

1 **Title:** The relationship between plumage colouration, problem-solving and learning
2 performance in great tits *Parus major*.

3 Cauchard Laure^{1*}, Stéphanie M. Doucet², Neeltje J. Boogert³, Bernard Angers¹ and
4 Blandine Doligez^{4,5}

5 1 Département de Sciences Biologiques, Université de Montréal, Pavillon Marie-Victorin,
6 bureau D-221, C.P. 6128, succ. Centre-ville, Montréal, Québec, H3C 3J7, Canada. Phone
7 number: 001 514 343 6111 # 1051. Email: laure.cauchard@umontreal.ca

8 2 Department of Biological Sciences, University of Windsor, Windsor, ON, Canada.

9 3 School of Psychology and Neuroscience, University of St Andrews, St Andrews, U.K.

10 4 CNRS UMR 5558, Department of Biometry and Evolutionary Biology, University Lyon
11 1, University of Lyon, Villeurbanne, France.

12 5 Animal Ecology, Department of Ecology and Genetics, Evolutionary Biology Centre,
13 Uppsala University, Uppsala, Sweden.

14 *Corresponding author

15 **Abstract:**

16 Recent studies suggest that individuals with better problem-solving and/or learning
17 performance have greater reproductive success, and that individuals may thus benefit from
18 choosing mates based on these performances. However, directly assessing these
19 performances in candidate mates could be difficult. Instead, the use of indirect cues related
20 to problem-solving and/or learning performance, such as condition-dependent phenotypic
21 traits, might be favored. We investigated whether problem-solving and learning
22 performance on a novel non-foraging task correlated with sexually selected plumage
23 colouration in a natural population of great tits *Parus major*. We found that males
24 successful in solving the task had darker blue-black crowns than non-solvers, and that
25 males solving the task more rapidly over multiple attempts (i.e. learners) exhibited blue-
26 black crowns with higher UV chroma and shorter-wavelength hues than non-learners. In
27 contrast, we found no link between behavioural performance on the task and the yellow
28 breast colouration in either sex. Our findings suggest that blue-black crown colouration
29 could serve as a signal of problem-solving and learning performance in wild great tit males.
30 Further research remains necessary to determine whether different sexually selected traits
31 are used to signal cognitive performance for mate choice, either directly (i.e. cognitive
32 performance influencing individual's health and ornamentation through diet for example)
33 or indirectly (i.e. due to a correlation with a third factor such as individual quality or
34 condition).

35 INTRODUCTION

36 Cognitive abilities allow animals to flexibly adjust their behaviour to new situations
37 (Shettleworth 2009). Such abilities include innovation, i.e. the propensity to invent a new
38 behaviour or to flexibly adjust established behaviours to solve new problems (Reader and
39 Laland 2003) and learning, i.e. the acquisition of information through experience that may
40 cause a change in behavior (Dukas 2013). Comparative studies have shown that these
41 abilities could be advantageous in various species, as reflected by a positive link with
42 invasion success, range expansion or even speciation (Sol et al. 2002; Sutter and Kawecki
43 2009; Cantalapiedra et al. 2014; Ducatez et al. 2014). Nevertheless, performance in
44 problem-solving and/or learning also varies within species (Cole et al. 2011; Aplin et al.
45 2013; Mery 2013) and such variation can have fitness consequences at the individual level
46 (Cole et al. 2012; Cauchard et al. 2013; Dukas 2013). Problem-solving and learning
47 performance have been associated with fitness benefits, such as higher mating success
48 (e.g., in satin bowerbirds *Ptilonorhynchus violaceus*: Keagy et al. 2011) and greater
49 reproductive success both in insects (e.g., in wasps *Biosteres arisanus*: Dukas and Duan
50 2000) and birds (e.g., in great tits *Parus major*: Cauchard et al. 2013). However, other
51 studies have reported fitness costs, such as decreased competitive ability (e.g., in fruit flies
52 *Drosophila melanogaster*: Mery and Kawecki 2003), increased energetic costs (e.g., in
53 honeybees *Apis mellifera*: Jaumann et al. 2013) and increased desertion rate (e.g., in great
54 tits: Cole et al. 2012).

55 Thus, depending on species-specific ecological conditions (Sol et al. 2011), it might
56 pay to choose a partner depending on its problem-solving and/or learning performance.
57 However, it may be challenging to directly assess these abilities in potential partners.

58 Instead, individuals may need to rely on indirect signals of cognitive abilities for mate
59 choice decisions. Which signals may be used remains poorly studied so far, with the
60 potential exception of song (Spencer et al. 2003; Boogert et al, 2008; Boogert et al. 2011).
61 Condition-dependent phenotypic traits could play a role in signalling individual problem-
62 solving or learning performance, and may thus be used in mate selection (reviewed in
63 Boogert et al. 2011), if individuals with high problem-solving and/or learning performance
64 succeed in maintaining high condition or vice versa. For example, colouration traits have
65 been shown to signal individual condition in many species and are important sexual signals
66 in many taxa (Kodric-Brown 1985; Hill 1990; Stuart-Fox 2004).

67 Feather or integument colouration in animals is produced by two main components,
68 which can act individually or together to produce colours: pigmentation and structural
69 colouration. The two most common pigment types in birds are carotenoid and melanin
70 pigments. Carotenoid pigments (responsible for yellow, orange and red colours) can only
71 be obtained from the diet and are limited in nature (Partali et al. 1987; Møller et al. 2000;
72 McGraw 2006a). Carotenoid-based colouration has been shown to be an honest signal of
73 foraging performance (Slagsvold and Lifjeld 1985, Senar et al. 2002, Senar et al. 2008; but
74 see Svensson and Wong 2011 for a review about the complexity of carotenoid-based
75 signals). In contrast, melanin pigments (responsible for black and brown colours) are
76 synthesized by individuals using basic amino acid precursors (McGraw 2006b).
77 Nevertheless, it has been shown that melanin-based colouration can reflect individual
78 variation in reproductive investment under certain environmental conditions (e.g. food
79 scarcity or predation pressure; Jacquin et al. 2012) and can be related to body condition,
80 parental care and reproductive success (reviewed in Roulin 2004; Hegyi et al. 2007).

81 Finally, structural colouration (responsible for ultraviolet, blue, and green colours) is
82 produced by differential reflection and refraction of nanostructural feather components
83 (Prum 2006). As with pigments, structural colours have been found to reflect health and
84 body condition in a number of species (e.g. Doucet 2002; Doucet and Montgomerie 2003;
85 Hegyi et al. 2007).

86 Both pigmentation and structural colouration can be affected by individuals' ability
87 to maintain high condition, for example through finding more or better-quality food
88 resources, and may therefore signal cognitive performance to conspecifics. Yet, the
89 potential role of colouration in signalling cognitive performance has only been investigated
90 once so far in birds (but see Karino et al. 2007, Shohet and Watt 2009, Kotrschal et al. 2015
91 for studies in guppies). In the siskin (*Carduelis spinus*), males with longer carotenoid-based
92 yellow wing stripes were faster to solve a novel foraging problem (Mateos-Gonzalez et al.
93 2011). In many bird species, individuals exhibit multiple plumage traits that may vary
94 independently from each other and signal different or redundant information depending on
95 the context (Freeman-Gallant et al. 2009; Bro-Jørgensen 2009). Whether and how multiple
96 colour traits may signal cognitive performance to conspecifics remains an open question.

97 In this study, we investigated whether individual variation in problem-solving and
98 learning performance on a novel non-foraging task correlates with variation in plumage
99 colour traits in a natural population of great tits. Using a food-motivated task to test
100 problem-solving performance in the wild can lead to differences in the level of response
101 between individuals if natural food is abundant in the environment and/or if birds vary in
102 their level of hunger. We thus used a string-pulling task motivated by accessing the young

103 during the peak of nestling food demand to test problem-solving performance (see
104 Cauchard et al. 2013). The great tit is a highly suitable model species to address this
105 question, because (i) it is known to show extensive individual variation in innovativeness
106 and problem-solving performance (Overington et al. 2009; Cole et al. 2011), (ii) problem-
107 solving performance and reproductive success correlate positively in our study population
108 (Cauchard et al. 2013) and (iii) great tits display several types of plumage colouration traits
109 (i.e. carotenoid, melanin and structural plumage) suggested to be under sexual selection. In
110 particular, assortative mating has been shown for the chroma of the yellow breast and the
111 UV reflectance of the blue-black crown (Hegyi et al. 2007). For both sexes, we measured
112 the carotenoid-based yellow breast colouration, which also exhibits UV reflectance. In
113 males, we also measured the blue-black crown colouration, which is a melanin patch with
114 a slight blue structurally-produced iridescence. If plumage colouration reflects problem-
115 solving and/or learning performance, we expect that birds able to solve the task and/or
116 learn to become more efficient at solving it should exhibit brighter or more chromatic
117 yellow and, for males, a darker blue-black colouration with greater UV reflectance.

118

119 **MATERIALS AND METHODS**

120 *Study site, population monitoring and morphological data*

121 We carried out the study in a breeding population of great tits on the island of Gotland,
122 Sweden (57°10' N, 18 ° 20' E) between April and June 2010 and 2011. Great tits readily
123 breed in nest boxes, thereby providing easy access to a large number of nests. We visited
124 nest boxes regularly from the beginning of the breeding season to record standard breeding

125 data. When chicks were 9 to 14 days old, both adults were captured with clap-traps or mist
126 nests, ringed if not ringed previously, aged (first-year vs. older) and sexed according to
127 plumage characteristics, weighed (to the nearest 0.1 g) and measured (tarsus length to the
128 nearest 0.1 mm). We collected 10 feathers from a standard position on the yellow breast
129 (at mid-height on the left flank) for both males and females and on the blue-black crown
130 for males only. We stored feathers in envelopes in the dark for later spectral measurements
131 in the laboratory. A previous study in great tits showed that laboratory measurements of
132 collected feathers are comparable to direct measurement in the field if 10 feathers or more
133 are used for the laboratory measurement (Quesada and Senar 2006).

134

135 *Problem-solving and learning performance*

136 To measure problem-solving and learning performance, we used a task for which the
137 solving motivation stems from parents' drive to feed their young during the nestling rearing
138 period (Cauchard et al. 2013). A door was placed in front of the entrance hole of the nest
139 box. The door was by default closed, preventing the birds from entering, but could be
140 opened by parents using their feet to pull a string placed below the door. Once opened, the
141 birds could slip their body under the door to enter. The door then closed automatically
142 behind the bird, but could be simply pushed open from inside the nest box by parents to
143 get out (Cauchard et al. 2013). Birds can thus go out and enter again several times during
144 the test. Removing natural obstacles (e.g. fallen leaves or branches) from the nest entrance
145 is very rare in this population (see Cauchard et al. 2013), thus problem-solving and learning
146 performance on the test were unlikely to be confounded by prior experience. The test was

147 conducted during the peak of nestling food demand (i.e. when chicks were 7 to 9 days old
148 and between 08:00 AM and 04:00 PM) and only if chicks were sufficiently satiated (e.g.
149 not strongly begging at the beginning of the test). The test lasted for 1 h only, to avoid
150 chick starvation if parents were not able to solve the task and enter to feed them. In 2010,
151 each pair was tested once. In 2011, we tried to increase our chances of measuring both
152 parents' participation in the test by presenting the task on two consecutive days, i.e. twice
153 in total. We randomly selected pairs to be tested and recorded the parents' behaviour during
154 the test using a camouflaged video recorder placed at a distance of approx. 6 m in front of
155 the nest box just before the test.

156 On video recordings, we first assessed the problem-solving performance of each
157 parent (N=152 individuals in total). Parents who succeeded in solving the task (i.e. in
158 opening the door and entering the box) were considered to be solvers, while those who
159 contacted the nest box but failed to enter were considered to be non-solvers (i.e. we defined
160 problem-solving status as a binary variable; see Cauchard et al. 2013). Second, among
161 solvers, when an individual came back to the task to try and enter again, we assessed its
162 learning performance based on the two subsequent entrances (i.e. second and third
163 entrances). To do this, we recorded the latency to enter the nest box as the time elapsed
164 between the first contact of the bird with the box and its entry, excluding the time spent
165 away from the nest box (i.e. solving latency; Cauchard et al. 2013). Individuals that
166 consistently solved the problem over the three attempts and became faster at solving it (i.e.
167 showed a decrease in solving latency over subsequent solving events, and thus a negative
168 latency vs. attempt number curve) were considered to be learners, while birds that failed to
169 enter again or did not become faster upon subsequent entries (i.e. showed an absence of

170 decrease in solving latency, and thus a flat or positive latency vs. attempt number curve)
171 were considered to be non-learners (i.e. we defined learning status as a binary variable).
172 Individuals that entered only once again after their first entrance were excluded from the
173 analysis because it was not possible to assess a learning curve with only two points
174 (N = 13). We used only the first three entrances to standardize our measure of learning
175 between individuals because the total number of entrances varied between individuals, as
176 they were free to participate or not. Using the reduction in number of trials (i.e. the number
177 of times a bird contacted the task before entering) instead of the reduction in solving time
178 for measuring learning performance did not change the results.

179 Neophobia, the fear of novelty, can have a confounding effect on behavioural
180 performances measured using a novel task. Thus, we measured neophobia for each parent
181 as the time elapsed between landing on the nest box and first contact with the task. We
182 included this measure in the statistical models to control for individuals' neophobia level
183 (see statistics).

184

185 *Spectral measurements of feathers*

186 To measure plumage reflectance, we taped together the 10 feathers from each body region
187 (i.e. breast and, for males, crown) onto matte black paper, overlapping the feathers to
188 approximate their normal position on the bird's body. We used an Ocean Optics USB4000
189 spectrometer paired with a PX-2 light source to collect spectral reflectance readings. Using
190 a bifurcated fibre optic probe, we collected five spectral readings per body region, lifting
191 the probe away from the feathers between each reading. The probe was tipped with a black

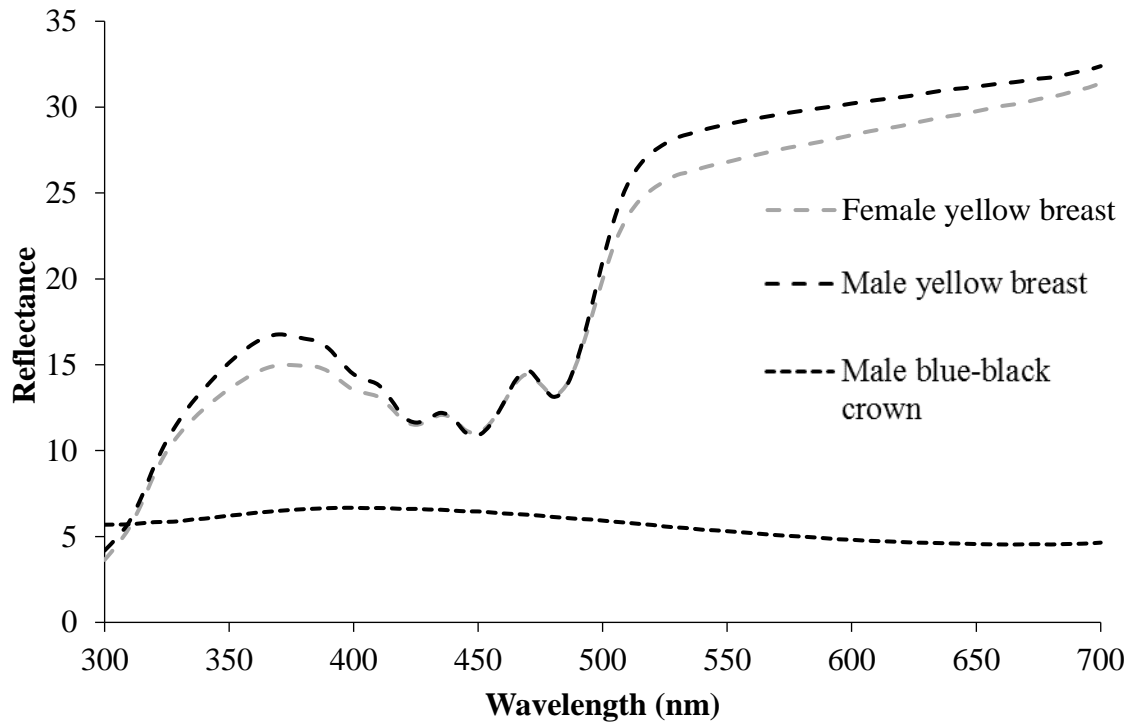
192 rubber stopper, which excluded external light and maintained the probe at a fixed 5 mm
193 distance from, and perpendicular to, the feathers. All measurements were made relative to
194 a white standard (WS-1), and were dark-corrected. We visually examined all spectral files
195 and omitted a few files from analyses (N = 9 out of a total of 152 individuals) because they
196 appeared abnormal probably due to measurement error (i.e. the probe was not fully
197 centered on feathers, or measurement was saved before the reflectance curve stabilized).

198 We calculated standard brightness, hue, and chroma colourimetric variables for each
199 of the two body regions using the software program CLR (Andersson et al. 2006;
200 Montgomerie 2006; 2008). As typically observed for yellow carotenoid-based colours
201 (Shawkey and Hill 2005; Shawkey et al. 2006), the yellow breast of great tits shows a
202 reflectance peak in the UV (300-400 nm) and a plateau at longer wavelengths (400-700
203 nm; Figure 1). The colouration of this body region results from both the feather
204 nanostructure, which produces an underlying white colour, and yellow carotenoid
205 pigments, which absorb wavelengths between 400 and 515 nm (Jacot et al. 2010). Yellow
206 carotenoids do not absorb wavelengths between 575 and 700 nm, and reflectance in this
207 region can therefore be considered as a measure of “brightness”, or background reflectance
208 of the structural colour (Jacot et al. 2010). We calculated the “UV chroma” of the yellow
209 breast as the ratio of reflectance between 300 and 400 nm relative to the background
210 reflectance between 575 and 700 nm (Jacot et al. 2010). This measurement focuses on the
211 structural colour that produces the UV peak. We calculated the “absolute carotenoid
212 chroma” of the yellow breast as the ratio of reflectance between 400 and 515 nm relative
213 to the background reflectance between 575 and 700 nm (Jacot et al. 2010). It is important
214 to note that this measurement *decreases* with carotenoid content as more carotenoid

215 absorption reduces the reflectance between 400 and 515 nm (Jacot et al. 2010). We
216 calculated the “hue” of the yellow breast as the wavelength at which the reflectance reached
217 50% of its maximum (Andersson et al. 2006). The blue-black crown of great tits has
218 generally low reflectance throughout with a small peak in UV and blue portions of the
219 reflectance spectrum (Figure 1). For the blue-black crown, we calculated “brightness” as
220 the mean reflectance across the entire spectrum from 300 to 700 nm. We calculated “UV
221 chroma” as the proportion of reflectance between 300 and 400 nm, and “blue chroma” as
222 the proportion of reflectance between 400 and 500 nm, relative to the total reflectance
223 across the spectrum from 300 nm to 700 nm. We calculated “hue” as the wavelength of
224 maximum reflectance. The repeatability of individual measurements (Lessels and Boag
225 1987) was relatively high ($R \geq 0.78 \pm 0.06$ and $P < 0.001$ in all cases; see Supplementary
226 material Appendix 1, Table S1), and we used the mean of the five measurements per body
227 region in all subsequent analyses (Figure 1) (Andersson et al. 2006; Montgomerie 2006;
228 2008).

229

230 **Figure 1:**



231

232

233

234 **Figure 1:** Spectral reflectance (mean) of the yellow breast feathers of both sexes and the

235 blue-black crown of males in our wild adult great tit population. Standard errors are not

236 shown to keep the figure readable (N = 106 females and N = 96 males).

237

238

239 *Statistical analyses*

240 To reduce the number of variables and analyse integrative measures of colouration, we ran
241 Principal Component Analyses with Varimax rotation on standardized feather
242 colourimetric variables and kept the first two components extracted with eigenvalues > 1,
243 which explained 72% and 80% of the variation in the yellow breast and blue-black crown
244 colour spectra respectively (Table 1). For both body regions, the first principal component
245 (PC1) summarizes the hue and chroma of the colour. For the yellow breast, high PC1 values
246 correspond to high absolute carotenoid chroma (low carotenoid-based absorption), high
247 UV chroma and shorter-wavelength hues, (i.e., individuals with less carotenoid-based
248 pigmentation and proportionally more UV reflectance; see Supplementary material
249 Appendix 1, Figure S1a). For the blue-black crown, high PC1 values correspond to longer-
250 wavelength hues, higher blue chroma, and lower UV chroma (i.e., males hues peaking
251 towards the blue part of the spectrum with proportionally more blue reflectance and
252 proportionally less UV reflectance; see Supplementary material Appendix 1, Figure S1b).
253 For both body regions, values of the second principal component (PC2) represent
254 brightness. For the yellow breast, high PC2 values correspond to duller colour (lower
255 reflectance) and somewhat lower absolute carotenoid chroma (higher carotenoid-based
256 absorption; see Supplementary material Appendix 1, Figure S1a) whereas for the blue-
257 black crown, PC2 values correspond to darker colour (lower reflectance; see
258 Supplementary material Appendix 1, Figure S1b). Yellow breast PC1 and blue-black
259 crown PC1 were negatively correlated ($r_p = -0.3$, $p = 0.015$, $N = 65$): individuals with less
260 carotenoid-based pigmentation and higher relative UV reflectance in the yellow breast also
261 had proportionally higher UV reflectance and proportionally less blue reflectance in the

262 blue-black crown. The brightness (PC2) of the two body regions was not correlated
 263 ($r_p = 0.1$, $p = 0.58$, $N = 65$).

264 **Table 1:**

	Rotated Factor loadings	
	PC1	PC2
Yellow Breast		
UV Chroma	0.896	0.136
Absolute carotenoid chroma	0.670	0.519
Hue	-0.708	0.267
Brightness	0.041	-0.883
<i>Eigenvalues</i>	<i>1.756</i>	<i>1.139</i>
<i>% of variance</i>	<i>43.90</i>	<i>28.47</i>
Black crown		
UV Chroma	-0.857	0.291
Blue Chroma	0.736	0.128
Hue	0.953	-0.048
Brightness	0.039	0.971
<i>Eigenvalues</i>	<i>2.185</i>	<i>1.046</i>
<i>% of variance</i>	<i>54.63</i>	<i>26.15</i>

265
 266 **Table 1:** Principal component analysis (PCA) of colour variables for yellow breast and
 267 blue-black crown colour spectra. The PCA was performed on colorimetric variables taken
 268 from individual for which both feathers and behavioural performance were collected.
 269 Yellow breast: $N = 142$; Blue-black crown: $N = 65$. See the methods section for a
 270 description of colour terms.

271 We then tested whether plumage principal components differed between solvers and
 272 non-solvers, on the one hand, and learners and non-learners, on the other hand. Because
 273 females may also signal their individual and maternal quality during mate choice, and both
 274 males and females might be choosy (Clutton-Brock 2007; Doutrelant et al. 2008; Remeš

275 and Matysioková 2013), we included both males and females in our analyses of yellow
276 breast colouration. For the analysis of problem-solving performance, we used linear mixed
277 models (LMM) with nest as a random effect to control for the non-independence of mates
278 when both parents were analysed (N = 58 nests out of a total of 93 nests). For the analysis
279 of learning performance, we used linear models (LM) because the learning performance of
280 both mates could be obtained only for one pair. For this one pair, we kept both mates in the
281 analysis but randomly excluding one of the mates did not qualitatively change the results.
282 For analyses of the blue-black crown colouration variables, we used LM because only
283 males were analysed. The full models included year, sex, age and problem-solving or
284 learning performance as fixed cofactors and their pairwise interactions. When analysing
285 both parents for breast colouration, year was nested within the random variable nest
286 because no pair was tested over the two years of the study. For models including learning
287 status, interactions with year were excluded because of a low sample size in 2010. We also
288 controlled for individual neophobia level in our analyses by including it as a fixed
289 covariate. Finally, the residual of mass on tarsus length was included in the initial models
290 to account for the potential effect of individual quality on feather colouration. However,
291 neither variable affected colourimetric variables in our population and these were therefore
292 excluded from the analyses.

293 We excluded from our analyses the individuals tested in 2011 that had already been
294 tested in 2010 to avoid pseudo-replication and potential habituation / learning effects over
295 the two years. We performed all analyses using SPSS 18.0 (Chicago, SPSS Inc. 2009). We
296 backward eliminated non-significant effects (starting from interactions) until the final
297 model contained only significant factors and/or interactions, and we checked the normality

298 and homoscedasticity of the residuals. Sample size varied between models because of
299 missing data. All tests were two-tailed.

300

301 **RESULTS**

302 Out of 152 individuals tested (N = 43 in 2010; N = 109 in 2011), 72 solved the task (N = 20
303 with 10 females and 10 males in 2010, N = 52 with 27 females and 25 males in 2011). The
304 problem-solving status (solver vs. non-solver) of an individual was not related to the status
305 of his/her mate ($\chi^2_1 = 1.13$, $p = 0.29$). Out of the 72 solvers, 28 returned to the nest box
306 following the first entrance and tried to enter again at least twice (N = 2 in 2010 and N = 26
307 in 2011), of which 18 succeeded (N = 1 male in 2010, N = 17 with 3 females and 14 males
308 in 2011). Learners and non-learners did not differ in their first solving latency (Independent
309 t-test: $t(25) = 0.2$, $p = 0.85$).

310 *Problem-solving and learning performance and yellow breast colouration*

311 The PC1 value of the yellow breast did not differ between solvers and non-solvers
312 ($F_{1,120.5} = 0.7$, $p = 0.41$) or between learners and non-learners ($F_{1,26} = 0.5$, $p = 0.49$). The
313 PC1 value of the yellow breast only varied depending on sex, with higher value for females
314 compared to males ($F_{1,73.2} = 20.9$, $p = <0.001$), and on the interaction between year and
315 age, with a tendency for lower values in yearlings compared to older individuals in 2010
316 becoming a tendency for higher values in yearlings compared to older individuals in 2011;
317 $F_{1,127.4} = 4.7$, $p = 0.031$).

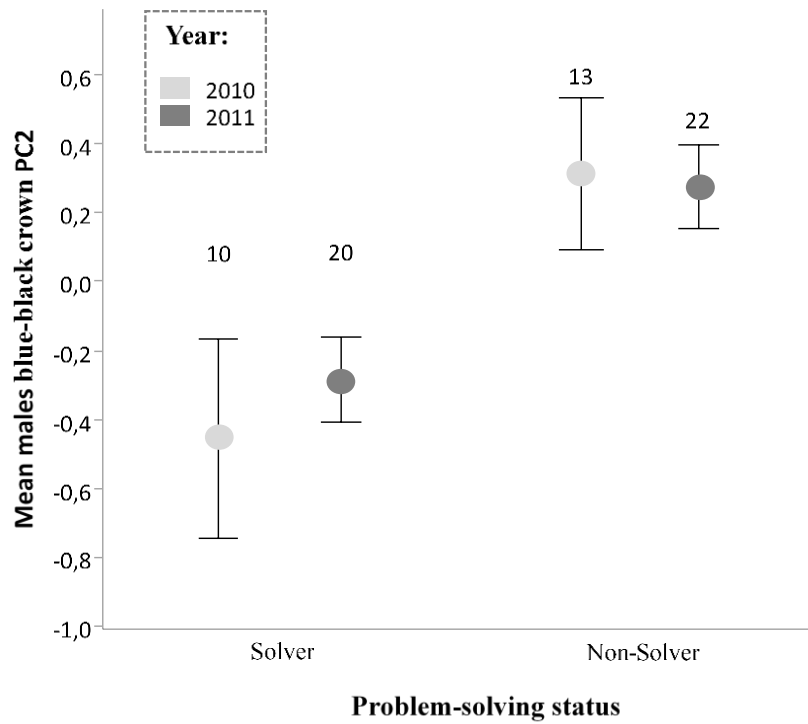
318 The PC2 value of yellow breast did not differ either between solvers and non-solvers
319 ($F_{1,130.0} = 0.4, p = 0.51$) or between learners and non-learners ($F_{1,25} = 0.3, p = 0.59$). It was
320 higher in males compared to females in 2011 only (interaction between year and sex: $F_{1,77.3}$
321 $= 13.4, p < 0.001$).

322 *Problem-solving and learning performance and blue-black crown colouration in males*

323 The PC1 value of the blue-black crown did not differ between solving and non-solving
324 males ($F_{1,63} = 0.2, p = 0.67$). However, learning males showed lower values of PC1 than
325 non-learning males ($F_{1,13} = 5.5, p = 0.035$; Figure 2): learners thus exhibited PC1 values
326 corresponding to shorter-wavelength hues, higher UV chroma, and lower blue chroma. In
327 this final model, the PC1 value of the blue-black crown also varied with year (i.e. lower
328 values of PC1 in 2010; $F_{1,13} = 11.8, p = 0.004$).

329

Figure 2 :



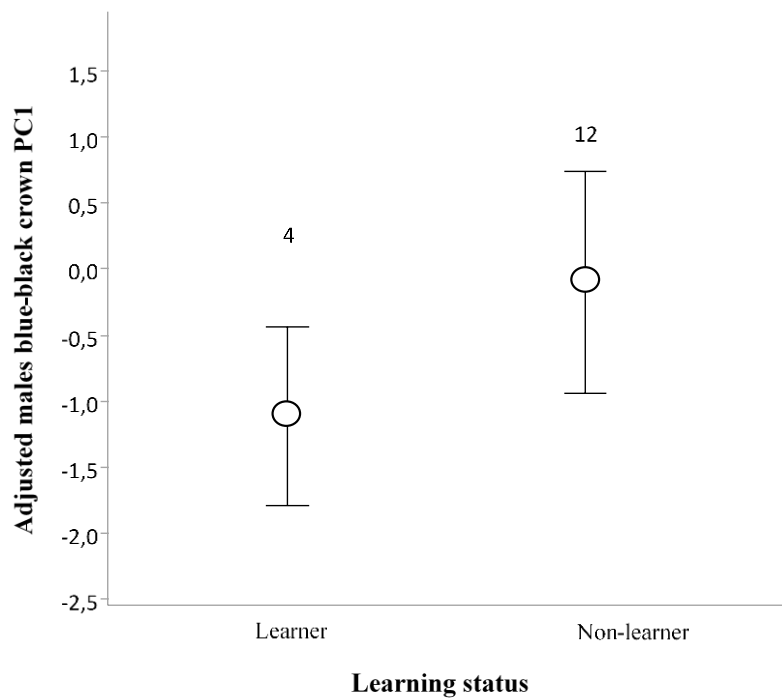
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331 **Figure 2:** Mean blue-black crown PC2 values \pm SE for solvers and non-solvers for 2010
332 and 2011. Numbers above are sample sizes.

333

334 The PC2 value of the blue-black crown was lower in solver males compared to non-solver
335 males ($F_{1,63} = 7.1, p = 0.010$; Figure 3): solvers had darker crowns than non-solvers.
336 However, the PC2 value of the crown did not differ between learning and non-learning
337 males ($F_{1,14} = 0.7, p = 0.41$).

Figure 3 :



338

339 **Figure 3:** Mean blue-black crown PC1 values \pm SE (adjusted for year) for learners and
340 non-learners. Numbers above are sample sizes.

341

342 **DISCUSSION**

343 In this study, we investigated whether different plumage colouration traits could possibly
344 signal individual problem-solving and/or learning performance in a natural population of
345 great tits. We found that in males, solvers had darker crowns than non-solvers and learners
346 had crowns with higher UV chroma, shorter-wavelength hues, and less blue chroma than
347 non-learners. However, we found no link between solving performance and yellow breast
348 colouration in either sex. Our findings suggest that crown colouration could signal male
349 problem-solving and learning performance in great tits.

350 The blue-black crown of males was darker in solvers compared to non-solvers. A
351 previous study in great tits found that birds in good condition (reflected by feather growth
352 rate) exhibited darker crowns than birds in worse condition (Hegyi et al. 2007). Moreover,
353 our results also showed that learners exhibited crowns with greater UV chroma and shorter-
354 wavelength hues than non-learners. Although the link between the chromatic attributes of
355 crown feathers and condition is not clear in great tits yet (Hegyi et al. 2007), studies in
356 other species have shown that the UV component of iridescent feather colour can be
357 positively associated with several measures of individual quality such as body condition,
358 intensity of infection from blood parasites, feather growth rate and body size (Doucet 2002;
359 Doucet and Montgomerie 2003). Taken together, these results suggest that the spectral
360 attributes of the crown may therefore signal overall individual ability to maintain high body
361 condition, e.g. via the ability to efficiently forage and find high quality food.

362 This association between crown colouration and cognitive ability could result from a
363 direct effect of cognition on condition during feather growth, for example through diet. In

364 great tits, plumage colours during the breeding season depend on the molting conditions in
365 the previous summer (Slagsvold and Lifjeld 1985; but see also Figuerola and Senar 2005).
366 Thus, individuals with higher problem-solving and/or learning performance could have
367 been better equipped to find food and recover faster after the reproduction season to
368 increase feather quality. These learning and problem-solving skills may allow individuals
369 to maintain a high body condition or health status by facilitating information use and
370 decision-making when exploiting regular food sources or breeding sites, finding novel ones
371 in times of scarcity as well as avoiding predators or parasites. Accordingly, we found in
372 the same population that solver pairs were more efficient in provisioning nestlings during
373 breeding (Cauchard et al. in prep), and in another population, performance in a food-based
374 task was also related to habitat use (Cole et al. 2012). The association between problem-
375 solving and learning performance and crown colouration traits could therefore be causal,
376 and these colouration traits could serve as honest signals of cognitive performance in great
377 tits.

378 Alternatively, the positive influence of a third variable on both cognitive abilities and
379 colouration could also explain the link between feather colouration and cognition, such as
380 the ability to cope with oxidative stress. Indeed, studies in humans and animal rodent
381 models have shown that a decrease in cognitive functions accompanies a decline in overall
382 health status, especially during the natural ageing process, associated with an increase in
383 oxidative stress (i.e. when oxidants that cause damage to biological macromolecules and
384 disturb cell and tissue functioning overwhelm antioxidant defences) (Finkel and Holbrook
385 2000; Keller et al. 2005). In both cases, our findings offer a possible mechanism whereby
386 crown colour could facilitate choice of mates based on cognitive performance. Because our

387 results are correlative, a causal link still needs to be demonstrated. This could be
388 challenging because of the difficulty to manipulate problem-solving or learning
389 performance, especially in natural populations. Captive populations may be useful to this
390 aim, using for example selection experiments or manipulating early growth conditions that
391 have been found to affect cognitive abilities later in life (Spencer et al. 2003) to investigate
392 subsequent colouration traits.

393 By contrast, the yellow breast colouration was not associated with problem solving
394 or learning performance in either males or females. Carotenoids are involved in a number
395 of physiological processes, among which immunity and oxidative balance (McGraw and
396 Ardia 2003, Sies 1997). The fact that they are limited in nature generates trade-offs
397 between investment in carotenoid-based colours and other functions (Simons et al. 2012).
398 We expected solvers and learners to be more efficient at finding high-quality, and in
399 particular carotenoid-rich, food (Dukas and Bernays 2000; Mateos-Gonzales et al. 2011),
400 resulting in a positive association between cognitive performance and yellow breast
401 colouration, as in the siskin (Mateos-Gonzales et al. 2011). However, we found no link
402 between the yellow breast colouration and problem-solving and learning performance in
403 our great tit study population. Yet, problem-solving performance has been found to
404 positively affect provisioning rates in the same population (Cauchard et al. in prep.),
405 suggesting a link between this performance and food provisioning. It is possible that better
406 problem solvers search for and utilize new food resources, i.e. increase their diet diversity,
407 allowing them to obtain a higher diversity of dietary antioxidants other than carotenoid
408 contents. Quantifying the diet of individuals that differ in problem-solving and/or learning

409 performance would be necessary to examine the link between cognitive performance and
410 its role in provisioning.

411 In great tits, mate choice according to crown brightness has not yet been investigated.
412 However, in closely related species, crown brightness is known to play an important role
413 in sexual selection. In chickadees (*Poecile atricapillus*), a darker crown has been shown to
414 offer higher contrast against the white cheeks than a lighter crown, and males with darker
415 crowns are dominant, in better condition, have higher reproductive success and are
416 favoured by females compared to males with lighter crowns (Mennill et al. 2003; Doucet
417 et al. 2005). Moreover, a previous study in great tits revealed assortative mating based on
418 the crown UV reflectance (Hegyi et al. 2007), suggesting mate choice based on this trait,
419 although other mechanisms may explain an assortative mating pattern, such as shared
420 habitat quality (Ferrer and Pentriani 2003). Females may thus use male melanin- and/or
421 UV-based crown colouration as a signal of individual problem-solving and/or learning
422 performance to select a mate, although this remains to be tested.

423

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435

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