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Avian sex allocation and ornamental coloration

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CHAPTER

7

Absence of status signalling by structurally based ultraviolet plumage in wintering blue tits

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Submitted

ABSTRACT

Structurally based ultraviolet-reflective plumage parts can be important cues in mate choice. However, it remains largely unknown if ultraviolet (UV) plumage variation can also function as a signal of social status during competitive interactions. In blue tits (*Parus 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 higher chances of over-winter survival. Possibly, the UV crown plumage acts as a status signal in 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.

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 coloured 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 (Rowher 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 & Harper 1988; Johnstone & 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 & Karter 1992; Slagsvold *et al.* 1995; Olson & Owens 1998; Buchanan *et al.* 2001).

Bright plumage colours in birds are produced by pigments, mostly carotenoids or melanins, which are deposited in the feathers, or by the nanostructure of the feather barbs (Hill & McGraw 2006a). In contrast to pigment-based plumage colour variation, which is primarily in the human-visible part of the spectrum, structurally based plumage coloration can also vary in the ultraviolet (UV) (Andersson 1999; Prum *et al.* 2003; Shawkey *et al.* 2003). Traditionally, studies of avian colour communication have mainly focused on pigment-based colour 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 & Lanyon 2003; Hausmann *et al.* 2003). These findings make it very likely that birds use UV plumage colours both as cues in mate choice and as signals of social status during conflicts. UV colour variation has indeed been shown to act as a mate choice cue in several bird species (Andersson & 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). However, until now the role of UV plumage colours in avian communication other than in a mate choice context, such as in inter-individual conflicts, or outside the breeding season remains largely unknown.

To evaluate if structurally based UV plumage coloration can function as a signal of social status during competitive interactions among non-breeding birds, we investigated if natural variation in UV reflectance of the crown feathers of blue tits (*Parus caeruleus*) indicates social dominance during winter. Blue tits often erect or flatten their crown feathers during agonistic interactions with conspecifics (Stokes 1962; Scott & Deag 1998), indicating a signalling function of the crown feathers in

the context of competition between individuals. The crown feathers, which appear bright blue to human observers, also reflect 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 Chapter 6). 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 *Parus* species) 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 in 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 the distances that these individuals had to travel 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 *et al.* 1984; Oberski & Wilson 1991; Dingemanse & de Goede 2004; Hansen & Slagsvold 2004). While controlling for sex, age and distance to territory, we tested if: (1) social dominance was related to crown UV reflectance; (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).

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 *ca.* 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 was monitored during the breeding seasons of 2001–2004, and during this period all breeding adults were routinely captured with mistnets or in nestboxes when feeding the nestlings. All captured adults and nestlings were marked with a uniquely numbered metal ring. In addition, all adults were marked with a unique combination of colour rings.

For the present study we provided a continuous food supply in the form of balls of seeds and fat at a feeding table near a fieldstation in the centre of the study area from October 2002–January 2003. We captured blue tits at the feeding table with baited cage traps from 26 November 2002–13 January 2003, and while roosting in nestboxes at night during two periods: from 19 November–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 tarsus length (± 0.1 mm). Spectrophotometric measurements of crown colour were made and blood samples (ca. 20 μ L) were taken by puncture of the brachial vein. DNA extracted from these blood samples was used to identify the sex of individuals using sex specific molecular makers (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; nonsurvivors 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 colour. Of these, 95 individuals were captured and measured once, 55 were captured and measured on two separate days, 14 on three days, and 2 on four 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 5 replicate readings and smoothed each of these reflectance spectra by calculating the running mean over 10 nm intervals. See Figure 7.1 for mean reflectance spectra of the crown plumage of first-year and older males and females. Following previous studies of UV colour signalling in blue tits (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 5 replicate spectra. ‘Brightness’ was the sum of reflectance between 320–700 nm ($R_{320-700}$), which corresponds to the spectral

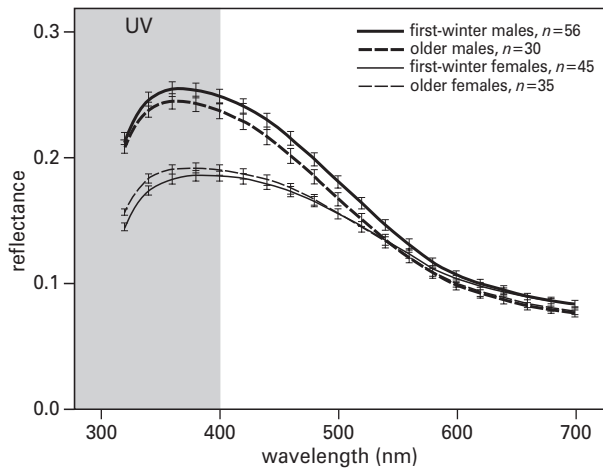


Figure 7.1 Mean crown reflectance spectra of first-year and older male and female blue tits during winter. Multiple measurements of same individuals taken on different days were averaged before calculation of the mean reflectance spectra. Standard errors around the means are depicted at 20 nm intervals. The shaded area indicates the UV part of the spectrum.

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 320–400 nm divided by the sum of reflectance between 320–700 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.* 2003; Griffith *et al.* 2003). Hue and UV chroma values were significantly correlated (Table 7.1).

In accordance with previous findings (Örnberg *et al.* 2002; Delhey *et al.* 2006), we found that blue tit crown colour changed over time, as indicated by significant regressions of all colour 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 two separate days (paired t -tests comparing crown colour 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 colour indices on capture date in our further analyses. Residual crown colour 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 & Boag 1987). When crown colour of an individual had been measured on more than one day we used the average values of these separate measurements in our analyses.

Table 7.1 Matrix of correlations between dominance, sex, age (first-winter versus older birds), crown colour indices (brightness, hue and UV chroma), distance from territory and survival to the following breeding season of wintering blue tits.

	Sex			Age			Brightness			Hue			UV chroma			Distance			Survival		
	r	n	P	r	n	P	r	n	P	r	n	P	r	n	P	r	n	P	r	n	P
Dominance	-0.39	36	0.018	0.15	36	0.37	0.02	35	0.91	-0.41	35	0.015	0.45	35	0.006	-0.52	31	0.003	0.27	36	0.12
Sex				0.02	172	0.80	-0.49	166	<0.001	0.59	166	<0.001	-0.72	166	<0.001	0.01	143	0.87	-0.04	172	0.64
Age							-0.05	166	0.49	-0.21	166	0.006	0.15	166	0.053	0.12	143	0.16	0.25	172	0.001
Brightness										-0.05	166	0.49	0.09	166	0.26	-0.02	138	0.82	-0.06	166	0.44
Hue													-0.82	166	<0.001	-0.05	138	0.56	-0.14	166	0.06
UV chroma																-0.06	138	0.52	0.13	166	0.10
Distance																			-0.14	143	0.09

Dominance is the proportion of all other individuals encountered over which an individual was dominant. Colour indices are residuals controlled for seasonal change in crown reflectance. In total 172 individuals were captured and/or observed at the feeding table during the 2002/2003 winter; crown coloration was measured for 166 individuals; distance to territory could be calculated for 143 individuals and dominance for 143 individuals. Correlations for different combinations of these subsets can have different sample sizes. Significant correlations ($P < 0.05$) are in bold.

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 5 m from inside the field station. The observations were made from 8–13 January 2003 during a single short period of snow cover and frost during that winter, which led to increased visitation rate and competition at the feeding table. During observation periods only a single ball of seeds and fat was provided to increase the competition among the feeding blue tits. Observations were made between 9:00 and 15:00 h when the largest numbers of birds were visiting the feeding table.

We recorded pairwise interactions between colour-banded individuals at the feeding table and inferred dominance when an individual (1) actively displaced another bird at the food source, either through a simple supplant, or by means of a postural display or attack, or (2) fed while an opponent waited to approach the food. Most of the observed conflicts were resolved with low intensity displays, and we rarely observed physical attacks (*cf* Scott & Deag 1998).

We observed 390 interactions between 55 colour-banded individuals, 31 males and 24 females. As a measure of social dominance we calculated the proportion of other individuals over which an individual was dominant (number individuals dominated / total number of individuals encountered; Hein *et al.* 2003). In total 350 interactions of 36 individuals, 25 males and 11 females, of which we observed 5 or more interactions, were included in this calculation (de Laet 1984). We chose to use the proportion of individuals dominated as a measure of dominance instead of calculating a ranking of individuals based on a win-loss matrix (de Vries 1998), because we believe this measure of dominance better reflects the site-dependent, and therefore spatially very dynamic, dominance relationships in the blue tit social system (Colquhoun 1942; Oberski & Wilson 1991; Hansen & Slagsvold 2004). Furthermore, the continuous scale nature of this measure of dominance allowed us to use parametric statistics for our analyses, which would not have been possible if we had used an ordinal dominance ranking of individuals. The measure of dominance we used was highly correlated with both the proportion of fights that an individual had won of all the fights in which it was involved ($r = 0.98$, $n = 36$, $P < 0.001$), and its dominance rank calculated according to de Vries (1998) ($r_s = 0.93$, $n = 36$, $P < 0.001$).

Calculation of travel distances

To control our analyses for the site-dependency of social dominance (*e.g.* Hansen & Slagsvold 2004), we calculated the travel distances (metres) from an individual's territory to the feeding table using GPS coordinates of the feeding table and the nestbox used for breeding and/or winter roosting. Territorial blue tits show high site fidelity and roost and breed in nestboxes inside their territories (Colquhoun 1942; P. Korsten & J. Komdeur, unpublished data). Therefore, the distance from an individual's territory to the feeding table was calculated as the average distance

between the feeding table's location and the locations of all nestboxes that an individual used for roosting during the winter of 2002/2003 and/or for breeding during the preceding (2002) or subsequent spring (2003). In this way we were able to estimate the travel distance for 143 individuals which were present in the study area during the 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 (during 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; P. Korsten & J. 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 & Slagsvold 2004). For a correlation matrix of the main variables included in our analyses see Table 7.1. P values < 0.05 are considered significant and significance tests are two-tailed throughout. The analyses were carried out with SPSS version 13.0.

RESULTS

Influence of sex and age on crown coloration

Crown colour indices – brightness, hue and UV chroma – showed rather continuous frequency distributions with considerable overlap between the sexes and the two age classes (Figure 7.2). Nevertheless, males had on average brighter, more UV-shifted (lower hue), and more UV-chromatic crown plumage than females (Table 7.2; Figure 7.2). First-winter birds had less UV-shifted and UV-chromatic crown colour than older birds (Table 7.2; Figure 7.2). The age difference for crown hue was more pronounced in females than in males, as indicated by the significant interaction term (Table 7.2; Figure 7.2). Brightness of first-winter and older birds did not differ (Table 7.2; Figure 7.2). Canonical discriminant analysis with the three crown colour 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

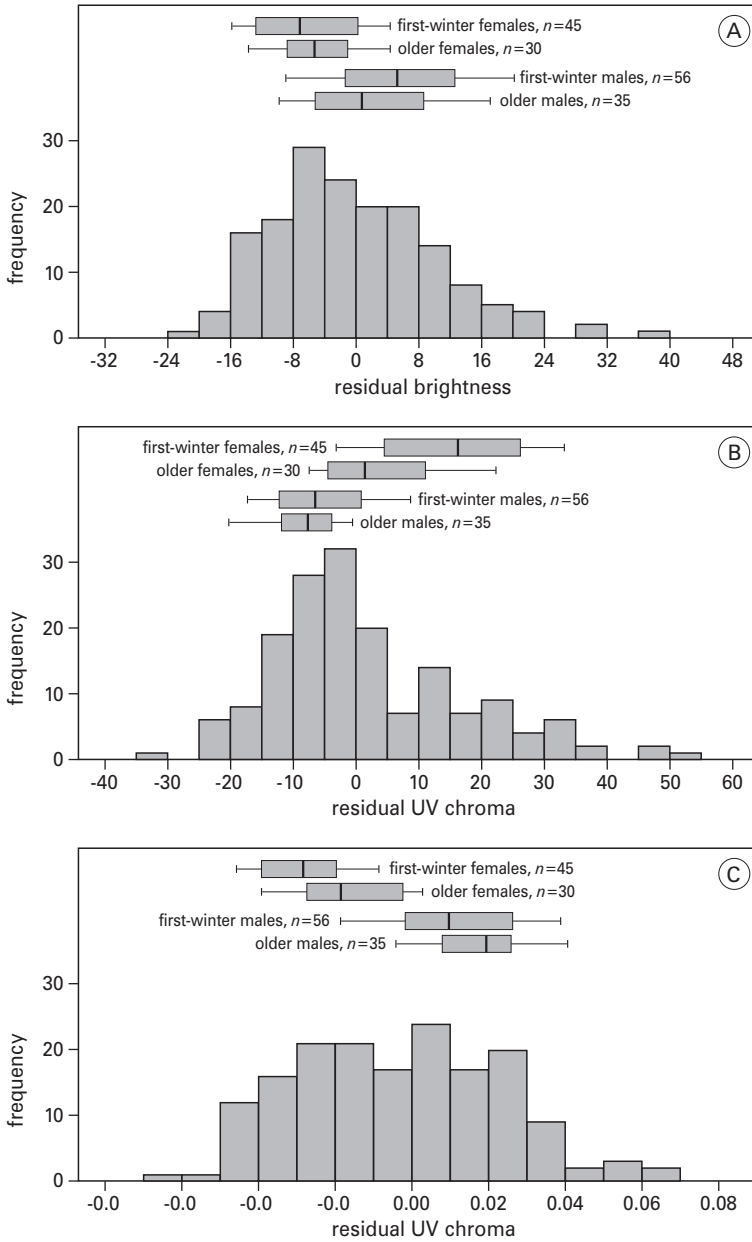


Figure 7.2 Frequency distributions of crown colour indices of wintering blue tits: residual brightness (A), hue (B), and UV chroma (C), controlled for the seasonal change of crown reflectance ($n = 166$; males and females, and different age classes combined). Horizontal box plots show brightness (A), 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 7.2.

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

Dominance was strongly correlated with both hue and UV-chroma, with more dominant individuals having more UV-shifted and more UV-saturated crown coloration (Table 7.1). However, crown coloration was correlated with both sex and age (Tables 7.1 and 7.2), making it difficult to separate the effects of crown colour versus the effects of sex and age on dominance. Therefore, we used a stepwise forward multiple regression analysis in which sex, age, and indices of crown coloration were all entered to test which of these predictors best explained the variation in dominance (Table 7.3). Dominance was also strongly correlated with distance from the

Table 7.2 Influence of sex and age on crown coloration in wintering blue tits ($n = 166$).

Crown colour indices	Sex		Age		Sex x age	
	$F_{1,162}$	P	$F_{1,162}$	P	$F_{1,162}$	P
Brightness	43.98	< 0.001	0.29	0.59	2.02	0.16
Hue	83.80	< 0.001	14.87	< 0.001	4.68	0.032
UV chroma	170.93	< 0.001	9.48	0.002	0.39	0.53

Results from ANOVAs with sex and age (first-winter versus older birds) as factors. Colour indices are residuals controlled for seasonal change in crown reflectance. Significant P values are in bold. See also Figure 7.2.

Table 7.3 Influence of sex, age, crown coloration, body size and distance from territory on dominance in wintering blue tits ($n = 30$).

Explanatory variables	Coefficient	t	P
Included			
Distance	-0.47	-4.79	<0.001
Sex	0.28	3.55	0.001
Age	0.22	2.75	0.011
Excluded			
Brightness		-0.28	0.78
Hue		0.11	0.91
UV chroma		-0.54	0.60
Body mass		-1.42	0.17
Tarsus length		0.03	0.97

Results from a stepwise forward linear regression analysis with dominance as dependent variable and sex, age (first-winter versus older birds), indices of crown colour (brightness, hue, and UV chroma), body mass, tarsus length, and distance from territory as explanatory variables. Colour indices are residuals after controlling for seasonal change in crown reflectance. Final model including sex, age and distance: $F_{3,26} = 12.16$, $P < 0.01$ ($r^2 = 0.58$). See also Figures 7.3 and 7.4.

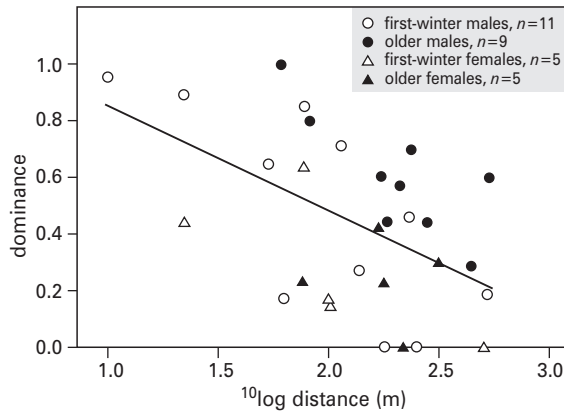


Figure 7.3 Influence of distance from territory on dominance of wintering blue tits. Overall regression line was added for visual purposes only. See also Table 7.3.

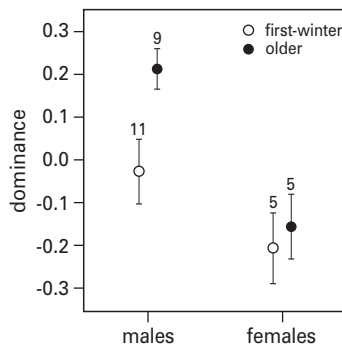


Figure 7.4 Influence of sex and age (first-winter or older) on residual dominance (controlled for distance from territory) of wintering blue tits. Means with standard errors. Numbers indicate sample size. See also Table 7.3.

territory (Table 7.1), which was therefore also entered as an explanatory variable. In addition, we entered body mass and tarsus length to control for the potential effects of body size on dominance. The regression analysis showed that distance from territory (Figure 7.3), and sex and age (Figure 7.4) together explained a large part of the total variation in dominance ($r^2 = 0.58$), whereas body mass, tarsus length and the three crown colour indices dropped from the final model as non-significant (Table 7.3). Adding the three crown colour indices as explanatory variables to this final model only led to a marginal and non-significant increase in the proportion of explained variation in dominance ($r^2 = 0.59$). An alternative model including distance and the crown colour indices, but not sex and age, explained considerably less variation in dominance ($r^2 = 0.44$) than the final model.

Influence of crown coloration on over-winter survival

Individuals with more UV-shifted and more UV-saturated crown coloration tended to have a higher probability of over-winter survival as indicated by their greater tendency for breeding in the study area the following spring (logistic regression, all $n = 166$: brightness: $\chi^2 = 0.60$, $df = 1$, $P = 0.44$; hue: $\chi^2 = 3.37$, $df = 1$, $P = 0.066$; UV chroma: $\chi^2 = 2.75$, $df = 1$, $P = 0.097$). However, as age and crown coloration were intercorrelated (Tables 7.1 and 7.2), it was difficult to separate the effects of age versus crown coloration on survival. A stepwise forward multiple logistic regression analysis in which age, crown colour indices, and also sex, body mass and tarsus length were entered as explanatory variables showed that only age had a significant effect on survival, whereas sex, crown coloration, body mass and tarsus length dropped from the model as non-significant terms (Table 7.4; Figure 7.5).

Table 7.4 Influence of sex, age, crown coloration and body size on survival to the following breeding season in wintering blue tits ($n=166$).

Explanatory variables	Coefficient	Wald (χ^2)	<i>P</i>
Included			
Age	1.14	11.10	0.001
Excluded			
Sex		0.15	0.70
Brightness		0.37	0.54
Hue		1.42	0.23
UV chroma		1.46	0.23
Body mass		1.81	0.18
Tarsus length		0.06	0.81

Results from logistic regression analysis with survival to the following breeding season as dependent variable and sex, age (first-winter versus older birds), indices of crown colour (brightness, hue, UV chroma), body mass and tarsus length as explanatory variables. Colour indices are residuals after correction for seasonal change in crown reflectance. See also Figure 7.5.

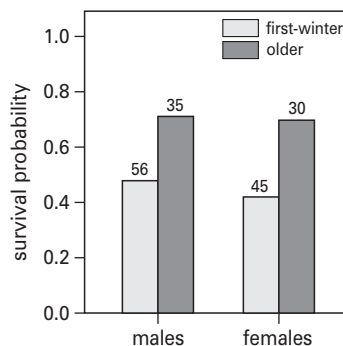


Figure 7.5 Probability of survival to the following breeding season for blue tit males and females of two age classes, first-winter and older birds. Numbers indicate samples sizes. See also Table 7.4.

DISCUSSION

Previous studies of social status signalling have mainly focused on pigment-based plumage colours and there is good evidence of a status signalling function for both melanin and carotenoid-pigmented plumage patches (e.g. Møller 1987; Pryke *et al.* 2001a, respectively). The present study has investigated if structurally based plumage coloration can also function as a signal of social status in the non-breeding 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 somewhat more UV reflective than first-winter birds (*cf* Delhey & Kempenaers 2006), which may be caused by age-dependent ornament expression (as we found no evidence for differential survival according to plumage colour), 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 colour 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 (Figure 7.2), 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, either within, or between, sex age classes. After controlling for the effects of sex, age and distance from territory, which together explained a remarkably large part of the variation in winter dominance ($r^2 = 0.58$), crown UV coloration did not significantly explain any additional variation in dominance. As males and older birds were both more dominant and more UV reflective than females and first-winter birds respectively, we cannot exclude the possibility that differences in UV crown plumage between sex and age classes have some influence on the outcome of aggressive interactions between birds of different sex and age, but this seems unlikely because sex and age class categories predicted individual dominance considerably better than did UV coloration. Furthermore, 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 excluded 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 *e.g.* Järvi *et al.* 1987b; Møller 1987; Pryke *et al.* 2001a)

UV coloration versus other determinants of dominance

Interestingly, we found distance from territory to be an important determinant of dominance (Figure 7.3), indicating that dominance was strongly site-dependent, which is in line with previous studies on winter dominance in blue tits and other *Parus* species (*e.g.* Dingemanse & de Goede 2004; Hansen & 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 inter-individual conflicts must have been resolved in different ways. As we rarely observed escalated fights we suggest that the birds may use subtle behavioural cues to assess a competitor's motivation and likeliness to escalate a conflict (*cf* Scott & Deag 1998). Such behavioural 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 & Wallin 1993), their relative durations of food deprivation (Lemel & Wallin 1993), prior residency (Krebs 1982), early social experiences (Hansen & Slagsvold 2004), personality (Dingemanse & de Goede 2004), and hormonal status (Järvi *et al.* 1987b). The use of status signalling through coloured 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 & 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 behavioural cues to assess the fighting ability or intentions of the (model) intruders, and apparently adjusted their aggressive behaviour 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 (Chapter 6).

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 nest-box 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 (*Guiraca 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.

Alternatively, plumage-based status signalling may be more important in northerly blue tit populations, possibly 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 & 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 versus 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 & Hill 2000a, 2000b), 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 non-breeding season (McGraw & Hill 2000a). Remarkably, during the breeding season bright males are even subordinate to drab males in competition over food (McGraw & 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, 2001b). 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 favoured by female choice (Pryke *et al.* 2001a, 2001b). These studies, together with our findings in the blue tit, show for several types of ornamentation (elongated tail feathers, structural and pigment-based plumage colours) 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 & Hartley 1998). Instead, melanin-pigmented plumage seems to be mainly important in agonistic signalling (Badyaev & Hill 2000; Jawor & Breitwisch 2003), while carotenoid-based plumage coloration may be important in both mate choice (Hill 1991; Badyaev & 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 inter-individual signalling in competitive interactions during winter.

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