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Mediating male-male interactions: the role of the UV-blue crest coloration in blue tits

1   **Title**

2   **Mediating male-male interactions: the role of the UV-blue crest**

3   **coloration in blue tits**

4

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18 **Abstract**

19 Badges of status, usually color patches, are hypothesised to serve as important

20 signals within natural populations by communicating individual's fighting ability or

21 aggressiveness before an interaction ever takes place. These signals, which may

22 evolve via sexual and/or social selection, mediate intra-specific competition by

23 influencing the outcome or escalation of contests between individuals. The last 10

24 years saw the rise of interest in the role of Ultraviolet (UV)-based coloration in

25 intra-sexual communication. However, the rare experimental studies that tested this

26 hypothesis found opposite results, which may originate from the different

27 methodological procedures used to assess badge of status theory. We present here

28 the results of an experiment testing whether male blue tits (*Cyanistes caeruleus*)

29 respond differently to unfamiliar conspecifics presenting contrasted UV crest

30 coloration. In an aviary, we simultaneously presented two caged blue tits with

31 enhanced (UV+) or reduced (UV-) crest coloration to a focal bird. We found that

32 focal males acted more aggressively towards the UV- males than UV+ males. In

33 addition, focal males fed more often close to males that were similar in brightness or

34 duller than themselves. We conclude that, in blue tits, UV-blue crest coloration

35 affects both social and aggressive responses towards unfamiliar individuals, and thus

36 it has some properties of a badge of status.

37

Introduction

In nature, animals frequently have to compete for food, mates, roosting or reproductive sites. Theoretical models showed that differences in fighting ability (i.e. resource holding potential), aggressiveness (i.e. willingness to escalate) or motivation can influence the outcome of these contests (Parker 1974; Maynard Smith and Harper 1988; Hurd 2006). The fighting ability and aggressiveness of opponents can be estimated through costly fights, but they could also be assessed relying on signals, providing a way of resolving contests without the cost of potential injuries (Maynard Smith and Harper 2003; Searcy and Nowicki 2005; Senar 2006). It has been suggested that some colorful ornaments, called badges of status, are used for such an assessment (Rohwer 1975). These color patches might evolve through both intra-sexual and social selection (Senar 2006). Signals evolving through intra-sexual selection are predicted to influence rivals' behaviors when competition is for mates or reproductive sites, whereas signals evolving through social selection are predicted to reflect dominance in a group when competing for food.

Several studies in many taxa including fish (e.g. Martin and Hengstebeck 1981), insects (e.g. Tibbetts and Dale 2004), lizards (e.g. Whiting et al. 2006) and birds (e.g. Senar 2006) confirmed that individuals presenting larger or more colorful badges are perceived differently from individuals presenting smaller or duller badges. These studies also found that individuals with higher badge expression won more conflicts and had higher fighting abilities or level of aggressiveness. Most studies which support the existence of such badges of status focused on melanin-

64 based coloration (Järvi and Bakken 1984; Møller 1987; Senar et al. 1993; see Jawor

65 and Breitwisch 2003; Tibbetts and Safran 2009 for review), although carotenoid-

66 based coloration has also recently been found to signal competitive abilities (Pryke

67 et al. 2001; Pryke and Andersson 2003; but see McGraw and Hill 2000). Melanin-

68 based colorations seem to be frequently used to signal aggressiveness and

69 dominance status in a group (Tibbetts and Safran 2009) due to the links between

70 melanin and testosterone (Buchanan et al. 2001; Gonzalez et al. 2001; Bokony et al.

71 2008; Safran et al. 2008) or corticosterone (McGraw 2008; Roulin et al. 2008).

72 Carotenoid-based colorations seem rather to be a sexual signal, used during

73 competition for mates and territories because they encode individuals' quality due to

74 the link between carotenoids, diet, and health (detoxification and implications for

75 the immune system: Lozano 1994; Olson and Owens 1998; von Schantz et al. 1999;

76 Faivre et al. 2003).

77   By contrast, the role of structural coloration (ultraviolet (UV), violet and

78 blue) in intra-sexual interactions has been less well investigated and is still

79 ambiguous. Some correlative studies have suggested a role of structural coloration in

80 male-male competition (Keyser and Hill 2000; Siefferman and Hill 2005b; Pryke

81 and Griffith 2006; Whiting et al. 2006), while two recent studies did not find any

82 relationship between UV coloration and dominance (Korsten et al. 2007b; Santos et

83 al. 2009). To date, only a few studies have experimentally manipulated structural

84 traits to assess their role in male-male interactions (Alonso-Alvarez et al. 2004;

85 Siebeck 2004; Korsten et al. 2007a; Poesel et al. 2007; Vedder et al. 2008). The

86 majority of these studies have been conducted on the UV-blue crest of blue tits

87 (*Cyanistes caeruleus*) and give opposing results, with some supporting a role in

88   male-male competition (Alonso-Alvarez et al. 2004; Poesel et al. 2007; Vedder et al.

89   2009) and others not (Korsten et al. 2007a; Vedder et al. 2008). So to date, no clear

90   general conclusion can be drawn on whether intra-sexual interactions drive the

91   evolution of structurally colored signals.

92   Our study aimed at determining whether structural coloration affects social

93   and/or aggressive interactions between male blue tits (*Cyanistes caeruleus*), taking

94   into account a major assumption of the badge of status hypothesis: namely badges of

95   status are used between unfamiliar individuals to signal at a distance fighting

96   abilities and aggressiveness (Maynard Smith and Harper 2003). Ignoring this

97   assumption could explain the disagreement in the past studies conducted in blue tits.

98   For example, during the non-breeding period, Vedder et al. (2008) did not find any

99   effect of crest reflectance on agonistic interactions between established and

100   potentially familiar individuals, whereas a second study (Vedder et al. 2009) found

101   that UV coloration influenced pairwise contest outcomes between unfamiliar males.

102   During winter, we conducted an experiment to assess whether focal birds

103   (the receivers of the signal) behave differently towards two unfamiliar birds

104   presenting different UV coloration: one UV enhanced (UV+) bird and one UV

105   reduced (UV-) bird. These UV modified birds were placed in small cages just above

106   a source of food. Two non-exclusive hypotheses were tested. First, we studied

107   whether UV treatment of the two introduced males influenced the aggressive

108   response of focal birds. We determined whether coloration of the focal male

109   explained variation in first attack behavior and the time spent on the cage of each

110   introduced male. Following badge of status theory, we predicted that less colorful

111   focal birds should attack the UV- male more, while more colorful focal birds are

112   expected to attack the UV+ bird, which represents a higher threat to the resource

113   holding. Second, we tested whether their choice of a feeding companion, measured

114   as the time spent feeding underneath each UV manipulated birds, was influenced by

115   the UV treatment of the intruders and by focal birds' coloration. If UV coloration is

116   a social signal used to assess the dominance rank in a group (e.g. for access to food),

117   we predicted that the choice of which UV modified conspecific to feed close to will

118   differ (Senar and Camerino 1998). Namely, focal males are expected to feed closer

119   to the intruder displaying a lower or similar coloration, representing a subordinate or

120   an individual of same social status, but avoid dominant individuals (presenting a

121   higher coloration), which might monopolize the food and represent a risk of injury

122   (Ekman 1989; Senar and Camerino 1998).

123

Material and methods

125   Capture, aging and sexing

126   For this experiment, we captured 54 blue tits during January and February 2007, in

127   six different localities around Montpellier, France. We first determined the sex and

128   age (yearling vs. adult) of the birds captured in the field, based on the color of their

129   wing coverts (Svensson 1992). After each trapping session and before the behavioral

130   trials in the aviary, birds were kept for one to two weeks in individual cages

131   (dimensions: 0.4 * 0.4 * 0.4 meter). Water and food (sunflower seeds, meal worms,

132   Orlux Uni paté® (Orlux, Deinze, Belgium) mixed with peanuts) were provided *ad*

133   *libitum*. Birds had no visual contact before behavioral trials (see below). After the

134   trials (n=18), we took a blood sample to confirm birds' sex by molecular sexing

135   (Griffiths et al. 1998). After migration of amplified fragments by electrophoresis,

136   two females were revealed among the 54 birds. The two trials involving these birds

137   were removed from the analyses, leaving a sample size of 48 birds and 16 trials. All

138   birds were released following the trials.

139

140   Experiment

141   Each trial consisted of monitoring the behavioral response of a focal male when we

142   introduced into its aviary two unfamiliar conspecifics with modified UV coloration

143   (see below for coloration methods): one UV reduced bird (named after UV-) and

144   one UV enhanced bird (named after UV+). The UV+ and UV- birds were males of

145   the same age class (yearlings or adults) from a different locality than the focal bird.

146   As distances between trapping localities were on average more than 10 km, we

147   assumed the probability that individuals had previously interacted and already knew

148   each other to be negligible. The two UV modified males were either from the same

149   area, or from different localities. To avoid pseudo-replication, each behavioral trial

150   involved a different focal bird and a different pair of intruders.

151   We used the same design as Senar and Camerino (1998; Fig. 1). The

152   behavioral trials took place in an outside aviary (dimensions 3 * 3 * 3 meters),

153   containing four perches (one in each corner), 2 open nest boxes and two central

154   feeding dishes (positioned 1.2 meter above the ground) with sunflower seeds, meal

155   worms, paté and water. Above each feeding dish stood a little cage (dimensions: 0.5

156   * 0.3 * 0.3 meter), within which a UV modified male was placed during the

157   experiment. Using cages rather than letting intruders free in the aviary has the

7

158   advantage of avoiding potential injuries. It was also a better design to test crest

159   coloration as a badge of status, since UV modified males could not reveal their

160   status by physical interactions with the focal male even if other signals could be

161   used, like postures or songs.

162   Each trial consisted of 5 steps. (i) The focal bird was introduced to the aviary

163   alone for two to four days to become familiar with this new environment, and to get

164   used to eating close to the two small empty cages (Senar and Camerino 1998). (ii)

165   At the end of this period of familiarization, we observed the focal bird for fifteen

166   minutes to check that it had no preference for one of the two cages or feeding dishes

167   which could represent a bias in the analyses. We did not find any significant

168   differences between the time spent on each cage and each feeding dish during these

169   fifteen minutes of observation (paired samples t-tests: t_{15} = -0.71, P = 0.488; t_{15} =

170   1.18, P = 0.259 respectively). (iii) Meal worms, a highly prized resource for blue tits

171   in captivity, were removed for one and a half hours to increase the motivation of the

172   focal bird to subsequently approach the cages (Braillet et al. 2002). During this

173   period, paté and sunflower seeds remained in the aviary allowing birds to continue

174   feeding. (iv) We then added meal worms and placed UV modified birds in the small

175   cages just above feeding dishes in the aviary. These birds were presented

176   simultaneously rather than sequentially, to facilitate their discrimination by the focal

177   bird (MacLaren and Rowland 2006). The choice of the cage ("left" or "right") for

178   each UV modified bird was determined randomly. (v) We then observed the

179   behavior of the focal bird for fifteen minutes following its first contact with either

180   one of the cages or one of the feeding dishes.

181   During the fifteen minutes of observation, we quantified four behavioral

182   responses in order to characterize the response of the focal bird: 1) the first cage

183   approached (the UV+ or UV- intruder). 2) the first feeding dish approached (under

184   the UV+ or UV- intruder's cage), 3) the total time spent on each cage and 4) the

185   total time spent on each feeding dish. As in previous studies (for instance Järvi and

186   Bakken 1984), we considered focal birds that landed on a cage to be displaying an

187   aggressive behavior. This estimation was reinforced by the fact that focal birds were

188   frequently observed hopping on the cages, trying to chase away the UV modified

189   birds. Finally, we considered that feeding below one of the two cages represents a

190   social choice of a feeding companion (Senar and Camerino 1998).

191   Color manipulation

192   Following Delhey et al. (2007) and Poesel et al. (2007), we changed the UV

193   reflectance of the intruder's crest with T-shirt markers *Edding 4500* (Edding,

194   Ahrensburg, Germany). A dark blue marker (color 003) and a pale blue marker

195   (color 10) were used to respectively reduce or increase the UV reflectance. Previous

196   studies that assessed the role of UV coloration in male-male interactions in blue tits

197   almost completely removed the UV reflectance (i.e. Alonso-Alvarez et al. 2004;

198   Korsten et al. 2007a; Vedder et al. 2008), creating unnatural colorations. Our

199   method has the major advantage of changing the UV spectra within the natural range

200   observed in male blue tits (Fig. 2). We assumed that this manipulation did not

201   produce a female phenotype since reflectance of UV- birds was significantly

202   different from the reflectance of females that we had (Wilcoxon-Mann-Whitney test:

203     $W = 32$, $P = 0.013$; see also Fig. 2). Moreover, no other male characteristics (wings,

204   tail, back mask, white crown, blue-black nape coloration, size) were manipulated.

205   Coloration measurements

206   At the end of each trial, we measured the crest coloration of all the birds with a

207   spectrophotometer Ocean Optics USB4000, having a Xenon light source (Ocean

208   Optics PS-2; covering the range 300-700 nm) and a 200 µm fiber-optic coaxial

209   probe, mounted with a black rubber cap to exclude ambient light (see methods of

210   Doutrelant et al. 2008). The probe was held at a 90° angle and at a fixed distance of

211   2 mm from the feather surface. Before each measurement, we reset the reflectance

212   with a white standard (WS1 Ocean Optics) and checked the reflectance of a dark

213   reference. Five replicates have been taken, changing position of the probe between

214   measurements. For each bird, four parameters of coloration were calculated from the

215   reflectance spectra using Avicol software v1 (Gomez 2006): brightness, hue, chroma

216   and UV chroma. Brightness corresponds to the average reflectance of feathers

217   (R_{mean}). Hue is the wavelength at the maximum reflectance, between 300 and 700

218   nm. Chroma, describing the spectral purity, is the ratio of the difference between the

219   maximum and the minimum reflectance and the mean reflectance: ($R_{max} - R_{min}$) /

220   R_{mean}. UV chroma corresponds to the proportion of the total reflectance located

221   between 300 and 400 nm: ($R_{300\ nm} - R_{400\ nm}$) / ($R_{300\ nm} - R_{700\ nm}$). For each color

222   parameter, we used the average of the five measurements taken.

223   Only brightness and UV chroma were chosen as variables in the statistical

224   analyses to characterize coloration. They represent respectively the achromatic and

225   chromatic components of the coloration. Brightness was not significantly correlated

226   to any of the 3 chromatic parameters ($r = 0.12$, $N = 16$, $P = 0.647$ with UV chroma; r

227   $= -0.09$, $N = 16$, $P = 0.752$ with hue; and $r = 0.44$, $N = 16$, $P = 0.087$ with chroma).

228   UV chroma was significantly correlated with the other chromatic color variables

229   (hue vs. UV chroma: *r* = -0.69; chroma vs. UV chroma: *r* = 0.87, hue vs. chroma: *r*

230   = -0.53; *N* = 16; all *P* < 0.05). Color measurements presented a statistically

231   significant difference between the UV+ and UV- males within dyads (Wilcoxon

232   signed rank test: for brightness: *V* = 127, *N* = 16, *P* = 0.001; for UV chroma: *V* =

233   109, *N* = 16, *P* = 0.036).

234   Statistical analyses

235   Two non-exclusive hypotheses were tested for the role of UV coloration: one for the

236   aggressive response of focal birds (first attack and time spent on each cage) and one

237   for the focal birds' choice of a feeding companion (time spent feeding close to each

238   UV manipulated birds). Consider here that in fourteen out of the sixteen replicates,

239   the focal bird went first to the cages containing the intruders and then to the feeding

240   dishes. Therefore, we did not analyze the choice of feeding close to a UV- or UV+

241   male first, since this variable was not the first approaching behavior expressed by

242   focal birds.

243   We used a General Linear Model (GLM), with a binomial error, to

244   investigate which intruder (UV+ or UV- male) focal males attacked first and

245   whether the coloration of the focal bird influenced this decision. The dependent

246   variable was the identity of the bird first attacked (1=UV+, 0=UV-) and the

247   independent variable was the coloration of the focal bird. A positive and significant

248   estimate for the intercept indicates that focal birds attacked the UV+ bird more. To

249   test whether the proportion of time spent attacking the UV+ male was not random

250   (i.e. significantly different from 50%) and was influenced by the focal bird's

251   coloration, we ran a regression model with a Gaussian error.

11

252   For the second hypothesis, we also ran a linear model to test whether the

253   proportion of time feeding under a specific cage was not random and influenced by

254   the focal bird's coloration.

255   For every test, we selected variables which had a significant effect on the

256   dependent variable by comparing nested models with an ANOVA (backward

257   stepwise procedure). We used $\alpha = 0.05$ for the significance level. All the analyses

258   were conducted with R software (Ihaka and Gentleman 1996).

259

260   **Results**

261   Focal males were significantly more likely to approach the UV- male first. In 11 out

262   of 14 trials, the focal birds first attacked the UV- bird (GLM: *intercept estimate* = -

263   1.30 ± 0.65, *Z* = -1.99, *P* = 0.046). However, the focal male coloration did not

264   influence the likelihood of attacking a UV- or UV+ male first (Table 1).

265   Focal males spent significantly less time perching on the UV+ male's cage

266   (LM: intercept estimate = 0.42 ± 0.09, *t* = 4.56, *P* = 0.0005). This behavior did not

267   differ according to the coloration of the focal bird (Table 1).

268   Finally, we found that the focal birds' coloration influenced the proportion of

269   time that they spent feeding under the UV+ and UV- males (Table 1). Brighter focal

270   birds fed underneath both the UV+ and UV- birds, while duller focal males fed

271   preferentially under UV- birds (LM: coefficient estimate = 0.06 ± 0.03, *t* = 2.23, *P* =

272   0.045; Fig. 3). We found no influence of the focal males' UV chroma on the time

273   spent feeding under the UV+ and UV- males (Table 1).

Discussion

Our results suggest that UV-blue crest in male blue tits has some properties of a badge of status. We found that focal birds attacked UV reduced birds first and spent significantly more time on their cages. Additionally, we found that the brightness of focal males influenced the time they spent feeding under the UV modified intruders, with duller focal males feeding nearly exclusively under UV- males while brighter focal males feeding under both UV- and UV+ males. These results showed that variation in UV coloration is discriminated by male blue tits and influences their initial response towards unfamiliar conspecifics.

In this study, we tried to dissociate the role of UV coloration on aggressive and social interactions. Concerning aggressive interactions, we found that the bird presenting the lower signal expression was attacked first and for longer periods, which is consistent with previous results found in other species (e.g. Møller 1987 for melanin-based signals; Pryke et al. 2001 for carotenoid-based signals; see also Senar 2006 for review). It is also in agreement with a recent study conducted on the same species (Vedder et al. 2009) in which experimentally UV reduced males had a higher probability of losing to control-treated opponents in pairwise trials of unfamiliar males. By contrast, Vedder et al. (2008) did not find any effect of reduced UV reflectance on agonistic interactions at a feeding table. However, their methods had the potential limitation of confounding effects, due to the release of manipulated birds into their original social groups, which implied that flock companions already knew the dominance status of their opponents (Senar 2006). The differences in these results (Vedder et al. 2008; 2009 and our study) show that

297   unfamiliarity between competitors is essential when testing the badge of status

298   hypothesis.

299   Surprisingly, the coloration of the focal birds did not influence which intruder

300   bird was attacked most; the UV- intruder was always attacked more than the UV+

301   intruder. We propose this is because it is less costly to attack the less threatening of

302   the two intruders first. This would be particularly true outside the breeding season

303   when the cost of fighting might be high relatively to the value of the resource (see

304   Tibbetts and Lindsay 2008 for an evaluation of the importance of the resource value

305   on the occurrence of aggressive interactions between individuals). Secondly,

306   interacting with the lower quality intruder first might simultaneously transfer

307   information to the higher quality intruder if this one is eavesdropping (McGregor

308   2005). Audience effects are suspected to increase the intensity of male-male

309   competition when males constitute the audience (Doutrelant et al. 2001).

310   Consequently, it may be more prudent to escalate with the lower quality individual

311   than the other.

312   In addition to aggressive interactions, our results strongly suggest that UV

313   coloration mediates social interactions as it clearly influenced the choice of a

314   feeding companion. We found that focal males preferentially ate close to the

315   intruder displaying a similar or lower brightness. This result is thus in agreement

316   with previous studies that showed that individuals avoided interactions with

317   dominants, and fed with companions of same or lower status (Fretwell 1969; Harper

318   1982; Metcalfe 1986; Ekman 1989; Senar and Camerino 1998). This result also

319   suggests that crest brightness might be a good candidate to encode the social status

320   in a group. Brightness has been found to be an indication of individual quality in

321   several species of birds (Doucet and Montgomerie 2003; Siefferman and Hill 2003).

322   Our color manipulation affected the hue, brightness and UV chroma of the

323   crest. Because we found that the overall crest coloration of intruders had an effect on

324   focal birds' aggressiveness, this suggests that at least one of these three color

325   dimensions is important to code for fighting ability. By contrast, the choice of a

326   feeding companion seems only influenced by the brightness of the birds, and not by

327   UV chroma. Why brightness and not UV chroma? Indeed, we expected a greater

328   influence of UV chroma on male-male interactions since chromatic components

329   were found to affect individuals' behaviors, in relation to female reproductive

330   strategies, in blue tits (assortative mating: Andersson et al. 1998; extra-pair

331   copulations: Delhey et al. 2003; sex ratio of the offspring: Sheldon et al. 1999;

332   Griffith et al. 2003). On the other hand, the expression of brightness, hue and UV

333   chroma of structural colorations has been experimentally shown to be condition-

334   dependent in several species (brightness: Siefferman and Hill 2007; Siitari et al.

335   2007; UV chroma: Jacot and Kempenaers 2007; overall reflectance: McGraw et al.

336   2002; Hill et al. 2005; Griggio et al. 2009). Therefore, each of these 3 color

337   parameters might encode information related to individuals' condition and affect

338   social interactions. Recent studies on the anatomical structure of feathers responsible

339   for structural coloration in eastern bluebirds (*Sialia sialis*) showed that UV chroma

340   and hue are predicted by barb structure in the inner spongy layer (Shawkey et al.

341   2003; Shawkey et al. 2005) whereas expression of brightness is related to the

342   thickness of the outer cortex layer of the barbs (Shawkey et al. 2005). Since the

343   outer cortex layer might be more exposed to feather abrasion, brightness is more

344   likely to signal individual condition than hue and UV chroma. However in blue tits,

345   only changes in UV chroma and hue over time were related to males' condition

346   (Delhey et al. 2006). So to date, more investigations are needed to propose a general

347   explanation for the greater effect of brightness compared to UV chroma on social

348   interactions.

349

350   If structural coloration is actually used as a badge of status, a next important step

351   would be to know the mechanisms that ensure the honesty of the structural

352   coloration. Honesty might be encoded by two types of costs: intrinsic and extrinsic

353   (Searcy and Nowicki 2005; Senar 2006). Intrinsic costs mean that signals are costly

354   to produce. Extrinsic costs mean that badges of status are conventional signals,

355   which are not costly to produce and honesty is maintained by social control (Rohwer

356   1977; Maynard Smith and Harper 2003). Under this second hypothesis, individuals

357   presenting higher signals are predicted to be systematically challenged by dominant

358   individuals and cheating would be prevented because the cost of fighting with a

359   more dominant individual would be too high for the cheater. Results of several

360   studies conducted on melanin-based signals are consistent with this hypothesis (e.g.

361   McGraw et al. 2003; Tibbetts and Dale 2004). For instance, in house sparrows,

362   melanin coloration does not seem to be nutritionally costly to produce (Gonzalez et

363   al. 1999; McGraw et al. 2002), but does seem to be socially controlled (Møller 1987;

364   McGraw et al. 2003; Nakagawa et al. 2008; but see Gonzalez et al. 2002). In blue

365   tits, a social cost for maintaining the honesty of signals seems unlikely as our results

366   and those of Vedder et al. (2009) showed that, contrary to the expectation, UV

367   reduced birds are always attacked more and the coloration of the owner does not

368   influence its response towards the intruder as predicted if social control is the

369   determinant mechanism for maintaining the honesty of the signal.

370   Intrinsic costs of signal production are often explained under the hypothesis of

371   condition dependence. This hypothesis states that a high level of signaling is more

372   costly for low than high quality individuals (Zahavi 1975; Grafen 1990). Concerning

373   color patches signaling aggressiveness, testosterone has been suggested to underline

374   the trade-offs between signaling and immunity (Folstad and Karter 1992). However,

375   whether there is enough testosterone during molt for this hypothesis to work is still

376   under discussion (Buchanan et al. 2001; but see Bokony et al. 2008). In addition, to

377   date the link between structural coloration and testosterone is not clear. In blue tits,

378   implants of testosterone during the molt do not increase the UV signal at the end of

379   the molt, although they seem to increase preening behavior, which would ensure a

380   high level of signaling later in the season (Roberts et al. 2009). Lastly, during the

381   reproductive season, no general relationship was found between UV-blue coloration

382   and testosterone in blue tits (Peters et al. 2006).

383   Intrinsic costs have also been proposed as a mechanism to ensure the honesty of

384   Resource Holding Potential (RHP) signals. As seen previously, development of UV

385   coloration is sensitive to individual condition. It seems to be linked to genetic

386   quality (Foerster et al. 2003; Garcia-Navas et al. 2009) and it is unambiguously

387   affected by condition during the molt (McGraw et al. 2002; Hill et al. 2005;

388   Siefferman and Hill 2005a; Siitari et al. 2007; see Griggio et al. 2009 for blue tits).

389   Because condition is important for dominance (RHP), the reliable link between

390   condition and coloration might explain why coloration honestly reflects dominance.

391   In conclusion, we provide here experimental evidence that UV signals mediate

392   male-male interactions at first encounter. In addition to other studies conducted with

393   blue tits (Alonso-Alvarez et al. 2004; Poesel et al. 2007; Vedder et al. 2009),

394   Broadley's flat lizards *Platysaurus broadleyi* (Whiting et al. 2006), damselfish

395   *Pomacentrus amboinensis* (Siebeck 2004) and sticklebacks *Gasterosteus aculeatus*

396   (Rick and Bakker 2008), our results support the hypothesis that structural coloration

397   could evolve under social or intra-sexual selection. Future investigations are needed

398   to test whether the influence of UV coloration during first interactions between

399   unfamiliar birds also occurs in a more natural environment. Finally, it would be

400   interesting to determine the fitness advantages in terms of food, mates and territory

401   acquisition of presenting a more colorful signal.

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635

636   **Tables**

637

638   **Table 1**   Best models describing the effects of focal birds' color parameters on both

639   aggressiveness (first attack and proportion of time spent attacking the UV+ male)

640   and social behavior (proportion of time spent feeding underneath the UV+ male)

Factors	Estimate ± SE	Test statistic	P
First attack			
Intercept	-1.30 ± 0.65	$Z = -1.99$	0.046
UV Chroma	-38.2 ± 41.5	LRT = 0.96	0.328
Brightness	0.36 ± 0.34	LRT = 1.39	0.238
Time spent attacking			
Intercept	0.42 ± 0.09	$t = 4.56$	0.0005
UV Chroma	-1.62 ± 5.33	LRT = 0.01	0.767
Brightness	-0.01 ± 0.04	LRT = 0.01	0.768
Time spent feeding			
Intercept	1.71 ± 2.13	$t = 0.80$	0.437
UV Chroma	-7.79 ± 6.17	$t = -1.26$	0.231
Brightness	0.062 ± 0.03	$t = 2.23$	0.045

641   For each test: N = 16

642   **Figure legends**

643   **Fig. 1** Schematic representation of the aviary used for the experiment. UV modified

644   birds (UV+ and UV-) were placed in small cages inside the aviary of the focal bird.

645   A feeding dish containing meal worms, sunflower seeds and paté was placed under
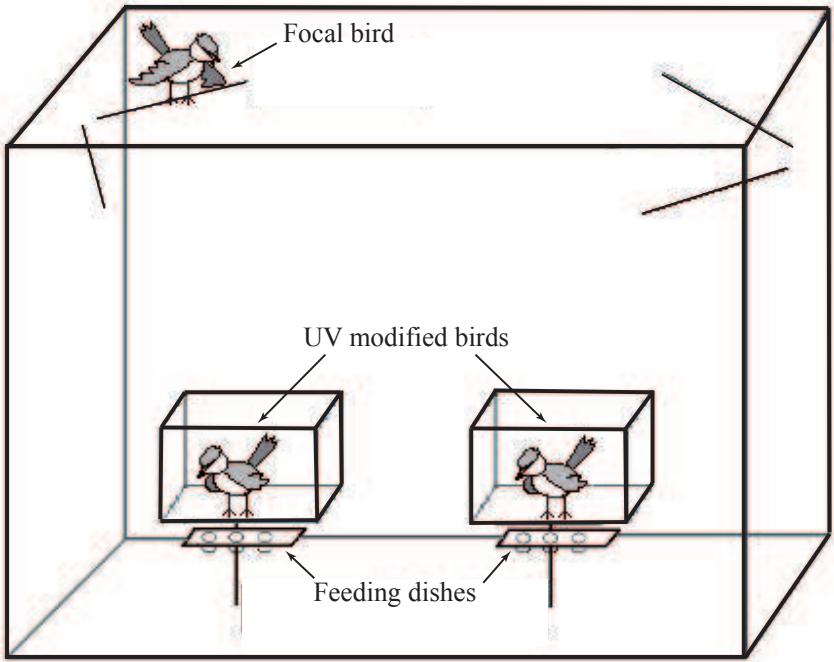
646   each small cage

647

648   **Fig. 2** Mean reflectance spectra of the crest of the three male groups: focal birds

649   (solid grey line), UV- birds (dashed black line), and UV+ birds (dotted dark-grey

650   line). N=16 for each group. Standard errors are indicated each 25nm intervals. Mean

651   reflectance spectrum of the crest of 2 females is also represented for comparison

652   (dot-dash light-grey line). UV reflectance ranges from 300 to 400 nm wavelengths

653

654   **Fig. 3** Relation between the brightness of the focal birds and the proportion of time

655   spent near the UV+ caged bird in comparison with the total time spent near both

656   caged birds. The dashed grey line represents the regression line (Y = 0.05730*X -
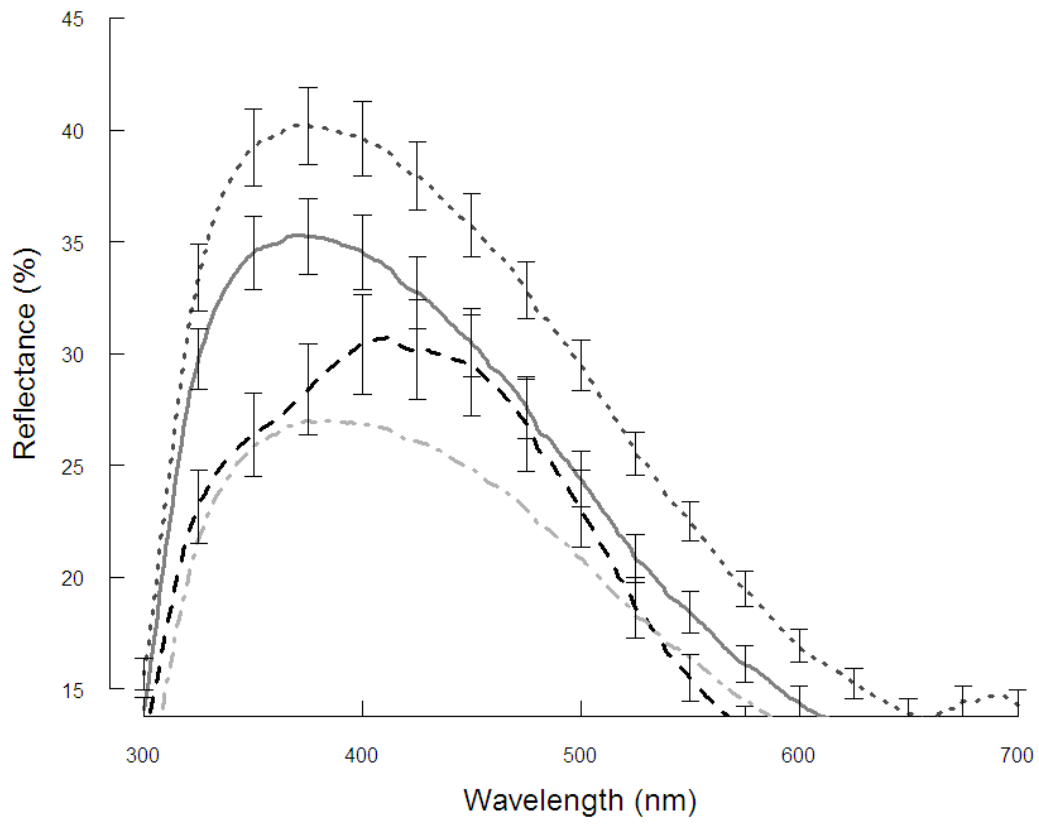
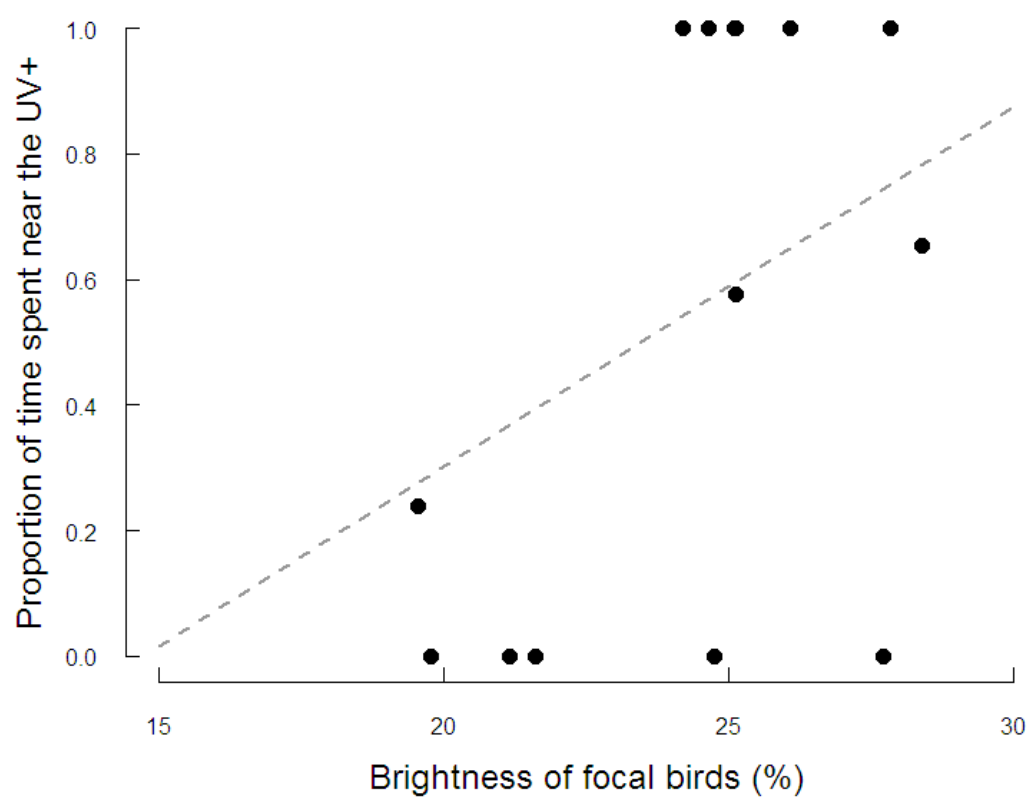657   0.84468)

658 **Figures**

659 **Fig. 1**

660

661

662 **Fig. 2**

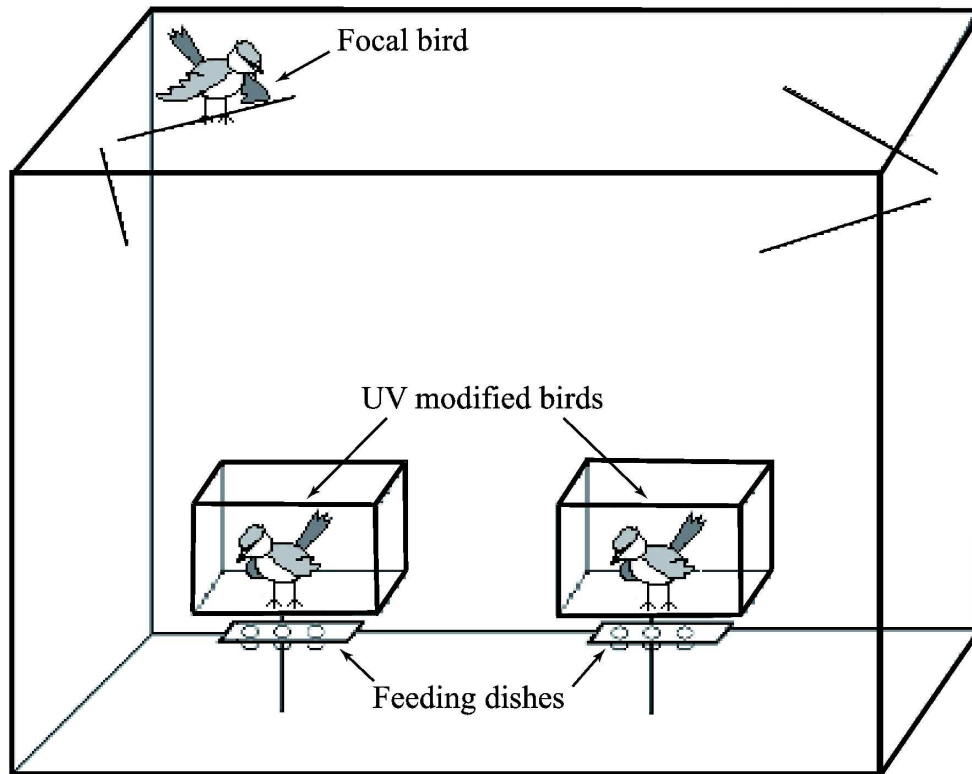

663

664   **Fig. 3**

665

666

Fig. 1 Schematic representation of the aviary used for the experiment. UV modified birds (UV+ and UV-) were placed in small cages inside the aviary of the focal bird. A feeding dish containing meal worms, sunflower seeds and paté was placed under each small cage
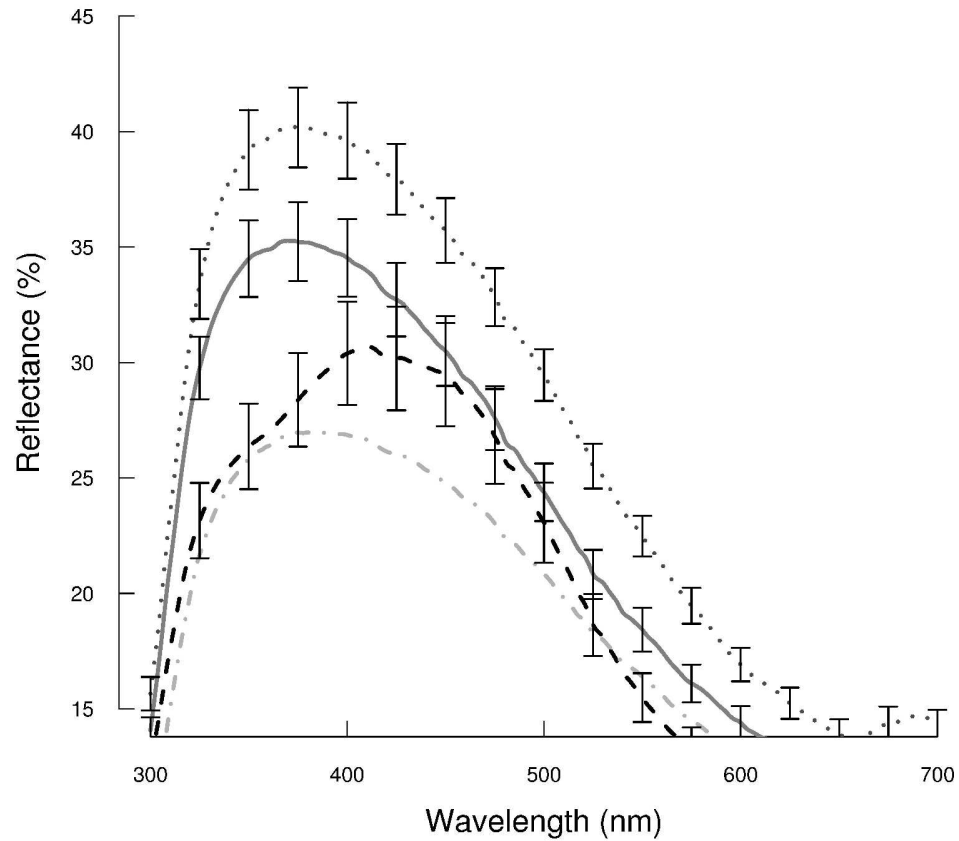153x121mm (600 x 600 DPI)

Fig. 2 Mean reflectance spectra of the crest of the three male groups: focal birds (solid grey line), UV- birds (dashed black line), and UV+ birds (dotted dark-grey line). N=16 for each group. Standard errors are indicated each 25nm intervals. Mean reflectance spectrum of the crest of 2 females is also represented for comparison (dot-dash light-grey line). UV reflectance ranges from 300 to 400 nm wavelengths
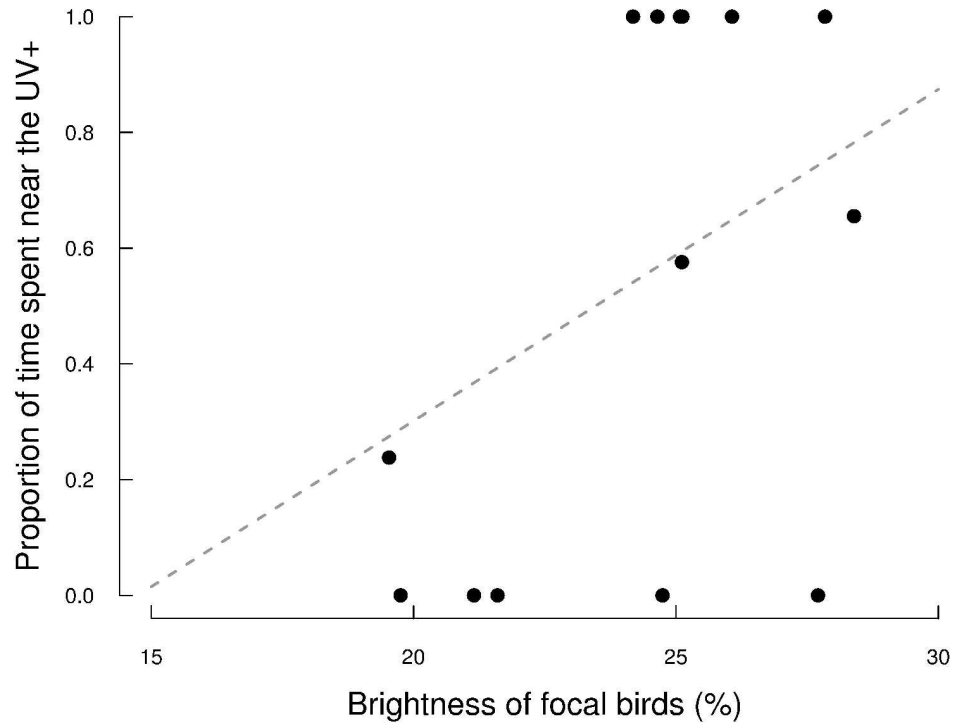203x182mm (600 x 600 DPI)

Fig. 3 Relation between the brightness of the focal birds and the proportion of time spent near the UV+ caged bird in comparison with the total time spent near both caged birds. The dashed grey line represents the regression line (Y = 0.05730*X - 0.84468)
201x155mm (600 x 600 DPI)