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Korsten, Peter; Vedder, Oscar; Szentirmai, István; Komdeur, Jan

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Absence of status signalling by structurally based ultraviolet plumage in wintering blue tits (*Cyanistes caeruleus*)

Peter Korsten · Oscar Vedder · István Szentirmai ·
Jan Komdeur

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Abstract Structurally based ultraviolet (UV)-reflective plumage parts can be important cues in mate choice. However, it remains largely unknown if UV plumage variation can also function as a signal of social status during competitive interactions. In blue tits (*Cyanistes caeruleus*), the UV-reflective crown plumage functions as a female mate choice cue that probably indicates male quality, as males with higher UV reflectance have been shown to have better chances of over-winter survival. Possibly, the UV crown plumage acts as a status signal in the competition over scarce food sources during winter. To test this idea, we related dominance of individuals at an artificial food source during adverse winter conditions to spectrophotometric measurements of their crown plumage. However, while controlling for the confounding effects of sex, age, and distance from territory, we found no significant effect of crown UV reflectance on dominance. Consistent with this result, we also found no relation between crown UV reflectance and over-winter survival. We conclude that the structurally based UV reflectance of the blue tit crown feathers plays little role in competition between individuals during winter despite its importance as a cue in mate choice.

Keywords Ultraviolet plumage · Status signalling · Site-dependent dominance · Winter flocks · Blue tit *Cyanistes* (formerly *Parus*) *caeruleus*

Introduction

Bright and conspicuous plumage colours in birds can function as cues in mate choice (Hill 1991; Andersson 1994) and as signals of social status, which individuals use to settle conflicts over food, territories and mates (Rohwer 1975; Møller 1990; Pryke et al. 2001a). The use of colored plumage patches ('badges of social status') to settle conflicts over limited resources is thought to be beneficial to both dominant and subordinate individuals because competing individuals of unequal fighting ability do not need to waste time and energy or risk injury in assessing each other's fighting ability (Rohwer 1982). To maintain the honesty of such status signals, individuals that express a signal of high dominance without actually having superior competitive ability ('cheaters') should pay some cost (e.g., Maynard Smith and Harper 1988; Johnstone and Norris 1993). Such costs of producing and maintaining bright plumage coloration could be increased predation risk, direct energetic or nutrient limitation, hormone-mediated immunosuppression, or an increase in the frequency of aggressive encounters with high-status individuals (Møller 1987; Folstad and Karter 1992; Slagsvold et al. 1995; Olson and Owens 1998; Buchanan et al. 2001).

Bright plumage colors in birds are produced by pigments, mostly carotenoids or melanins, which are deposited in the feathers, or by the nanostructure of the feather barbs (reviewed in Hill and McGraw 2006). In contrast to pigment-based plumage color variation, which is primarily in the human-visible part of the spectrum, structurally based

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P. Korsten (✉) · O. Vedder · J. Komdeur
Animal Ecology Group, Centre for Ecological
and Evolutionary Studies, University of Groningen,
P.O. Box 14, 9750 AA Haren, The Netherlands
e-mail: p.korsten@rug.nl

I. Szentirmai
Department of Ethology, Eötvös University,
Pázmány P. sétány 1/C,
Budapest 1117, Hungary

plumage coloration can also vary in the ultraviolet (UV; Andersson 1999; Prum et al. 2003; Shawkey et al. 2003). Traditionally, studies of avian color communication have mainly focused on pigment-based color variation that is visible to human observers (Bennett et al. 1994). However, many bird species, including most passerine species tested to date, are capable of detecting wavelengths in the UV section of the spectrum (320–400 nm; Cuthill 2006), and structurally based, UV-reflective plumage parts are widespread among many avian taxa (Eaton and Lanyon 2003; Hausmann et al. 2003). These findings make it very likely that birds use UV plumage colors both as cues in mate choice and as signals of social status during conflicts. UV color variation has indeed been shown to act as a mate choice cue in several bird species (Andersson and Amundsen 1997; Bennett et al. 1997; Andersson et al. 1998; Hunt et al. 1998; Siitari et al. 2002; Delhey et al. 2003; Komdeur et al. 2005; but see Liu et al. 2007). However, until now, the role of UV plumage colors in avian communication other than in a mate choice context, such as in interindividual conflicts (but see Pryke and Griffith 2006), or outside the breeding season remains largely unknown.

To evaluate if structurally based UV plumage coloration functions as a signal of social status during competitive interactions among nonbreeding birds, we investigated if natural variation in UV reflectance of the crown feathers of blue tits (*Cyanistes caeruleus*) indicates social dominance during winter. Blue tits often erect or flatten their crown feathers during agonistic interactions with conspecifics (Stokes 1962; Scott and Deag 1998), indicating a signalling function of the crown feathers in the context of competition. The crown feathers, which appear bright blue to human observers, reflect also substantially in the UV. Blue tits are sexually dimorphic with respect to this UV component of the crown reflectance, i.e., males reflect more UV than females (Andersson et al. 1998; Hunt et al. 1998). Furthermore, the UV reflectance of the crown plumage is an important cue in both social and extra-pair mate choice (Andersson et al. 1998; Hunt et al. 1998; Delhey et al. 2003). The UV reflectance may also function as a signal in male–male territorial conflicts during the breeding season, as breeding males were shown to react more aggressively towards a mounted conspecific male with natural crown UV reflectance than towards a mount with reduced crown UV reflectance (Alonso-Alvarez et al. 2004; but see Korsten et al. 2007). Possibly, blue tit crown UV reflectance signals individual viability or quality, as in a Swedish population, males with higher UV reflectance during the breeding season were found to have higher subsequent over-winter survival (Sheldon et al. 1999; Griffith et al. 2003).

We hypothesize that blue tit UV coloration has not only a signalling function in mate choice and male–male territorial conflicts during the breeding season but also

functions as a signal of social status within flocks of wintering birds. During winter, blue tits (and some other species of the *Paridae* family) aggregate in loosely organized foraging flocks ('basic flocks') that roam the area in search for food (Colquhoun 1942; Ekman 1989). We suggest that, within these flocks, highly UV-reflective individuals may be more successful at monopolizing food sources, which could be a proximate explanation for their demonstrated greater survival chances (Sheldon et al. 1999; Griffith et al. 2003). To evaluate if highly UV-reflective individuals have higher dominance and priority access to food sources, we related the dominance of individuals at an artificial food source to spectrophotometric measurements of their crown plumage. Furthermore, we measured travel distances that these individuals had to cover from their territories to the food source. This enabled us to control our analyses for the potentially confounding effects of site-dependent dominance, i.e., the phenomenon that individuals are more dominant at sites closer to their own territory (Colquhoun 1942; De Laet 1984; Oberski and Wilson 1991; Dingemanse and De Goede 2004; Hansen and Slagsvold 2004). While controlling for sex, age, and distance to territory, we tested if (1) social dominance was related to crown UV reflectance and (2) individuals with higher UV reflectance had a greater probability of survival to the following breeding season as reported previously (Sheldon et al. 1999; Griffith et al. 2003; but see Delhey and Kempenaers 2006).

Materials and methods

Study area and population

This research was conducted during the winter of 2002/2003 on the estate of 'De Vosbergen', near Groningen, The Netherlands (53°08'N, 06°35'E). The study area of approximately 50 ha contains about 185 nestboxes designed for blue tits and consists of patches of mixed deciduous and coniferous forest interspersed by patches of open grassland. The blue tit population breeding at the Vosbergen estate has been monitored during the breeding seasons of 2001–2004, and during this period, all breeding adults were routinely captured with mist nets or in nestboxes when feeding the nestlings. All captured adults and nestlings were marked with a uniquely numbered metal band. In addition, all adults were marked with a unique combination of color bands.

For the present study, we provided continuous food supply in the form of balls of clumped seeds and fat at a feeding table near a field station in the center of the study area from October 2002 to January 2003. We captured blue tits at the feeding table with baited cage traps from 26

November 2002 to 13 January 2003 and while roosting in nestboxes at night during two rounds: from 19 November to 4 December 2002 and from 20–27 January 2003. Individuals were aged as first-winter birds or older (see Svensson 1992). We measured body mass (± 0.1 g) and length of tarsus (± 0.1 mm). Spectrophotometric measurements of crown color were made, and blood samples (about 20 μ l) were taken by a puncture of the brachial vein. DNA extracted from these blood samples was used to identify the individuals' sex using sex-specific molecular markers (P2 and P8; Griffiths et al. 1998). Following Sheldon et al. (1999) and Griffith et al. (2003), we defined over-winter survivors as birds that were recaptured when breeding in the study area the following spring; non-survivors were defined as birds that were not recaptured.

Measurements of crown UV reflectance

We captured 166 individual blue tits, 91 males and 75 females, of which we made spectrophotometric measurements of crown color. Of these, 95 individuals were captured and measured once, 55 were captured and measured on 2 separate days, 14 on 3 days, and 2 on 4 days, yielding a total of 255 measurements. Mean number of days (\pm SD) between first and second, second and third, and third and fourth captures were 44 ± 17 , 22 ± 11 , and 25 ± 10 days, respectively.

The spectral reflectance of the crown feathers was measured with an USB-2000 spectrophotometer with illumination by a DH-2000 deuterium-halogen light source (both Avantes, Eerbeek, The Netherlands). The measuring probe was held at a right angle against the plumage, i.e., both illumination and recording were at 90° to the feathers. During each crown reflectance measurement, we took five replicate readings and smoothed each of these reflectance spectra by calculating the running mean over 10-nm intervals. See Fig. 1 for mean reflectance spectra of the crown plumage of first-year and older males and females. Following previous studies of UV color signalling in blue tits (e.g., Andersson et al. 1998; Sheldon et al. 1999; Griffith et al. 2003; Delhey et al. 2003), we calculated three indices describing the variation in crown coloration—'brightness,' 'hue,' and 'UV chroma'—from each reflectance spectrum and averaged these across the five replicate spectra. 'Brightness' was the sum of reflectance between 320 and 700 nm ($R_{320-700}$), which corresponds to the spectral range visible to blue tits (Hart et al. 2000). 'Hue' was the wavelength of maximum reflectance, $\lambda(R_{\max})$. 'UV chroma' was the sum of reflectance between 320 and 400 nm divided by the sum of reflectance between 320 and 700 nm ($R_{320-400}/R_{320-700}$). Both the 'hue' and 'UV chroma' indices have previously been identified as important predictors of male attractiveness and viability in blue tits (Andersson et al. 1998; Sheldon et al. 1999; Delhey et al.

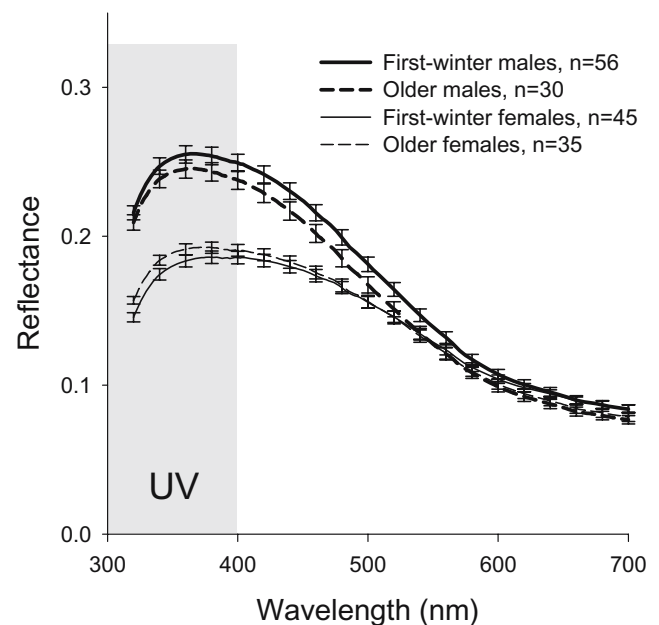


Fig. 1 Mean crown reflectance spectra of first-year and older male and female blue tits during winter. Multiple measurements of same individuals taken on different days were averaged before calculation of the mean reflectance spectra. Standard errors of the means are depicted at 20-nm intervals. The shaded area indicates the UV part of the spectrum

2003; Griffith et al. 2003). Hue and UV chroma values were significantly correlated (Table 1).

In accordance with previous findings (Örnberg et al. 2002), we found that blue tit crown color changed over time, as indicated by significant regressions of all color indices on date of capture (brightness: $R=0.52$, $P<0.001$; hue: $R=0.26$, $P<0.001$; UV chroma: $R=-0.20$, $P=0.001$; all $n=255$). This pattern was also present within individuals that were captured on at least 2 separate days (paired t -tests comparing crown color of first and last capture: brightness: $t=-10.51$, $P<0.001$; hue: $t=-4.67$, $P<0.001$; UV chroma: $t=3.04$, $P=0.003$; all $df=70$) and is probably due to feather wear or the accumulation of dirt or fat (Örnberg et al. 2002). Therefore, we used the residuals of the regressions of crown color indices on capture date in our further analyses. Residual crown color measurements were repeatable within individuals between separate days of capture (brightness: repeatability= 0.50 , $F_{70,89}=3.26$, $P<0.001$; hue: repeatability= 0.60 , $F_{70,89}=4.40$, $P<0.001$; UV chroma: repeatability= 0.75 , $F_{70,89}=7.86$, $P<0.001$; Lessells and Boag 1987). In case crown color of an individual had been measured on more than 1 day, we used average values of these separate measurements in our analyses.

Competitive interactions and estimation of social dominance

We observed competitive interactions between blue tits competing for food at the feeding table from a distance of

winter of 2002/2003 (84 males, 59 females). Individual males and females were recorded at up to two breeding locations (one in 2002 and one in 2003) and three roosting locations (in the winter of 2002/2003). Based on these repeated individual recordings, we calculated the repeatability of travel distances. This analysis showed that distances were highly repeatable within individuals, both in males (repeatability=0.94, $F_{59,116}=46.25$, $P<0.001$) and in females (repeatability=0.90, $F_{40,76}=26.15$, $P<0.001$; Lessells and Boag 1987).

Statistical analyses

Body mass was significantly related to time of day, both for captures at the feeding table during daytime ($R=0.58$, $n=76$, $P<0.001$) and captures in the nestboxes at night ($R=-0.22$, $n=179$, $P=0.003$). Therefore, we used residual body mass controlled for the time and period of day (day or night) in our further analyses. Multiple residual measures of body mass of single individuals were averaged. Also, tarsus length, which is constant over life, (Korsten and Komdeur, unpublished data) was averaged over repeated measurements within individuals. We used the $^{10}\log$ values of the calculated distances from the individuals' territories to the feeding table in our analyses because the distance-related decrease in dominance diminished at larger distances (see also Hansen and Slagsvold 2004). The distribution of residual values of hue deviated significantly from normal (Kolmogorov–Smirnov goodness of fit: $Z=1.51$, $P=0.021$; Fig. 2). Therefore, we log-transformed residual hue values using $^{10}\log(X+c)$ with a constant c which was equal to the absolute value of the smallest residual hue value+1 ($c=31.49$; following Quinn and Keough 2002). The constant was added because the residual hue distribution also contained negative values, and it is not possible to take the log of values ≤ 0 . The transformation substantially improved the distribution, and it was no longer deviating from normal ($Z=1.07$, $P=0.20$). Distributions of residual brightness and UV chroma values were not deviating from normal (both $Z<0.86$, $P>0.46$).

We used multilevel models with a binomial error distribution with a logit-link function to analyze the effect of sex, age, indices of crown coloration, and distance from territory on the proportion of interactions won, with interactions nested within individuals. The models were implemented using restricted iterative generalized least squares and second-order penalized quasi-likelihood approximation (Rasbash et al. 2004). Initially, sex, age, indices of crown coloration, and distance from territory were all simultaneously entered in the model. In addition, we entered body mass and tarsus length to control for potential effects of body size on dominance. Nonsignificant terms were excluded from the full model through backward

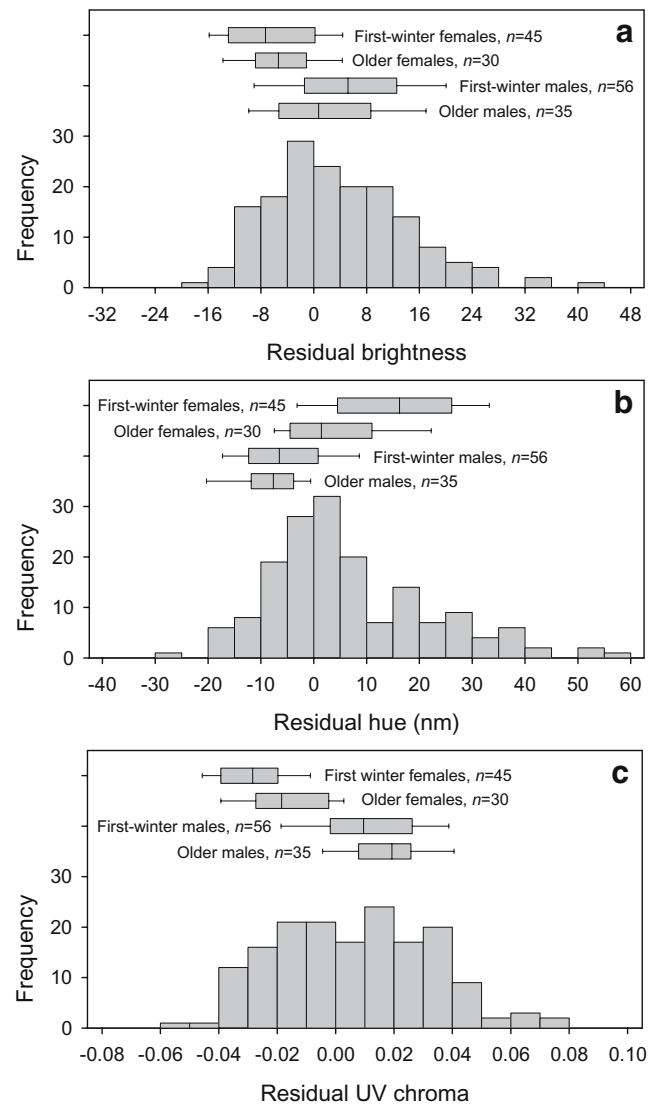


Fig. 2 Frequency distributions of crown color indices of wintering blue tits: residual brightness (a), hue (b), and UV chroma (c), controlled for the seasonal change of crown reflectance ($n=166$; males and females, and different age classes combined). Horizontal box plots show brightness (a), hue (b), and UV chroma (c) for males and females, and for first-winter and older birds. Boxes indicate the 25th and 75th percentiles, and whiskers indicate the 10th and 90th percentiles of the median. See also Table 2

selection of least significant terms. The significance of variables was tested using the Wald statistic, which follows a χ^2 distribution. Thereafter, all excluded variables were included, one by one, in the final model to confirm that they were not significant. Reported statistics and probabilities correspond to the inclusion of variables in the final model. Survival was analyzed using binary logistic regression models. Initially, sex, age, crown color indices, and also body mass and tarsus length were simultaneously entered. Again, we followed a backward selection procedure in which nonsignificant terms were sequentially excluded from the final model. For a correlation matrix of the main variables

Table 2 Influence of sex and age on crown coloration in wintering blue tits ($n=166$)

Crown color indices	Sex		Age		Sex×age	
	$F_{1,162}$	<i>P</i>	$F_{1,162}$	<i>P</i>	$F_{1,162}$	<i>P</i>
Brightness	43.98	<0.001	0.29	0.59	2.02	0.16
Hue	68.31	<0.001	10.52	0.001	0.811	0.37
UV chroma	170.93	<0.001	9.48	0.002	0.39	0.53

Results from ANOVAs with sex and age (first-winter vs older birds) as factors. Color indices are residuals controlled for seasonal change in crown reflectance. Residuals of hue were log-transformed (see “Materials and methods”). Significant *P* values ($P<0.05$) are in italics. See also Fig. 1

included in our analyses, see Table 1. An alpha significance level of 0.05 was used, and significance tests are two-tailed throughout. Multilevel models were carried out using MLwiN 2.02 and all other statistical tests using SPSS 13.0.

Results

Influence of sex and age on crown coloration

Crown color indices—brightness, hue, and UV chroma—showed rather continuous frequency distributions with considerable overlap between the sexes and the two age classes (Fig. 2). Nevertheless, males had, on average, brighter, more UV-shifted (lower hue), and more UV-chromatic crown plumage than females (Table 2; Fig. 2). First-winter birds had less UV-shifted and UV-chromatic crown color than older birds (Table 2; Fig. 2), whereas brightness was not different between the two age classes (Table 2; Fig. 2). Canonical discriminant analysis with the three crown color indices as predictor variables classified the individuals' sexes with an overall accuracy of 95.8% (84 of 91 males and 75 of 75 females were correctly classified). The age of 56.0% of males (51 out of 91) and

72.0% of females (54 out of 75) could be classified correctly.

Influence of crown coloration on dominance and survival

Multilevel models showed that distance from territory (Fig. 3), and sex and age (Fig. 4) together explained a significant part of the variation in dominance, whereas body mass, tarsus length, and the three crown color indices dropped from the final model as nonsignificant (Table 3). Logistic regression analysis showed that only age had a significant effect on survival, whereas sex, crown coloration, body mass, and tarsus length dropped from the model as nonsignificant terms (Table 4; Fig. 5).

Discussion

Previous studies of social status signalling have mainly focused on pigment-based plumage colors, and there is good evidence of a status signalling function for both

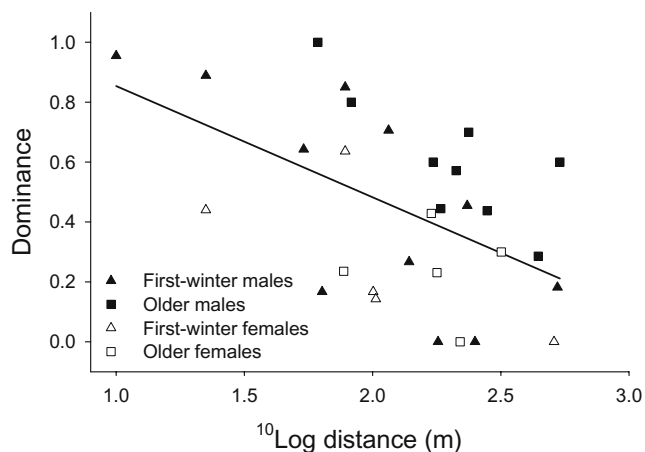


Fig. 3 Influence of distance from territory on dominance of wintering blue tits. Overall regression line was added for visual purposes only. See also Table 3

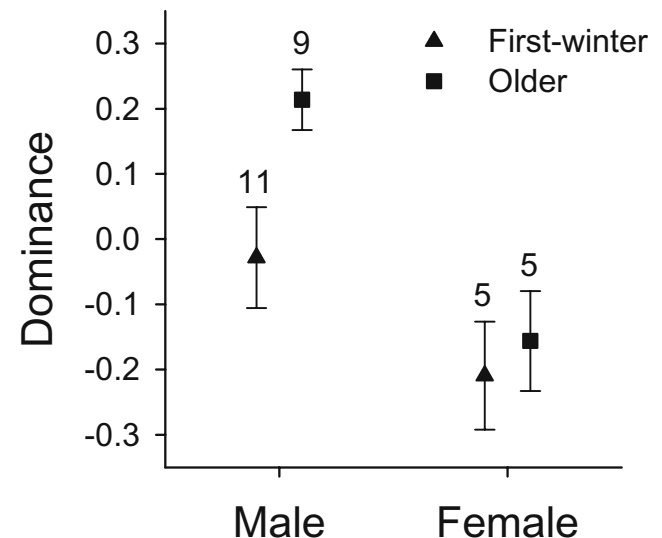


Fig. 4 Influence of sex and age (first-winter or older) on residual dominance (controlled for distance from territory) of wintering blue tits. Means with standard errors. Numbers indicate sample size. See also Table 3

Table 3 Influence of sex, age, crown coloration, body size, and distance from territory on dominance in wintering blue tits ($n=30$)

Explanatory variables	Coefficient (SE)	Wald (χ^2)	Δdf	<i>P</i>
Included				
Distance	−3.09 (0.65)	22.71	1	<0.001
Sex	2.05 (0.50)	16.80	1	<0.001
Age	1.44 (0.52)	7.65	1	0.006
Excluded				
Brightness	0.01 (0.02)	0.08	1	0.78
Hue	1.15 (1.53)	0.57	1	0.45
UV chroma	−9.58 (13.85)	0.48	1	0.49
Body mass	−1.03 (0.60)	2.93	1	0.09
Tarsus length	0.03 (0.59)	0.003	1	0.96

Results from a multilevel model analysis with a binomial error distribution with a logit-link function to analyze the effect of sex, age (first-winter vs older birds), indices of crown color (brightness, hue, and UV chroma), body mass, tarsus length, and distance from territory on the proportion of interactions won. Color indices are residuals after controlling for seasonal change in crown reflectance. Residuals of hue were log-transformed (see “Materials and methods”). See also Figs. 2 and 3.

melanin and carotenoid-pigmented plumage patches (e.g., Møller 1987; Pryke et al. 2001a, respectively). The present study investigated if structurally based plumage coloration can function as a signal of social status in the nonbreeding season. Contrary to our prediction, the results show that the structurally based UV coloration of the blue tit crown feathers plays no apparent role in competition between individuals during winter and is not significantly related to winter survival, despite its importance as a cue in mate choice.

UV coloration and dominance

Blue tits in our study population were clearly sexually dimorphic for crown UV coloration, which confirms previous studies in other populations and supports the idea that the UV crown plumage is a sexually selected trait important in female mate choice (Andersson et al. 1998; Hunt et al. 1998; Delhey et al. 2003). Furthermore, we

found that older birds of both sexes were more UV reflective than first-winter birds, which may be caused by age-dependent ornament expression (as we found no evidence for differential survival according to plumage color), and is typical for condition-dependent sexually selected characters (Andersson 1994; Siefferman et al. 2005). Given that the blue tit’s crown UV coloration is an important mate choice cue, crown color is also expected to act as a signal of social status in agonistic interactions because ornamental traits mostly have dual signalling functions in both mate choice and intra-sexual competition (Berglund et al. 1996). We found considerable and continuous variation in plumage UV reflectance (Fig. 2), also within sex and age classes, suggesting that there is scope for UV status signalling in wintering blue tits. However, we found no evidence for UV status signalling. After controlling for the effects of sex, age, and distance from territory, crown UV coloration did not significantly explain any additional variation in dominance. As males

Table 4 Influence of sex, age, crown coloration, and body size on survival to the following breeding season of wintering blue tits ($n=166$)

Explanatory variables	Coefficient (SE)	Wald (χ^2)	Δdf	<i>P</i>
Included				
Age	1.14 (0.34)	11.10	1	0.001
Excluded				
Sex	−0.13 (0.33)	0.15	1	0.70
Brightness	−0.01 (0.02)	0.37	1	0.54
Hue	−0.40 (0.75)	0.28	1	0.60
UV chroma	7.59 (6.31)	1.45	1	0.23
Body mass	−0.46 (0.34)	1.79	1	0.18
Tarsus length	−0.08 (0.34)	0.06	1	0.81

Results from logistic regression analysis with survival to the following breeding season as the dependent variable and sex, age (first-winter vs older birds), indices of crown color (brightness, hue, UV chroma), body mass, and tarsus length as explanatory variables. Color indices are residuals after correction for seasonal change in crown reflectance. Residuals of hue were log-transformed (see “Materials and methods”). See also Fig. 4.

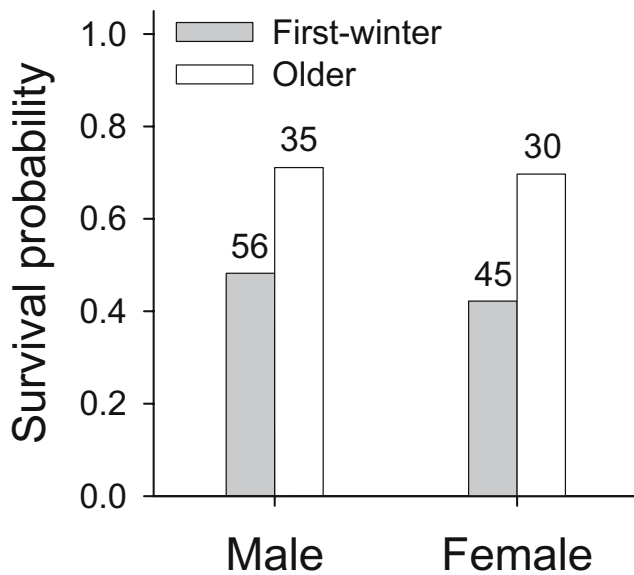


Fig. 5 Probability of survival to the following breeding season for blue tit males and females of two age classes, first-winter and older birds. Numbers indicate samples sizes. See also Table 4

and older birds were both more dominant and more UV reflective than females and first-winter birds, respectively, we cannot entirely exclude the possibility that individuals actually use UV crown plumage as a cue to assess other birds' sex and age, which information in turn determines the outcome of the individuals' interactions. But, although crown UV coloration was a good predictor of sex (95.8% of individuals correctly classified based on crown coloration), it was a rather poor predictor of age, especially in males (56.0% of males and 72.0% of females correctly classified). Consequently, crown UV coloration would be an unreliable indicator of age in competitive interactions. Although our correlational results strongly suggest that UV coloration does not function as a signal of social status, ultimately, experimental manipulations of crown UV coloration are necessary to unequivocally refute any link between winter dominance and crown UV coloration in blue tits. Another possibility that still needs to be tested is that between-individual variation in the size of the area of the UV reflecting crown plumage relates to individual dominance (for examples of such badge area related status signalling, see Järvi et al. 1987; Møller 1987; Pryke et al. 2001a).

UV coloration vs other determinants of dominance

Interestingly, we found distance from territory to be an important determinant of dominance (Fig. 2), indicating that dominance was strongly site-dependent, which is in line with previous studies on winter dominance in blue tits and some other species of the *Paridae* family (e.g., Dingemans and De Goede 2004; Hansen and Slagsvold 2004). Thus, the relative dominance of individual birds

within highly mobile flocks will be continuously changing depending on proximity to their territories, while obviously the appearance of their plumage or actual fighting ability does not. Therefore, an important part of the variation in dominance among individuals could not be caused by variation in plumage characteristics, and interindividual conflicts must have been resolved in different ways. As we rarely observed escalated fights, we suggest that the birds may use subtle behavioral cues to assess a competitor's motivation and likeliness to escalate a conflict (cf. Scott and Deag 1998). Such behavioral cues may also play a role in the resolution of conflicts between individuals of different sex and/or age classes.

Sex, age, and site-related effects are well documented and generally important determinants of social dominance in birds (reviewed by Piper 1997). In addition, many other factors have been identified that may influence the outcome of contests between individuals. These include contestants' prior experiences with each other (Lemel and Wallin 1993), their relative durations of food deprivation (Lemel and Wallin 1993), prior residency (Krebs 1982), early social experiences (Hansen and Slagsvold 2004), personality (Dingemans and De Goede 2004), and hormonal status (Järvi et al. 1987). The use of status signalling through colored plumage badges in the resolution of conflicts may in fact be limited to some quite specific contexts, given the large number of other factors which can potentially influence social dominance. It has indeed been suggested that status signalling through 'badges of social status' would only be evolutionary stable if the competing individuals are unfamiliar with each other and if there are no asymmetries between individuals in, for example, territorial status at the location of the conflict (Maynard Smith and Harper 1988; Wilson 1992). This may also explain why studies of status signalling have often found equivocal or inconsistent results, probably depending on the exact circumstances during the observations and/or the experimental design, leading to an ongoing debate on the generality of badge status signalling in birds (Wilson 1992; Senar 1999).

Similarly in blue tits, status signalling by the crown UV coloration may only be important under specific circumstances. For example, Alonso-Alvarez et al. (2004) showed that, during the breeding season, territorial males reacted more aggressively towards male taxidermic mounts with natural UV reflectance than towards mounts with reduced UV. In this experiment, territory owners could obviously not have used behavioral cues to assess the fighting ability or intentions of the (model) intruders and apparently adjusted their aggressive behavior to the relative UV reflectance of the models, which was the only perceivable difference between them. Note that a similar experiment in our study population which also involved model intruders,

but had a slightly modified experimental design, showed no evidence for a role of crown UV coloration in territorial conflict during the breeding season (Korsten et al. 2007).

In addition to the blue tit study of Alonso-Alvarez et al. (2004), two other recent studies in different species have suggested that structurally based coloration could be important as a status signal in male–male competition during the breeding season. Siefferman and Hill (2005) found a negative correlation between date of nestbox occupation and UV/blue coloration in male Eastern bluebirds (*Sialia sialis*), and Keyser and Hill (2000) found a positive correlation between territory quality and blue coloration of the owners in male blue grosbeaks (*Passerina caerulea*).

UV coloration and over-winter survival

The absence of a status signalling function of UV plumage in our population of wintering blue tits is consistent with the lack of a relation between survival to the following breeding season and UV coloration. Instead, over-winter survival was strongly dependent on age, with older birds having higher chances of survival (or acquisition of a breeding territory in the study area) than first-winter birds. This result is in contrast with two previous studies on a more northerly population in Sweden (Gotland) that reported higher chances of over-winter survival for more UV-reflective males (Sheldon et al. 1999; Griffith et al. 2003). In these previous studies, survival was measured from one breeding season to the next, whereas for the present study, we measured survival of birds that were present in winter to the following breeding season, which could have caused a discrepancy. However, a recent study on an Austrian blue tit population also showed no evidence for crown color-related survival, while survival in this study was estimated from one breeding season to the next (Delhey and Kempenaers 2006).

Possibly, plumage-based status signalling is more important in northerly blue tit populations, perhaps because these are less sedentary during winter. In these populations, individuals often leave their breeding areas when there is low food availability during cold weather (Smith and Nilsson 1987, and references therein). Under these circumstances, encounter rates between non-territorial, unfamiliar birds will be greater, and UV status signalling might be used to settle conflicts over food and shelter. This may eventually lead to higher over-winter survival of more UV-reflective individuals, as reported by Sheldon et al. (1999) and Griffith et al. (2003).

Mate choice cues vs signals of social status

The present study indicates that the UV coloration of the blue tit crown feathers may primarily function as a cue in

mate choice and not as an indicator of dominance during winter. This would be similar to the situation in the well-studied house finch (*Carpodacus mexicanus*; e.g. Hill 1991; McGraw and Hill 2000a, b), where females prefer mates with bright red carotenoid-based plumage coloration (Hill 1991), but red coloration does not reliably indicate male social status during the nonbreeding season (McGraw and Hill 2000a). Remarkably, during the breeding season, bright males may even be subordinate to drab males in competition over food (McGraw and Hill 2000b). Comparable results have been found in the red-collared widowbird (*Euplectes ardens*), in which long male tail feathers are selected by female choice, but males do not use tail length as a signal in agonistic interactions (Pryke et al. 2001a, b). In addition to their long tail, red-collared widowbird males have a red carotenoid collar badge, which they do use as a status signal in male–male competition, but which is in turn not favored by female choice (Pryke et al. 2001a, b). These studies, together with our findings in the blue tit, show for several types of ornamentation (elongated tail feathers, structural and pigment-based plumage colors) that male ornaments selected through female mate choice are not necessarily always important as signals of social status in competitive interactions or vice versa.

Interestingly, a recent comparative study suggested that the occurrence of sexually dimorphic structural plumage coloration among socially monogamous birds is related to especially sexual selection through extra-pair fertilizations, whereas this is not the case for melanin- and carotenoid-based coloration (Owens and Hartley 1998). Instead, melanin-pigmented plumage seems to be mainly important in agonistic signalling (Badyaev and Hill 2000; Jawor and Breitwisch 2003), while carotenoid-based plumage coloration may be important in both mate choice (Hill 1991; Badyaev and Hill 2000) and agonistic signalling (Pryke et al. 2001a). These findings suggest that the different types of plumage coloration may have been largely selected by different forms of social and/or sexual selection. This idea is consistent with our results that show that a structurally based and sexually selected plumage character plays little role in interindividual signalling in competitive interactions during winter.

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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 M (1994) Sexual selection. Princeton University Press, Princeton
- Andersson S (1999) Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *J Avian Biol* 30:193–204
- Andersson S, Amundsen T (1997) Ultraviolet colour vision and ornamentation in bluethroats. *Proc R Soc Lond B* 264:1587–1591
- Andersson S, Örnborg J, Andersson M (1998) Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc R Soc Lond B* 265:445–450
- Badyaev AV, Hill GE (2000) Evolution of sexual dichromatism: contribution of carotenoid-versus melanin-based coloration. *Biol J Linn Soc* 69:153–172
- Bennett ATD, Cuthill IC, Norris K (1994) Sexual selection and the mismeasure of color. *Am Nat* 144:848–860
- Bennett ATD, Cuthill IC, Partridge JC, Lunau K (1997) Ultraviolet plumage colors predict mate preferences in starlings. *Proc Natl Acad Sci USA* 94:8618–8621
- Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc* 58:385–399
- 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* 268:1337–1344
- Colquhoun MK (1942) Notes on the social behaviour of blue tits. *Br Birds* 35:234–240
- Cuthill IC (2006) Color perception. In: Hill GE, McGraw KJ (eds) *Bird coloration, vol 1: mechanisms and measurements*. Harvard University Press, Cambridge, pp 3–40
- De Laet J (1984) Site-related dominance in the great tit *Parus major major*. *Ornis Scand* 15:73–78
- Delhey K, Kempenaers B (2006) Age differences in blue tit *Parus caeruleus* plumage colour: within-individual changes or colour-biased survival? *J Avian Biol* 37:339–348
- 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* 270:2057–2063
- De Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim Behav* 55:827–843
- Dingemans NJ, De Goede P (2004) The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav Ecol* 15:1023–1030
- Eaton MD, Lanyon SM (2003) The ubiquity of avian ultraviolet plumage reflectance. *Proc R Soc Lond B* 270:1721–1726
- Ekman J (1989) Ecology of non-breeding social systems of *Parus*. *Wilson Bull* 101:263–288
- Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Griffith SC, Örnborg 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
- Hansen BT, Slagsvold T (2004) Early learning affects social dominance: interspecifically cross-fostered tits become subdominant. *Behav Ecol* 15:262–268
- Hart NS, Partridge JC, Cuthill IC, Bennett ATD (2000) Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J Comp Physiol A* 186:375–387
- Hausmann F, Arnold KE, Marshall NJ, Owens IPF (2003) Ultraviolet signals in birds are special. *Proc R Soc Lond B* 270:61–67
- Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337–339
- Hill GE, McGraw KJ (eds) (2006) *Bird coloration, vol 1: mechanisms and measurements*. Harvard University Press, Cambridge
- Hunt S, Bennett ATD, Cuthill IC, Griffith R (1998) Blue tits are ultraviolet tits. *Proc R Soc Lond B* 265:451–455
- Järvi T, Walsø Ø, Bakken M (1987) Status signalling by *Parus major*: an experiment in deception. *Ethology* 76:334–342
- Jawor JM, Breitwisch R (2003) Melanin ornaments, honesty, and sexual selection. *Auk* 120:249–265
- Johnstone RA, Norris K (1993) Badges of status and the cost of aggression. *Behav Ecol Sociobiol* 32:127–134
- Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav Ecol* 11:202–209
- Komdeur J, Oorebeek M, Van Overveld T, Cuthill IC (2005) Mutual ornamentation, age and reproductive performance in the European starling. *Behav Ecol* 16:805–817
- Korsten P, Dijkstra TH, Komdeur J (2007) Is UV signalling involved in male–male territorial conflict in the blue tit (*Cyanistes caeruleus*)? A new experimental approach. *Behaviour* 144:447–470
- Krebs JR (1982) Territorial defence in the great tit (*Parus major*): do residents always win? *Behav Ecol Sociobiol* 11:185–194
- Lemel J, Wallin K (1993) Status signalling, motivational condition and dominance: an experimental study in the great tit, *Parus major* L. *Anim Behav* 43:549–558
- Lessells CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. *Auk* 104:116–121
- Liu M, Siefferman L, Hill GE (2007) An experimental test of female choice relative to male structural coloration in eastern bluebirds. *Behav Ecol Sociobiol* 61:623–630
- Maynard Smith J, Harper DGC (1988) The evolution of aggression: can selection generate variability? *Philos Trans R Soc Lond B* 319:557–570
- McGraw KJ, Hill GE (2000a) Carotenoid-based ornamentation and status signaling in the house finch. *Behav Ecol* 11:520–527
- McGraw KJ, Hill GE (2000b) Plumage brightness and breeding-season dominance in the house finch: a negatively correlated handicap? *Condor* 102:456–461
- Møller AP (1987) Social control of deception among status signalling house sparrows *Passer domesticus*. *Behav Ecol Sociobiol* 20:307–311
- Møller AP (1990) Sexual behavior is related to badge size in the house sparrow *Passer domesticus*. *Behav Ecol Sociobiol* 27:23–29
- Oberski IM, Wilson JD (1991) Territoriality and site-related dominance: on two related concepts in avian social organization. *Ethology* 87:225–236
- Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol* 13:510–514
- Örnborg J, Andersson S, Griffith SC, Sheldon BC (2002) Seasonal changes in a ultraviolet structural colour signal in blue tits, *Parus caeruleus*. *Biol J Linn Soc* 76:237–245
- Owens IPF, Hartley IR (1998) Sexual selection in birds: why are there so many different forms of dimorphism? *Proc R Soc Lond B* 265:397–407
- Piper WH (1997) Social dominance in birds. Early findings and new horizons. *Curr Ornithol* 14:125–187

- Prum RO, Andersson S, Torres RH (2003) Coherent scattering of ultraviolet light by avian feather barbs. *Auk* 120:163–170
- Pryke SR, Griffith SC (2006) Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc R Soc Lond B* 273:949–957
- Pryke SR, Lawes JL, Andersson S (2001a) 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
- Pryke SR, Andersson S, Lawes JL (2001b) Sexual selection of multiple handicaps in red-collared widowbirds: female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Rasbash J, Steele F, Brown W, Prosser B (2004) A user's guide to MLwiN version 2.0. Institute of Education, London
- Rohwer SA (1975) The social significance of avian winter plumage variability. *Evolution* 29:593–610
- Rohwer SA (1982) The evolution of reliable and unreliable badges of fighting ability. *Am Zool* 33:531–546
- Scott GW, Deag JM (1998) Blue tit (*Parus caeruleus*) agonistic displays: a reappraisal. *Behaviour* 135:665–691
- Senar JC (1999) Plumage colouration as a signal of social status. In: Adams NJ, Slotow RH (eds) Proceedings of the 22nd international ornithological congress, Durban. BirdLife South Africa, Johannesburg, pp 1669–1686
- Shawkey MD, Estes AM, Siefferman LM, Hill GE (2003) Nanostructure predicts intraspecific variation in ultraviolet-blue plumage colour. *Proc R Soc Lond B* 270:1455–1460
- Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J (1999) Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402:874–877
- Siefferman L, Hill GE (2005) UV-blue structural coloration and competition for nestboxes in male eastern bluebirds. *Anim Behav* 69:67–72
- Siefferman L, Hill GE, Dobson FS (2005) Ornamental plumage coloration and condition are dependent on age in eastern bluebirds *Sialia sialis*. *J Avian Biol* 36:428–435
- Siitari H, Honkavaara J, Huhta E, Viitala J (2002) UV reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Anim Behav* 63:97–102
- Slagsvold T, Dale S, Kruszewicz A (1995) Predation favours cryptic coloration in breeding male pied flycatchers. *Anim Behav* 50:1109–1121
- Smith HG, Nilsson J-Å (1987) Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): an evaluation of different hypotheses. *Auk* 104:109–115
- Stokes AW (1962) Agonistic behaviour among blue tits at a winter feeding station. *Behaviour* 19:118–138
- Svensson L (1992) Identification guide to European passerines. Fingraf, Stockholm
- Wilson JD (1992) A re-assessment of the significance of status signalling in populations of wild great tits, *Parus major*. *Anim Behav* 43:999–1009