Is UV signalling involved in male-male territorial conflict in the blue tit (*Cyanistes caeruleus*)? A new experimental approach

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Summary

Structurally-based ultraviolet (UV) coloration of plumage can signal male quality and plays a role in female mate choice in many bird species. UV-reflecting badges could also be important signals in male-male competition. We tested if territorial blue tit (*Cyanistes caeruleus*) males discriminate between conspecific male intruders which differ in the UV reflectance of their crown feathers. To this aim, we used a new experimental approach in which we simultaneously (instead of sequentially) introduced two male blue tit taxidermic mounts in the territories of resident males during the female fertile period; one mount with natural crown UV reflectance and one mount with reduced crown UV. The two mounts provoked strong aggressive reactions from resident males. Males specifically directed their aggression to conspecific intruders, as a male blue tit mount received substantially more aggression than a mount of a European robin (*Erithacus rubecula*). However, aggression of resident males did not vary between the UV-reduced and the control mount. Furthermore, the variation in natural crown UV reflectance of the resident males did not predict the intensity of their aggressive response. Contrary to previous findings our results suggest that UV signals play only a limited role in male-male interactions during territorial intrusions in the female fertile period.

Keywords: ultraviolet plumage, ultraviolet signalling, male-male competition, territorial conflict, sexual selection, blue tit *Cyanistes* (formerly *Parus*) *caeruleus*.

Introduction

Competition between males over limited resources and potential mates occurs in many avian mating systems and can, together with female mate choice, drive the evolution of male plumage colours that have social signalling functions (Andersson, 1994). Such colour badges of status allow competitors to assess each others fighting ability from a distance, and hence to settle contests without risking injury during aggressive interactions (Rowher, 1975, 1982; Whitfield, 1987). In order to ensure reliability and to prevent cheaters providing dishonest information such status signals have to be associated with costs (Maynard Smith & Harper, 1988; Johnstone & Norris, 1993). Costs of the production and maintenance of bright plumage coloration could be socially induced, increased predation risk, direct energetic or nutrient limitation, or hormone mediated (Møller, 1987; Folstad & Karter, 1992; Andersson, 1994; Slagsvold et al., 1995).

Plumage colours are either due to pigment deposition in the feathers (carotenoids or melanins; Olson & Owens, 1998; Jawor & Breitwisch, 2003) or to microstructures in the feather barbs (Fox, 1976; Prum et al., 2003). These microstructures can not only produce blue, violet and iridescent colours, but also ultraviolet (UV), which is invisible to humans. UV-reflective plumage parts are widespread among many avian taxa (Burkhardt, 1989; Eaton & Lanyon, 2003; Hausmann et al., 2003), and many bird species can detect wavelengths in the UV portion of the spectrum (320-400 nm; Parrish et al., 1984; Cuthill et al., 2000). UV plumage colours can signal several aspects of male quality, such as survival prospects (Sheldon et al., 1999; but see Delhey & Kempenaers, 2006), parasite load (Doucet & Montgomerie, 2003), nutritional condition (Keyser & Hill, 1999; McGraw et al., 2002) and territory quality (Keyser & Hill, 2000). Furthermore, several studies have shown female preferences for males with high plumage UV reflectance over less UV-reflective males (Andersson & Amundsen, 1997; Andersson et al., 1998; Hunt et al., 1998; Johnsen et al., 1998).

Male secondary sexual characters that function as female mate choice cues often also play an important role in male-male competition and vice versa (Berglund et al., 1996). However, few studies have investigated the role of UV ornaments in male-male competition. In the Eastern bluebird (*Sialia sialis*), males with higher plumage UV reflectance had a competitive advantage over less colourful males in the acquisition of vacant nestboxes

(Siefferman & Hill, 2005). In males of the Gouldian finch (*Erythrura gouldiae*), the intensity and size of their UV-blue collar determined the outcome of the staged contests (Pryke & Griffith, 2006). In the blue tit (*Cyanistes caeruleus*), in which both sexes have UV-reflecting blue crown feathers, territorial males showed higher levels of aggression towards male taxidermic mounts with natural crown UV reflectance than towards mounts with reduced crown UV, when tested in a population of the *ultramarinus* subspecies on the Mediteranean island Pantelleria (Alonso-Alvarez et al., 2004). The UV crown plumage of both male and female blue tits is probably important in inter-sexual signalling during mutual mate choice, as indicated by the occurrence of assortative pairing with respect to crown UV reflectance (Andersson et al., 1998; Alonso-Alvarez et al., 2004). In addition, the UV crown plumage of male blue tits was found to play a role in inter-sexual signalling during extra-pair mate choice (Delhey et al., 2003, 2007a), offspring sex allocation (Sheldon et al., 1999; Griffith et al., 2003; Korsten et al., 2006; Delhey et al., 2007b) and allocation of maternal care (Limbourg et al., 2004). However, in our blue tit study population, which is of the nominate subspecies, we observed no assortative pairing with respect to crown UV reflectance (Korsten, 2006), which suggests that the signalling function of blue tit UV crown plumage may vary among populations and/or subspecies.

Therefore, we aimed to test if ultraviolet signalling of the crown plumage is involved in male-male agonistic interactions during territorial intrusions in our blue tit study population. We introduced two taxidermic male blue tit mounts – of which one had reduced crown UV reflectance and the other had natural crown UV reflectance after a control treatment – into territories of resident males during the presumed female fertile period, and we measured if resident males varied their aggressive responses towards the two different mount types. Alonso-Alvarez et al. (2004) presented both mounts sequentially to territorial males, separated by at least one-hour intervals. To control for possible mount effects, Alonso-Alvarez et al. (2004) used one single male's mounted body fitted with either one of two detachable male heads, of which one had reduced crown UV reflectance and the other had natural crown UV. We presented the two male mounts with the different UV treatments simultaneously. This new experimental set-up has the advantage of a direct comparison of resident males' reactions to the different intruder types, while controlling for irrelevant variation in male reactions due to for

example differences in the timing of the mount presentation, the motivation of the males, or the presence or absence of the female mate during the simulated intrusion (for further discussion of sequential versus simultaneous stimulus presentations in choice tests, see also MacLaren & Rowland, 2006). To control for possible mount effects we switched the UV-reduced and control treatment regularly between both mounts. We predicted that if the UV reflectance of the crown feathers is indeed used as an indicator of male competitive ability, territorial males should behave less aggressively towards the mount 'signalling' the highest degree of asymmetry with the territory owner, that is the UV-reduced mount (Rohwer, 1975; Alonso-Alvarez et al., 2004).

In addition to the replication of the original mount intrusion experiment of Alonso-Alvarez et al. (2004), we measured the natural crown UV reflectance of the resident males to investigate the relationship between the UV signal of focal males and their aggressive response towards the 'intruding' male mounts. In birds, males searching for a territory probably mostly attack territory owners with relatively low intensity colour signals indicating lower fighting ability (Røskaft & Rohwer, 1987; Pryke et al., 2002). Furthermore, male blue tits with more UV-shifted crown plumage were found to be less cuckolded (Delhey et al., 2003; see also Delhey et al., 2007a), which may indicate that they are better mate guarders than less UV-shifted males. Therefore, we expected that males with more intense UV signals would on average show fiercer reactions towards the mounts than less UV-reflective males, which would be similar to the positive correlation between the intensity of pigment-based plumage coloration and resident male aggression that was found in several other bird species (Studd & Robertson, 1985; Järvi et al., 1987; Pryke et al., 2001). The function of avian structural/UV colour signalling in competitive interactions is relatively unexplored and to our knowledge this is the first study in which the extent of male aggressive behaviour has been related to the extent of males' own UV coloration.

Materials and methods

Study area and population

We conducted this research from 14 March to 30 May, 2003, in a blue tit population of the nominate subspecies breeding on the estate of de Vosbergen (ca. 50 ha; 53°08′N, 06°35′E), near Groningen, the Netherlands. The

study area 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 was monitored during the breeding seasons of 2001-2003, and during this period we marked all breeding adults with a uniquely numbered metal ring and a unique combination of coloured rings.

For the present study we regularly checked nestboxes for occupation from March 14 onwards. Once we discovered nest building activity, we recorded the stage of nest building, and the dates of laying of the first egg, clutch completion and hatching. We conducted territorial intrusion trials with taxidermic mounts of male blue tits, both in territories where nests were completed, but laying had not commenced, and in territories where the female had started laying, but not completed her clutch. We captured parent birds during nestling feeding with spring traps in nestboxes. We sexed adults by the presence (=female) or absence (=male) of an incubation patch, and aged them as first year or older (see Svensson, 1992). We measured body mass (±0.1 g, using a Pesola spring balance) and the spectral reflectance of the crown feathers.

Measurements of crown colour

The spectral reflectance of the crown feathers of all but two resident males ($N = 42$) in whose territories we conducted successful intrusion trials 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. Following previous studies of UV colour signalling in blue tits (e.g., Sheldon et al., 1999; Griffith et al., 2003; Korsten et al., 2006; Delhey et al., 2007a) we calculated three indices describing the variation in crown colouration – '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 and 700 nm ($R_{320\text{-}700}$), which corresponds to the spectral range visible to blue tits (Hart et al., 2000). Hue was the wavelength of maximum reflectance, $\lambda(R_{max})$. 'UV chroma' was the sum

of reflectance between 320 and 400 nm divided by the sum of reflectance between 320 and 700 nm ($R_{320\text{-}400}/R_{320\text{-}700}$). Both the 'hue' and 'UV chroma' indices have previously been identified as important predictors of male attractiveness and viability in blue tits (e.g., Sheldon et al., 1999; Delhey et al., 2003, 2007a; Griffith et al., 2003). Males were captured for crown colour measurements within a relatively short period (14-29 May) leading to little variation in crown feather wear (Örnborg et al., 2002; Delhey et al., 2006), and consequently crown coloration was not significantly related to the date of capture (brightness: $r = 0.28$, $p = 0.08$; hue: $r = -0.05$, $p = 0.73$; UV chroma: $r = 0.22$, $p = 0.16$; all $N = 42$).

Territorial intrusion experiment

We used two taxidermic mounts of male blue tits (mount A and B), which had a neutral pose (body straight, wings down alongside the body and the tail straight extending from the back). We reduced the original UV reflectance of the crown feathers of one of the two mounts by applying a 40/60% (by weight) mixture of duck preen gland fat and UV-blocking chemicals, 50% Parsol 1789 and 50% Parsol MCX (also by weight) (Roche, Basel, Switzerland; Figure 1). As a control, preen gland fat only was applied to the crown feathers of the other mount, which left the original UV reflectance unaltered (Figure 1). The method of UV reduction followed the procedures of previous UV manipulations of wild male blue tits (Sheldon et al., 1999; Limbourg et al., 2004; Korsten et al., 2006, in press) and the procedure used by Alonso-Alvarez et al. (2004) to manipulate the UV of a male blue tit taxidermic mount. The mounts were switched in treatment ($5\times$) after variable numbers of trials (9.6 ± 6.0 SD) to control for differences in reactions of resident birds based on other physical differences between the mounts (total number of trials: $N = 49$). We switched the treatment after a variable number of trials to be able to balance the number of trials in which either mount A was UV-reduced or mount B was UV-reduced specifically for those trials in which the resident male closely approached (<1 m) or attacked at least one of the mounts ($N = 17$ trials; mount A UV-reduced: $N = 8$; mount B UV-reduced: $N = 9$; see below for more details on sample sizes). To switch the mounts in treatment both the UV-reducing chemicals and the duck preen gland fat were removed from the feathers by rinsing with 96% ethanol after which the crown feathers were blown until dry. The presence or absence of a
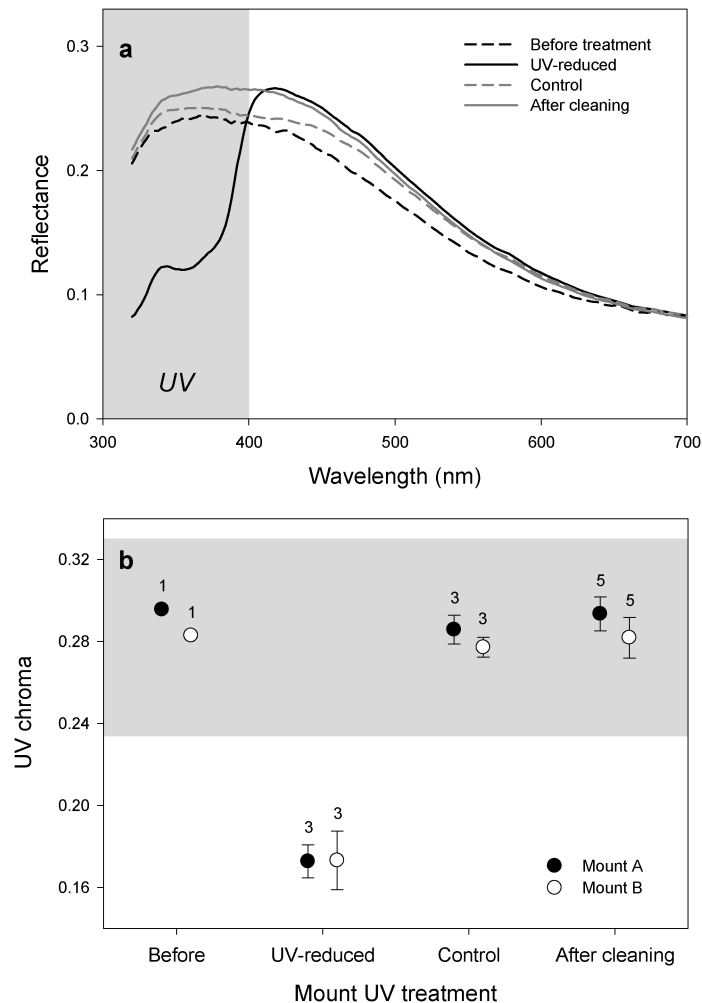
Figure 1. Top panel (a) shows mean reflectance spectra of the crown plumage of two male blue tit taxidermic mounts (A and B) used to simulate territorial intrusions. Mean reflectance spectra were calculated from crown reflectance measurements taken before the first UV treatment ($N = 2$), after each UV-reduction treatment ($N = 6$), after each control treatment ($N = 6$), and after each cleaning ($N = 10$). Lower panel (b) shows the UV chroma values of crown plumage of male blue tit mounts A and B. Depicted are the initial UV chroma values of both mounts before the first UV treatment, means after UV reduction and control treatment, and means after cleaning. Means were calculated from crown color measurements taken each time the UV treatment was switched between the mounts. Whiskers indicate SDs. Numbers indicate sample sizes. The shaded area indicates the range of natural UV chroma values of the 42 resident blue tit males of which we measured crown coloration that were included in our analyses.
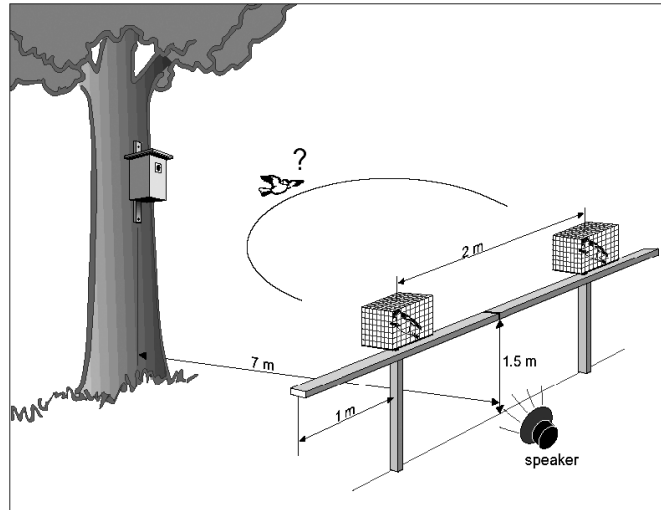
Figure 2. Experimental set-up of territorial intrusion trials with male blue tit taxidermic mounts.

UV-reduction effect caused by the treatment was invisible to the human eye, but spectrophotometric measurements proved that the cleaning method was effective and entirely restored the original UV reflectance of the mounts (Figure 1). After we ascertained that the original UV reflectance of the mounts was restored, the treatments were re-applied. In summary, mount A and B each received both the UV-reduction and control treatment 3 times, and each mount was cleaned 5 times (Figure 1).

During the intrusion trials both mounts were simultaneously presented in the territory of a resident male on top of two T-formed sticks (horizontal 2×1.0 m on a 1.5 m vertical stick; Figure 2). To prevent the mounts from damage due to the aggressive responses of the resident males both mounts were put in two equally sized green wire cages ($7.0 \times 12.0 \times 15.0$ cm). The sticks with the mounts were placed alongside each other, at 7 meters distance of a tree with an occupied nestbox, in such a manner that both mounts were equally accessible from surrounding trees and nearby branches (Figure 2). The sticks including two empty wired cages were placed in position one day before each trial to habituate the resident birds to the foreign objects in their territory. At the start of each intrusion trial we placed both mounts in the cages on the T-sticks after we ascertained that none of the resident birds were in the vicinity. Each trial the UV-reduced and control-treated mounts

were randomly assigned to the left and right sticks. To attract the resident birds, song of an unfamiliar blue tit male was played from a speaker placed on the ground in between both mounts (Figure 2). The sexes of the resident birds were identified by their colour rings. In case the resident male did not respond to the presence of the mounts and song playback, i.e., when the male did not appear within a distance of 10 m from one of the mounts within 15 minutes (recorded with a stopwatch) we stopped the intrusion trial. If the male responded within 15 minutes we recorded the latency from the start of song playback until the moment of first arrival within 10 m (hereafter referred to as 'latency of response'). At the arrival of the male we started an observation protocol of five minutes (see Alonso-Alvarez et al., 2004). We measured the latencies from the moment of the male's arrival until his first approach within 1 m from one of the mounts (hereafter referred to as 'latency to approach'), and until the moment he first landed on one of the cages to physically attack the mount inside (hereafter referred to as 'latency to attack'). Because distance of resident birds to intruders is a good estimate of the intensity of aggression (Studd & Robertson, 1985; Pryke et al., 2001; Alonso-Alvarez et al., 2004; Penteriani et al., 2007) we recorded the distance between the focal male and the nearest mount every five seconds on a voice recorder. We recorded the following distance categories: (1) contact with cage, hereafter referred to as 'attack'; (2) between 0-1 m, but no contact with cage, hereafter referred to as 'approach'; (3) >1 m from cage. When the male was exactly in between the mounts only the distance to both mounts (0-1 m) but no nearest mount was recorded (Figure 2). Only one trial per nestbox was conducted. All trials were conducted without the observer (TD) knowing which type of treatment was used on which of the two mounts (treatment applied by PK).

During the presumed female fertile period we conducted intrusion trials at 49 nestboxes with nest stages ranging from 11 days before to 7 days after laying of the first egg (average clutch size: 11.0 ± 1.67 SD). Although the precise onset of the fertile period of females is unknown in most wild birds (Birkhead & Møller, 1998), the fertile period of female blue tits probably starts at least 5-6 days before laying, when resident males are frequently challenged by male territorial intrusions (Kempenaers et al., 1992) and intensify mate guarding. The female subsequently remains fertile until one day before completion of the clutch (Kempenaers et al., 1995). Four trials conducted in the territories of what turned out to be two polygynous males

were excluded from the analyses. This was to avoid pseudo-replication, and because polygynous males may react differently to the territorial intrusions. This could occur, because polygynous males may preferentially defend one of the two occupied nestboxes in their territory or may focus their attention on one of the two nestboxes, and consequently have a longer delay until the detection of intruders near the other nestbox. One more trial was excluded, because the resident male directed courting behaviour, instead of aggression, to the models. Additional exclusion of the 7 trials that were conducted more than 6 days before the female laid her first egg did not lead to a qualitative change in the results. Therefore, we only report the results of analyses including these 7 trials (total $N = 44$).

Of the 44 individual resident males included in the analysis 25 males responded to the mounts and song playback and arrived within 10 m from the mounts in less than 15 minutes. Seventeen of these 25 males approached at least one of the mounts within 1 m, of which 14 males attacked one or both mounts. In 8 of these trials mount A was UV-reduced and mount B control-treated; in 9 trials mount B was UV-reduced and mount A control-treated. There was an almost significant tendency for males to preferentially first approach mount B within 1 m (4 first approaches to mount A versus 13 to mount B, Yates' corrected $\chi^2 = 3.76$, df $= 1$, $p = 0.052$). However, there was no difference in the number of first attacks that males directed to either mount A or mount B (8 first attacks of mount A versus 6 of mount B, Yates' corrected $\chi^2 = 0.07$, df $= 1$, $p = 0.79$). Also the number of males that approached or attacked either mount A or mount B during the intrusion trials was not different, as 16 of 25 males approached mount A versus 17 of 25 males that approached mount B (Yates' corrected $\chi^2 = 0.00$, df $= 1$, $p = 1.0$) and 11 of 25 males attacked mount A versus 14 of 25 males that attacked mount B (Yates' corrected $\chi^2 = 0.32$, df $= 1$, $p = 0.57$). Males also spent a similar amount of time within 1 m from each mount (mean number of five-second intervals $\pm$ SE: mount A, 5.88 ± 0.98; mount B, 7.76 ± 1.22; paired t-test: $t = -1.69$, df $= 16$, $p = 0.11$) and attacking each mount (mean number of five-second intervals $\pm$ SE: mount A, 14.8 ± 2.68; mount B, 16.4 ± 2.10; paired t-test: $t = -0.60$, df $= 13$, $p = 0.56$). Given this overall result, we consider it unlikely that differences in appearance between the two mounted blue tit males, other than manipulated crown UV reflectance, would have influenced our results. The near-significant tendency of males to preferentially first approach mount B was not corroborated by any of

the other measures of male aggression directed to the two models and may represent a type-I statistical error, especially given the substantial number of tests we performed. To check if the aggression by the resident males towards the male blue tit mounts was specifically directed to conspecific intruders we presented a mount of a European robin (*Erithacus rubecula*), which is also a common species in our study area, together with a male blue tit mount in the territories of 8 resident males following the same protocol as described above.

Data analyses

To investigate if aggression of resident males was specifically directed to one of the two simultaneously presented mount treatment types we tested: (1) if one of the mounts was more often first approached (within 1 m) or first attacked (physical contact with protecting cage) by the resident males; (2) if a greater number of resident males approached or attacked one of the mounts during the 5-minute intrusion trial (see Alonso-Alvarez et al., 2004); (3) if the time (=number of five-second intervals) resident males spent within 1 m from each mount or attacking each mount differed between the two mount types.

To investigate if the intensity of the aggressive reaction of resident males was related to their own UV coloration we tested: (1) if indices of crown colour differed between: males that responded to the simulated intrusion, males that approached at least one of the mounts, males that attacked at least one of the mounts, and males that did none of these; (2) if male crown colour indices were correlated with the latency of response to the simulated intrusion, and with the latencies to approach or attack; (3) if male crown colour indices were correlated with the time males spent within 1 m from the mounts or attacking the mounts.

To investigate if resident males directed their aggression to either the UV-reduced or control-treated mount depending on their own UV coloration we tested if crown colour indices differed between males that first approached or attacked the UV-reduced mount and males that first approached or attacked the control-treated mount. Furthermore, we tested if male crown colour indices were related to the proportion of 5-second intervals spent within 1 m from the UV-reduced mount or attacking the UV-reduced mount when compared to the total number of 5-second intervals spent within 1 m and attacking respectively. Distributions of the proportions of time spent within

1 m from the UV-reduced mount and attacking the UV-reduced mount did not deviate from normal and we used weighted linear regression for this analysis. The linear regression models were weighted for the total number of intervals spent within 1 m from both mounts and attacking both mounts respectively, because these numbers varied considerably among males (Figure 3). All statistical tests were two-tailed and *p*-values smaller than 0.05 were regarded significant. Following the recent recommendation of Nakagawa (2004) we provide measures of standardised effect size with our main statistical results to facilitate the use of these results in meta-analyses. The reported measures of standardized effect size are r for correlations, Cohen's d for *t*-tests comparing means and Cohen's w for χ^2 tests for goodness of fit (Cohen, 1992). Cohen's (1992) benchmark values are $r = 0.10, 0.30$ and 0.50, $d = 0.20, 0.50$ and 0.80, and $w = 0.10, 0.30$ and 0.50, for small, medium, and large effects, respectively. Statistical analyses were carried out using SPSS 14.0 (2005) and G*Power (version 3.0.3; Faul et al., in press).

Results

Blue tit mount versus European robin mount

Five of eight resident blue tit males responded within 15 minutes when we simultaneously presented mounts of a male blue tit and a European robin in their territories. Resident males specifically directed their aggression to the blue tit mount; four of five males first approached the blue tit mount and four males landed on the cage with the blue tit mount, whereas only one male landed on the cage with the robin mount. Although males did not spend more time within 1 m from the blue tit mount than within 1 m from the robin mount (mean number of five-second intervals $\pm$ SE: blue tit, 1.80 ± 1.56; robin, 1.40 ± 0.51; paired *t*-test: $t = 0.27$, df $= 4$, $p = 0.80, d = 0.17$), males spent substantially more time on the cage with the blue tit mount, while attacking it, than on the cage with the robin mount (mean number of 5-second intervals $\pm$ SE: blue tit, 39.6 ± 10.8; robin, 0.80 ± 0.80; paired *t*-test: $t = 3.66$, df $= 4$, $p = 0.022, d = 2.53$).

UV-reduced versus control-treated blue tit mounts

Twenty-five of 44 individual resident males responded to the mounts and song playback during our trials and arrived within 10 m in less than 15
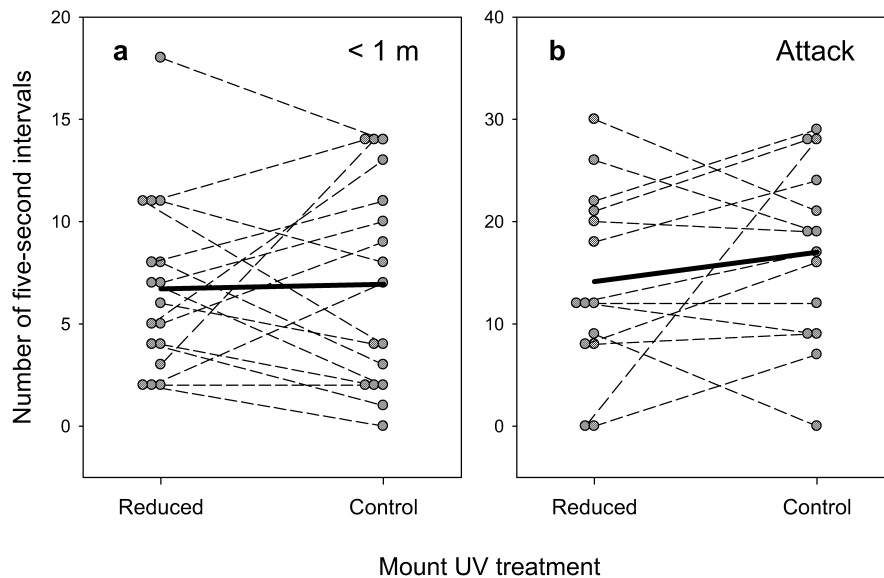
Figure 3. Number of five-second intervals spent by territorial male blue tits within 1 m distance ($N = 17$) (a) or attacking ($N = 14$) (b) each of the two simultaneously presented intruder mounts (UV-reduced and control) during five minute trials. Dots connected by dashed lines indicate paired observations of individual resident males. Bold solid lines indicate average slopes. Paired t-tests of UV-reduced versus control: Approach < 1 m, $t = -0.20$, df $= 16$, $p = 0.85$, $d = 0.05$; Attack, t-test: $t = -1.13$, df $= 13$, $p = 0.28$, $d = 0.33$.

min. Seventeen of these males approached at least one of the mounts within 1 m, of which 14 males attacked one or both mounts. Resident males did not preferentially first approach either the UV-reduced (11 males) or the control-treated mount (6 males) within 1 m (Yates' corrected $\chi^2 = 0.94$, df $= 1$, $p = 0.33$, $w = 0.29$), or more often first attack either the UV-reduced (6 males) or the control-treated mount (8 males; Yates' corrected $\chi^2 = 0.07$, df $= 1$, $p = 0.79$, $w = 0.14$). Also the number of males that approached or attacked either the UV-reduced or control-treated mount during the intrusion trials was not different, as 17 of 25 males approached the UV-reduced mount versus 16 males that approached the control-treated mount (Yates' corrected $\chi^2 = 0.00$, df $= 1$, $p = 1.0$, $w = 0.04$) and 12 of 25 males attacked the UV-reduced mount versus 13 males that attacked the control-treated mount (Yates' corrected $\chi^2 = 0.00$, df $= 1$, $p = 1.0$, $w = 0.04$). Males spent similar amounts of time within 1 m from the UV-reduced and within 1 m from the control-treated mount and attacking the two mount types (Figure 3).

Table 1. Comparisons of crown colour indices of blue tit males with different aggressive reactions to male blue tit mounts.

Colour indices	Response			No response			Independent samples t-tests			
	Mean	SE	$N^{1)}$	Mean	SE	$N^{1)}$	t	df	p	d
Brightness	71.7	2.29	23	72.7	2.78	19	−0.27	40	0.79	0.09
Hue	394.0	2.60	23	392.9	2.93	19	0.30	40	0.77	0.09
UV chroma	0.290	0.003	23	0.290	0.004	19	0.03	40	0.98	0.00
	Approach < 1 m			No approach < 1 m						
Brightness	72.0	2.15	15	71.2	5.46	8	0.15	$9.23^{2)}$	0.89	0.07
Hue	396.5	2.83	15	389.3	5.11	8	1.33	21	0.20	0.62
UV chroma	0.288	0.004	15	0.294	0.005	8	−0.92	21	0.37	0.40
	Attack			No attack						
Brightness	72.2	2.19	13	71.2	4.58	10	0.20	$13.1^{2)}$	0.85	0.09
Hue	398.3	2.63	13	388.5	4.46	10	1.88	$15.0^{2)}$	0.08	0.87
UV chroma	0.286	0.003	13	0.296	0.006	10	−1.61	21	0.12	0.71

[1] Note that sample sizes are reduced, because crown reflectance of 2 males was not measured.

[2] Adjusted for unequal variances.

Influence of resident male crown colour

There was no difference between the crown colour of resident males that responded within 15 minutes to the presentation of the blue tit mounts and males that did not respond (Table 1). Similarly, there was no difference between the crown colour of males that approached (<1 m) or attacked at least one of the mounts and males that did not (Table 1).

Crown colour of males was unrelated to: 1) their latency of response after we presented the male blue tit mounts in their territories; 2) their latency to approach and their latency to attack; 3) the amount of time they spent within 1 m from the mounts or attacking the mounts (Table 2).

Crown colour was not different between males that first approached the UV-reduced mount and males that first approached the control mount (Table 3). Similarly, crown colour was not different between males that first attacked the UV-reduced mount and males that first attacked the control-treated mount (Table 3). Male crown colour was unrelated to the proportions of 5-second intervals spent within 1 m of the UV-reduced mount and attacking the UV-reduced mount (Table 4).

Finally, male age and body mass were unrelated to the likelihood of response to the simulated territorial intrusion or any measure of aggressive

Table 2. Relationships between crown colour indices of blue tit males, and latency and intensity of aggressive reactions to male blue tit mounts.

	Brightness			Hue			UV chroma		
	r	$N^{2)}$	p	r	$N^{2)}$	p	r	$N^{2)}$	p
Latency of response	−0.01	23	0.95	−0.00	23	0.98	0.06	23	0.80
Latency to approach (<1 m)	0.45	15	0.09	0.11	15	0.70	0.13	15	0.64
Latency to attack	0.33	13	0.27	0.11	13	0.72	0.11	13	0.71
Time spent[1] within 1 m	0.06	23	0.78	−0.08	23	0.73	0.21	23	0.34
Time spent[1] attacking	−0.01	23	0.97	0.340	23	0.06	−0.37	23	0.09

[1] Number of 5-second intervals.

[2] Note that sample sizes are reduced, because crown reflectance of 2 males was not measured.

Table 3. Comparisons of crown colour indices of blue tit males that first approached (<1 m) or attacked either the UV-reduced or control mount.

	Colour indices	UV-reduced			Control			Independent samples t-tests			
		Mean	SE	$N^{1)}$	Mean	SE	$N^{1)}$	t	df	p	d
First approach	Brightness	71.2	2.64	10	73.7	4.03	5	−0.54	13	0.60	0.32
	Hue	396.7	3.23	10	396.0	6.11	5	0.12	13	0.91	0.07
	UV chroma	0.288	0.006	10	0.288	0.006	5	0.01	13	0.99	0.01
First attack	Brightness	71.1	4.40	5	72.8	2.51	8	−0.32	11	0.71	0.23
	Hue	395.5	6.04	5	400.0	2.29	8	−0.58	11	0.44	0.50
	UV chroma	0.288	0.008	5	0.284	0.004	8	0.33	11	0.60	0.34

[1] Note that sample sizes are reduced, because crown reflectance of 2 males was not measured.

behaviour (all p-values > 0.17). Neither were male age or body mass related to the UV treatment of the mount to which the males directed their aggression (all p-values > 0.38).

Discussion

In contrast to a previous study by Alonso-Alvarez et al. (2004) in a blue tit population of the *ultramarinus* subspecies, we found no significant difference in the likelihood of territorial blue tit males of the nominate subspecies to attack a conspecific male mount with natural crown UV reflectance (after

Table 4. Relationships between crown colour indices of blue tit males and the proportions of 5-second intervals these males spent near (within 1 m) and attacking the UV-reduced male blue tit mount.

	Brightness			Hue			UV chroma		
	r	$N^{2)}$	p	r	$N^{2)}$	p	r	$N^{2)}$	p
Proportion time spent <1 m of UV-reduced mount[1]	0.19	15	0.51	0.12	15	0.68	0.13	15	0.64
Proportion time spent attacking UV-reduced mount[1]	0.18	13	0.57	0.15	13	0.62	0.08	13	0.80

[1] Proportion of five-second intervals spent near (<1 m) or attacking the UV-reduced mount. Linear regression models were weighted for total number of 5-second intervals spent near (<1 m) or attacking either the UV-reduced or control mount.

[2] Note that sample sizes are reduced, because crown reflectance of 2 males was not measured.

control treatment) and a mount with reduced crown UV, when we simultaneously introduced these different mount types in males' territories. Given the marginal effect that we found – 13 of 25 males attacked the control-treated mount, whereas 12 of those 25 males attacked the UV-reduced mount (which equates to an standardized effect size of $w = 0.04$) – we conclude that the UV coloration of the intruder mount had at most a negligibly small effect on the aggressive response of the territorial males in our blue tit population. This conclusion was confirmed by the absence of a significant effect of mount UV treatment on all other parameters of resident male aggression we measured, such as which mount type was first approached or attacked, and the time that males spent near (<1 m) or attacking the differently treated mounts. Furthermore, resident males' own crown UV coloration was not significantly related to the intensity of their aggressive reaction to the mounts, which is another indication that crown UV signalling is of little importance in conflict between male territory owners and intruders in our study population.

The UV reduction treatment distorted the spectral profile of the crown reflectance and reduced UV chroma values outside the natural range (Figure 1). This may have lead to an unnatural appearance of the UV-reduced mount as perceived by the resident blue tit males, which could potentially have caused artifactual results. Nevertheless, we believe that our conclusions are valid for the following reasons. Firstly, the UV-reduced blue tit mount was certainly recognised as a conspecific, since resident males directed their aggression equally to the UV-reduced and control-treated mount. Furthermore, it is very

unlikely that resident males would discriminate between intruders that vary more subtly in their crown colour (i.e., within the natural range), given that they did not vary their responses in relation to the extreme difference in crown coloration between the two intruder mounts in our experiment. Lastly, we used the same UV-reduction treatment as Alonso-Alvarez et al. (2004), who to the contrary did find an effect of the treatment on resident male aggression in their study population.

An important factor that could potentially affect the validity of these sort of choice experiments using models of conspecifics, is that mostly only a small number of different models is used (e.g., Bright & Waas, 2002; Alonso-Alvarez et al., 2004; Penteriani et al., 2007; this study). This holds the risk of pseudo-replication and could lead to erroneous conclusions due to individual model effects (Kroodsma et al., 2001; Wiley, 2003). A possible solution to minimize this problem is to switch the treatments within single models (Bright & Waas, 2002). Alonso-Alvarez et al. (2004) did this by using either one of two differently treated detachable blue tit heads (UV-reduced and control) in combination with a single mounted blue tit body. Although these authors showed plumage colour differences between the two heads to be minor (Alonso-Alvarez et al., 2004), it cannot be completely excluded that the two heads differed in other respects, such as the relative size of the differently coloured plumage patches (black eye-stripes, white cheeks, UV/blue crown feathers). We have attempted to solve this problem by repeatedly switching the UV treatment of the two different models we used, and we show that it is feasible to repeatedly remove (with 96% ethanol) and re-apply a commonly-used treatment for plumage UV manipulation (although we do not recommend this method of treatment removal for use in live birds).

At this stage it is speculative why the importance of crown UV reflectance as a signal in owner-intruder conflict differs between the study of Alonso-Alvarez et al. (2004) and ours. We cannot entirely exclude that the difference in outcome is due to the fact that we presented the intruder mounts simultaneously in the resident males' territories, whereas Alonso-Alvarez et al. (2004) presented the models sequentially. However, this methodological difference seems an unlikely explanation for the lack of effect in our study, because choice tests with simultaneous presentation of test stimuli are believed to generally give higher resolution in discrimination by the focal animal (Mac-Laren & Rowland, 2006). Also, the encounter of more than one opponent at the same time is not an unusual situation for wild blue tits, because agonistic

interactions regularly involve more than two individuals, especially within winter foraging flocks (Korsten, P., personal observation).

Interestingly, Alonso-Alvarez et al. (2004) both found evidence for a role of crown UV coloration in male-male conflict, and in male and female mate choice, as indicated by the occurrence of assortative mating with respect to crown UV reflectance, whereas in our population we neither found evidence for a role of crown UV reflectance in male-male conflict nor in mutual mate choice as indicated by the absence of assortative pairing (Korsten, 2006). There seems to be a remarkable parallel here with the studies on the signalling function of the melanin-pigmented black bib feathers of the house sparrow (*Passer domesticus*), where the role of the black bib in male-male competition and female mate choice also varies between populations, possibly in relation to the intensity of male-male competition over suitable nest sites (Griffith et al., 1999). It is possible that differences in the local ecological circumstances between blue tit populations, such as for example differences in light environment, breeding densities, food situation, opportunity for extra-pair copulations, and abundance of suitable breeding territories and nest cavities, also cause variation in the signalling function of the crown UV coloration among blue tit populations.

Some of these factors may indeed be different between the population of the *ultramarinus* subspecies studied by Alonso-Alvarez et al. (2004) and our study population of the nominate subspecies, for example: (1) the light environment in the natural habitat of the *ultramarinus* subspecies, which natural range is at lower latitudes than the nominal subspecies' range, is more luminant (Alonso-Alvarez C, personal communication). In this context it seems interesting that the *ultramarinus* subspecies has darker crown plumage with lower overall reflectance (see Alonso-Alvarez et al. 2004). (2) Furthermore, the study population of Alonso-Alvarez et al. (2004) was breeding on a small island (83 km^2) in the Mediterranean Sea (Pantelleria, Italy; 36°82′N, 11°97′E), whereas we studied a mainland population. In passerine birds, rates of extra-pair paternity are generally lower in island than in mainland populations (Griffith, 2000; but see Krokene & Lifjeld, 2000). If extra-pair paternity rates are indeed lower in Alonso-Alvarez et al.'s (2004) study population than in ours, male territorial intrusions may pose less of a paternity threat and a relatively greater territorial threat in Alonso-Alvarez et al.'s (2004) than in our population. Male blue tits with low crown UV were found to sire more extra-pair offspring than high-UV males (whereas

high-UV males were less cuckolded, which may suggest different mating strategies in high and low-UV males; Delhey et al., 2003; see also Delhey et al., 2007a). However, low-UV males may be less successful in territory take-over than high UV-males. Therefore, between-population variation in the relative importance of the territorial and the paternity threat posed by intruding males may lead to different defence strategies of territory owners based on the intruder's crown colour in the different study populations.

Prior residency is generally the main determinant of the outcome of aggressive interactions during territorial intrusions (Davies, 1978; Krebs, 1982) often overruling indicators of fighting ability, such as for example colour badges of status (Holberton et al., 1990) or body size (Chellappa et al., 1999; Dale & Slagsvold, 1995; Turner, 1994). This could be another explanation why we found no effect of either residents own crown colour, body mass or age on their aggressive responses. Also several other studies found no evidence for structurally-based plumage colour signalling during conflicts between territory owners and intruders. Territorial male purple martins (*Progne subis*) with experimentally lightened structural plumage coloration and control-treated males defended their territories with equal success (Stutchbury, 1992). Also territorial bluethroat males (*Luscinia svecica*) did not differ in their ability to retain their territories when either UV-reduced or control-treated (Johnsen et al., 1998). Even so, structural plumage signals may still be important in male-male competition when the ownership of vacant territories has to be established and the competing males have similar aggressive motivation. For example, in purple martins, subadult males that were dyed to appear adult-like obtained a territory more quickly than control subadults (Stutchbury, 1991). Also male eastern bluebirds (*Sialia sialis*) with high UV reflectance were more successful during the acquisition of nest sites than males with low UV reflectance (Siefferman & Hill, 2005).

If structurally-based coloration acts as a signal during territory acquisition, individuals that are more colourful may be able to obtain territories of higher quality. To date the relationship between territory quality and structural plumage coloration remains still largely unstudied, but Keyser & Hill (2000) found in blue grosbeaks (*Passerina caerulea*) that males with brighter structural coloration defend larger territories of higher quality than duller males. Territory quality is an important determinant of breeding success in blue tits (Blondel et al., 2000; Przybylo et al., 2001) and it would be interesting to investigate if a relationship exists between crown UV coloration

and territory quality in blue tits. The existence of such a relationship would support the idea that the intensity of the UV signal influences the outcome of competition over still vacant territories. Another context in which blue tit UV plumage could act as a signal of competitive ability is in foraging flocks during winter. However, we found no evidence for this in our blue tit population (Korsten et al., 2006).

In summary, while using a new experimental approach (simultaneous presentation of model intruders) we found no evidence for UV signalling playing a role in the agonistic interactions between male territory owners and intruders, which is contrary to a previous study in the same species (which used sequential presentations of model intruders). This illustrates the strong need for the replication of studies in behavioural and evolutionary ecology in different populations of the *same* species to evaluate the robustness and generality of the patterns found. Future research of avian visual communication should aim at improving our understanding of the relative importance of structural/UV colour signalling during competitive interactions in different bird populations and (sub)species and in different contexts such as during owner-intruder conflict, territory establishment and in winter foraging flocks.

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