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

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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

## 38 **Keywords**

39 Badge of status; Structural coloration; Blue Tit (*Cyanistes caeruleus*); Intra-specific  
40 competition

## 41 **Introduction**

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

57 Several studies in many taxa including fish (e.g. Martin and Hengstebeck  
58 1981), insects (e.g. Tibbetts and Dale 2004), lizards (e.g. Whiting et al. 2006) and  
59 birds (e.g. Senar 2006) confirmed that individuals presenting larger or more colorful  
60 badges are perceived differently from individuals presenting smaller or duller  
61 badges. These studies also found that individuals with higher badge expression won  
62 more conflicts and had higher fighting abilities or level of aggressiveness. Most  
63 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

## 124 **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

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  $\mu\text{m}$  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 ( $R_{\text{mean}}$ ). 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:  $(R_{\text{max}} - R_{\text{min}}) /$   
220  $R_{\text{mean}}$ . UV chroma corresponds to the proportion of the total reflectance located  
221 between 300 and 400 nm:  $(R_{300 \text{ nm}} - R_{400 \text{ nm}}) / (R_{300 \text{ nm}} - R_{700 \text{ nm}})$ . 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.

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  $1.30 \pm 0.65$ ,  $Z = -1.99$ ,  $P = 0.046$ ). 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* =  $0.42 \pm 0.09$ ,  $t = 4.56$ ,  $P = 0.0005$ ). 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* =  $0.06 \pm 0.03$ ,  $t = 2.23$ ,  $P =$   
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).

## 274 **Discussion**

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

283 In this study, we tried to dissociate the role of UV coloration on aggressive  
284 and social interactions. Concerning aggressive interactions, we found that the bird  
285 presenting the lower signal expression was attacked first and for longer periods,  
286 which is consistent with previous results found in other species (e.g. Møller 1987 for  
287 melanin-based signals; Pryke et al. 2001 for carotenoid-based signals; see also Senar  
288 2006 for review). It is also in agreement with a recent study conducted on the same  
289 species (Vedder et al. 2009) in which experimentally UV reduced males had a  
290 higher probability of losing to control-treated opponents in pairwise trials of  
291 unfamiliar males. By contrast, Vedder et al. (2008) did not find any effect of  
292 reduced UV reflectance on agonistic interactions at a feeding table. However, their  
293 methods had the potential limitation of confounding effects, due to the release of  
294 manipulated birds into their original social groups, which implied that flock  
295 companions already knew the dominance status of their opponents (Senar 2006).  
296 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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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 $\pm$ SE	Test statistic	<i>P</i>
<i>First attack</i>			
Intercept	-1.30 $\pm$ 0.65	<i>Z</i> = -1.99	0.046
UV Chroma	-38.2 $\pm$ 41.5	LRT = 0.96	0.328
Brightness	0.36 $\pm$ 0.34	LRT = 1.39	0.238
<i>Time spent attacking</i>			
Intercept	0.42 $\pm$ 0.09	<i>t</i> = 4.56	0.0005
UV Chroma	-1.62 $\pm$ 5.33	LRT = 0.01	0.767
Brightness	-0.01 $\pm$ 0.04	LRT = 0.01	0.768
<i>Time spent feeding</i>			
Intercept	1.71 $\pm$ 2.13	<i>t</i> = 0.80	0.437
UV Chroma	-7.79 $\pm$ 6.17	<i>t</i> = -1.26	0.231
Brightness	0.062 $\pm$ 0.03	<i>t</i> = 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

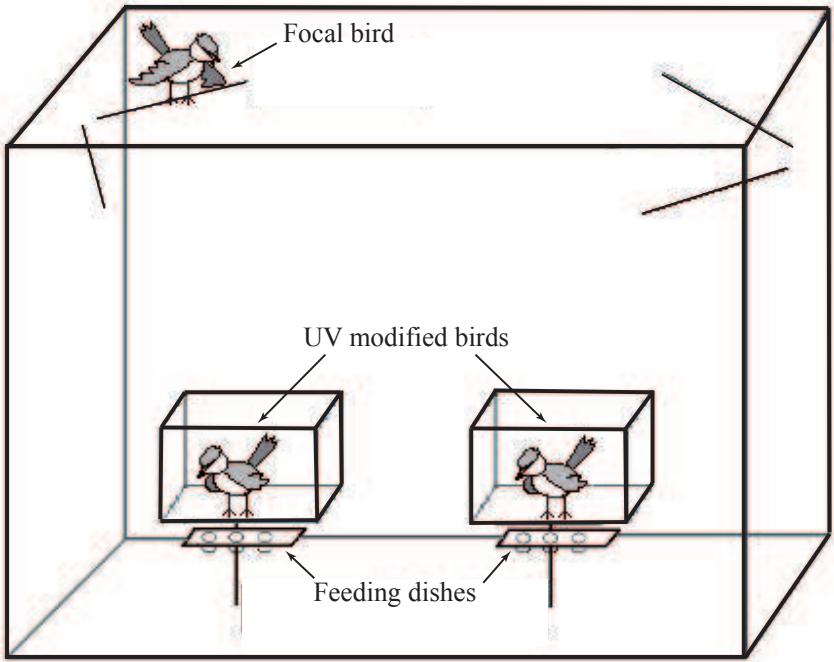
648 **Fig. 2** Mean reflectance spectra of the crest of the three male groups: focal birds  
649 (solid grey line), UV- birds (dashed black line), and UV+ birds (dotted dark-grey  
650 line). N=16 for each group. Standard errors are indicated each 25nm intervals. Mean  
651 reflectance spectrum of the 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**

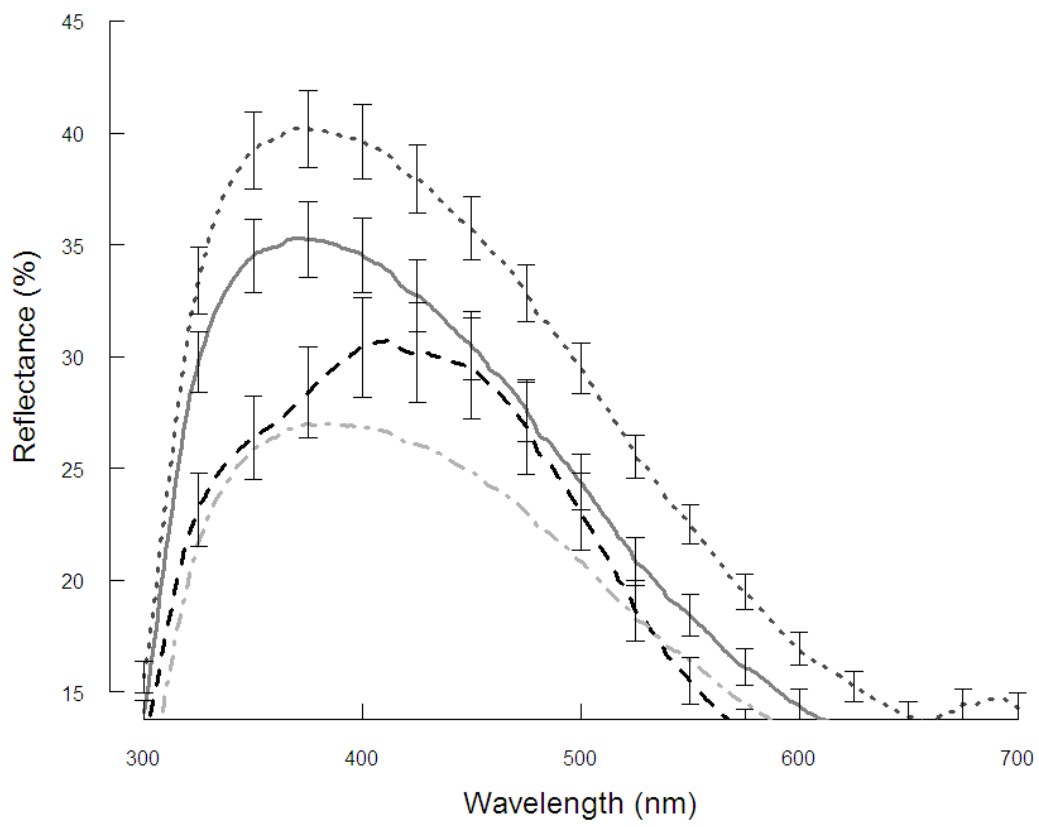


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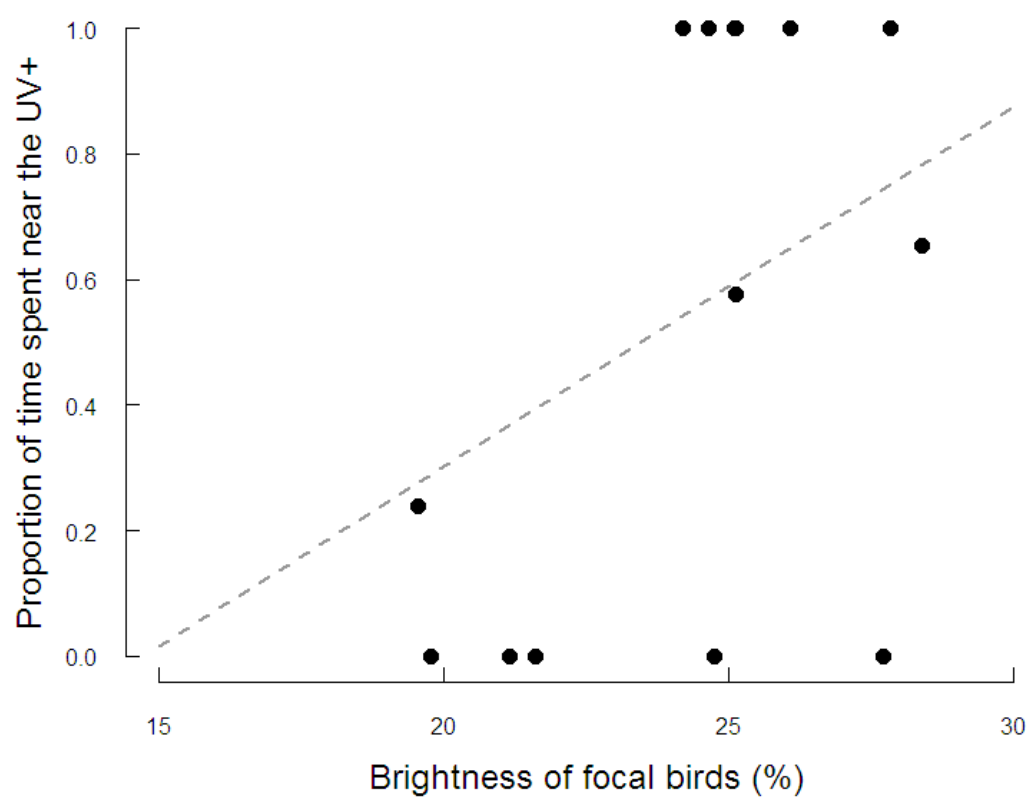
662 Fig. 2



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664 Fig. 3



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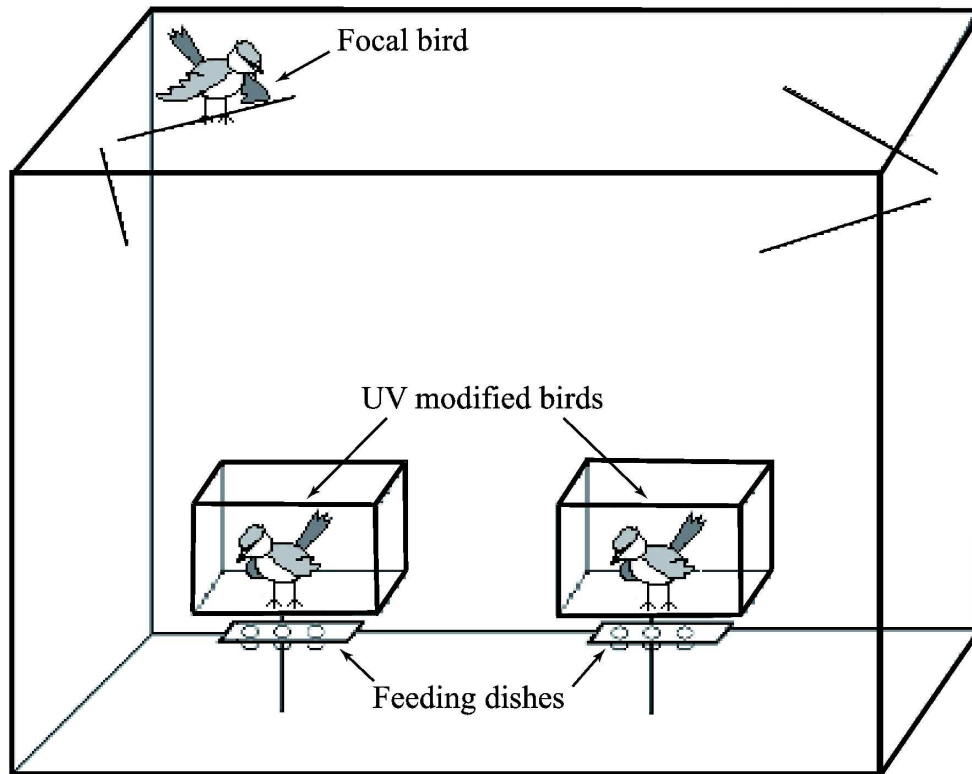


Fig. 1 Schematic representation of the aviary used for the experiment. UV modified birds (UV+ and UV-) were placed in small cages inside the aviary of the focal bird. A feeding dish containing meal worms, sunflower seeds and paté was placed under each small cage 153x121mm (600 x 600 DPI)

Only

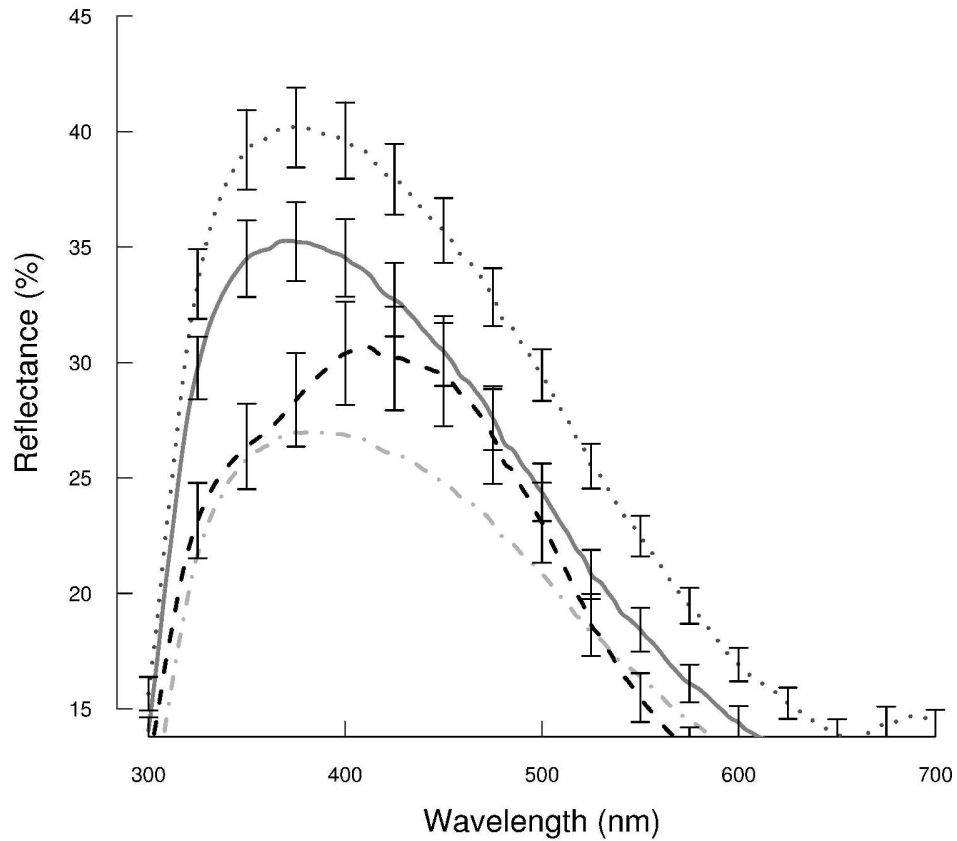


Fig. 2 Mean reflectance spectra of the crest of the three male groups: focal birds (solid grey line), UV- birds (dashed black line), and UV+ birds (dotted dark-grey line). N=16 for each group. Standard errors are indicated each 25nm intervals. Mean reflectance spectrum of the crest of 2 females is also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

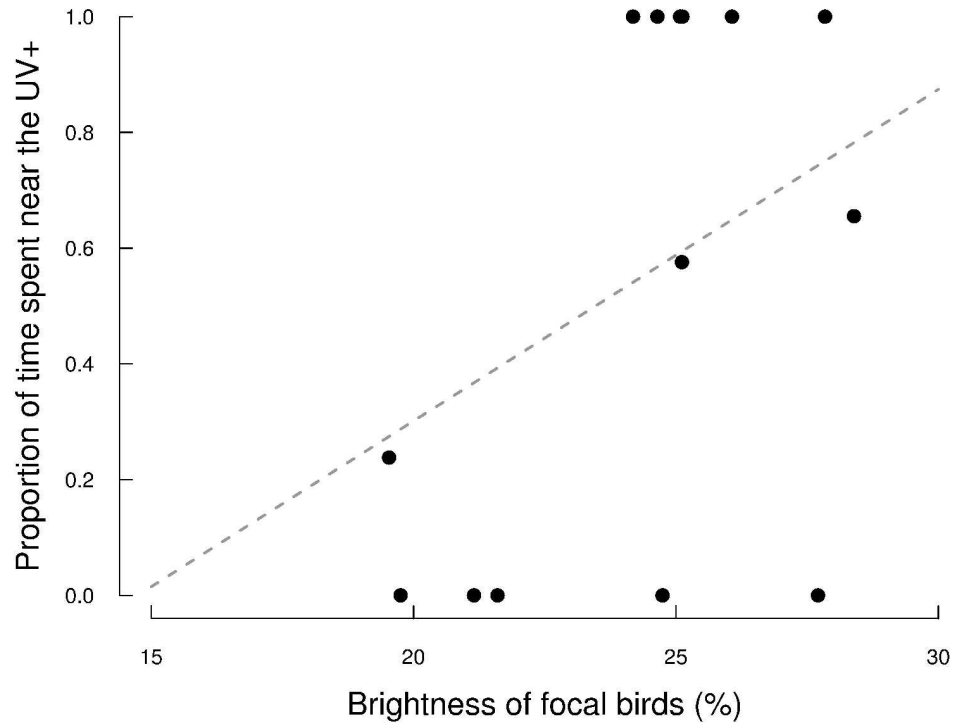


Fig. 3 Relation between the brightness of the focal birds and the proportion of time spent near the UV+ caged bird in comparison with the total time spent near both caged birds. The dashed grey line represents the regression line ( $Y = 0.05730 \cdot X - 0.84468$ )  
201x155mm (600 x 600 DPI)