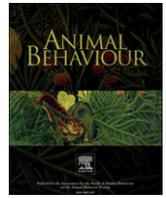




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Female–female aggressiveness is influenced by female coloration in blue tits

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Social and intrasexual competition for access to food, territory and reproduction is a major selection force acting on male phenotypes. In contrast, its evolutionary consequences for female phenotypes, especially female ornamentation, have been overlooked. Because fighting is costly for individuals, physical indicators of status that are correlated with aggressiveness or fighting ability are predicted to evolve. Under the badge of status hypothesis, individuals are predicted to attack unknown rivals that present signals of similar size or intensity more vigorously than dissimilar rivals. We used blue tits, *Cyanistes caeruleus*, to test whether UV/blue and yellow coloration mediates female aggression. We exposed territorial birds to two female blue tit decoys during nest building: one had a UV/blue crown with an enhanced UV signal (UV+) and the other had a reduced UV signal (UV–). We found that resident females with higher UV signal more often landed on the cage containing the UV+ decoys whereas females with a lower UV signal more often landed on the cage containing the UV– decoys. This result suggests that UV/blue crown coloration is a badge of status and supports the hypothesis that female–female competition can generate or maintain female ornamentation. Resident females with darker yellow chests also attacked the decoys with greater intensity. Previous studies suggest that brighter yellow females invest more in reproduction and consequently could be more sexually attractive. So, this last result may be explained by a higher motivation of darker yellow females or a trade-off between aggressiveness and female investment in reproduction.

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In species in which both males and females have ornaments, there is ongoing debate as to whether female ornaments are sexually selected signals (Amundsen 2000; Clutton-Brock 2009) or are nonfunctional by-products of selection on male ornaments (Lande 1980). The potential role of sexual selection (i.e. male mate choice and female–female competition) in the evolution of female ornaments has only recently been studied (Amundsen 2000; Lebas 2006; Clutton-Brock 2009). There is an increasing number of examples of males choosing mates based on female ornaments (Amundsen et al. 1997; Amundsen & Forsgren 2001; Griggio et al. 2005; Torres & Velando 2005; Bateman & Fleming 2006), which suggests that ornaments can signal quality. However, there are few demonstrations that female ornaments are involved in female–female competition (Murphy et al. 2009a; Swaddle & Witter 1995), even though three reviews have recently underlined the importance of investigating female–female competition experimentally (Lebas 2006; Kraaijeveld et al. 2007; Clutton-Brock 2009).

Competition is a major selection force that shapes the evolution of life history traits and strategies. In males, it can result in impressive morphological traits such as deer antlers or beetle horns; such

traits can serve as weapons during male–male competition. In various taxa, females also compete for access to food or reproduction (birds: Rosvall 2008; mammals: Robinson & Kruuk 2007; reptiles: While et al. 2009; insects: Papadopoulos et al. 2009; Watson & Simmons 2010; fishes: Dijkstra et al. 2009b). Various factors can determine the willingness to engage in escalating and potentially injurious fights: (1) the value of the defended resource and the motivation of the opponents (Brown et al. 2006; Jonart et al. 2007); (2) the individual level of aggressiveness, which could be consistent across different situations (i.e. personality trait: Sih et al. 2004) and (3) the individual's fighting ability, linked to his or her ability to control a given resource (i.e. resource-holding potential: Jonart et al. 2007).

Because fighting is costly for both opponents, phenotypic signals that reliably signal an individual's fighting ability or aggressiveness to their opponents are predicted to influence behaviour (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Senar 1990; Chaine & Lyon 2008). Both opponents can avoid costly fights and injuries by using these badges of status (Rohwer 1977; Rohwer & Ewald 1981) with the prediction that individuals with similar signals would be more likely to fight with each other. Badges of status have been studied extensively in males of many species (birds: reviewed in Senar 2006; fishes: e.g. Dijkstra et al. 2009a; Grether 1996; mammals: e.g. Bergeron et al. 2010; reptiles: e.g. Anderholm et al. 2004). In general, pigment-based colorations of plumage

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patches have been identified as important badges of status. In males, it has been shown that melanin-based plumage is linked to individual status and aggressiveness (e.g. Lemel & Wallin 1993; Gonzalez et al. 2002; Tarof et al. 2005; Bokony et al. 2008; Tibbetts & Safran 2009) while carotenoid-based plumage is related to individual fighting ability (e.g. Evans & Hatchwell 1992; Mateos & Carranza 1997; Pryke et al. 2001). Ducrest et al. (2008) proposed that melanin-based coloration could be tied to aggressiveness because of the pleiotropic effects of genes controlling melanin production and aggressiveness. Carotenoid-based coloration could be linked to fighting ability because carotenoid pigments are a limited resource that can only be acquired from one's diet and are used in signalling, detoxification and immune function. Consequently, it is predicted that only high-quality individuals would be able to allocate carotenoids to signalling (Lozano 1994; Olson & Owens 1998; von Schantz et al. 1999; Faivre et al. 2003). Although the role of plumage structural coloration in intrasexual competition has only recently been investigated, it seems that this type of coloration also has some impact on male competitive interactions (Alonso-Alvarez et al. 2004; Siebeck 2004; Siefferman & Hill 2005b; Whiting et al. 2006; Korsten et al. 2007b; Rémy et al. 2010).

Although West-Eberhard (1979) proposed that status signalling should occur in both sexes, only a few studies have linked female ornaments and female aggressiveness or fighting ability (Swaddle & Witter 1995; Murphy et al. 2009a, b; Griggio et al. 2010). Moreover, female ornamentation is rarely manipulated (Murphy et al. 2009a), which is an essential step to prove its function as a badge of status. Lastly, no study has ever controlled for asymmetry in female ornament intensity or size between opponents, even though it is this asymmetry between opponents that is predicted to influence the interaction between unfamiliar individuals.

Here, we tested whether female plumage structural and carotenoid-based colorations in blue tits, *Cyanistes caeruleus*, were linked to female aggressive response and whether they influenced female–female contests over nest sites and mates in the wild. Blue tits are territorial (Dhondt et al. 1982) and can breed in nestboxes. They are socially monogamous and social partners can engage in extrapair copulations (Dhondt 1987; Kempenaers et al. 1992; Charmantier & Blondel 2003). In the studied population, 14% of the offspring in 46% of the nests come from extrapair copulations (Charmantier & Blondel 2003). Polygyny can also occur when females settle on an already occupied territory and nestlings in polygynous males' nests usually receive less parental care. In blue tit populations, about 20% of males and 35% of females are engaged in a polygynous mating (Kempenaers 1994). In our population this is rarer (about 1–2%; P. Perret et al. unpublished data). Resident females are known to be very aggressive against intruding females, especially early in the breeding season and this aggressiveness affects the probability of settlement by female intruders (Kempenaers 1994). In males, several studies suggest that the UV reflectance of the UV/blue crown influences male–male interactions (Alonso-Alvarez et al. 2004; Rémy et al. 2010; Vedder et al. 2010; but see Korsten et al. 2007a; Vedder et al. 2008). The UV/blue crown is sexually dichromatic, with that of females reflecting less UV and being overall less bright than that of males (Hunt et al. 1998). The female's UV/blue crown seems to be linked to female survival (Doutrelant et al. 2008), but whether it can also have a role in female–female competition remains untested. Moreover, the chest carotenoid-based coloration is known to be linked to female maternal quality (Doutrelant et al. 2008; A. Midamegbe et al., unpublished data) and male parental quality (Senar et al. 2002). However, it is unknown whether it could serve as a badge of status and be involved in intrasexual competition in blue tits.

We tested the effect of the UV/blue crown coloration of the female intruder on female territorial response by simultaneously presenting two stuffed female decoys to resident females during nest building;

one model had a crown with an enhanced UV signal (UV+) and the other had a reduced UV signal (UV–). We then recorded female and male behaviour and tested whether female response towards each decoy was related to the UV/blue crown coloration of both the intruding and the resident females. According to the badge of status hypothesis, we predicted that resident females with higher UV reflectance would show greater territorial responses to the UV+ decoy, whereas females with lower UV reflectance would invest more in defending against the UV– decoy.

We also tested the relationship between female coloration (both yellow chest and UV/blue crown) and overall female aggressiveness towards both decoys. In these analyses, we included other phenotypic female traits such as body size (Olsson 1992) and age (Smith & Metcalfe 1997) that could affect reaction towards the decoys.

METHODS

Study Population

We studied a population of blue tits located in southern France (Montarnaud; 43°40'N, 03°40'E). Their habitat is a broadleaved deciduous forest of downy oaks. The population has been studied since 1991 and breeds in nestboxes. Each year, breeding birds are captured and their reproduction is monitored (Blondel et al. 2006).

Behavioural trials were conducted on 48 pairs of birds from 23 March to 22 April 2009. Because the focal individuals had to be identified individually to have their behaviour scored, we captured as many individuals as possible before the trials took place. During these captures, we gave each bird a unique colour ring combination. In addition, we collected six UV/blue crown feathers and eight yellow chest feathers from each bird for colour measurements and measured tarsus lengths with a digital calliper to the nearest 0.02 mm. Bird sex and age were determined based on the colour of the wing coverts (Svensson 1992). Birds were ringed under CRBPO authorization and captured under the authorization of the Prefecture de l'Hérault.

We captured 30 females and 38 males before the behavioural trials. On average \pm SD, they were captured 24 ± 20 days before the trial (range 3–61 days), either with mist nets (79%) or in their nests at night (21%). We used caged birds to attract the focal birds into the net. To evaluate whether this could have affected future responses towards the decoys, we tested whether the time since the capture had an effect on behavioural responses during trials. The number of days between the capture and the trial did not influence the individual behaviours towards the intruders (i.e. the number of times they attacked the intruders: GLM: estimate \pm SE = -0.004 ± 0.003 , $N = 68$ females and males, $P = 0.16$).

Some birds were captured only after the trial ($N = 5$ females and $N = 1$ male) with mist nets. There were no effects of the capture mode (i.e. mist net capture versus capture at night and captured before versus after the trial) on the individual behaviour during trials (two-tailed t tests, respectively: $t_{12,91} = 0.38$, $P = 0.71$ and $t_{19,57} = 0.75$, $P = 0.46$).

Colour Measurements and Colour Variables

The reflectance of the feathers collected from the focal males and females was measured with an AVASPEC-2048 spectrophotometer (Avantes, Eerbeek, The Netherlands), a deuterium–halogen light source (AVALIGHT-DH-S lamp, Avantes) that covers the spectral range of 300–700 nm visible to blue tits (Hart et al. 2000), and a 200 μ m fibre-optic probe. Feather coloration was measured following the same procedure as in Doutrelant et al. (2008).

Colour spectra information was extracted using Avicol software v3 (available upon request from D. Gomez at dodogomez@yahoo.fr). For both colour patches, brightness was calculated as the mean

reflectance over the range of 300–700 nm (computed as the area under the curve divided by the width of the interval 300–700 nm), in order to include the whole range of bird colour sensitivity (Hart et al. 2000). Chroma and hue were computed based on the shape of the reflectance spectra (e.g. Andersson et al. 1998; Delhey et al. 2003; Doutrelant et al. 2008). To estimate UV/blue crown coloration, UV chroma was defined as the mean reflectance between 300 and 400 nm divided by the mean reflectance over the range 300–700 nm. We computed hue as the wavelength at maximum reflectance. For yellow chest coloration, we computed chroma as the difference between the maximal reflectance between 500 and 700 nm and the reflectance at 450 nm divided by the average reflectance ($R_{\max(500-700\text{ nm})} - R_{450}$)/ R_{AV} . This approach should directly indicate the influence of carotenoids, which maximally absorb around 450 nm (Andersson & Prager 2006). We did not compute hue parameters for yellow coloration because of the double-peaked nature of these carotenoid-based spectra.

All our measurements were significantly repeatable with $P < 10^{-3}$ (Lessells & Boag 1987; in focal females and males: UV/blue crown: brightness repeatability $R = 0.81$; hue $R = 0.77$; UV chroma $R = 0.74$; yellow chest: brightness $R = 0.52$; chroma $R = 0.63$; in models: brightness_{UV/blue crown} $R = 0.75$; hue_{UV/blue crown} $R = 0.99$; UV chroma_{UV/blue crown} $R = 0.89$). In males, all the colour variables of the UV/blue crown were significantly correlated (brightness/hue: $r_{24} = 0.43$, $P = 0.03$; brightness/UV chroma: $r_{24} = -0.67$, $P < 10^{-2}$; hue/UV chroma: $r_{24} = -0.66$, $P < 10^{-2}$), whereas the colour variables of the yellow chest (yellow brightness and yellow chroma) were not significantly correlated ($r_{24} = -0.18$, $P = 0.36$). In females, UV chroma_{UV/blue crown} and hue_{UV/blue crown} were highly correlated ($r_{28} = -0.62$, $P < 10^{-2}$), whereas brightness_{UV/blue crown} was not significantly correlated with hue_{UV/blue crown} ($r_{28} = -0.28$, $P = 0.14$) and UV chroma_{UV/blue crown} ($r_{28} = -0.21$, $P = 0.27$). Yellow chest brightness and chroma were negatively correlated ($r_{28} = -0.53$, $P < 10^{-2}$).

In the following analyses, we chose to use brightness and hue to describe female UV/blue crown coloration. UV chroma was excluded because it was highly correlated with hue and because the focal birds' hues were below the values of the UV+ decoys and above the values of the UV- decoys (Table 1), which was not the case for the UV chroma because of its higher sensitivity to brightness (UV chroma = $(R_{\max(500-700\text{ nm})} - R_{450})/R_{AV}$). None the less, the analyses using UV chroma instead of hue gave similar results (see the Appendix for more information). Both brightness_{yellow chest} and chroma_{yellow chest} were used because they were less strongly correlated and are supposed to indicate different components of yellow coloration: brightness is related to feather structure, whereas chroma is tied to carotenoid incorporation in the feathers (Shawkey & Hill 2005).

Simulated Territorial Intrusions

Six 1-year-old female blue tit decoys were used. These females died naturally over the course of the long-term monitoring programme and were conserved at -20°C . During taxidermic preparation, they were placed in neutral life-like perched postures and

their heads were made removable. This allowed us to randomize the combinations of bodies and heads during the experiments and to test whether the crown UV reflectance (versus correlated aspects of individual phenotype) was responsible for the focal pair behaviours (Alonso-Alvarez et al. 2004).

Shortly before the start of the experiments, we changed the coloration of the decoys. To this purpose, we painted the decoy crowns with Edding 4500 'T-shirt markers' to modify UV reflectance (Delhey et al. 2007; Poesel et al. 2007). The light-blue marker (colour 10) was used to increase UV reflectance (UV+) and the dark blue (colour 003) to reduce UV reflectance (UV-). Crown reflectance was measured before and after treatment and was frequently checked over the course of the trials. The crown was repainted with the same marker as before if it was necessary.

After treatment, the reflectance spectra of both decoy groups were different but still resembled those of untreated birds in overall shape (Fig. 1). UV+ heads reflected more in the UV (higher UV chroma), had a more UV-shifted peak (lower hue) and were brighter than UV- heads, whereas before UV manipulation, these values were intermediate (Table 1, Fig. 1). All colour variables of the decoy UV/blue crown were significantly correlated (brightness/hue: $r_4 = -0.87$, $P = 0.02$; brightness/UV chroma: $r_4 = 0.91$, $P < 10^{-2}$; hue/UV chroma: $r_4 = -0.96$, $P < 10^{-2}$).

On average, focal females (females tested in our experiment) had intermediate values of hue between UV-treated decoys, lower brightness and higher UV chroma (Table 1, Fig. 1). Phenotypes equivalent to our manipulated ones have been found in our population and other female characteristics remained unchanged (sexual dimorphism for multiple regions of plumage, e.g. upper side of tail, white crown, Hunt et al. 1998, and size, Blondel et al. 2002), so we believe that UV-manipulated decoys represented realistic females.

The behavioural trials took place during nest building. Each focal pair was exposed to two decoys at the same time: a UV+ and a UV- decoy. We presented the decoys simultaneously rather than sequentially to facilitate their discrimination by the focal bird (Leitao & Riebel 2003; MacLaren & Rowland 2006; Korsten et al. 2007a). Indeed, studies showed that behavioural responses could be weaker when manipulated decoys are presented in sequence (e.g. MacLaren & Rowland 2006) and many variables other than coloration could explain a difference in bird behaviour on different days (motivation, condition, presence of predators, competitors). The decoys were placed in individual small wire cages (9×11 cm and 13 cm high) to avoid damage to them by focal individuals. These cages were attached to either end of a pole 1.2 m long. Before each experiment, we secured the pole to the top of the nestbox with string such that each decoy was 60 cm from the box (Fig. 2). The two observers (A.M. and C.D.) were not aware of which decoy (UV+ or UV-) was in which cage.

To attract the resident pair to the nestbox, we placed a loudspeaker that produced a male blue tit song about 2 m away. To attract the male to the loudspeaker rather than to the female decoy, we let the playback run during the experiment. Previous playback experiments show that blue tit males react aggressively towards male song (e.g. Doutrelant et al. 2000; Poesel & Dabelsteen 2006). The observers were hidden below the vegetation at about 10 m from

Table 1

Mean values of the UV/blue crown coloration of the focal females and of the UV+ and UV- decoys before and after UV/blue crown manipulation

| | Brightness (%) | Hue in nm | UV chroma |
|-------------------------|---------------------------|------------------------|------------------------|
| Focal females | 10.87±3.75 (4.05, 22.61) | 380.83±8.47 (363, 399) | 0.38±0.03 (0.32, 0.43) |
| UV+ decoys | 23.52±2.11 (21.14, 25.18) | 362.67±6.81 (355, 368) | 0.33±0.00 (0.33, 0.34) |
| UV- decoys | 13.60±4.88 (7.98, 16.78) | 452.33±2.31 (451, 455) | 0.26±0.01 (0.25, 0.28) |
| Decoys before treatment | 17.51±2.84 (14.40, 21.03) | 384.83±7.49 (375, 394) | 0.31±0.02 (0.29, 0.34) |

Means ± SDs are given, with minimum and maximum values in parentheses.

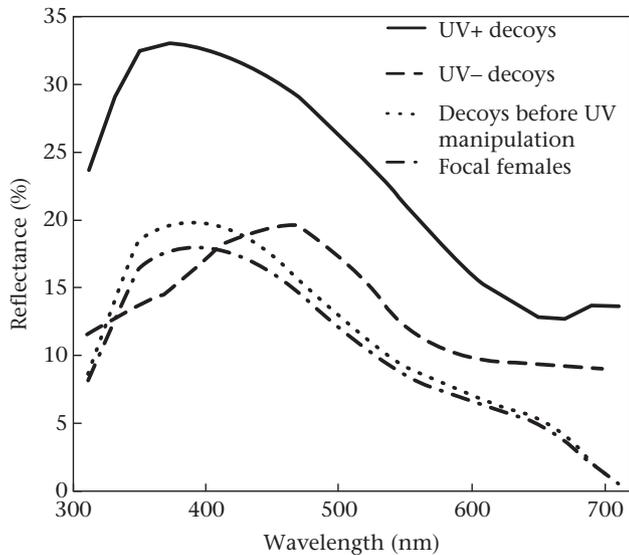


Figure 1. Mean reflectance spectra of the UV/blue crowns of the UV+ and UV- decoys before and after UV manipulation and of the focal females. $N_{UV+ \text{ decoys}} = 3$, $N_{UV- \text{ decoys}} = 3$, $N_{\text{focal females}} = 28$.

the nestbox. They recorded the behaviours of both the focal male and female over the first 10 min following the female's arrival within 5 m of the nestbox.

Trials were performed on a total of 48 pairs of birds. Eight of the 48 pairs did not show up at the trial and, in three trials, only the male showed up whereas the female was not seen. In comparing

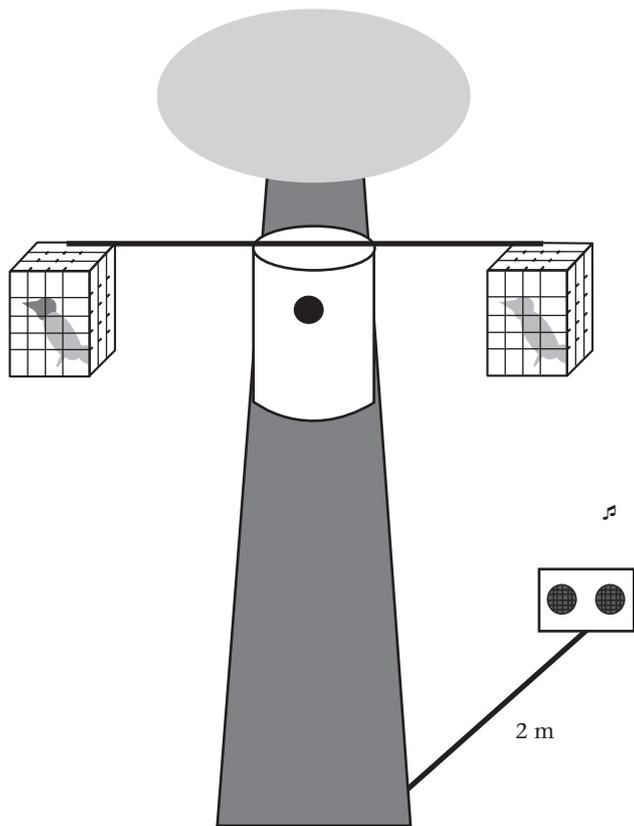


Figure 2. Schematic representation of the experiment. UV-modified female decoys were placed in small wire cages. The cages were attached to a 1.2 m pole that was placed on an occupied nestbox with a nest in construction. A loudspeaker that produced a male blue tit song during the trials was placed approximately 2 m from the nestbox tree.

female and male behaviours, we took into account all the trials performed where both reacted ($N = 37$). In contrast, only the pairs in which females were present during the trial and had been captured were considered in further analyses ($N = 30$).

We assessed focal female behaviour using the following estimates of intensity of aggression: (1) the number of times the focal individual touched each wire cage containing the decoys, (2) the proportion of time spent on each wire cage and (3) the proportion of time spent at less than 2 m at the side of each decoy and from both decoys. These variables are commonly used to describe aggressiveness in this type of experiment (e.g. Slagsvold 1993; Alonso-Alvarez et al. 2004; Rémy et al. 2010). The same behaviours were recorded for focal males. Female and male behaviours during the trials are described in Table 2.

Behavioural responses towards the decoy were highly variable between individuals (Table 2) and females were significantly more aggressive towards the female decoys than males (two-tailed t tests: all $P < 10^{-2}$; Table 2).

Within females, variables describing behavioural responses towards the decoys were highly correlated (all Spearman rank correlations: $r_s > 0.81$, $P < 10^{-3}$). Because of this high correlation between the aggressiveness variables, we retained only one behavioural response in the analyses. First, as touching an opponent represents the ultimate and unambiguous aggressive behaviour, we omitted the proportion of time spent at less than 2 m. Then, we kept the number of times each intruder was touched (rather than proportion of time on each opponent's cage), as this behaviour represents independent repeated aggressive events that could better represent aggressiveness than time spent on the cage if the focal individual had stayed on the cage for unrelated reasons. Lastly, the number of times each intruder was touched has the additional advantage of representing a more natural behaviour than the fact of standing on an opponent's cage. However, similar results were found with either variable.

The male behaviour as well as the number of days between the trial and the laying date did not have any significant effect on the females' overall aggressiveness towards both decoys (i.e. on whether or not they touched the decoy cages and on the number of times females touched the decoy cages; GLMs: all $P > 0.48$).

Data Analyses

All data analyses were performed with R 2.8.1 (Ihaka & Gentleman 1996).

Responses towards decoys in relation to coloration

We tested whether the females reacted differently towards the two decoys (UV+ or UV-) and whether female focal coloration influenced this reaction.

Table 2
Description of female and male behaviour during behavioural trials

| | Minimum | Maximum | Mean | SD |
|---|---------|---------|------|-------|
| Females | | | | |
| Proportion of time spent on both cages | 0 | 0.95 | 0.21 | 0.28 |
| Number of times the cages were touched | 0 | 43 | 9.49 | 12.21 |
| Proportion of time spent at less than 2 m from decoys | 0 | 1 | 0.56 | 0.48 |
| Males | | | | |
| Proportion of time spent on both cages | 0 | 0.52 | 0.03 | 0.09 |
| Number of times the cages were touched | 0 | 24 | 2.05 | 5.24 |
| Proportion of time spent at less than 2 m from decoys | 0 | 1 | 0.18 | 0.26 |

$N = 48$ trials.

First, for the 30 captured females, we used as the dependent variable a binomial variable indicating whether or not the female touched the caged decoy ($N = 18$ females touched at least one of the two caged decoys: 13 touched both, three touched only the UV+ decoy and two touched only the UV– decoy; 12 females did not touch either). In this model, we specified a binomial family error.

Second, we considered the 18 females that touched at least one of the decoy cages and used as the dependent variable the number of times the females touched one or the other decoy cage. In this model, we specified a Poisson family error. In both cases, we used generalized linear models with mixed effects (GLMMs) fitted by the Laplace approximation with type III errors in which female identity was included as a random effect. Wald Z tests were used to calculate the P values (Bolker et al. 2009).

The explanatory variables used in these two GLMMs were the decoy phenotype (UV+ or UV–) and the following double interactions: decoy phenotype*brightness_{UV/blue crown} and decoy phenotype*hue_{UV/blue crown}.

We used a backward procedure to select the best model with only variables with a significant effect ($P \leq 0.05$).

Overall female aggressiveness and coloration

We subsequently tested, for the 30 captured females, which factor could explain the important variation observed in females' overall aggressiveness towards the two decoys (Table 2). Our two dependent variables were (1) whether or not the female touched one of the caged decoys and (2) the total number of times both cages were touched by the 18 females that touched one at least once.

We used GLMs with type III errors, using binomial family error and Poisson family error, respectively.

The explanatory colour variables included in the models were female brightness_{UV/blue crown}, hue_{UV/blue crown}, brightness_{yellow chest} and chroma_{yellow chest}. In addition, to test the effect of the mate's attractiveness (and thus his coloration), we included male coloration in the analyses (brightness_{UV/blue crown}, hue_{UV/blue crown}, brightness_{yellow chest} and chroma_{yellow chest}). We also tested the effect of female age (yearling versus more than 1 year old) and body size (tarsus length), which could both be correlated with female fighting ability (age: Smith & Metcalfe 1997; body size: Olsson 1992).

Because of the high number of variables tested and the small sample sizes, we used a forward procedure to select the best model (Reunanen 2003). First, we separately tested the effect of each variable. We then included one by one in the model only the variables with a $P \leq 0.05$, starting with those with the lowest P values. In the final model, we only kept the variables and interactions with a P that remained ≤ 0.05 .

To confirm our results, we also used backward procedures with only the female variables (i.e. blue and yellow coloration, age and tarsus length) and found the same final models.

RESULTS

Responses Towards Decoys in Relation to Coloration

None of the variables tested had a significant effect on whether or not the female touched one of the caged decoys at least once (all $P > 0.61$).

The number of times a female touched a caged decoy was significantly explained by the interaction between the decoy's UV/blue crown phenotype and the female hue_{UV/blue crown} (Table 3, Fig. 3). Less UV females (i.e. those with a higher value of hue) were more aggressive against the UV– decoys and more UV females (i.e. those with a lower value of hue) were more aggressive against the UV+ decoy (Fig. 3).

Table 3

Results of the GLMMs conducted to determine whether female aggressiveness was influenced by the decoy's UV/blue crown coloration

| Number of times the female touched the decoy cage | Estimate | SE | P |
|---|----------|-------|-------|
| Minimal adequate model | | | |
| Intercept | 9.32 | 9.78 | 0.341 |
| Decoy (UV+ or UV–) | 13.90 | 6.22 | 0.025 |
| Female hue | –0.02 | 0.02 | 0.446 |
| Female hue*decoy (UV+ or UV–) | –0.04 | 0.02 | 0.024 |
| Nonsignificant variables | | | |
| Female brightness | 0.007 | 0.081 | 0.932 |
| Female brightness*decoy (UV+ or UV–) | 0.04 | 0.05 | 0.371 |

For the nonsignificant variables not included in the final model, we report estimate, SE and P values when they were excluded from the model. $N = 18$ trials in which females touched the decoy cages at least once.

Overall Female Aggressiveness and Coloration

None of the tested variables had a significant effect on whether or not the female touched at least one caged decoy (all $P > 0.11$).

Among the females that touched the decoys, only female brightness_{yellow chest} had a significant effect on the number of times the female touched them (Table 4). Those that touched more of the decoys were darker (Table 4, Fig. 4). All the other variables tested were nonsignificant.

DISCUSSION

Using an experimental approach, we tested whether UV/blue and yellow coloration mediates female physical aggression in blue tits. As predicted by the badge of status hypothesis, we found that female UV/blue crown coloration affected the female's reaction towards female intruders. More UV females (i.e. lower hue) were more aggressive towards UV-enhanced intruders, whereas less UV females (i.e. higher hue) were more aggressive towards UV-reduced intruders. Furthermore, we found a high degree of variability in females' overall aggressiveness (Table 2); some females never attacked intruders whereas others landed on the caged decoys up to 43 times in 10 min. Part of this variability was associated with female coloration. Females with darker yellow chests were more aggressive towards the intruders.

Using UV-manipulated females allowed us to ascertain that female aggressiveness was influenced by the coloration of the female intruder. Manipulating the UV/blue coloration of intruding birds to investigate intrasexual competition has been done in only five studies, all on male blue tits (Alonso-Alvarez et al. 2004; Korsten et al. 2007a; Vedder et al. 2008, 2010; Rémy et al. 2010). We can

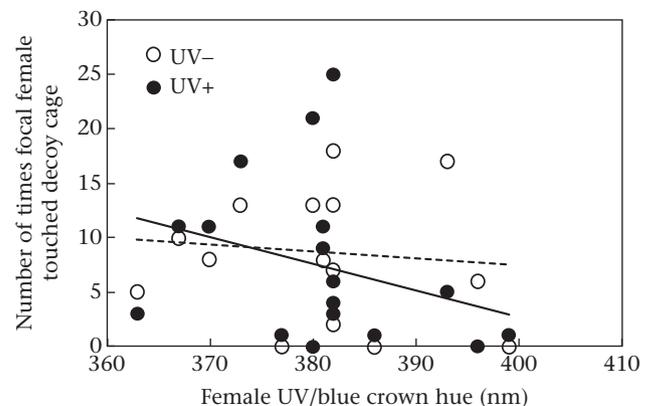


Figure 3. Relationship between focal female UV/blue crown hue and the number of times the female touched the UV+ and the UV– decoy cages.

Table 4

Results of the GLMs conducted to determine which variables influenced the overall female aggressiveness estimated by the number of times the female touched the caged decoys

| Number of times the female touched the caged decoys | Estimate | SE | P |
|---|----------|------|------------|
| Minimal adequate model | | | |
| Intercept | 5.44 | 0.94 | $<10^{-3}$ |
| Female brightness _{yellow chest} | -0.17 | 0.06 | 0.014 |
| Nonsignificant variables tested separately | | | |
| Female brightness _{UV/blue crown} | 0.02 | 0.06 | 0.739 |
| Female hue _{UV/blue crown} | 2.45 | 6.65 | 0.718 |
| Female chroma _{yellow chest} | 1.31 | 1.01 | 0.211 |
| Female tarsus length | 0.02 | 0.42 | 0.963 |
| Female age (yearling versus more than 1 year old) | 0.39 | 0.35 | 0.281 |
| Male brightness _{UV/blue crown} | -0.02 | 0.06 | 0.720 |
| Male hue _{UV/blue crown} | 5.00 | 8.19 | 0.552 |
| Male brightness _{yellow chest} | -0.02 | 0.09 | 0.861 |
| Male chroma _{yellow chest} | -0.72 | 1.46 | 0.629 |

$N = 18$ trials in which females touched the decoy cages at least once.

conclude from these studies, in particular from those that manipulated unfamiliar individuals (Alonso-Alvarez et al. 2004; Rémy et al. 2010; Vedder et al. 2010), that UV/blue crown coloration influences the initial reaction of territorial males. In males, however, the results were different from what we found in females. Indeed, in males, the signal asymmetry between the focal males and the decoy did not influence their aggressiveness (Rémy et al. 2010). This difference could be due to the way in which the experiments were conducted (e.g. in a natural population during spring versus in captivity during the winter). It could also reveal a real dissimilarity in the way males and females react towards the UV/blue crown coloration of same-sex opponents. It is important to highlight that all of these studies, including the present one, suggest that UV/blue crown coloration is used in intrasexual interactions in both sexes and that it has the potential to evolve under sexual or social selection.

In our experiment, we presented the decoys simultaneously to facilitate the discrimination of the decoy coloration by the focal females (Leitao & Riebel 2003; MacLaren & Rowland 2006; Korsten et al. 2007a). Outside the breeding season, females are likely to be faced with several females with different phenotypes during agonistic interactions (e.g. for access to food). However, our experimental set-up may represent more unrealistic agonistic interactions during the nest-building period. The unrealistic situation could explain the fact that many females did not touch any of the decoys (12 out of 30) and that we did not find any correlation between the

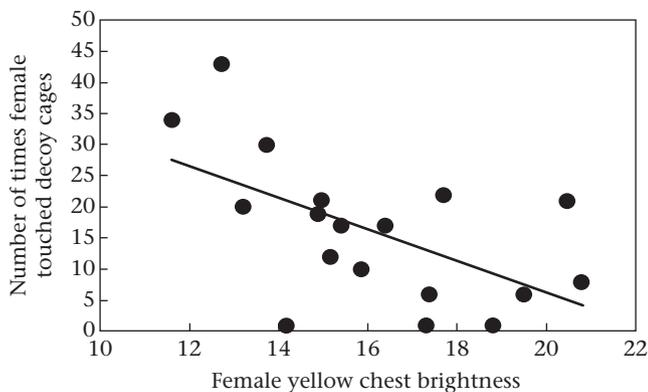


Figure 4. Relationship between female yellow chest brightness and the number of times that females attacked the decoys among females that touched the decoy cages at least once. $N = 18$ trials.

likelihood to attack the decoy and female coloration. Only a study testing an intrusion with a single female could tell us whether or not the results are comparable.

Badges of status might reflect aggressiveness or fighting ability. Aggressive individuals possess a high propensity to escalate contests independently of their real fighting ability (Barlow et al. 1986; Maynard Smith & Harper 1988). The UV/blue coloration of the female decoys affected the reaction of the resident females in an assortative manner (i.e. females with higher UV reflectance were more aggressive towards the UV+ decoy and vice versa), yet we did not find any association between the overall aggressiveness of the resident female and her UV/blue coloration. Such a result suggests that the UV/blue crown coloration signals fighting ability rather than aggressiveness. This suggestion is in agreement with previous studies in male blue tits that did not establish a clear link between testosterone and UV/blue crown coloration (Peters et al. 2006; Roberts et al. 2009), testosterone being linked more to aggressiveness than to real fighting ability. It also agrees with previous studies that suggested a link between UV/blue crown coloration and quality (e.g. in blue tits: Doutrelant et al. 2008; C. Doutrelant et al., unpublished data). In other species, structural coloration has been found to be condition dependent (McGraw et al. 2002; Hill et al. 2005; Siefferman & Hill 2005a; Siitari et al. 2007) as well as involved in intrasexual competition (Siebeck 2004; Siefferman & Hill 2005b; Whiting et al. 2006), suggesting it could commonly be associated with fighting ability.

In contrast, we found that the variability in female aggressiveness towards both decoys was associated with the brightness of their yellow chest. Darker yellow females were more aggressive towards female intruders. Because no effect of yellow chroma was found, this result contrasts with previous studies in which yellow chroma or size of the yellow patch was found to affect aggression (e.g. Pryke et al. 2001; Murphy et al. 2009a; Griggio et al. 2010).

At least three explanations can account for the fact that darker yellow females were more aggressive. First, darker yellow plumage could indicate that females deposited more carotenoid in the chest plumage (Andersson & Prager 2006). So, more ornamented females that were able to allocate more carotenoid to signalling may also have been more capable of being more aggressive against female intruders. However, in this case we would have expected to find also an effect of yellow chroma, which is the variable directly influenced by carotenoid deposition in feathers (Andersson & Prager 2006).

Second, this result might reflect a difference of motivation rather than a difference in fighting ability or aggressiveness (e.g. Lemel & Wallin 1993). McGraw et al. (2007) also found that drab male house finches, *Carpodacus mexicanus*, tended to be more aggressive than bright males during the breeding season and the winter. They explained their results by proposing that because drab males are less sexually attractive, they could gain more by elevating aggression. In female blue tits, it has been shown that brighter yellow females are better quality females (higher reproductive success: Doutrelant et al. 2008; higher transfer of carotenoids in eggs: A. Midamegbe et al., unpublished data). Consequently, if males choose mates using this trait, a similar explanation might apply. Compared to brighter females, darker resident females (who are potentially less attractive) may have more to gain by being more aggressive against intruding females to defend their nest site and/or mate.

A last alternative explanation is that brightness of the yellow chest is linked to female aggressiveness as part of a behavioural syndrome. It has been shown that some behavioural traits are correlated and are consistent across situations (Sih et al. 2004). Recent studies have suggested that melanin-based plumage coloration is associated with behavioural traits owing to the pleiotropic effect of hormones influencing both pigmentation and behaviour (Ducrest et al. 2008), and that individuals with more melanin are more aggressive. In tits,

Isaksson et al. (2008) have proposed that variation in yellow brightness also depends on the difference in levels of melanin pigment incorporated into the greyish basal part of the feather; more incorporated melanin renders the feathers darker. As a result, darker yellow females in our study could have had more melanin incorporated into their feathers and could have been more aggressive because of the pleiotropic link between melanin and aggressiveness. To explain the observed link and to discriminate between these different hypotheses, further investigation is needed. The use of decoys with manipulated yellow coloration in a more neutral context is especially essential.

We found that males were less aggressive than females. This result was expected given that our experimental approach included distracting the male with played-back song. This finding supports the hypothesis that there is a sexual difference in territorial defence. Because same-sex intruders are more likely to challenge territorial tenure and to take over mates, it is expected that males would turn their aggressiveness towards other males whereas females would be more aggressive towards intruding females. In the streak-backed oriole, *Icterus pustulatus* (Murphy et al. 2009a), there was also an observed sexual difference in territorial defence: females were more aggressive than males against female intruders, especially when female intruders were more colourful. These results suggest that the females perceived a greater risk of losing their territory or mate than the males when the intruders were females. This could be also the case in blue tits.

In conclusion, this study suggests that UV/blue crown coloration could be used as a badge of status among blue tit females and that yellow coloration is linked to aggressiveness. These differing results for differing coloration types are an additional example of multiple signalling in a context of intrasexual competition. Indeed, both Bokony et al. (2008) and Chaîne & Lyon (2008) found that different signals provided different information: some signals are used at short versus long distances in lark buntings, *Calamospiza melanocorys*, and some signals are used in aggression versus defence in house sparrows, *Passer domesticus*.

The evidence found in our study that coloration affects female–female interactions supports the hypothesis that female–female competition generates and/or maintains female ornamentation. This is especially interesting as traits selected through female–female competition could also be used by males to choose higher quality females, as previously proposed by Lebas (2006), thus reinforcing female ornamentation.

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APPENDIX

We present here the analyses that included UV chroma instead of hue for the UV/blue crown coloration.

Methods

The statistical procedures were exactly the same as described above.

Results

Responses towards decoys in relation to coloration

None of the variables tested had a significant effect on whether or not the female touched one of the caged decoys. The number of times a female touched a caged decoy was significantly explained by the interaction between the decoy's UV/blue crown phenotype and the female's UV chroma (Table A1, Fig. A1). Less UV females (i.e. those with a lower value of the UV chroma) were more aggressive against the UV– decoys and more UV females were more aggressive against the UV+ decoy (Fig. A1). This result is similar to that found with the analyses conducted with the UV/blue crown hue and leads to the same interpretations (see the Discussion below).

Overall female aggressiveness and coloration

As described in the Results in the main text, only the female's brightness_{yellow chest} had a significant effect (Table 4).

Discussion

As expected given the strong positive correlation between UV chroma and hue, the results obtained using both colour indexes were similar. Females with a short-wave hue and a higher UV chroma reacted more to UV-enhanced decoys, whereas females with long-wave hue and lower UV chroma reacted more to UV-reduced decoys. This suggests that the UV-coloration of a female intruder affects the reactions of territorial females.

However, both UV-manipulated decoys had a UV chroma value inferior to the value of the focal females (Table 1). Indeed, although our manipulation produced decoys with significantly different hue, brightness and UV chroma (i.e. below and above the values of the decoys before treatment: Table 1) and with higher and lower values of hue and brightness than the focal females, it did not strongly increase the UV chroma.

The moderate value of the UV chroma of the UV+ decoys is explained by the way the UV chroma is calculated. This index is computed as the ratio of the reflectance over the UV range 300–400 nm to the reflectance over the whole range 300–700 nm. In the manipulated UV+ decoys, our treatment did increase the reflectance in the UV range, but also more generally in the whole range (see Table 1, Fig. 1). As a consequence, the UV chroma was only slightly increased by our manipulation and because the decoys before manipulation presented a lower UV chroma than the focal females (Table 1), the difference in UV chroma remains.

What are the consequences for our results? Because we successfully changed the appearance of both types of decoy in the expected direction, and the focal female could choose to react to a UV-increased or UV-decreased opponent (Fig. 1), we think the

consequences are moderate. In agreement with this idea, if we consider the mean reflectance in the UV of the UV+ decoys (i.e. UV chroma*brightness), it is higher than the mean reflectance in the UV of the focal females (UV+: 7.82 ± 0.68 ; UV–: 3.64 ± 1.44 ; decoys before treatment: 5.44 ± 0.71 ; focal females: 4.08 ± 1.39).

This discussion, however, leads us to a more general note on the use of UV chroma and hue to represent an achromatic index of coloration. UV chroma is interesting because it describes the response in the UV relative to the other parts of the spectrum, as a relative photoreceptor excitation would do. However, as we saw above, it is also very sensitive to variation in brightness. Hue is computed as the wavelength of maximal reflectance and is thus not mathematically linked to brightness. As a consequence, brightness can change without affecting hue and hue seems, at least in our case, a better chromatic parameter than UV chroma.

Table A1

Results of the GLMMs conducted to determine whether female aggressiveness was influenced by the model's UV/blue crown coloration

| Number of times the female touched the decoy cage | Estimate | SE | P |
|---|----------|------|-------------------|
| Intercept | 4.36 | 3.49 | 0.211 |
| Decoy (UV+ or UV–) | –7.44 | 2.22 | <10 ^{–3} |
| Female UV chroma | –6.85 | 9.42 | 0.477 |
| Female UV chroma*decoy (UV+ or UV–) | 19.55 | 5.93 | <10 ^{–3} |

The final model contains only variables or two-way interactions with $P \leq 0.05$. $N = 18$ trials in which females touched the decoy cages at least once.

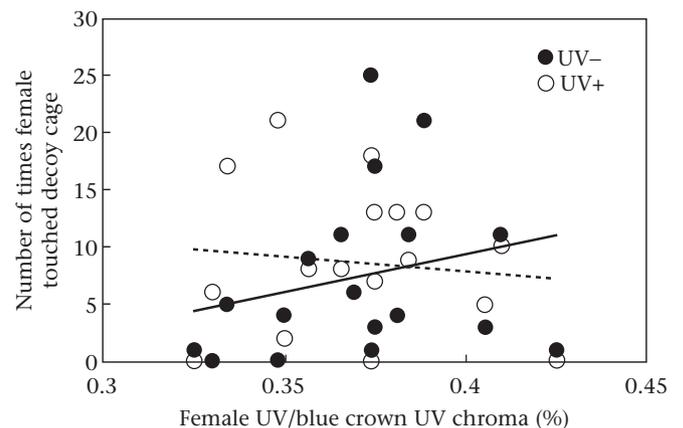


Figure A1. Relationship between female UV chroma and the number of times the female touched the UV+ and the UV– decoy cages.