

Ultraviolet plumage does not signal social status in free-living blue tits; an experimental test

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Ultraviolet (UV) signals are suggested to be sexually selected in a wide range of taxa. Most research, however, has focused on the role of UV signals in mate choice, whereas possible functions in intraspecific competition remain largely untested. Studies on other colors indicate that ornaments preferred by females can also function as signals of social status in competitive interactions between individuals. Whereas these colors are mainly pigment based, UV reflectance is generally caused by selective reflectance of light from surface structures. Here we test experimentally whether the structurally based UV-reflective crown plumage in the blue tit (*Cyanistes caeruleus*) serves as a signal of status in interindividual competition. We reduced the crown UV reflectance of free-living blue tits in winter and compared their probability of winning conflicts over food at a feeding table with control-treated and untreated individuals. Although we controlled for effects of sex, age, and distance from territory, we found no effect of reduced UV reflectance on the probability of winning nor were conflicts involving UV-reduced individuals more likely to escalate. Therefore, we conclude that the UV reflectance of the blue tit's crown does not serve as a signal of status in competition over food in winter. We suggest that the observed site-dependent dominance structure may constrain the opportunity for a status signal to evolve and that enhancing attractiveness in mate choice may be the sole function of the crown's UV reflectance. *Key words:* armament, male–male competition, sexual selection, site-related dominance, status signaling, structural coloration. [*Behav Ecol* 19:410–416 (2008)]

The evolution of conspicuous secondary sexual traits has traditionally been explained in terms of 2 main selective benefits. Conspicuous traits could give their bearers an advantage via mate choice by the opposite sex or an advantage in competition for a mate or other resources (Darwin 1871). It has long been recognized that these functions are not mutually exclusive (Fisher 1915), and in most cases where a trait functions in mate choice it also functions in competition (reviewed by Berglund et al. 1996). This has even led to the suggestion that the function of a trait in mate choice arises after its initial evolution as an armament in intrasexual competition (Berglund et al. 1996).

Some of the most striking examples of secondary sexual traits are the bright and conspicuous colors exhibited in many taxa throughout the animal kingdom. These colors result either from selective absorption of light from pigments or from selective reflectance of light from surface structures (Land 1972). Structurally based ultraviolet (UV) reflectance has long been neglected in studies on the function of color signaling, in part because it lies outside the visible color spectrum of humans (Bennett et al. 1994). However, with the development of new color-measuring techniques, it has become apparent that UV reflectance may have sexually selected functions in species from a wide range of taxa (e.g., Actinopterygii; Smith et al. 2002; Arachnida; Lim et al. 2007; Insecta; Brunton and Majerus 1995; Reptilia; LeBas and Marshall 2000). Birds (Aves) are particularly popular as model species for investigating mechanisms and functions of UV signaling (Hill and McGraw 2006a, 2006b), but to date exact functions in sexual selection remain enigmatic.

An extensive comparative analysis among bird species by Owens and Hartley (1998) reveals a positive correlation between the degree of structural sexual dichromatism and the levels of extrapair paternity, suggesting that structurally based colors are particularly important in mate choice. However, mate choice trials in which UV-blue structural plumage of males was manipulated are scarce and the findings inconsistent. Two studies that manipulated plumage coloration within the natural range both found no female preference for brighter colored males (blue grosbeaks, *Passerina caerulea*, Ballentine and Hill 2003; eastern bluebirds, *Sialia sialis*, Liu et al. 2007), but another study that more specifically decreased male UV reflectance did find a female preference for unreduced control males (bluethroats, *Luscinia s. svecica*, Andersson and Amundsen 1997). In the extensively studied blue tit (*Cyanistes caeruleus*), females have been shown to alter reproductive strategies when their mates had the UV reflectance of their crown experimentally reduced (Sheldon et al. 1999; Limbourg et al. 2004; Johnsen et al. 2005; Korsten et al. 2006; Delhey et al. 2007a; Kingma SA, Komdeur J, Vedder O, von Engelhardt N, Korsten P, Groothuis TGG, unpublished data). These findings are often interpreted as a response to a perceived lower attractiveness of the male but could also arise from changes in male behavior. Moreover, a cross-fostering study on the heritability of variation in UV color expression in blue tits failed to find a strong heritable component (Hadfield et al. 2006), which is a prerequisite for indirect, genetic benefit models of mate choice (Mead and Arnold 2004). Given these results, it is somewhat surprising that alternative functions of UV structural plumage, such as competition outside a mate choice context, have not received more attention.

For a colorful plumage patch to function in competition, it should serve as a reliable indicator of social status (Rohwer 1975). This requires that conflicts over limited resources are settled with the display of a plumage patch that signals

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competitive ability or level of aggression (Maynard Smith and Harper 1988). This would be beneficial for both the dominant and the subordinate individual because they avoid wasting time, wasting energy, or risking injury to assess each other's competitive abilities (Rohwer 1982). To maintain the honesty of such a status-signaling system, it should be unprofitable or impossible for individuals to signal more or less than their true capabilities, which could be enforced by a production or maintenance cost of the signal, genetic constraints, or social control of deception (Owens and Hartley 1991; Johnstone and Norris 1993).

There is good experimental evidence for pigment-based colors signaling status (melanins: e.g., Møller 1987, Gonzalez et al. 2002; carotenoids: e.g., Pryke et al. 2002, Pryke and Andersson 2003). For UV reflectance, however, currently only 1 study has provided experimental evidence for a signaling function in competition. In Augrabies flat lizards (*Platysaurus broadleyi*), conflicts were more likely to escalate when they involved experimentally UV-reduced males (Stapley and Whiting 2006). In birds, there is only limited evidence for a causal function of UV reflectance in status signaling. In black-capped chickadees (*Poecile atricapillus*), socially dominant males are generally favored in female choice and exhibit more UV reflectance from dark body regions than subordinates (Woodcock et al. 2005). In eastern bluebirds, males that settled earlier at limited nest-boxes had more intense UV coloration (Siefferman and Hill 2005). In Gouldian finches (*Erythrura gouldiae*), the intensity and size of the UV-blue collar were positively related to the outcome of male dominance interactions (Pryke and Griffith 2006), and in blue tits, territorial males with fertile females acted less aggressively toward taxidermic mounts with reduced crown UV reflectance, than to control males (Alonso-Alvarez et al. 2004). However, the latter finding could also be interpreted in a mate choice context if, for example, a UV-reduced male poses less threat to a focal male's paternity (see Delhey et al. 2007b). Furthermore, the result could not be repeated in a different population when UV-manipulated mounts were presented simultaneously instead of sequentially (Korsten, Dijkstra, et al. 2007). Hence, our understanding of the function of UV reflectance in competition is insufficient to draw general conclusions, in large part because of the lack of an experimental approach.

To determine if plumage coloration has a role in signaling status, it is essential to solely manipulate the trait of interest because color expression may simply be correlated with social dominance but unrelated to the cues used to estimate an opponent's social status. Here, we aim to perform such an experiment, for the first time, to investigate the potential importance of UV-reflective plumage outside a mate choice context. To this end, we manipulated the UV-reflective crown of free-living, individually recognizable male and female blue tits in winter and scored the outcome and degree of escalation of competitive interactions over artificially provided food. We hypothesize that if the UV-reflective crown coloration acts as a status signal, UV-reduced individuals will either lose more interactions or that interactions involving UV-reduced individuals are more likely to escalate, as individuals will acquire unreliable information about the competitive ability of their opponent. In a previous correlative study, we were unable to separate the effects of sex and crown UV reflectance on social status (Korsten, Vedder, et al. 2007). Hence, the possibility that the observed sex difference in social status primarily reflects variation in crown UV reflectance could not be discarded. With our experimental approach, we are able to determine whether the UV reflectance of the crown feathers per se is a signal of social status.

METHODS

Study area and general procedures

The experiment was performed in the winters of 2005/2006 and 2006/2007 at the estate "De Vosbergen" near Groningen in the north of the Netherlands (53°08'N, 06°35'E). The study area (50 ha) contains approximately 185 nest-boxes for blue tits, and from 2001 the population of blue tits has been monitored every year. Each breeding season, all breeding adults and nestlings were marked with uniquely numbered metal bands and the adults also fitted with a unique combination of 3 color bands.

From December 2005 to February 2006 and from January 2007 to February 2007, we put up a feeding table close to the field station in the center of the study area, which was continuously supplied with commercially available food balls comprising seed and clumped fat. Both winters, all nest-boxes were checked at least once at night for the presence of roosting blue tits. Birds were caught by taking them out of the nest-box at night and/or by catching them with baited cage traps and mist nets at the feeding table. Individuals were aged as first-winter birds or older (Svensson 1992) and color banded. Spectrophotometric measurements of the crown (see below) were taken at each capture. A blood sample, by puncture of the brachial vein, was taken at least once from each individual (for more details, see Korsten et al. 2006) and the extracted DNA used to sex all individuals with sex-specific molecular markers (P2 and P8; Griffiths et al. 1998).

Crown reflectance measurements and UV treatment

The spectral reflectance of the crown feathers was measured with a USB-2000 spectrophotometer with illumination from a DH-2000 deuterium-halogen light source (both Avantes, Eerbeek, The Netherlands), following the protocol described in Korsten, Vedder, et al. (2007). Five replicate readings were taken from the center of the crown from each individual at each capture. These 5 readings were smoothed by calculating the running mean over 10 nm, and the average of a typically used color index (i.e., "UV chroma") in UV color-signaling studies was calculated. This was done by dividing the sum of UV reflectance (320–400 nm) by the sum of reflectance between 320 and 700 nm ($R_{320-400}/R_{320-700}$), which corresponds to the spectral range visible to blue tits (Hart et al. 2000). The UV chroma index has previously been identified as an important predictor of male viability in blue tits (Sheldon et al. 1999; Griffith et al. 2003).

In both winters, all individuals that were caught at the feeding table from 14 January onward were sequentially assigned to either a "UV-reduced" or a "control" treatment. The UV-reduced treatment consisted of applying a mixture of duck preen gland fat and UV-blocking chemicals (50% Parsol 1789 and 50% Parsol MCX; Roche, Basel, Switzerland) onto the crown feathers, after initial spectrophotometric measurements were taken. The control treatment consisted of only applying the duck preen gland fat. To confirm the direct effect of both treatments, 3 replicate crown reflectance readings were taken directly after the treatment, following the protocol described above. This experimental procedure has been widely used in studies on wild blue tits (e.g., Sheldon et al. 1999; Limbourg et al. 2004; Korsten et al. 2006), and its effects are well described (Korsten, Limbourg, et al. 2007). The UV-reduced treatment led on average to a 37% ($n = 55$) reduction in UV chroma (Figures 1 and 2), and the difference in UV chroma between the 2 treatments lasted approximately 20 days (Figure 2). Previous work in male blue tits has shown that, although initially the reduction in UV chroma falls outside the natural range, within 2 days UV-reduced males

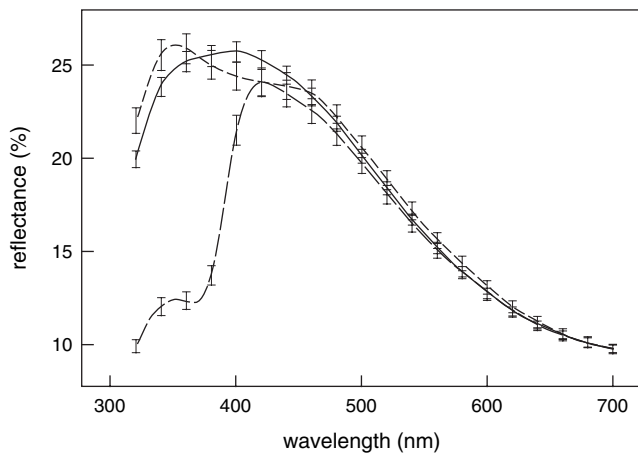


Figure 1
Average crown reflectance spectra of all UV-manipulated individuals before manipulation (solid line, $n = 109$), immediately after the UV-reduced treatment (long-barred line, $n = 55$) and immediately after the control treatment (short-barred line, $n = 54$). Standard errors of the means are depicted at 20-nm intervals.

exhibit UV chroma within the natural range for males (Korsten, Limbourg, et al. 2007). On average, the interactions of manipulated individuals (UV reduced and control) were observed 7.81 (standard deviation = 5.30) days after they were treated, and 2 interactions involving manipulated individuals that occurred more than 20 days after treatment application were discarded.

Competitive interactions

In January–February 2006, 539 pairwise competitive interactions between blue tits over food at the feeding table were

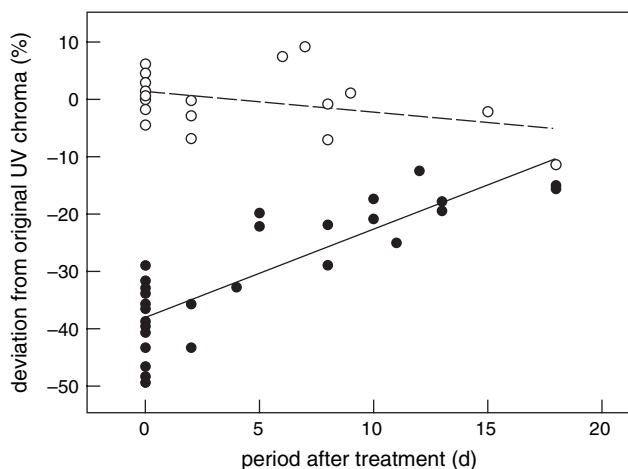


Figure 2
Deviation from original crown UV chroma before manipulation (expressed as a percentage) for birds that were remeasured in the same winter plotted against the period in days after treatment. For every remeasured UV-reduced (filled circles, $n = 15$) and control (open circles, $n = 11$) individual, both the deviation in UV chroma immediately after treatment is plotted (x value of 0) as well as the deviation in UV chroma of the later measurement. Fitted lines (solid for UV reduced and dashed for control) were calculated with least squares regression. Note that the regression lines suggest that the difference in UV treatments disappeared after approximately 20 days.

observed from inside the field station at a distance of 5 m. In January–February 2007, an extra 145 interactions were observed following the same procedures. For each interaction, both birds were identified by their color bands and the winner was determined as the individual that either actively displaced its opponent or fed while its opponent waited to approach the food. Furthermore, we recorded whether the conflict was settled with 1) a simple supplant of the winner or by passive waiting of the loser (“no display”), 2) by postural displays of both winner and loser, in which crown feathers were flattened and erected, until the loser retreated (“active display”), or 3) through actual fights with physical contact and peck attacks (“physical fights”). All interactions were observed and classified by the same observer (O.V.) in both years. In general, conflicts were settled without display, but when neither competitor retreated they tended to progressively escalate to active display and, very rarely, physical fights (see also Scott and Deag 1998).

Distance from territory

In blue tits and other species of the Paridae family, it is well known that the social dominance status of an individual decreases as it moves further away from its territory (e.g., Colquhoun 1942; Oberski and Wilson 1991; Dingemanse and De Goede 2004; Hansen and Slagsvold 2004; Korsten, Vedder, et al. 2007). To control for this effect, we estimated the distance in meters between an individual's territory and the feeding table (hereon referred to as “distance from territory”) using Global Positioning System coordinates of the feeding table and the nest-boxes used for breeding and/or roosting. This distance from territory was calculated as the average of the distances between the feeding table and all nest-boxes used by an individual for roosting during winter and for breeding during the preceding and/or after breeding season. Previous work has shown that these distances are highly repeatable within individuals (Korsten, Vedder, et al. 2007), which may be expected because territorial blue tits are known to be very site faithful between years and to roost within their territories (Colquhoun 1942).

Statistical analyses

To test for effects on the probability of winning a conflict at the feeding table, we used hierarchical linear mixed models with a binomial error distribution with a logit link function. The models were implemented using restricted iterative generalized least squares (Rasbash et al. 2004). Because the probability that an individual wins an interaction is not independent of the chance that the opponent loses, we randomly assigned half of all interactions to the point of view of the winner and the other half to the point of view of the loser. In this way, we avoided pseudoreplication, as each interaction was only counted as a single datapoint, and the outcome of an interaction can be analyzed as a binary response (i.e., win or lose). Hierarchical random effects in the model were the identity of the focal individual and the identity of the opponent, respectively. This results in a 3-level structure with the focal individual at the highest level, the unique dyads of the focal individual (i.e., each different opponent) at the intermediate level, and each interaction within a unique dyad at the lowest level. To test whether our manipulation affected the probability of winning, we assessed significance in a full model, with UV treatment entered as a categorical explanatory variable (untreated, control treated, and UV reduced) together with sex, age, distance from territory, and the 2-way interaction between the UV treatment and sex. The additional variables were included because previous work in the study population

Table 1
Model summary examining the effects of the UV manipulation and individual characteristics on the probability of winning competitive interactions in blue tits

Explanatory variables	Coefficient (standard error)	Wald (χ^2)	Δ df	<i>P</i>
Distance from territory	-0.011 (0.001)	54.93	1	<0.001
Sex (female as reference)	2.014 (0.588)	11.75	1	<0.001
Age (1st year as reference)	0.632 (0.370)	2.92	1	0.087
UV treatment (control as reference)	0.401 (0.621) untreated	0.76	2	0.684
	-0.195 (0.763) UV reduced			
Sex × UV treatment	-0.179 (0.736) untreated	0.52	2	0.771
	0.402 (0.880) UV reduced			

n = 559 interactions of 48 focal individuals.

showed that sex, age, and distance from territory affected social status (Korsten, Vedder, et al. 2007). The interaction term was included to account for the possibility that UV reflectance only functions as a status signal in males. Significance (*P* < 0.05, 2 tailed) was tested using the Wald statistic, which follows a chi-square distribution. This analysis was repeated without the conflicts of untreated focal individuals. This has the advantage of more specifically comparing UV-reduced with control-treated individuals but has the disadvantage that the effects of sex, age, and distance from territory are not corrected as reliably because of the smaller sample size. We used the same dataset and model structure to examine how social conflicts were settled. Because conflicts that were settled by physical fights were extremely rare (0.7%, *n* = 684), we pooled these with the conflicts settled by active display. Consequently, “type of conflict” was analyzed as a binary response (i.e., active display or no display). Explanatory variables included in the model were UV treatment (untreated, control treated, and UV reduced), sex, age, and distance from territory. Furthermore, because conflicts may have been more likely to escalate when the focal bird was more evenly matched to its opponent, we also included in the model, as independent variables, the absolute difference between the 2 opponents for distance from territory and whether or not opponents were in the same category for UV treatment, sex, and age.

Although we observed 684 interactions involving 64 focal individuals, some focal individuals were never caught in a nest-box, prohibiting the estimation of a distance from territory. Hence, statistical analyses were performed on a dataset consisting of 48 focal individuals (559 interactions), of which 17 had their UV reflectance reduced (174 interactions divided over 5 first-winter males, 6 older males, 4 first-winter females, and 2 older females) and 11 were control treated (160 interactions divided over 3 first-winter males, 3 older males, and 5 older females). There was no significant difference in distance from territory between individuals of the 2 treatment categories (*t* = -0.83, degrees of freedom [df] = 26, *P* = 0.417). The remaining focal individuals were categorized as untreated (100 interactions), and the interactions before treatment for focal individuals that later received a UV treatment were also categorized as untreated (125 interactions). There were an additional 81 interactions for which we could not calculate an absolute difference in distance from territory between opponents. There were 8 individuals for which we observed interactions in both years, but the explanatory variables, age, distance from territory, and UV treatment, are year specific for these individuals.

We also analyzed whether for UV-treated individuals, the probability of occupying a nest-box and breeding in the subsequent season was affected by the treatment they received in winter. This was analyzed using a binary logistic regression

model. Together with UV treatment (UV reduced or control), we entered year, date of treatment, sex, age, and the 2-way interaction between UV treatment and sex in the model. When individuals received a UV treatment in both years, we only included them for analyses in the first year of treatment, resulting in a sample size of 51 UV-reduced individuals (25 males and 26 females) and 52 control individuals (24 males and 28 females). All analyses were carried out using MLwiN 2.02.

RESULTS

The probability of winning a conflict over food at the feeding table was significantly influenced by an individual’s sex and the distance between its territory and the feeding table. Males were more likely to win conflicts than females (Table 1, Figure 3A), and the probability of winning decreased with distance from territory (Table 1, Figure 3C). There was a nonsignificant trend for older birds to win more conflicts than first-winter birds (Table 1, Figure 3B). The experimental reduction of crown UV reflectance had no significant effect on the probability of winning a conflict nor was the effect of the manipulation dependent on the sex of an individual (Table 1, Figure 3). The model with only the experimentally treated individuals (UV reduced or control) included also showed no effect of the UV manipulation ($\chi^2 = 0.58$, Δ df = 1, *P* = 0.447)

The overall percentage of conflicts that were settled with active display or physical fights was low (6.4%, *n* = 684). Whether or not opponents had the same UV treatment or whether they were of the same sex or age did not affect the probability of the conflict escalating to display (Table 2). Similarly, the probability of conflict escalation was not dependent on the UV treatment, sex, or age of the focal individual (Table 2), although there was a nonsignificant trend for conflicts to escalate more often when the absolute difference in distance from territory between opponents was less and when the focal individual resided closer to the feeding table (Table 2).

Overall, 54.4% (*n* = 103) of the individuals that were treated in winter were observed breeding in the study area in the subsequent breeding season. The probability of breeding in the subsequent season was not affected by the UV manipulation ($\chi^2 = 0.21$, Δ df = 1, *P* = 0.647) nor did any of the other entered variables (year, date of treatment, sex, age) or the 2-way interaction between UV treatment and sex significantly explain any variation (all *P* > 0.10).

DISCUSSION

The experimental reduction of UV reflectance has often been used to show that female reproductive strategies can be

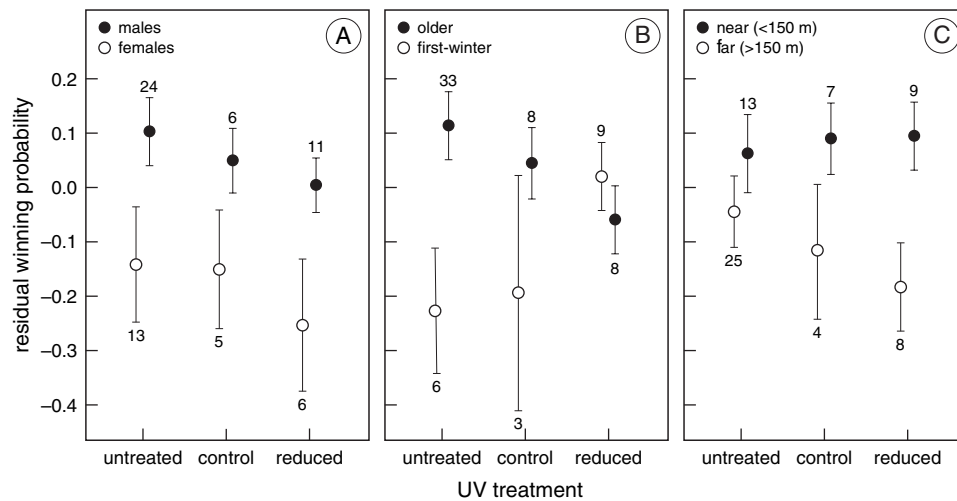


Figure 3

Average residual winning probability \pm standard error plotted against UV treatment, for both sexes (A), both age classes (B), and 2 categories for distance from territory (C). When plotted for sex, winning probability is corrected for age and distance. When plotted for age, winning probability is corrected for sex and distance. When plotted for distance from territory, winning probability is corrected for sex and age. Sample sizes are presented adjacent to each estimate and represent the number of individuals. The division in distance categories for distance from territory is performed for visual purposes only. All statistical analyses are performed with distance as a continuous variable (see Table 1).

influenced by the UV reflectance of male plumage (social mate choice: Andersson and Amundsen 1997; extrapair mate choice: Johnsen et al. 1998, Delhey et al. 2007b; brood sex ratio: Sheldon et al. 1999, Korsten et al. 2006, Delhey et al. 2007a; prenatal maternal hormones: Kingma SA, Komdeur J, Vedder O, von Engelhardt N, Korsten P, Groothuis TGG, unpublished data; nestling provisioning: Limbourg et al. 2004, Johnsen et al. 2005). However, in this study we used this technique, for the first time, to investigate the role of UV-reflective plumage in free-living birds outside a mate choice context. Despite this apparently successful experimental protocol, we found no effect of the treatment on the probability of winning a social conflict over food at a feeding table in winter nor were conflicts more likely to escalate when they involved UV-reduced individuals. Hence, we have no indication that the degree of UV reflectance of the crown serves as a status signal in competition between blue tits.

After manipulation, there are basically 2 possible scenarios that would serve as evidence for a status-signaling function of the trait. In the first scenario, the status of an individual changes according to the manipulation of its signal. This may occur if constraints, such as production costs or pleiotropic gene effects, ensure that under natural circumstances it is

impossible to signal unreliably. Thus, opponents should simply accept the change in status of the manipulated individuals, particularly when signals of focal individuals are increased (for experimental evidence, see Pryke et al. 2002; Pryke and Andersson 2003). Alternatively, when the costs that maintain the honesty of the system are more of a social nature, like enhanced aggression to individuals that signal a high status (Møller 1987) or when signals are decreased, status might not change but conflicts involving manipulated individuals would be more likely to escalate (for experimental evidence, see Stapley and Whiting 2006). For example, when a focal individual with a decreased signal encounters an opponent, the opponent would perceive the focal individual as low in status and attack whereas the focal individual would not retreat as its actual status remains unchanged. These scenarios are not mutually exclusive as, in the latter scenario, signal-reduced individuals may not be able to withstand an increased competitive pressure and decline in status (Pryke et al. 2002). In our experiment, we observed neither of these scenarios, so we conclude that crown UV reflectance does not serve as a signal of social status, at least in the social situation encountered at our feeding table.

Table 2

Model summary examining the effects of the UV manipulation, individual characteristics, and asymmetries between opponents on the nature of conflict resolution (display or not) in blue tits

Explanatory variables	Coefficient (standard error)	Wald (χ^2)	Δ df	P
Distance from territory	-0.004 (0.002)	2.76	1	0.097
Sex (female as reference)	-0.716 (0.473)	2.29	1	0.130
Age (1st year as reference)	-0.165 (0.568)	0.08	1	0.777
UV treatment (control as reference)	0.500 (0.550) untreated	1.10	2	0.576
	0.025 (0.595) UV reduced			
Difference in distance	-0.004 (0.002)	2.96	1	0.085
Different sex	-0.184 (0.458)	0.16	1	0.689
Different age	0.030 (0.595)	0.00	1	0.951
Different UV treatment	0.204 (0.434)	0.22	1	0.639

$n = 477$ interactions of 48 focal individuals. The coefficients of asymmetries between opponents are based on "no difference" as reference category.

It has been hypothesized that signals of social status will only be used in competition over resources of low value and when asymmetries in motivation between opponents are small (Maynard Smith and Harper 1988; Wilson 1992). The low incidence of conflicts that escalate to displays suggests that the food we provided was not highly valued by the blue tits. However, the strong effect of distance from territory on the probability of winning a conflict may imply that conflicts over territories have been resolved previously and that encounters at the feeding table were merely social conformations of the territorial structure in the area. Consequently, there may be little scope to use a status signal in conflict resolution because of the site-dependent dominance structure in the study area. However, the prediction concerning the value of the contested resource has little empirical support (Maynard Smith and Harper 1988). More generally, it has been found that status signals also function to settle conflicts over high-value resources, such as territories (Part and Qvarnström 1997; Pryke et al. 2002; Pryke and Andersson 2003). We found that the probability for breeding in the subsequent season was independent of the UV treatment, again inconsistent with a role for UV plumage in conflict resolution, although our treatment was only temporary. Furthermore, site-dependent dominance appears to be a consistent finding in the blue tit (Colquhoun 1942; Hansen and Slagsvold 2004; Korsten, Vedder, et al. 2007). Hence, if this social structure is an important constraint on the evolution of a status signal, there is no reason to expect such a signal to have evolved in blue tits. In this light, it would be interesting to assess the role of structural UV coloration in competition in less territorial or migratory species.

The distinct sexual dichromatism in blue tits, with males reflecting more UV than females (e.g., Andersson et al. 1998; Hunt et al. 1998), strongly suggests that this trait has evolved by sexual selection. As our study indicates that a function in intrasexual competition is unlikely, female choice would seem the best explanation for the evolution of this dichromatism. This is further supported by a range of studies that show female blue tits alter reproductive strategies when mated to UV-reduced males (Sheldon et al. 1999; Limbourg et al. 2004; Johnsen et al. 2005; Korsten et al. 2006; Delhey et al. 2007a, 2007b; Kingma SA, Komdeur J, Vedder O, von Engelhardt N, Korsten P, Groothuis TGG, unpublished data). However, the exact process and function of female choice for more UV-reflective males remain unclear as the trait was found to have low heritability (Hadfield et al. 2006), and correlative patterns of extrapair paternity in relation to male UV reflectance contradict experimental findings (Delhey et al. 2003, 2007b). Similar findings of traits functioning in mate choice but not competition, or vice versa, have been reported for house finches (*Carpodacus mexicanus*; McGraw and Hill 2000), red-collared widowbirds (*Euplectes ardens*; Pryke et al. 2001), red-shouldered widowbirds (*Euplectes axillaris*; Pryke and Andersson 2002), and Eurasian siskins (*Carduelis spinus*; Senar et al. 2005). Hence, empirical evidence is now accumulating that sexually selected traits need not have dual utility (but see Berglund et al. 1996).

In our previous correlative study (Korsten, Vedder, et al. 2007), we were unable to reject the possibilities that the difference in crown UV reflectance between the sexes was the primary reason for their difference in social status and even served as the principle mechanism of conspecific sex recognition. However, in this study, we show that the effect of sex on social status is more than 10 times greater than that of our experimental reduction in UV (Table 1), allowing us to discard these possibilities. Hence, other cues must contribute to the sex difference in social status in blue tits. Similar results have been obtained in the closely related great tit (*Parus major*),

where females were still able to recognize the sex of conspecific females that were dyed to appear like males (Slagsvold 1993). Interestingly, the converse was found in the migratory pied flycatcher (*Ficedula hypoleuca*), where plumage color manipulations corrupted sex recognition in conspecifics (Sætre and Slagsvold 1992). Again, this suggests that territorial structure may be a key factor in determining the importance of sexually selected color signals.

Whether structurally based plumage coloration can be regarded as a distinct class of secondary sexual traits that is more important in mate choice than in competition, compared with pigment-based coloration (Owens and Hartley 1998), remains to be unambiguously tested. To date, the 3 studies that test for a function of structurally based UV plumage coloration in competition, that manipulated the trait of interest, are limited to 1 species (i.e., blue tits). Two of these were performed within a mate choice context and are equivocal in their results (Alonso-Alvarez et al. 2004; Korsten, Dijkstra, et al. 2007), whereas this study failed to find any evidence for a function in competition. However, as UV reflectance has been clearly demonstrated to serve as a status signal in a lizard species (Stapley and Whiting 2006), there is no physiological basis to reject the possibility that structurally based UV signals can be used in competition. Clearly, more experimental work on the role of structural plumage coloration in competition is needed in other species in order to resolve this issue more generally.

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