally, the third possibility is  
586 developmental and functional linkage among multiple ornamental traits (Badyaev, 2004).  
587 There is apparently great among-species variation in the interrelations and relative roles of  
588 multiple ornamental traits (Candolin 2003). In perhaps the most comprehensive empirical  
589 study conducted to date, the information content of multiple display traits in lark buntings  
590 (*Calamospiza melanocorys*) fluctuated among years of different environmental conditions,  
591 and sexual selection on these traits also fluctuated in both strength and direction (Chaine &  
592 Lyon, 2008a). Furthermore, in that signal system, different traits conveyed very different  
593 information about their bearers (Chaine & Lyon, 2008b). By contrast, in a population of  
594 collared flycatchers (*Ficedula albicollis*), mating patterns suggested a special function for the  
595 plumage-level parallel variation of colour in mate acquisition (Laczi *et al.*, 2011) and life-  
596 history correlates revealed multiple independent, composite colour axes with different  
597 information content in the same plumage (Laczi *et al.*, 2013). In our great tit population, we  
598 found correlated expression between some colour traits, but no functional integration, at least  
599 in terms of assortative mating. The differences from collared flycatchers could be due to the  
600 fewer proximate determination pathways of plumage colour (carotenoids are lacking), and the  
601 integration of both brightness and chroma traits at the whole plumage level in that species.  
602 Future studies on great tits should pay more attention to the hitherto largely unknown role of  
603 plumage reflectance in sexual selection (but see Quesada & Senar 2009), with special  
604 attention to breast yellow chroma, a highly informative trait (Senar *et al.*, 2003; Jacot *et al.*,  
605 2010; this study), and crown UV chroma, a trait with great sexual dichromatism and a  
606 possible role in mutual mate choice (Hegyi *et al.*, 2007b, this study).

607           Our results convey an important warning for empirical studies of multiple signals. At  
608 present, when researchers encounter significant correlations among colour traits, the general  
609 reaction (if any) is apparently to combine these into a composite colour measure (Merilä *et*  
610 *al.*, 1999; Siefferman & Hill, 2003, 2005b; but see Jacot *et al.*, 2010 for an exception). Our  
611 results suggest that correlated ornaments require more careful treatment. In particular, before  
612 considering the traits “together”, we must examine whether their composite has any special  
613 information to provide to the receiver, and also whether it plays a special role in sexual  
614 selection combined to the individual traits. In the absence of special information content or  
615 function, the optimal solution is probably to identify the real sexually selected trait “among  
616 the trees”, and use this in further analyses. This identification may need to be done separately  
617 for different contexts (Andersson *et al.*, 2002) and different populations (Dunn *et al.*, 2010)  
618 and should ideally be experimental. Any correlative test must pay attention to the statistical  
619 problems of multiple testing (Nakagawa & Cuthill, 2007) and collinearity (Graham, 2003).  
620 Sexual selection research will greatly benefit from the proper handling of relationships  
621 between multiple ornamental traits (Cornwallis & Uller, 2009).

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934 **Table 1.** Results from general linear models testing the effects of year, season, sex and age on raw plumage colour traits. We employed  
 935 backward stepwise model simplification with reintroduction, and adjusted  $r^2$  refers to the final model

	Breast brightness		Breast yellow chroma		Crown brightness		Crown UV chroma		Stripe brightness		Stripe UV chroma	
	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df
Year	1.90	6, 933	8.43***	6, 933	26.49***	6, 927	39.99***	6, 927	11.24***	6, 926	42.88***	6, 926
Season	86.13***	1, 933	6.71**	1, 933	41.77***	1, 927	606.14***	1, 927	0.30	1, 926	588.15***	1, 926
Sex	51.41***	1, 933	1.08	1, 932	244.29***	1, 927	1390.49***	1, 927	283.53***	1, 926	563.59***	1, 926
Age	0.146	1, 932	13.93***	1, 933	2.35	1, 926	0.13	1, 926	2.58	1, 925	7.79**	1, 926
Year x season	10.29***	6, 933	4.86***	6, 933	74.65***	6, 927	9.73***	6, 927	17.13***	6, 926	32.25***	6, 926
Year x sex	0.89	6, 927	1.20	6, 926	2.06	6, 921	2.21*	6, 927	0.49	6, 920	0.67	6, 920
Year x age	0.89	6, 926	1.14	6, 927	1.51	6, 920	1.24	6, 920	0.60	6, 919	0.54	6, 920
Season x sex	0.00	1, 932	1.93	1, 931	3.43	1, 926	0.29	1, 926	8.85**	1, 926	0.02	1, 925
Season x age	0.99	1, 931	2.66	1, 932	0.01	1, 925	0.61	1, 925	0.02	1, 924	0.54	1, 925
Sex x age	2.72	1, 931	0.87	1, 931	0.02	1, 925	1.70	1, 925	2.46	1, 924	3.62	1, 925
Year x season x sex	1.99	6, 927	1.35	6, 926	10.86***	6, 927	0.87	6, 921	2.65*	6, 926	2.33*	6, 926
Adjusted model $r^2$	0.188		0.088		0.579		0.764		0.365		0.673	

936  
 937 \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$



938 **Table 2** AIC values from the common principal component (CPC) analyses to assess the  
 939 similarity of the correlation matrices of our six individual colour traits (group-corrected  
 940 residuals) between sexes, ages (yearling versus older), seasons (autumn versus spring) and  
 941 years. The selected models are highlighted by boldface

Model	Sex	Age	Season	Year autumn	Year spring
Equality	18.45	41.44	76.81	161.34	138.59
Proportionality	<b>20.44</b>	43.05	78.45	170.84	149.77
Full CPC	23.94	28.65	40.20	<b>153.66</b>	<b>139.16</b>
4 CPC	25.04	<b>26.27</b>	38.36	160.14	142.55
3 CPC	28.36	29.54	<b>36.39</b>	163.15	160.08
2 CPC	31.68	34.62	40.86	188.85	177.54
1 CPC	35.98	37.74	38.44	213.76	209.64
Unrelated	42.00	42.00	42.00	252.00	252.00

942

943 **Table 3** Component loadings (Pearson  $r$ ) and explained variances of the main principal  
 944 component axes of variation among individual colour traits (group-corrected residuals).  
 945 Correlations larger than 0.5 are shown in bold

	PC1	PC2	PC3
Breast brightness	-0.177	<b>-0.765</b>	0.112
Breast yellow chroma	-0.210	<b>0.770</b>	-0.020
Crown brightness	0.032	-0.024	<b>0.792</b>
Crown UV chroma	<b>0.791</b>	-0.060	-0.013
Breast stripe brightness	-0.079	-0.096	<b>0.730</b>
Breast stripe UV chroma	<b>0.765</b>	0.033	-0.037
<i>Explained variance</i>	<i>0.216</i>	<i>0.199</i>	<i>0.196</i>
<i>Eigenvalue</i>	<i>1.294</i>	<i>1.193</i>	<i>1.175</i>

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947 **Table 4** Within-individual repeatability (all categories pooled), condition-dependence and assortative mating for individual colour traits (group-  
 948 corrected residuals) and colour PCs. None of the significances disappears after Bonferroni correction (3 x 3 non-independent variables)

	Repeatability					Condition					Assortative mating				
	$R_I$	SE	Pearson $R$	CI lower	CI upper	$N$	Pearson $R$	CI lower	CI upper	$N$	Pearson $R$	CI lower	CI upper	$N$	
Breast brightness	-0.025	0.106	-0.028	-0.234	0.180	90	-0.049	-0.145	0.048	410	0.015	-0.134	0.163	175	
Breast yellow chroma	0.280	0.098	0.277**	0.074	0.458	90	0.129*	0.032	0.223	410	0.107	-0.042	0.252	175	
Crown brightness	-0.037	0.106	-0.042	-0.247	0.167	90	0.022	-0.075	0.119	410	-0.060	-0.206	0.089	175	
Crown UV chroma	0.275	0.098	0.280**	0.077	0.460	90	0.068	-0.029	0.164	410	0.194**	0.047	0.333	175	
Breast stripe brightness	0.020	0.106	0.022	-0.186	0.228	90	-0.001	-0.098	0.096	410	0.122	-0.027	0.265	175	
Breast stripe UV chroma	0.131	0.104	0.137	-0.072	0.335	90	0.011	-0.086	0.107	410	0.122	-0.027	0.266	175	
PC1	0.185	0.102	0.182	-0.026	0.345	90	0.041	-0.056	0.138	410	0.188*	0.041	0.327	175	
PC2	0.101	0.105	0.100	-0.109	0.301	90	0.120*	0.024	0.214	410	0.049	-0.101	0.195	175	
PC3	-0.029	0.106	-0.029	-0.235	0.179	90	0.029	-0.068	0.126	410	0.046	-0.103	0.193	175	

949 CI, confidence interval;  $r_I$ , intraclass correlation coefficient; SE, standard error; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$

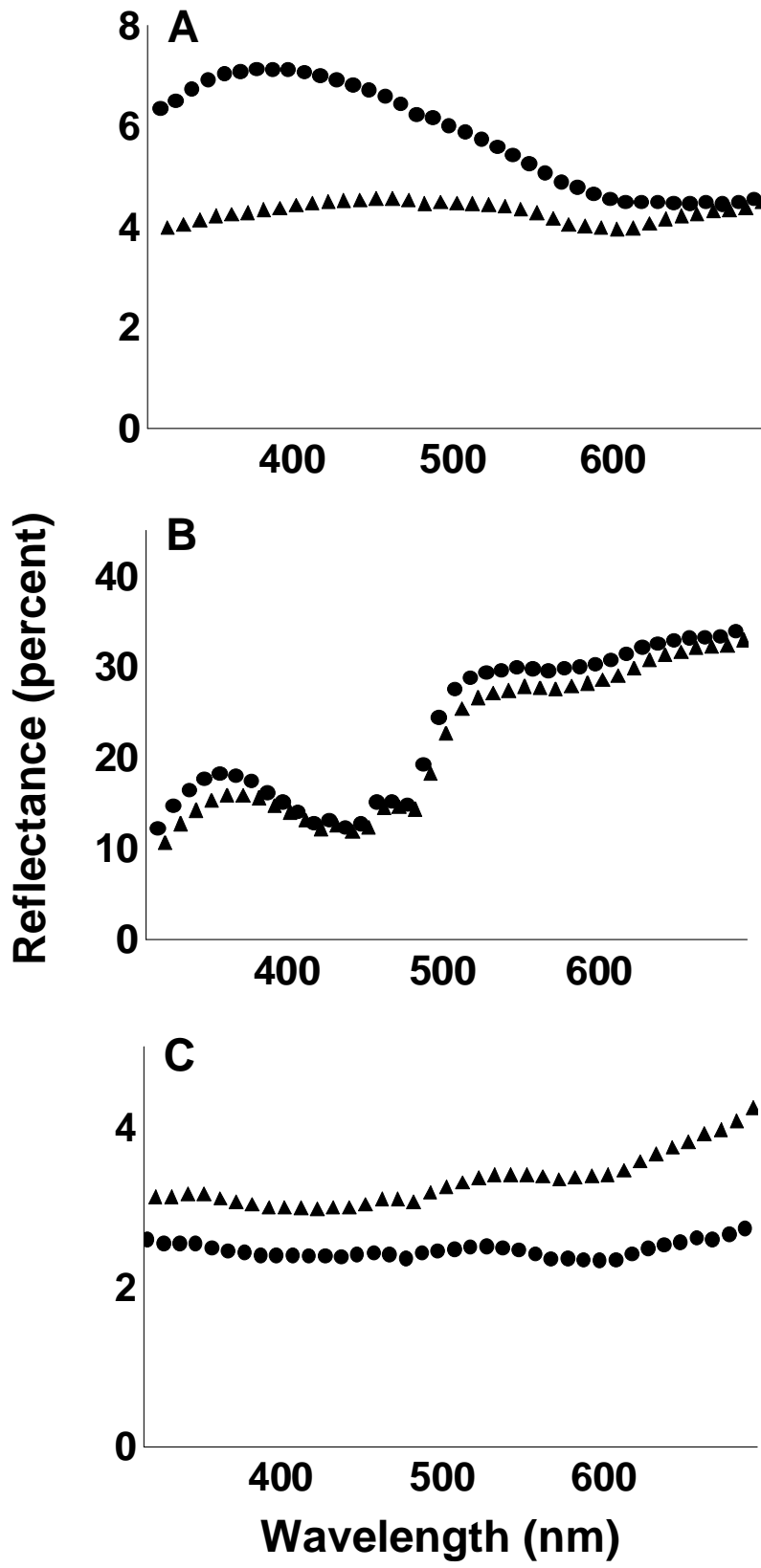
950 **Figure 1.** Sexual dichromatism in raw reflectance spectra of three plumage areas; A, crown;  
951 B, breast; C, breast stripe. Circles refer to males ( $N = 484$ ) while triangles to females ( $N =$   
952 374). Mean values are shown. Bars of 95% confidence intervals are smaller than the symbols  
953 so they cannot be shown in this figure

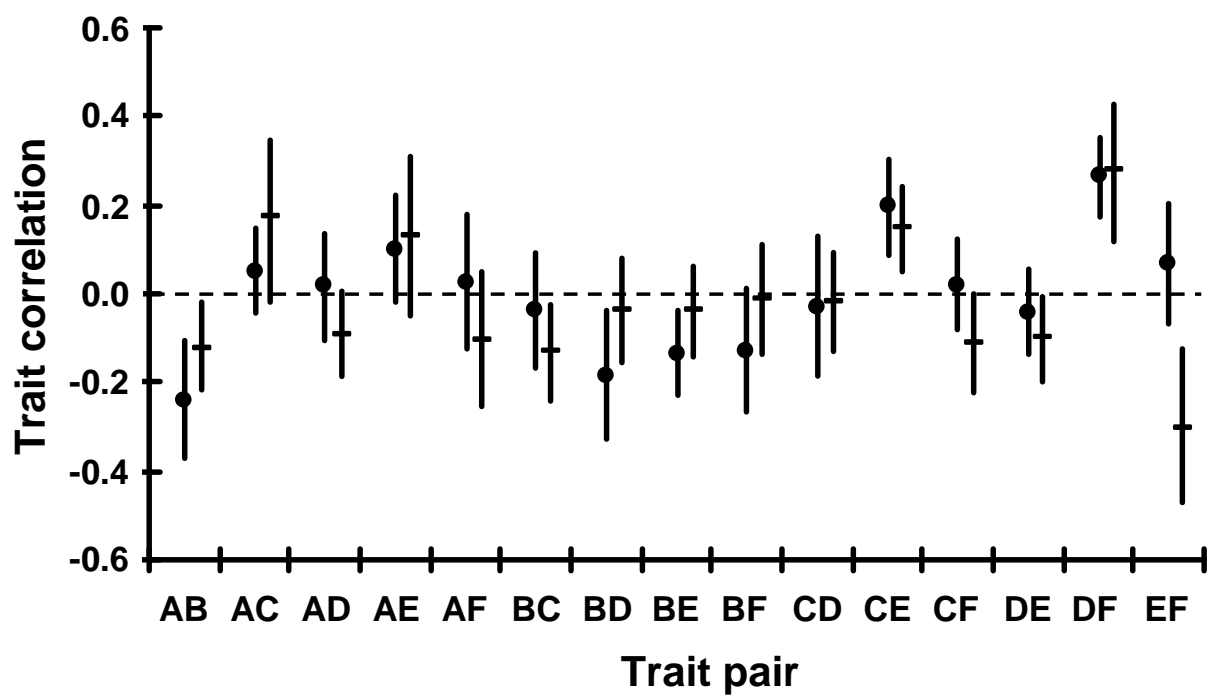
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955 **Figure 2.** Among-year weighted mean correlations (Pearson  $r \pm 95\%$  CI) of given individual  
956 colour trait pairs (group-corrected residuals) in autumn (filled circles) and spring (horizontal  
957 lines). 'AB' denotes correlation between trait A and trait B. Capital letters refer to breast  
958 brightness (A), breast yellow chroma (B), crown brightness (C), crown UV chroma (D),  
959 breast stripe brightness (E) and breast stripe UV chroma (F). The dashed line marks zero  
960 correlation

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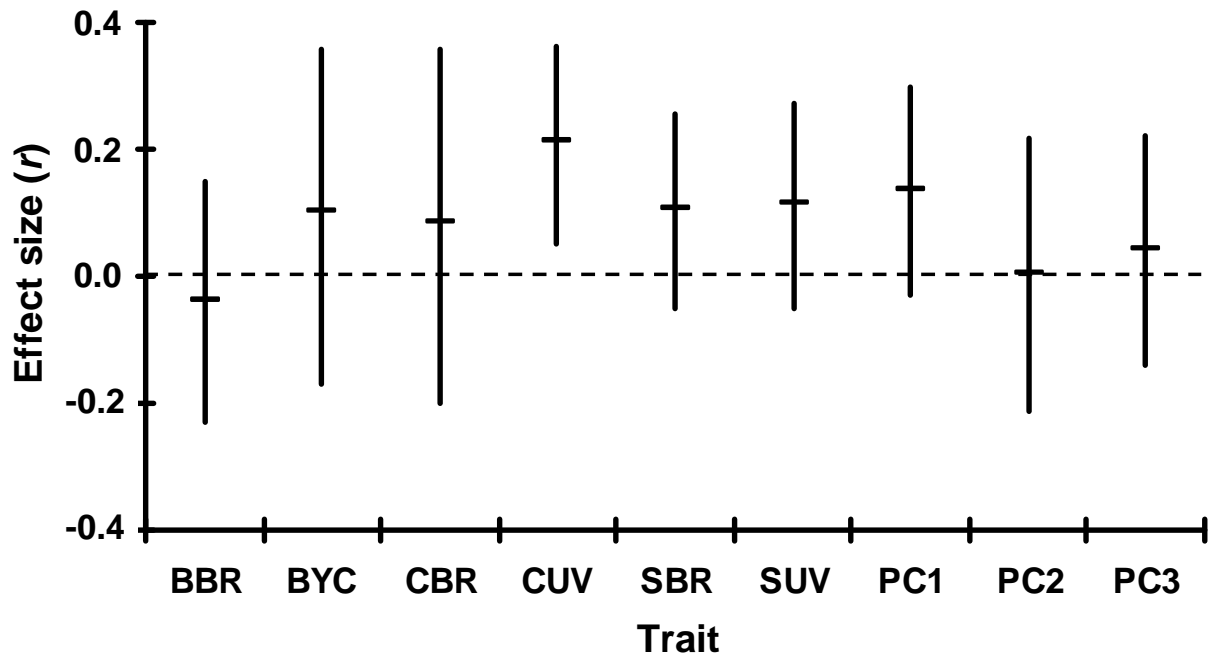
962 **Figure 3.** Among-year weighted means of assortative mating estimates (Pearson  $r \pm 95\%$  CI)  
963 for individual (residual) and composite plumage colour traits. Codes of individual colour traits  
964 consist of area (B, breast; C, crown; S, breast stripe) and colour variable (BR, brightness; YC,  
965 yellow chroma; UV, UV chroma). The dashed line marks zero correlation





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