

Ultraviolet reflectance affects male-male interactions in the blue tit (*Parus caeruleus ultramarinus*)

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Several animal species have been shown to use phenotypic traits to assess the competitive ability of opponents and adjust their aggressiveness depending on the likelihood to win the contest. In birds, these phenotypic traits usually involve patches of colored feathers. The benefit to harbor honest signals of male quality is the avoidance of wasteful aggressive interactions. Recent work has shown that ultraviolet (UV) plumage reflectance is an important signal used by females during mate choice. Surprisingly, however, the role of UV signaling on intrasexual selection has been neglected. In the present study, we aimed to test whether UV reflectance of crown feathers was used as a signal of male competitive ability during male-male interactions. Breeding male blue tits (*Parus caeruleus ultramarinus*) were exposed during the female egg-laying period to blue tit taxidermic mounts with either control or reduced UV reflectance of crown feathers. In agreement with the prediction that UV reflectance advertises male quality, we found that breeding blue tits behaved less aggressively toward the UV-reduced decoy. To our knowledge, this is the first experimental evidence suggesting a role for UV signaling on intrasexual selection. *Key words*: animal contests, male-male competition, sexual selection, sexual signals. [*Behav Ecol* 15:805–809 (2004)]

The evolution of aggressive behavior in animals has attracted considerable attention from evolutionary biologists, and several theoretical and empirical studies have investigated the factors potentially affecting the optimal level of investment into an aggressive interaction (for a recent review, see Riechert, 1998). Contests may considerably vary in the degree of escalation from ritualized displays to fighting. However, if opponents can assess the relative likelihood to win the contest, then the outcome of the interaction can be settled with no need of escalating fights (Maynard Smith and Parker, 1973, 1976). The value of the defended resource, however, also affects the willingness to accept escalating and potentially injuring fights (Poole, 1989; Riechert, 1998). Recently, another type of benefits of male contests has been put forward. Social interactions might participate in a process of transfer of public information among members of the group. Males might therefore benefit from engaging in aggressive interactions if females eavesdrop on the issue of the contest (Doutrelant and McGregor, 2000; Doutrelant et al. 2001; Mennill et al., 2002; Otter et al., 1999). Here again the benefit is likely to depend on the vigor of the opponent.

How do animals weigh up the competitive ability of potential opponents to adjust the intensity of their aggressive behavior? In addition to eavesdropping (McGregor and Peake 2000; Oliveira et al., 1998), phenotypic cues or signals that reliably inform opponents about their asymmetry in quality and affect the probability to win a particular contest might be particularly important to predict the optimal level of aggression. Rohwer (1975) suggested that patches of colored feathers might play that role in birds. Accordingly, if these

traits honestly reflect the quality of the individuals harboring them, then both high- and low-quality birds might benefit from such signals to avoid wasteful and potentially injuring fights.

Ultraviolet (UV) reflectance in avian plumage is ubiquitous across the avian tree of life (Eaton and Lanyon, 2003). Since the first studies reporting UV visual sensitivity in birds, three decades ago (Huth and Burkhardt, 1972; Wright, 1972), the interest in the role of UV signals in avian biology in general, and sexual selection in particular, has considerably increased. In 1990s, Bennett and Cuthill (1994) suggested that UV reflectance could play a role during mate choice or male-male interactions, signaling individual quality. This idea has been subsequently tested in several avian species. Mate choice experiments with captive birds showed that females prefer males with higher UV plumage reflectance (Andersson and Amundsen, 1997; Bennett et al., 1996, 1997; Hunt et al., 1999; Pearn et al., 2001; Siitari et al., 2002). However, to our knowledge, the role of UV signals in male-male conflicts has never been investigated.

In the past years, the blue tit (*Parus caeruleus*) has become one of the most-studied model species with respect to UV signaling. In particular, correlative and experimental work has suggested a role of UV reflectance of crown feathers on intersexual selection. Several lines of evidence have been provided: (1) sexual dichromatism and assortative mating (Andersson et al., 1998; Hunt et al., 1998), (2) reciprocal mate preference (Hunt et al., 1998, 1999), and (3) female adjustment of brood sex-ratio, depending on the level of UV reflectance of male crown feathers (Sheldon et al., 1999).

If male blue tits are able to discriminate females with different UV signals during mate choice trials (Hunt et al., 1999), it seems plausible that males can also evaluate the quality of other males on the basis of the same trait. Moreover, a recent study shows that male blue tits with a more UV-shifted crown were less cuckolded (Delhey et al., 2003), which may suggest a role of UV signal in mate guarding. Therefore, the

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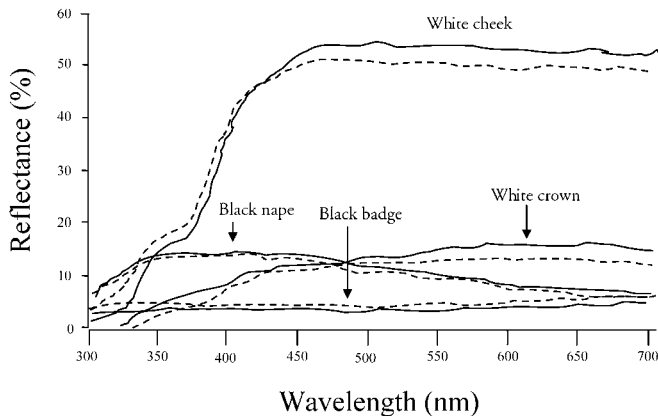


Figure 1
Reflectance spectra of blue tit feathers from different areas of two heads used in the experiment. Continuous line indicates control head; dotted lines, UV-reduced head.

main objective of the present study was to test whether UV reflectance can affect the outcome of intrasexual interactions in blue tits. More specifically, we studied the role of a UV signal on male-male agonistic behavior. The present study was performed in an insular population of blue tits belonging to the *ultramarinus* subspecies. Like the nominal subspecies, the *ultramarinus* tits show both sexual dimorphism and assortative mating with respect to UV chroma, hue, and color contrast of the crown feathers (Doutrelant C and Sorci G, unpublished data). We compared the level of aggression against taxidermic mounts, either with unmanipulated crown color or with a crown with a reduced UV signal (UVR). We predict that if the UV signal of the crown feathers is used as a cue of male competitive ability, males should behave less aggressively toward the mount with the highest degree of asymmetry in quality that is the UV-reduced mount.

METHODS

The present study was carried out in the island of Pantelleria (36°82' N, 11°97' E, Italy) during April–May 2002. We analyzed the response of territorial blue tits against taxidermic mounts presented close to the nest during the female egg-laying period. One single male body and two different male heads were used in the experiment. Both heads were separated just under the mandible and fixed on the body by means of a metallic wire and plasticine. The use of a single body was required to test whether crown UV reflectance per se and not some correlated aspects of individual phenotype could be responsible for a difference in the behavior of focal males. Although subtle differences in other parts of the head could have been present, the spectral properties of the black and white parts of the facial plumage of both models were almost identical (Figure 1).

Manipulation of UV reflectance was achieved following protocols described in Andersson and Amundsen (1997) and Sheldon et al. (1999). Namely, we smeared the crown plumage with a 40%/60% (w/w) mixture of duck preen gland fat and UV-absorbing chemicals (50/50 w/w blend of Parsol 1789 and MCX, Roche). Control was obtained by smearing the crown feathers with the duck preen gland fat alone. Changes in spectral shape of crown feathers for the two treatments are showed in Figure 2. Reflectance was measured by using a portable spectroradiometer (Ocean Optics S-2000) and a deuterium-halogen source (DH-2000). The light source

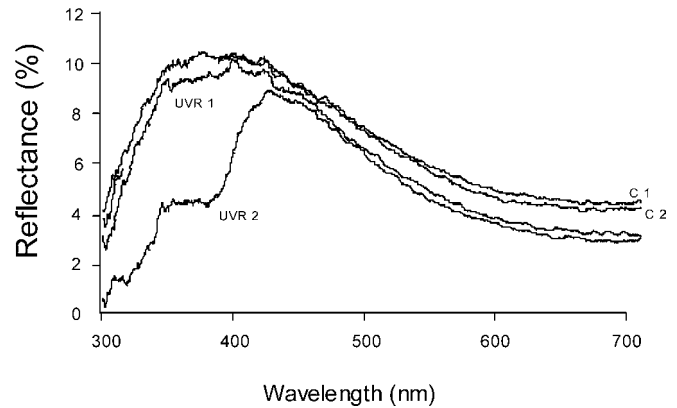


Figure 2
Reflectance spectra of blue tit crown feathers: C1 and C2 spectra refer to control mount before and after the application of duck preen gland fat; UVR1 and UVR2 spectra refer to UV-reduced mount before and after the application of UV-blocking chemicals.

illuminated the feathers through an optic fiber (FCR-7UV200-2-45 ME) and was reflected through a silica window cut at 45 degrees. A DAQ 700 card converted the data collected by the spectrometer and transferred them to a computer, where a software package (Spectrawin 4.1) computed reflectance spectra relative to a Spectralon white standard. The sampling frequency was set at 102.4 kHz, and each spectrum was averaged from five scans of 40 ms stabilized for maximal chroma. The persistence of the chemicals on the feathers was previously checked on another blue tit mount. According to these previous results, the chemicals were applied once a week.

Each focal male was exposed to both mounts (UVR and control) with at least an 1-hour interval between the two trials (mean = 71 min, range = 63–87 min). Presentation order was randomized to avoid training effect. A total of 24 focal males were tested, using the control head in the first trial in 12 cases. The mount was hanged about 3 m apart from the nest. To mimic a natural situation as much as possible, we played back the same vocal stimulus during each trial. A loudspeaker placed close to the mount produced 5 min of male song previously recorded in the same blue tit population. Because preliminary tests revealed that aggressive responses could seriously damage the mounts, they were placed in a small cage (40 × 30 × 30 cm) that simultaneously assured that focal males and females could see the mount and protected it. Only one cage was used. It was hanged on a branch by means of a wire and carefully placed at the same position during the two trials.

The behavior of focal individuals was recorded during 5 min per trial (UVR and control tests), using a digital video camera (Panasonic NV-MX7EG, Osaka, Japan). We started to record from the first moment the male discovered the mount. The behavior of focal males was assessed by the following variables indicating decreasing intensity of aggressive responses: (1) attack to the mount (scored as 0, no contact between the bird and the cage during the 5-min trial; 1, contact between the bird and the cage), (2) minimal distance to the mount (scored as 1, perched on the cage; 2, less than 40 cm to the cage but no contact; and 3, more than 40 cm to the cage); (3) time spent in proximity to the mount (within 40 cm to the cage); and (4) number of exhibition flights (Cramp and Perrins, 1993: 237) that males performed over the mount with no physical contact with the cage.

We also recorded whether the female was present during the trial (i.e., 26 out of 48 trials), her minimal distance to the

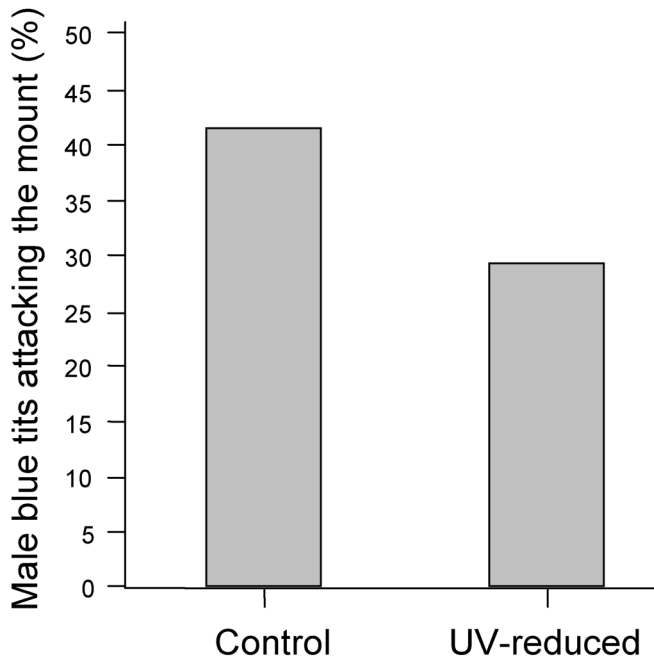


Figure 3
Percentage of male blue tits attacking a mount with control or UV-reduced crown feathers ($n = 24$ in each group).

mount, and the time spent in proximity to the mount. This allowed us to take into account a possible audience effect on male behavior.

Statistical analyses

We used generalized linear models (McCullagh and Nelder, 1989) to investigate whether focal males adjusted their aggressive behavior to the UV reflectance of the mounts. Generalized linear models allow the selection of an appropriate link function and response probability distribution depending on the nature of the data (binomial, multinomial, Poisson). The statistical analyses were performed with SAS Macro program GLIMMIX and PROC GENMOD (version SAS 8.2; SAS Institute, 2001). To evaluate the influence of female presence on male behavior and its interaction with the treatment (UVR versus control mounts) each model included nest as a random factor, treatment, female presence, and the treatment \times female presence interaction. We started with the saturated model and subsequently dropped the nonsignificant terms ($p > .05$). Explained deviance is the change in deviance when a term is removed from the model and is expressed as the percentage of the total deviance in the model including the nest.

RESULTS

Male blue tits exhibited a more aggressive response toward the control mount, as shown by a higher propensity to attack the control decoy (explained deviance in the null model: 24.45%; parameter estimate \pm SE: 1.496 ± 0.633 , $F_{1,23} = 5.57$, $p = .027$, nest effect: $Z = 2.19$, $p = .014$) (Figure 3), and by a shorter approach distance (explained deviance: 45.64%, parameter estimate: 3.892 ± 1.512 , $\chi^2 = 6.63$, $p = .010$, nest effect: $\chi^2 = 80.54$, $p < .001$). In seven cases the male was closer to the control than to the UVR mount, whereas the opposite was true in only one case. Time spent close to the mounts was

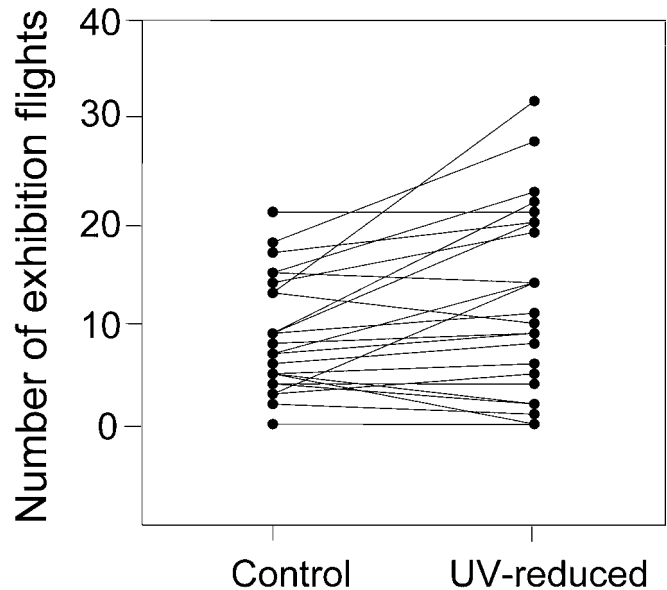


Figure 4
Number of exhibition flights performed by male blue tits toward a mount with control or UV-reduced crown feathers ($n = 24$ in each group).

not affected by the treatment (parameter estimate: -0.065 ± 0.170 , $F_{1,23} = 0.15$, $p = .705$, nest effect: $Z = 2.13$, $p = .017$).

Finally, the number of exhibition flights over the cage was significantly higher for the UV-reduced mount (explained deviance: 33.15%, parameter estimate: 0.327 ± 0.101 , $F_{1,23} = 10.48$, $p = .0036$, nest effect: $Z = 2.37$, $p = .009$) (Figure 4).

DISCUSSION

Our results suggest that UV signals affect the outcome of aggressive interactions in male blue tits. We found that nest-defending males adjusted their behavior against an intruder depending on the UV properties of the crown feathers of the opponent. To our knowledge this is the first experimental evidence indicating that UV signals may play a role in male contests.

Asymmetries between opponents in terms of individual quality are known to affect the intensity of the aggressive behavior, the probability of escalation being negatively correlated with the degree of asymmetry (Riechert, 1998). In agreement with this view, we found that focal males behaved less aggressively toward the UV-reduced mount that is in contests in which the asymmetry between opponents was greatest. It is possible that ritualized displays such as exhibition flights are sufficient to discourage a low-quality intruder from pursuing the contest, with no need to escalate into a potentially injurious fight. This hypothesis could explain our result of higher probability of attack and closer approach to the control mount, but higher number of exhibition flights against the UV-reduced decoy.

Studies dealing with the evolution of animal conflicts have often focused on pairwise interactions in which two opponents "fight" for a resource, and the costs and benefits of the contest directly arise from the outcome of the conflict. However, social as well as aggressive interactions usually take place in a wider context of information exchange among several members of a group (McGregor and Peake, 2000). As such, individuals might gather information on the competitive ability of conspecifics involved in aggressive interactions

and use it during the decision making to fight or to retreat (Johnstone, 2001). Females can also assess the quality of partners during male-male contests and use this information to adjust their investment into reproduction (Doutrelant and McGregor, 2000; Mennill et al., 2002; Otter et al., 1999). In a dynamical game, opponents are also expected to adjust their willingness to fight to the benefit arising from the effect of the contest outcome on the audience (Doutrelant et al., 2001; Matos and McGregor, 2002). According to this scenario, we predicted that focal males should modulate their reaction toward the mount depending on whether the female was present or absent. However, contrary to this prediction, we did not find any effect of female presence on the intensity of aggressive behaviors expressed by males. Further experiments specifically designed to test this hypothesis are needed to draw final conclusions.

In a recent review, Berglund et al. (1996) suggested that male-male competition could be the promoting force for many secondary sexual traits, female choice playing a reinforcement role later on. Could this hypothesis work for blue tit UV colors? Several lines of evidence suggest that this might be the case. First, recent findings showed that UV reflectance of blue tit crown feathers is maximal in winter (Örnberg et al., 2002), when tits form large flocks (Cramp and Perrins, 1993). Dominance status within the flock is related to body condition, predation risk, and survival rate in tits (see Gosler and Carruthers, 1999; Hegner, 1985; Koivula et al., 1996; Poysa, 1988). Thereafter, when flocks break up at the end of winter, male-male contests for territory acquisition and defense are common (Cramp and Perrins, 1993), and territory quality has a strong effect on blue tit breeding success (see Blondel et al., 2000; Przybylo et al., 2001). If highly ornamented males (with highest UV reflectance) establish and defend better territories, there might be strong intrasexual selection going on these traits. Intersexual selection could reinforce such pattern if females choose mates based on territory quality and male ornaments.

To conclude, we should remember that debate is open on the specificity of UV signals in birds. Although some studies claim that information offered in the UV spectrum is no more special than that offered in other wavelengths (Banks, 2001; Hunt et al., 2001), a recent comparative approach suggest that signals based on UV contrast are of special importance in the context of active courtship displays in avian species (Hausmann et al., 2003). Now, a similar approach including UV role in intrasexual signaling is needed.

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