

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

Alice Rémy · Arnaud Grégoire · Philippe Perret ·
Claire Doutrelant

Received: 5 January 2010 / Revised: 21 May 2010 / Accepted: 24 May 2010 / Published online: 8 June 2010
© Springer-Verlag 2010

Abstract Badges of status, usually color patches, are hypothesized to serve as important signals within natural populations by communicating an individual's fighting ability or aggressiveness before an interaction ever takes place. These signals, which may evolve via sexual and/or social selection, mediate intra-specific competition by influencing the outcome or escalation of contests between individuals. The last 10 years saw the rise of interest in the role of ultraviolet (UV)-based coloration in intra-sexual communication. However, the rare experimental studies that tested this hypothesis found opposite results, which may originate from the different methodological procedures used to assess the badge of status theory. We present here the results of an experiment testing whether male blue tits (*Cyanistes caeruleus*) respond differently to unfamiliar conspecifics presenting contrasted UV crest coloration. In an aviary, we simultaneously presented two caged blue tits with enhanced (UV+) or reduced (UV−) crest coloration to a focal bird. We found that focal males acted more aggressively towards the UV− males than UV+ males. In

addition, focal males fed more often close to males that were similar in brightness or duller than themselves. We conclude that, in blue tits, UV blue crest coloration affects both social and aggressive responses towards unfamiliar individuals, and thus it has some properties of a badge of status.

Keywords Badge of status · Structural coloration · Blue tit (*Cyanistes caeruleus*) · Intra-specific competition

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 the 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.

Communicated by: K. McGraw

A. Rémy · A. Grégoire · P. Perret · C. Doutrelant (✉)
CEFE-CNRS UMR5175,
1919 Rte de Mende,
34293 Montpellier, France
e-mail: claire.doutrelant@cefe.cnrs.fr

Present Address:

A. Rémy
Faculty of Forestry and Wildlife Management,
Hedmark University College,
2480 Koppang, Norway

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-based coloration (Järvi and Bakken 1984; Møller 1987; Senar et al. 1993; see Jawor and Breitwisch 2003; Tibbetts and Safran 2009, for review), although carotenoid-based coloration has also recently been found to signal competitive abilities (Pryke et al. 2001; Pryke and Andersson 2003; but see McGraw and Hill 2000). Melanin-based colorations seem to be frequently used to signal aggressiveness and dominance status in a group (Tibbetts and Safran 2009) due to the links between melanin and testosterone (Buchanan et al. 2001; Gonzalez et al. 2001; Bokony et al. 2008; Safran et al. 2008) or corticosterone (McGraw 2008; Roulin et al. 2008). Carotenoid-based colorations seem rather to be a sexual signal, used during competition for mates and territories because they encode the individuals' quality due to the link between carotenoids, diet, and health (detoxification and implications for the immune system; Lozano 1994; Olson and Owens 1998; von Schantz et al. 1999; Faivre et al. 2003).

By contrast, the role of structural coloration (ultraviolet (UV), violet, and blue) in intra-sexual interactions has been less well investigated and is still ambiguous. Some correlative studies have suggested a role of structural coloration in male–male competition (Keyser and Hill 2000; Siefferman and Hill 2005b; Pryke and Griffith 2006; Whiting et al. 2006), while two recent studies did not find any relationship between UV coloration and dominance (Korsten et al. 2007b; Santos et al. 2009). To date, only a few studies have experimentally manipulated structural traits to assess their role in male–male interactions (Alonso-Alvarez et al. 2004; Siebeck 2004; Korsten et al. 2007a; Poesel et al. 2007; Vedder et al. 2008, 2009). The majority of these studies have been conducted on the UV blue crest of blue tits (*Cyanistes caeruleus*) and give opposing results, with some supporting a role in male–male competition (Alonso-Alvarez et al. 2004; Poesel et al. 2007; Vedder et al. 2009) and others not (Korsten et al. 2007a; Vedder et al. 2008). So, to date, no clear general conclusion can be drawn on whether intra-sexual interactions drive the evolution of structurally colored signals.

Our study aimed at determining whether structural coloration affects social and/or aggressive interactions between male blue tits (*C. caeruleus*), taking into account a major assumption of the badge of status hypothesis: namely, badges of status are used between unfamiliar individuals to signal fighting abilities and aggressiveness at a distance

(Maynard Smith and Harper 2003). Ignoring this assumption could explain the disagreement in the past studies conducted in blue tits. For example, during the non-breeding period, Vedder et al. (2008) did not find any effect of crest reflectance on agonistic interactions between established and potentially familiar individuals, whereas a second study (Vedder et al. 2009) found that UV coloration influenced pairwise contest outcomes between unfamiliar males.

During winter, we conducted an experiment to assess whether focal birds (the receivers of the signal) behave differently towards two unfamiliar birds presenting different UV coloration: one UV enhanced (UV+) bird and one UV reduced (UV-) bird. These UV modified birds were placed in small cages just above a source of food. Two non-exclusive hypotheses were tested: first, we studied whether the UV treatment of the two introduced males influenced the aggressive response of focal birds. We determined whether the coloration of the focal male explained a variation in the first attack behavior and the time spent on the cage of each introduced male. Following the badge of status theory, we predicted that less colorful focal birds should attack the UV- male more, while more colorful focal birds are expected to attack the UV+ bird, which represents a higher threat to the resource holding. Second, we tested whether their choice of a feeding companion, measured as the time spent feeding underneath each UV manipulated bird, was influenced by the UV treatment of the intruders and by the focal birds' coloration. If UV coloration is a social signal used to assess the dominance rank in a group (e.g., for access to food), we predicted that the choice of which UV modified conspecific to feed close to will differ (Senar and Camerino 1998), namely, focal males are expected to feed closer to the intruder displaying a lower or similar coloration, representing a subordinate or an individual of same social status, but avoid dominant individuals (presenting a higher coloration), which might monopolize the food and represent a risk of injury (Ekman 1989; Senar and Camerino 1998).

Materials and methods

Capture, aging, and sexing

For this experiment, we captured 54 blue tits during January and February 2007 in six different localities around Montpellier, France. We first determined the sex and age (yearling vs. adult) of the birds captured in the field, based on the color of their wing coverts (Svensson 1992). After each trapping session and before the behavioral trials in the aviary, birds were kept for 1 to 2 weeks in individual cages (dimensions, 0.4×0.4×0.4 m). Water and food (sunflower seeds, meal worms, Orlux Uni paté® (Orlux, Deinze, Belgium) mixed with peanuts) were provided ad libitum.

Birds had no visual contact before the behavioral trials (see below). After the trials ($n=18$), we took a blood sample to confirm the birds' sex by molecular sexing (Griffiths et al. 1998). After migration of amplified fragments by electrophoresis, two females were revealed among the 54 birds. The two trials involving these birds were removed from the analyses, leaving a sample size of 48 birds and 16 trials. All birds were released following the trials.

Experiment

Each trial consisted of monitoring the behavioral response of a focal male when we introduced into its aviary two unfamiliar conspecifics with modified UV coloration (see below for coloration methods): one UV reduced bird (named after UV⁻) and one UV enhanced bird (named after UV⁺). The UV⁺ and UV⁻ birds were males of the same age class (yearlings or adults) from a different locality than the focal bird. As distances between trapping localities were on average more than 10 km, we assumed the probability that individuals had previously interacted and already knew each other to be negligible. The two UV modified males were either from the same area or from different localities. To avoid pseudo-replication, each behavioral trial involved a different focal bird and a different pair of intruders.

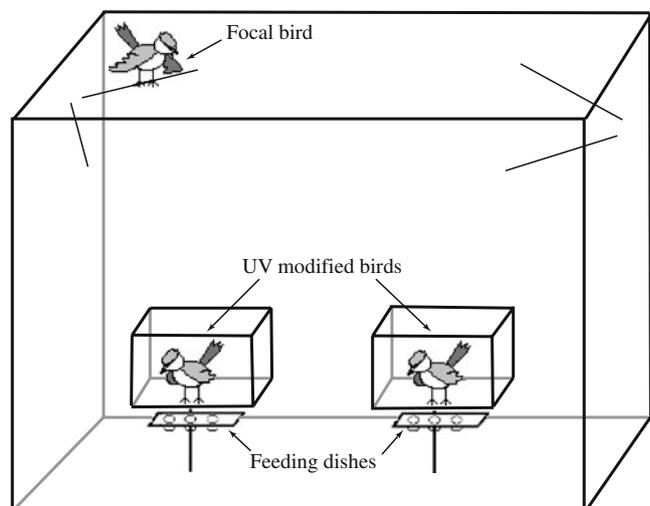
We used the same design as Senar and Camerino (1998; Fig. 1). The behavioral trials took place in an outside aviary (dimensions, 3×3×3 m) containing four perches (one in each corner), two open nest boxes, and two central feeding dishes (positioned 1.2 m above the ground) with sunflower seeds, meal worms, paté, and water. Above each feeding dish stood a little cage (dimensions, 0.5×0.3×0.3 m), within which a UV modified male was placed during the experiment. Using cages rather than letting intruders free

in the aviary has the advantage of avoiding potential injuries. It was also a better design to test the crest coloration as a badge of status since UV modified males could not reveal their status by physical interactions with the focal male even if other signals could be used, like postures or songs.

Each trial consisted of five steps: (1) the focal bird was introduced to the aviary alone for 2 to 4 days to become familiar with this new environment and to get used to eating close to the two small empty cages (Senar and Camerino 1998); (2) at the end of this period of familiarization, we observed the focal bird for 15 min to check that it had no preference for one of the two cages or feeding dishes which could represent a bias in the analyses. We did not find any significant differences between the time spent on each cage and each feeding dish during these 15 min of observation (paired samples *t*-tests: $t_{15}=-0.71$, $P=0.488$; $t_{15}=1.18$, $P=0.259$, respectively); (3) meal worms, a highly prized resource for blue tits in captivity, were removed for 1.5 h to increase the motivation of the focal bird to subsequently approach the cages (Braillet et al. 2002). During this period, paté and sunflower seeds remained in the aviary, allowing birds to continue feeding; (4) we then added meal worms and placed UV modified birds in the small cages just above the feeding dishes in the aviary. These birds were presented simultaneously rather than sequentially to facilitate their discrimination by the focal bird (MacLaren and Rowland 2006). The choice of the cage ("left" or "right") for each UV modified bird was determined randomly; (5) we then observed the behavior of the focal bird for 15 min following its first contact with either one of the cages or one of the feeding dishes.

During the 15 min of observation, we quantified four behavioral responses in order to characterize the response of the focal bird: (1) the first cage approached (the UV⁺ or

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



UV– intruder), (2) the first feeding dish approached (under the UV+ or UV– intruder’s cage), (3) the total time spent on each cage, and (4) the total time spent on each feeding dish. As in previous studies (for instance, Järvi and Bakken 1984), we considered focal birds that landed on a cage to be displaying an aggressive behavior. This estimation was reinforced by the fact that the focal birds were frequently observed hopping on the cages, trying to chase away the UV modified birds. Finally, we considered that feeding below one of the two cages represents a social choice of a feeding companion (Senar and Camerino 1998).

Color manipulation

Following Delhey et al. (2007) and Poesel et al. (2007), we changed the UV reflectance of the intruder’s crest with T-shirt markers Edding 4500 (Edding, Ahrensburg, Germany). A dark blue marker (color 003) and a pale blue marker (color 10) were used to respectively reduce or increase the UV reflectance. Previous studies that assessed the role of UV coloration in male–male interactions in blue tits almost completely removed the UV reflectance (i.e., Alonso-Alvarez et al. 2004; Korsten et al. 2007a; Vedder et al. 2008), creating unnatural colorations. Our method has the major advantage of changing the UV spectra within the natural range observed in male blue tits (Fig. 2). We assumed that this manipulation did not produce a female phenotype since the reflectance of UV– birds was significantly different from the reflectance of females that

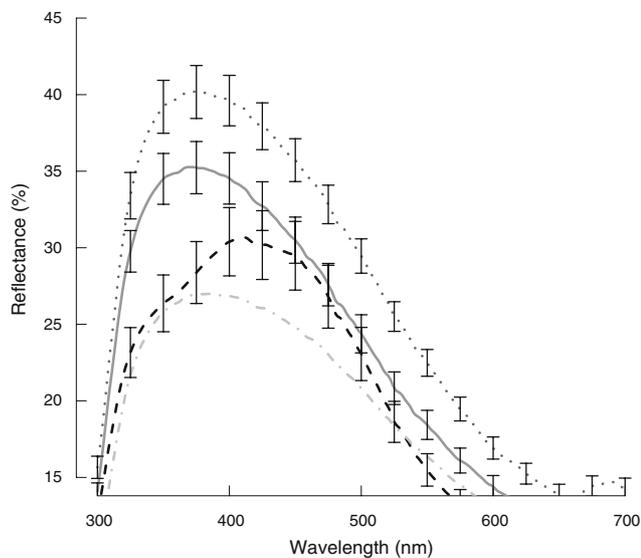


Fig. 2 Mean reflectance spectra of the crest of the three male groups: focal birds (solid gray line), UV– birds (dashed black line), and UV+ birds (dotted dark-gray line). $N=16$ for each group. Standard errors are indicated each at 25-nm intervals. Mean reflectance spectrum of the crest of two females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

we had (Wilcoxon–Mann–Whitney test: $W=32$, $P=0.013$; see also Fig. 2). Moreover, no other male characteristics (wings, tail, back mask, white crown, blue-black nape coloration, size) were manipulated.

Coloration measurements

At the end of each trial, we measured the crest coloration of all the birds with a spectrophotometer Ocean Optics USB4000 having a xenon light source (Ocean Optics PS-2; covering the range 300–700 nm) and a 200- μm fiber-optic coaxial probe, mounted with a black rubber cap to exclude ambient light (see methods of Doutrelant et al. 2008). The probe was held at a 90° angle and at a fixed distance of 2 mm from the feather surface. Before each measurement, we reset the reflectance with a white standard (WS1 Ocean Optics) and checked the reflectance of a dark reference. Five replicates have been taken, changing the position of the probe between measurements. For each bird, four parameters of coloration were calculated from the reflectance spectra using Avicol software v1 (Gomez 2006): brightness, hue, chroma, and UV chroma. Brightness corresponds to the average reflectance of feathers (R_{mean}). Hue is the wavelength at the maximum reflectance, between 300 and 700 nm. Chroma, describing the spectral purity, is the ratio of the difference between the maximum and the minimum reflectance and the mean reflectance: $(R_{\text{max}}-R_{\text{min}})/R_{\text{mean}}$. UV chroma corresponds to the proportion of the total reflectance located between 300 and 400 nm: $(R_{300\text{ nm}}-R_{400\text{ nm}})/(R_{300\text{ nm}}-R_{700\text{ nm}})$. For each color parameter, we used the average of the five measurements taken.

Only brightness and UV chroma were chosen as variables in the statistical analyses to characterize coloration. They represent respectively the achromatic and chromatic components of the coloration. Brightness was not significantly correlated to any of the three chromatic parameters ($r=0.12$, $N=16$, $P=0.647$ with UV chroma; $r=-0.09$, $N=16$, $P=0.752$ with hue; and $r=0.44$, $N=16$, $P=0.087$ with chroma). UV chroma was significantly correlated with the other chromatic color variables (hue vs. UV chroma: $r=-0.69$; chroma vs. UV chroma: $r=0.87$, hue vs. chroma: $r=-0.53$; $N=16$; all $P<0.05$). Color measurements presented a statistically significant difference between the UV+ and UV– males within dyads (Wilcoxon signed rank test: for brightness, $V=127$, $N=16$, $P=0.001$; for UV chroma, $V=109$, $N=16$, $P=0.036$).

Statistical analyses

Two non-exclusive hypotheses were tested. The first one was that UV coloration influenced the aggressive response of focal birds in relation to their own coloration. Aggressiveness was assessed through two variables: identity of the birds attacked first and total spent one each cage containing an UV modified

bird. The second hypothesis was that UV coloration influenced the focal birds' choice of a feeding companion in relation to its own coloration. The choice of a feeding companion was assessed through one variable: the total time feeding close to each UV manipulated bird. Here, we did not consider whether the focal bird chose to feed first near the UV- or UV+ bird, since this was not the first approaching behavior expressed by focal birds. Indeed, in fourteen out of the sixteen replicates, the focal bird went first to the cages containing the intruders and then to the feeding dishes.

We used a general linear model (GLM), with a binomial error, to investigate which intruder (UV+ or UV- male) focal males attacked first and whether the coloration of the focal bird influenced this decision. The dependent variable was the identity of the bird first attacked (1=UV+, 0=UV-) and the independent variable was the coloration of the focal bird. A positive and significant estimate for the intercept indicates that focal birds attacked the UV+ bird more. To test whether the proportion of time spent attacking the UV+ male was not random (i.e., significantly different from 50%) and was influenced by the focal bird's coloration, we ran a regression model with a Gaussian error.

For the second hypothesis, we also ran a linear model to test whether the proportion of time feeding under a specific cage was not random and influenced by the focal bird's coloration.

For every test, we selected variables which had a significant effect on the dependent variable by comparing nested models with an ANOVA (backward stepwise procedure). We used $\alpha=0.05$ for the significance level. All the analyses were conducted with R software (Ihaka and Gentleman 1996).

Results

Focal males were significantly more likely to approach the UV- male first. In 11 out of 14 trials, the focal birds first attacked the UV- bird (GLM: intercept estimate = -1.30 ± 0.65 , $Z = -1.99$, $P = 0.046$). However, the focal male coloration did not influence the likelihood of attacking a UV- or UV+ male first (Table 1).

Focal males spent significantly less time perching on the UV+ male's cage (LM: intercept estimate = 0.42 ± 0.09 , $t = 4.56$, $P = 0.0005$). This behavior did not differ according to the coloration of the focal bird (Table 1).

Finally, we found that the focal birds' coloration influenced the proportion of time that they spent feeding under the UV+ and UV- males (Table 1). Brighter focal birds fed underneath both the UV+ and UV- birds, while duller focal males fed preferentially under UV- birds (LM: coefficient estimate = 0.06 ± 0.03 , $t = 2.23$, $P = 0.045$; Fig. 3). We found no influence of the focal males' UV chroma on the time spent feeding under the UV+ and UV- males (Table 1).

Table 1 Best models describing the effects of focal birds' color parameters on both aggressiveness (first attack and proportion of time spent attacking the UV+ male) and social behavior (proportion of time spent feeding underneath the UV+ male)

Factors	Estimate \pm SE	Test statistic	<i>P</i>
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

For each test, $N = 16$

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.

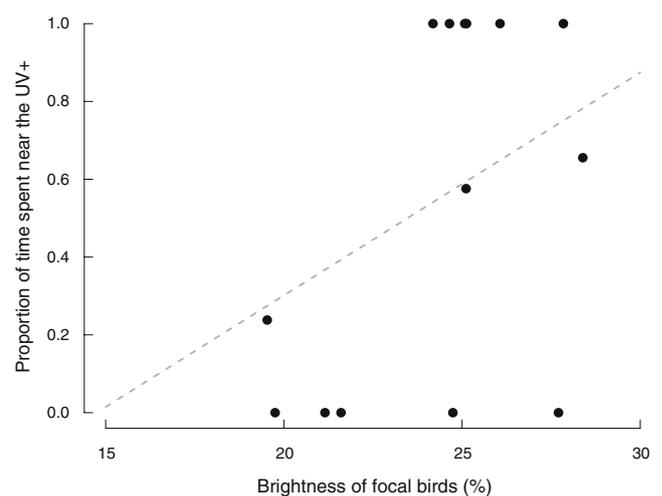


Fig. 3 Relation between the brightness of the focal birds and the proportion of time spent near the UV+ caged bird in comparison with the total time spent near both caged birds. The dashed gray line represents the regression line ($Y = 0.05730 \times X - 0.84468$)

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; our study) show that unfamiliarity between competitors is essential when testing the badge of status hypothesis.

Surprisingly, the coloration of the focal birds did not influence which intruder bird was attacked most; the UV–intruder was always attacked more than the UV+ intruder. We propose that this is, firstly, because it is less costly to attack the less threatening of the two intruders first. This would be particularly true outside the breeding season when the cost of fighting might be high relatively to the value of the resource (see Tibbetts and Lindsay (2008) for an evaluation of the importance of the resource value on the occurrence of aggressive interactions between individuals). Secondly, interacting with the lower-quality intruder first might simultaneously transfer information to the higher-quality intruder if this one is eavesdropping (McGregor 2005). Audience effects are suspected to increase the intensity of male–male competition when males constitute the audience (Doutrelant et al. 2001). Consequently, it may be more prudent to escalate with the lower-quality individual than the other.

In addition to aggressive interactions, our results strongly suggest that UV coloration mediates social interactions as it clearly influenced the choice of a feeding companion. We found that focal males preferentially ate close to the intruder displaying a similar or lower brightness. This result is thus in agreement with previous studies that showed that individuals avoided interactions with dominants and fed with companions of the same or lower status (Fretwell 1969; Harper 1982; Metcalfe 1986; Ekman 1989; Senar and Camerino 1998). This result also suggests that crest brightness might be a good candidate to encode the social status in a group. Brightness has been found to be an indication of individual quality in several species of birds (Doucet and Montgomerie 2003; Siefferman and Hill 2003).

Our color manipulation affected the hue, brightness, and UV chroma of the crest. Because we found that the overall crest coloration of intruders had an effect on the focal birds' aggressiveness, this suggests that at least one of these three color dimensions is important to code for fighting ability. By contrast, the choice of a feeding companion seems only influenced by the brightness of the birds and not by UV chroma. Why brightness and not UV chroma? Indeed we expected a greater influence of UV chroma on male–male interactions since chromatic components were found to affect the individuals' behaviors, in relation to female reproductive strategies, in blue tits (assortative mating: Andersson et al. 1998; extra-pair copulations: Delhey et al. 2003; sex ratio of the offspring: Sheldon et al. 1999; Griffith et al. 2003). On the other hand, the expression of brightness, hue, and UV chroma of structural colorations has been experimentally shown to be condition dependent in several species (brightness: Siefferman and Hill 2007; Siitari et al. 2007; UV chroma: Jacot and Kempenaers 2007; overall reflectance: McGraw et al. 2002; Hill et al. 2005; Griggio et al. 2009). Therefore, each of these three color parameters might encode information related to the individuals' condition and affect social interactions. Recent studies on the anatomical structure of feathers responsible for structural coloration in eastern bluebirds (*Sialia sialis*) showed that UV chroma and hue are predicted by barb structure in the inner spongy layer (Shawkey et al. 2003, 2005), whereas expression of brightness is related to the thickness of the outer cortex layer of the barbs (Shawkey et al. 2005). Since the outer cortex layer might be more exposed to feather abrasion, brightness is more likely to signal individual condition than hue and UV chroma. However, in blue tits, only changes in UV chroma and hue over time were related to males' condition (Delhey et al. 2006). So, to date, more investigations are needed to propose a general explanation for the greater effect of brightness compared to UV chroma on social interactions.

If structural coloration is actually used as a badge of status, a next important step would be to know the mechanisms that ensure the honesty of the structural coloration. Honesty might be encoded by two types of costs: intrinsic and extrinsic (Searcy and Nowicki 2005; Senar 2006). Intrinsic costs mean that signals are costly to produce. Extrinsic costs mean that badges of status are conventional signals, which are not costly to produce and honesty is maintained by social control (Rohwer 1977; Maynard Smith and Harper 2003). Under this second hypothesis, individuals presenting higher signals are predicted to be systematically challenged by dominant individuals and cheating would be prevented because the cost of fighting with a more dominant individual would be too high for the cheater. Results of several studies conducted on melanin-based signals are consistent with this hypothesis (e.g., McGraw et al. 2003;

Tibbetts and Dale 2004). For instance, in house sparrows, melanin coloration does not seem to be nutritionally costly to produce (Gonzalez et al. 1999; McGraw et al. 2002) but does seem to be socially controlled (Møller 1987; McGraw et al. 2003; Nakagawa et al. 2008; but see Gonzalez et al. 2002). In blue tits, a social cost for maintaining the honesty of signals seems unlikely as our results and those of Vedder et al. (2009) showed that, contrary to the expectation, UV reduced birds are always attacked more and the coloration of the owner does not influence its response towards the intruder as predicted if social control is the determinant mechanism for maintaining the honesty of the signal.

Intrinsic costs of signal production are often explained under the hypothesis of condition dependence. This hypothesis states that a high level of signaling is more costly for low- than high-quality individuals (Zahavi 1975; Grafen 1990). Concerning color patches signaling aggressiveness, testosterone has been suggested to underline the trade-offs between signaling and immunity (Folstad and Karter 1992). However, whether there is enough testosterone during molt for this hypothesis to work is still under discussion (Buchanan et al. 2001; but see Bokony et al. 2008). In addition, to date, the link between structural coloration and testosterone is not clear. In blue tits, implants of testosterone during the molt do not increase the UV signal at the end of the molt, although they seem to increase preening behavior, which would ensure a high level of signaling later in the season (Roberts et al. 2009). Lastly, during the reproductive season, no general relationship was found between UV blue coloration and testosterone in blue tits (Peters et al. 2006).

Intrinsic costs have also been proposed as a mechanism to ensure the honesty of resource holding potential (RHP) signals. As seen previously, development of UV coloration is sensitive to individual condition. It seems to be linked to genetic quality (Foerster et al. 2003; Garcia-Navas et al. 2009) and it is unambiguously affected by condition during the molt (McGraw et al. 2002; Hill et al. 2005; Siefferman and Hill 2005a; Siitari et al. 2007; see Griggio et al. 2009 for blue tits). Because condition is important for dominance (RHP), the reliable link between condition and coloration might explain why coloration honestly reflects dominance.

In conclusion, we provide here experimental evidence that UV signals mediate male–male interactions at first encounter. In addition to other studies conducted with blue tits (Alonso-Alvarez et al. 2004; Poesel et al. 2007; Vedder et al. 2009), Broadley's flat lizards *Platysaurus broadleyi* (Whiting et al. 2006), damselfish *Pomacentrus amboinensis* (Siebeck 2004), and sticklebacks *Gasterosteus aculeatus* (Rick and Bakker 2008), our results support the hypothesis that structural coloration could evolve under social or intrasexual selection. Future investigations are needed to test whether the influence of UV coloration during first

interactions between unfamiliar birds also occurs in a more natural environment. Finally, it would be interesting to determine the fitness advantages in terms of food, mates, and territory acquisition of presenting a more colorful structural signal.

Acknowledgments We thank Marie Pierre Dubois for helping with the molecular sexing, Marcel Lambrechts for the stimulating discussions, Mireille Son for helping with ringing permits, Eric Dincuff for the efficient help during the trapping sessions, Jos Milner for English corrections and comments, and two anonymous referees for their constructive comments on the manuscript. Birds were ringed under CRBPO authorization and kept in an aviary under the authorizations of the DSV. This work was supported by the Centre National de la Recherche Scientifique (C.N.R.S.) and the Agence Nationale de la Recherche (A.N.R. JC05_43762 and 09-JCJC-0050-01).

References

- Alonso-Alvarez C, Doutrelant C, Sorci G (2004) Ultraviolet reflectance affects male–male interactions in the blue tit (*Parus caeruleus ultramarinus*). *Behav Ecol* 15:805–809
- Andersson S, Ornborg J, Andersson M (1998) Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc R Soc Lond B Biol Sci* 265:445–450
- Bokony V, Garamszegi LZ, Hirschenhauser K, Liker A (2008) Testosterone and melanin-based black plumage coloration: a comparative study. *Behav Ecol Sociobiol* 62:1229–1238
- Braillet C, Charmantier A, Archaux F, Dos Santos A, Perret P, Lambrechts MM (2002) Two blue tit *Parus caeruleus* populations from Corsica differ in social dominance. *J Avian Biol* 33:446–450
- Buchanan KL, Evans MR, Goldsmith AR, Bryant DM, Rowe LV (2001) Testosterone influences basal metabolic rate in male house sparrows: a new cost of dominance signalling? *Proc R Soc Lond B Biol Sci* 268:1337–1344
- Delhey K, Johnsen A, Peters A, Andersson S, Kempenaers B (2003) Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (*Parus caeruleus*). *Proc R Soc Lond B Biol Sci* 270:2057–2063
- Delhey K, Peters A, Johnsen A, Kempenaers B (2006) Seasonal changes in blue tit crown color: do they signal individual quality? *Behav Ecol* 17:790–798
- Delhey K, Peters A, Johnsen A, Kempenaers B (2007) Fertilization success and UV ornamentation in blue tits *Cyanistes caeruleus*: correlational and experimental evidence. *Behav Ecol* 18:399–409
- Doucet SM, Montgomerie R (2003) Structural plumage colour and parasites in satin bowerbirds *Ptilonorhynchus violaceus*: implications for sexual selection. *J Avian Biol* 34:237–242
- Doutrelant C, Gregoire A, Grnac N, Gomez D, Lambrechts MM, Perret P (2008) Female coloration indicates female reproductive capacity in blue tits. *J Evol Biol* 21:226–233
- Doutrelant C, McGregor PK, Oliveira RF (2001) The effect of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens*. *Behav Ecol* 12:283–286
- Ekman J (1989) Group-size in dominance-structured populations. *Ornis Scandinavica* 20:86–88
- Faivre B, Gregoire A, Preault M, Cezilly F, Sorci G (2003) Immune activation rapidly mirrored in a secondary sexual trait. *Science* 300:103–103
- Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B (2003) Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* 425:714–717

- Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Fretwell S (1969) Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-Banding* 40:1–25
- Garcia-Navas V, Ortego J, Sanz JJ (2009) Heterozygosity-based assortative mating in blue tits (*Cyanistes caeruleus*): implications for the evolution of mate choice. *Proceedings of the Royal Society B-Biological Sciences* 276:2931–2940
- Gomez D (2006) AVICOL©: a program to analyse spectrometric data.
- Gonzalez G, Sorci G, Moller AP, Ninni P, Haussy C, De Lope F (1999) Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *J Anim Ecol* 68:1225–1234
- Gonzalez G, Sorci G, Smith LC, de Lope F (2001) Testosterone and sexual signalling in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 50:557–562
- Gonzalez G, Sorci G, Smith LC, de Lope F (2002) Social control and physiological cost of cheating in status signalling male house sparrows (*Passer domesticus*). *Ethology* 108:289–302
- Grafen A (1990) Biological signals as handicaps. *J Theor Biol* 144:517–546
- Griffith SC, Ornborg J, Russell AF, Andersson S, Sheldon BC (2003) Correlations between ultraviolet coloration, overwinter survival and offspring sex ratio in the blue tit. *J Evol Biol* 16:1045–1054
- Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. *Mol Ecol* 7:1071–1075
- Griggio M, Serra L, Licheri D, Campomori C, Pilastro A (2009) Moulting speed affects structural feather ornaments in the blue tit. *J Evol Biol* 22:782–792
- Harper DGC (1982) Competitive foraging in mallards: ‘ideal free’ ducks. *Anim Behav* 30:575–584
- Hill GE, Doucet SM, Buchholz R (2005) The effect of coccidial infection on iridescent plumage coloration in wild turkeys. *Anim Behav* 69:387–394
- Hurd PL (2006) Resource holding potential, subjective resource value, and game theoretical models of aggressiveness signalling. *J Theor Biol* 241:639–648
- Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5:299–314
- Jacot A, Kempenaers B (2007) Effects of nestling condition on UV plumage traits in blue tits: an experimental approach. *Behav Ecol* 18:34–40
- Järvi T, Bakken M (1984) The function of the variation in the breast stripe of the great tit (*Parus major*). *Anim Behav* 32:590–596
- Jawor JM, Breitwisch R (2003) Melanin ornaments, honesty, and sexual selection. *Auk* 120:249–265
- Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav Ecol* 11:202–209
- Korsten P, Dijkstra TH, Komdeur J (2007a) Is UV signalling involved in male–male territorial conflict in the blue tit (*Cyanistes caeruleus*)? A new experimental approach. *Behaviour* 144:447–470
- Korsten P, Vedder O, Szentirmai I, Komdeur J (2007b) Absence of status signalling by structurally based ultraviolet plumage in wintering blue tits (*Cyanistes caeruleus*). *Behav Ecol Sociobiol* 61:1933–1943
- Lozano GA (1994) Carotenoids, parasites, and sexual selection. *Oikos* 70:309–311
- MacLaren RD, Rowland WJ (2006) Differences in female preference for male body size in *Poecilia latipinna* using simultaneous versus sequential stimulus presentation designs. *Behaviour* 143:273–292
- Martin FD, Hengstebeck MF (1981) Eye color and aggression in juvenile guppies, *Poecilia reticulata*. *Anim Behav* 29:325–331
- Maynard Smith J, Harper DGC (1988) The evolution of aggression: can selection generate variability? *Philos Trans R Soc Lond B Biol Sci* 319:557–570
- Maynard Smith J, Harper DGC (2003) *Animal signals*. Oxford University Press, Oxford
- McGraw KJ (2008) An update on the honesty of melanin-based color signals in birds. *Pigment Cell Melanoma Res* 21:133–138
- McGraw KJ, Hill GE (2000) Carotenoid-based ornamentation and status signaling in the house finch. *Behav Ecol* 11:520–527
- McGraw KJ, Mackillop EA, Dale J, Hauber ME (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J Exp Biol* 205:3747–3755
- McGraw KJ, Dale J, Mackillop EA (2003) Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 53:116–122
- McGregor PK (2005) *Animal communication networks*. Cambridge University Press, Cambridge
- Metcalfe NB (1986) Variation in winter flocking associations and dispersion patterns in the turnstone *Arenaria interpres*. *J Zool* 209:385–403
- Møller AP (1987) Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Anim Behav* 35:1637–1644
- Nakagawa S, Lee JW, Woodward BK, Hatchwell BJ, Burke T (2008) Differential selection according to the degree of cheating in a status signal. *Biol Lett* 4:667–669
- Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol* 13:510–514
- Parker GA (1974) Assessment strategy and evolution of fighting behavior. *J Theor Biol* 47:223–243
- Peters A, Delhey K, Goymann W, Kempenaers B (2006) Age-dependent association between testosterone and crown UV coloration in male blue tits (*Parus caeruleus*). *Behav Ecol Sociobiol* 59:666–673
- Poesel A, Dabelsteen T, Darden SK, Delhey K, Peters A (2007) Territorial responses of male blue tits, *Cyanistes caeruleus*, to UV-manipulated neighbours. *J Ornithol* 148:179–187
- Pryke SR, Andersson S (2003) Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition. *Behav Ecol Sociobiol* 53:393–401
- Pryke SR, Griffith SC (2006) Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proceedings of the Royal Society B-Biological Sciences* 273:949–957
- Pryke SR, Lawes MJ, Andersson S (2001) Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. *Anim Behav* 62:695–704
- Rick IP, Bakker TCM (2008) Males do not see only red: UV wavelengths and male territorial aggression in the three-spined stickleback (*Gasterosteus aculeatus*). *Naturwissenschaften* 95:631–638
- Roberts ML, Ras E, Peters A (2009) Testosterone increases UV reflectance of sexually selected crown plumage in male blue tits. *Behav Ecol* 20:535–541
- Rohwer S (1975) The social significance of avian winter plumage variability. *Evolution* 29:593–610
- Rohwer S (1977) Status signaling in harris sparrows: some experiments in deception. *Behaviour* 61:107–129
- Roulin A, Almasi B, Rossi-Pedrucci A, Ducrest AL, Wakamatsu K, Miksik I, Blount JD, Jenni-Eiermann S, Jenni L (2008) Corticosterone mediates the condition-dependent component of melanin-based coloration. *Anim Behav* 75:1351–1358

- Safran RJ, Adelman JS, McGraw KJ, Hau M (2008) Sexual signal exaggeration affects physiological state in male barn swallows. *Curr Biol* 18:R461–R462
- Santos ESA, Maia R, Macedo RH (2009) Condition-dependent resource value affects male–male competition in the blue-black grassquit. *Behav Ecol* 20:553–559
- Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton
- Senar JC (2006) Color displays as intrasexual signals of aggression and dominance. In: Hill GE, McGraw KJ (eds) Bird coloration (volume II): function and evolution. Harvard University Press, Cambridge, pp 87–136
- Senar JC, Camerino M (1998) Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). *Proc R Soc Lond B Biol Sci* 265:1515–1520
- Senar JC, Camerino M, Copete JL, Metcalfe NB (1993) Variation in black bib of the Eurasian siskin (*Carduelis spinus*) and its role as a reliable badge of dominance. *Auk* 110:924–927
- Shawkey MD, Estes AM, Siefferman L, Hill GE (2005) The anatomical basis of sexual dichromatism in non-iridescent ultraviolet–blue structural coloration of feathers. *Biol J Linn Soc* 84:259–271
- Shawkey MD, Estes AM, Siefferman LM, Hill GE (2003) Nanostructure predicts intraspecific variation in ultraviolet–blue plumage colours. *Proc R Soc Lond B Biol Sci* 270:1455–1460
- Sheldon BC, Andersson S, Griffith SC, Ornborg J, Sendecka J (1999) Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402:874–877
- Siebeck UE (2004) Communication in coral reef fish: the role of ultraviolet colour patterns in damselfish territorial behaviour. *Anim Behav* 68:273–282
- Siefferman L, Hill GE (2003) Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behav Ecol* 14:855–861
- Siefferman L, Hill GE (2005a) Male eastern bluebirds trade future ornamentation for current reproductive investment. *Biol Lett* 1:208–211
- Siefferman L, Hill GE (2005b) UV–blue structural coloration and competition for nestboxes in male eastern bluebirds. *Anim Behav* 69:67–72
- Siefferman L, Hill GE (2007) The effect of rearing environment on blue structural coloration of eastern bluebirds (*Sialia sialis*). *Behav Ecol Sociobiol* 61:1839–1846
- Siitari H, Alatalo RV, Halme P, Buchanan KL, Kilpimaa J (2007) Color signals in the black grouse (*Tetrao tetrix*): signal properties and their condition dependency. *Am Nat* 169:S81–S92
- Svensson L (1992) Identification guide to European passerines, 4th edn. British Trust for Ornithology, Stockholm
- Tibbetts EA, Dale J (2004) A socially enforced signal of quality in a paper wasp. *Nature* 432:218–222
- Tibbetts EA, Lindsay R (2008) Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. *Biol Lett* 4:237–239
- Tibbetts EA, Safran RJ (2009) Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows. *J Evol Biol* 22:2376–2386
- Vedder O, Korsten P, Magrath MJL, Komdeur J (2008) Ultraviolet plumage does not signal social status in free-living blue tits: an experimental test. *Behav Ecol* 19:410–416
- Vedder O, Schut E, Magrath MJL, Komdeur J (2009) Ultraviolet crown coloration affects contest outcomes among male blue tits, but only in the absence of prior encounters. *Functional Ecology* 24:417–425
- von Schantz T, Bensch S, Grahn M, Hasselquist D, Wittzell H (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proc R Soc Lond B Biol Sci* 266:1–12
- Whiting MJ, Stuart-Fox DM, O'Connor D, Firth D, Bennett NC, Blomberg SP (2006) Ultraviolet signals ultra-aggression in a lizard. *Anim Behav* 72:353–363
- Zahavi A (1975) Mate selection: selection for a handicap. *J Theor Biol* 53:205–214