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Male sexual attractiveness and parental effort in blue tits: a test of the differential allocation hypothesis

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When the reproductive value of a breeding attempt is related to attributes of the breeding partner, an individual is expected to allocate more resources to parental care when mated to a high-quality partner. We tested predictions of the differential allocation hypothesis, by experimentally increasing and decreasing male blue tit, *Parus caeruleus*, sexual attractiveness and recording subsequent measures of male and female parental effort during the chick-feeding period. We used marker pens, to create two distinct male phenotypes: one more attractive phenotype with a shift in peak reflectance towards the ultraviolet (UV) part of the spectrum (UV+) and one less attractive phenotype with a shift towards the human-visible part of the spectrum (UV−). There was no significant difference in absolute or relative female feeding rate with respect to treatment. However, there were significant interaction effects between treatment and female age on female feeding rate, indicating that 1-year-old females provisioned more when mated to a UV+ male than a UV− male. UV− males fed their chicks at a higher rate than UV+ males, but there was no significant difference between the groups in total feeding rate. Females contributed less to nest defence relative to their mates when they were mated to UV− males, whereas the opposite was true for females mated to UV+ males. The behavioural responses did not translate into differences in measures of reproductive output. Our study suggests that male phenotypic appearance at the chick-feeding stage influences female decisions about level of parental effort.

In socially monogamous species with biparental care, variance in male reproductive success may arise through a variety of mechanisms such as differential pairing with respect to female quality (Darwin 1871; Fisher 1930), differential fertilization success (Birkhead & Møller 1992) or differential allocation of resources by the mate (Burley 1986). Differential allocation can occur whenever the reproductive value of a brood is related to the attractiveness of the mate (Burley 1986; Sheldon 2000). Such a relation may arise because attractive males provide better resources or genes for increased offspring quality. Females with attractive mates should be willing to pay the costs of investing more in the current breeding attempt, if these are more than compensated by the benefits in terms of increased offspring quality. As a consequence, attractive males are expected to reduce their parental effort in the current brood and save resources for future breeding attempts, which may result in higher lifetime reproductive success and, in turn, directional selection on secondary sexual characters (Burley 1986).

The differential allocation hypothesis has received support from experimental studies on insects, amphibians, birds and mammals (Sheldon 2000). In birds, differential allocation occurs at various stages of the breeding cycle, for example through differential maternal investment in the quality or quantity of eggs produced (Petrie & Williams 1993; Gil et al. 1999; Cunningham & Russell 2000), or through differential parental effort (Burley 1988; de Lope & Møller 1993; Limbourg et al. 2004). Several avian studies have manipulated male phenotypic traits known to affect attractiveness (Burley 1988; de Lope & Møller 1993; Swaddle 1996; Limbourg et al. 2004). Although there are many strengths and advantages of this approach (Sheldon 2000), a shortcoming has been that the manipulated traits are artificial (i.e. leg bands, Burley 1988; Swaddle 1996) or manipulated outside the natural variation of the ornament (de Lope

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& Møller 1993; Limbourg et al. 2004). It is therefore difficult to infer from such studies that differential allocation occurs within the range of natural variation in male attractiveness. In the present study of wild blue tits, *Parus caeruleus*, we improved on previous designs by manipulating a male ornament to resemble more closely the extremes of the natural variation.

The blue tit is a short-lived passerine, in which most individuals that reach adulthood are able to reproduce only once, and lifetime fledgling production correlates strongly with the number of breeding seasons (Dhondt 1989). Hence, there is a potentially important trade-off between current and future reproduction that may affect individuals differently, for example depending on their age and quality. Blue tits are sexually dichromatic with respect to several plumage traits. In particular, the plumage regions that appear blue to humans (i.e. the crown, wing patches and tail) show pronounced sex differences in the ultraviolet (UV)/blue part of the spectrum (Andersson et al. 1998; Hunt et al. 1998). Studies have found assortative mating with respect to UV/blue crown coloration (Andersson et al. 1998), and a male-biased brood sex ratio and higher paternity for males with a stronger UV component (Sheldon et al. 1999; Delhey et al. 2003). Based on this information, the blue tit crown ornament seems an ideal candidate for an experimental study of differential allocation. Previous experimental manipulations of structurally coloured feather ornaments have consisted of an almost complete removal of the UV component of the signal, which creates phenotypes that do not occur naturally (Andersson & Amundsen 1997; Johnsen et al. 1998; Sheldon et al. 1999). Indeed, Limbourg et al. (2004) used this method to show that female blue tits paired with UV-reduced males fed their offspring less than those paired with control males, thus providing evidence for differential allocation of parental effort in this species. While this method is valid for experimental tests of whether the UV component matters or not, it cannot be used to make inferences about the importance of the natural variation in the amount of UV reflection.

We used two types of marker pens to create two phenotypically distinct groups of males, one with a shift in hue (peak reflectance) towards the UV part of the spectrum (UV+) and the other with a shift towards longer wavelengths (UV−). Based on previous studies (Andersson et al. 1998; Hunt et al. 1999; Sheldon et al. 1999; Delhey et al. 2003), we expected females to perceive the UV+ males as more attractive than the UV− males. If so, the differential allocation hypothesis makes the following predictions about the relation between treatment and measures of parental effort and reproductive output. First, females with a UV+ mate will invest more in parental care (as measured by feeding rate and intensity of nest defence) than females with a UV− mate. Second, as a consequence of the elevated investment by their females, UV+ males will invest less than or the same as UV− males in parental care, depending on whether the birds adjust investment completely or incompletely (Burley 1986). Finally, the reproductive output should be similar in the two groups or even higher for the UV+ males, depending on the total investment in such broods (Burley 1986).

METHODS

General Field Procedures

We conducted the field experiment on a colour-banded blue tit population breeding in nestboxes at Kolbeterberg, Vienna, Austria (48°13′N, 16°20′E) in 2003. The study area covers about 35 ha of mixed deciduous forest and contains about 250 nestboxes, 96 of which were occupied by blue tits in 2003. Further details can be found in Delhey et al. (2003). We surveyed the population on a daily basis from mid-March to the beginning of June and did the experiments between 8 and 31 May. In this population, females are single brooded, although some do renest after complete brood failure. All experimental broods were regular first breeding attempts (i.e. no renestings).

We first describe the general field protocol and provide details in the sections below. On day 6 posthatch (day 1 being the day of hatching), we attached a dummy antenna to the inside of the entrance hole of the nestbox. On days 8 and 9 posthatch, we captured each of the parents, recorded their age (yearling or 2 years and older, according to Svensson 1992), body mass (electronic balance, $\pm$0.1 g), wing length (flattened and straightened; ruler, $\pm$0.5 mm) and tarsus length (standard technique in Svensson 1992; calliper, $\pm$0.05 mm) and fitted a transponder to the two colour bands on one of their legs (the other leg having one metal ring and one colour band). We also measured plumage colour of both sexes and manipulated the crown colour of the males. On the evening of day 10, we mounted a transponder system on focal boxes and left them until the evening of day 11 or 12. On one of the days 13–16, we recorded nest defence behaviour. We ringed, measured (body mass and tarsus length) and took a small blood sample by brachial venipuncture ($\leq$25 µl) from nestlings on day 14, and remeasured them (body mass, wing length) on day 19. Finally, we checked nestboxes for fledging from day 19 onwards until all chicks had fledged.

Colour Measurements and Manipulations

We measured the plumage colour of males and females with a S-2000 spectroradiometer with a DH-2000-FHS deuterium–halogen lamp (Ocean Optics, Eerbek, The Netherlands) following the procedure described in Delhey et al. (2003). In brief, measurements from five different standardized spots were taken from the crown and breast plumage and objective colour coefficients (Hailman 1977) were calculated based on averaged and smoothed reflectance spectra. For the crown spectra, hue was defined as the wavelength of peak reflectance (λ (R_{max})), brightness as the average reflectance (R_{av}) in the 300–700-nm interval, chroma as the difference between maximum and minimum reflectance divided by average reflectance (($R_{max} - R_{min}$)/R_{av}), and UV chroma as $R_{300–400}/R_{300–700}$. For the breast spectra, brightness was again estimated as average reflectance (R_{av}) in the 300–700-nm interval, whereas carotenoid chroma was estimated by (($R_{700} - R_{450}$)/R_{700}), a measure that indicates the influence

of carotenoids absorbing maximally at 450 nm. Owing to the double-peaked nature of the breast plumage spectra, we did not calculate the hue of this plumage region (Cuthill et al. 1999).

We altered male phenotypic appearance by applying two different Edding 4500 T-shirt marker pens (Ahrensburg, Germany) on their UV/blue crown feathers. One group of males (UV+) was painted with a light blue pen (colour code 0.10) only, whereas the other group (UV−) was painted first with a dark blue pen (colour code 0.03) and then with the light blue pen (colour code 0.10). For both treatments, we added a final layer of silicon paste (Balzer Silicone Fett, Lauterbach, Germany) to ensure that the effect of the treatment would remain for the period required. The nontoxic silicon paste had no obvious effect on male behaviour and no long-lasting effect on plumage (K. Delhey, A. Peters, A. Johnsen & B. Kempenaers, unpublished data; see also Siitari et al. 2002). Figure 1 shows the resulting average reflectance spectrum of each treatment. Even though the treatment faded over time, measures of 16 males recaptured between 7 and 25 days (mean 15.4 days) after treatment revealed that there was still a significant difference in hue between the two groups of males (K. Delhey, A. Peters, A. Johnsen & B. Kempenaers, unpublished data). We are therefore confident that the colour treatment was significant at the time of the feeding-rate recordings (days 11–12, maximally 4 days after treatment) and the nest defence experiment (days 13–16, maximally 8 days after treatment).

Since the treated birds were unable to observe the colour of their crown feathers directly, the time spent preening or in other ways being distracted or irritated by the treatment should not differ between the treatment groups. Furthermore, the fact that the two treatments differed only with respect to the application of one of the marker pens (i.e. they were both painted with the other pen and both received the silicon overlay) implies that the chemical properties of the two treatments, and thus their odours, are likely to have been very similar.

In total, we manipulated 28 males (15 UV+, 13 UV−) from which we later obtained data on feeding rate and/or nest defence behaviour. The colour manipulations took place between 11 and 21 May. Most of the males ($N = 25$; 13 UV+ and 12 UV−) had received the same treatment at the beginning of the same reproductive attempt, as part of a different project (K. Delhey, A. Peters, A. Johnsen & B. Kempenaers, unpublished data). These birds received their first treatment on average 49.4 days (range 29–57) before the second treatment. Importantly, all males were paired before the first treatment and they were mated to the same females when they received the second treatment. The effect of the first treatment was no longer detectable when the birds were measured immediately before the second treatment: there were no significant pretreatment differences in crown colour characteristics (brightness, hue, chroma and UV chroma) between the two groups (Table 1). Furthermore, there was no significant difference between the treatment groups in the change of body mass from the first to the second treatment (*t* test: $t_{23} = 0.35$, $P = 0.73$), indicating that there was no treatment-related long-term effect of the first treatment on male condition. Such an effect could be expected if, for example, males of either treatment experienced more stress because of an increase in the frequency of interactions with other males and/or extrapair females.

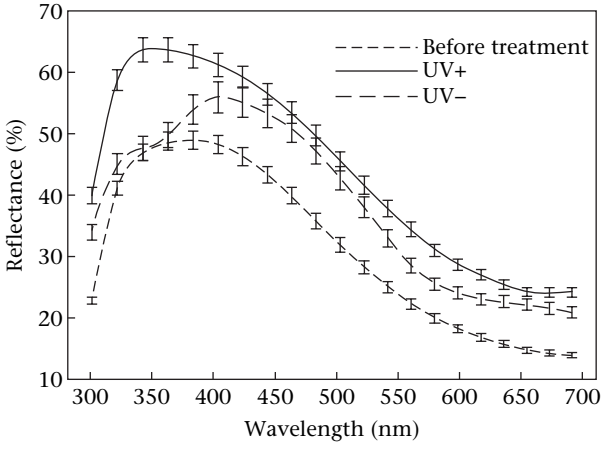

Figure 1. Average ± SE reflectance spectra from the crown feathers of male blue tits, measured before treatment ($N = 28$), after the UV+ treatment ($N = 15$) and after the UV− treatment ($N = 13$).

Parental Effort

To record feeding rates we used four Trovan RF identification systems (Euro I.D., Weilerswist, Germany). Upon capture, both members of focal pairs were fitted with small cylindrical transponders (ID 101; length: 11.5 mm, mass: 0.1 g). The transponders were attached to two colour bands with superglue and a piece of black isolation tape. Thus, the transponder was not attached directly to the leg, but moved freely with the colour bands. We attached a dummy antenna to the inside of the entrance hole of focal nestboxes several days before the actual feeding-rate recordings, to allow the birds to get used to having a foreign object inside their box. The real antenna was then mounted and connected to a battery-driven OEM board/data logger unit. The OEM board/logger unit and the battery were placed in a waterproof plastic bag and mounted on the tree somewhat higher than and at the opposite side of the nestbox (to avoid disturbance by the general public). The transponder system works by recording the time when a bird with a transponder enters (individual transponder number recorded) and leaves (general stop code recorded) the magnetic field surrounding the antenna. Hence, every time a bird enters a nestbox, there will be one record of each type in rapid succession unless the bird stops in the entrance hole, in which case the two recordings will either be further apart in time or, if the transponder touches the border of the magnetic field, many recordings in rapid succession will occur.

We extracted feeding rates from the recorded data in the following way. First, we calculated the time difference between each record and removed all the zero time differences (assuming that these represented the time of exit from the magnetic field or multiple recordings on the same visit). Then we sorted the data for each sex and again

Table 1. Pretreatment characteristics of males and females in the two treatment groups

	Males		Test		Females		Test	
	UV+ (N=15)	UV− (N=13)	t_{26}	P	UV+ (N=15)	UV− (N=13)	t_{26}	P
Crown brightness	30.2±1.5	31.8±1.1	−0.84	0.40	26.1±0.9	26.0±1.2	0.03	0.98
Crown chroma	1.15±0.02	1.17±0.03	−0.56	0.58	0.89±0.03	0.83±0.03	1.13	0.27
Crown UV chroma	0.342±0.003	0.341±0.006	0.13	0.90	0.298±0.004	0.289±0.003	1.82	0.08
Crown hue (nm)	376.5±2.0	378.4±2.1	−0.66	0.52	382.1±2.3	390.6±2.9	−2.30	0.03
Breast brightness	29.5±0.9	32.1±1.3	−1.66	0.11	27.4±0.8	28.1±0.8	−0.67	0.51
Breast chroma	0.64±0.01	0.56±0.03	2.92	0.01	0.61±0.01	0.60±0.02	0.31	0.76
Tarsus length (mm)	17.1±0.1	17.3±0.1	−1.43	0.17	16.8±0.1	16.6±0.1	1.01	0.32
Wing length (mm)	68.1±0.4	69.0±0.7	−1.16	0.26	65.4±0.3	65.2±0.4	0.45	0.65
Body mass (g)	10.8±0.1	11.0±0.2	−1.18	0.25	11.0±0.1	10.9±0.1	0.94	0.36

Values are means ± SE.

calculated the time difference between each record, this time within each sex. We then excluded all time differences that amounted to 6 s or less, assuming that such short time differences did not represent actual feeding events but were probably due to repeated entering on the same visit. We chose 6 s as the cutoff point based on detailed examination of the logged data from the first two nests. Finally, we counted the remaining records for each hour and divided this number by two to reach an hourly rate of feeding. This procedure provides an estimate of feeding rate that is likely to contain some degree of error. Errors could be the result of (1) not counting feeding visits that took less than 6 s, and (2) counting visits longer than 6 s that did not involve feeding. However, such errors should be random with respect to the experimental treatments.

We attached transponders to both members of 28 pairs, but because of various problems (female disappearance ($N = 2$), nest abandonment ($N = 1$), transponder loss ($N = 4$), logger breakdown ($N = 2$)) we got complete data from 19 pairs (11 UV+ and 8 UV−) and incomplete data from another four pairs (1 UV+ and 3 UV−; 2 male-only and 2 female-only). One UV+ male fed only twice during the entire recording and we excluded the data from this pair. For the 22 remaining nestboxes, the data were collected on day 11 ($N = 21$) or 12 ($N = 1$). The overall feeding rate of each individual (feeds/h) was calculated by averaging over the time interval 0600–1800 hours ($N = 16$), 0600–1700 hours ($N = 3$), 0700–1800 hours ($N = 2$) and 0800–1800 hours ($N = 1$). We also calculated the proportion of female feeds (number of female feeds/total number of feeds) and the total feeding rate (male plus female) per nest. In summary, sample sizes vary in the different analyses of feeding rates, with $N = 18$ in analyses involving both pair members, and $N = 20$ in analyses involving either the male or the female parent, respectively.

We compared the feeding rates obtained using transponders with those obtained during direct feeding observations in 2002, during which male and female feeding rates were determined with binoculars from hides for one ($N = 25$ pairs) or two ($N = 8$ pairs) 1-h observations on day 13 posthatch. We found no significant differences in male feeding rate/chick per h ($\overline{X}$±SE for transponder data: 2.05 ± 0.13; feeding observations: 1.89 ± 0.13; Mann–Whitney U test: $U = 283.0$, $N_1 = 20$, $N_2 = 33$, $P = 0.39$), female feeding rate/chick per h (transponders: 1.46 ± 0.08; observations: 1.65 ± 0.16; $U = 295.0$, $N_1 = 20$, $N_2 = 33$, $P = 0.52$) or total feeding rate chick per h (transponders: 3.35 ± 0.09; observations: 3.54 ± 0.24; $U = 291.0$, $N_1 = 18$, $N_2 = 33$, $P = 0.91$). Even though these data sets were collected in different years and on different birds, the similarity of the two sets of estimates shows that the transponder method resulted in realistic estimates of feeding rates. We used the 33 pairs involving unmanipulated males as untreated controls in comparisons with each treatment group.

We estimated the intensity of nest defence by placing a rubber snake on the roof of the nestbox and recording nest defence behaviour for 20 min from the moment the first member of the pair appeared. The aesculapian snake, *Elaphe longissima*, is a natural predator of nestlings in our study population. The observer (B.K., E.S. or K.D.) was blind with respect to the treatment, stood fully visible to the birds at 10 m from the nestbox, and noted for each member of the pair (1) the distance to the box once every minute, (2) the presence/absence of alarm calling during each 1-min period, and (3) the shortest distance to the box during the entire 20-min period. From the raw data, we calculated for each bird the proportion of observation units (maximally 20) spent within 5 and 20 m of the nestbox, respectively, and the proportion of time units spent calling. Owing to structural differences between territories (e.g. differences in the proximity of suitable perches (trees/branches) to the nestbox), the exact distance measures were not comparable between birds in different territories. Hence, we calculated the difference between pair members (male minus female) in these variables as measures of the relative nest defence investment of each sex.

The four measures of relative nest defence intensity (difference between the sexes in (1) proportion ≤ 5 m, (2) proportion ≤ 20 m, (3) calling rate and (4) minimal distance) were significantly correlated (Spearman rank correlations: all $|r_S| > 0.39$, all $N = 27$, all $P < 0.04$), with the exception of the correlation between difference in calling rate and difference in minimal distance ($r_S = -0.25$, $N = 27$, $P = 0.21$). Owing to this

interdependence, we performed a principal components analysis on all four variables and used the first principal component (PC1) in further analyses. This component had an eigenvalue of 2.5, explained 62.4% of the variance and had high positive factor loadings for difference in proportion ≤ 5 m (0.80), difference in proportion ≤ 20 m (0.89) and difference in calling rate (0.73) and a high negative loading for difference in minimal distance (-0.73). Thus, a positive PC1 value represents a situation where the male spends more effort on nest defence (higher proportion ≤ 5 m and ≤ 20 m, higher calling rate and smaller minimum distance), whereas a negative value represents a situation where the female invests more. To assess whether treatment-related differences in relative nest defence were due to changes in the behaviour of males, females or both, we also did tests on the absolute values of each of the four variables for each sex. However, as noted above, the absolute values are not directly comparable between territories because of structural habitat differences, and these analyses should therefore only be taken as indicative.

Nest defence observations were carried out on 28 experimental pairs, but for one of them (UV+) the female did not appear. This pair was excluded from further analysis. The remaining 27 pairs (14 UV+ and 13 UV−) were observed once each between 0748 and 1337 hours (mean 0956 hours), on day 13 ($N = 21$), 14 ($N = 4$), 15 ($N = 1$) or 16 ($N = 1$) posthatch. There were no differences between the two treatment groups in the time or day of observation (both $P > 0.86$). We also obtained data on nest defence from 12 pairs (mean time of day: 1157 hours, range 0839–1606 hours; mean day posthatch: 13.5, range 13–15) where the male had not been manipulated, and used these as untreated controls in comparisons with each treatment group.

Characteristics of the Treatment Groups

Only socially monogamous pairs were included in this study. There were no significant differences between males in the two treatment groups in premanipulation measurements of colour and size, except that UV+ males had a significantly more chromatic breast plumage than UV− males (Table 1). Given that an aspect of yellow coloration has been shown to correlate with parental abilities in this species (Senar et al. 2002), we included yellow chroma as a covariate in the analyses of treatment effects on measures of parental effort. There was no bias in male age structure in the two groups (Fisher's exact test: $P = 0.70$). Females in the two groups did not differ significantly with respect to the measured variables, with the exception that females mated to UV+ males had a somewhat more UV-shifted crown hue (Table 1). We therefore entered female crown hue as a covariate in the analyses. There was no bias in female age structure between the groups (Fisher's exact test: $P = 1.00$). There was no significant difference between the two male groups in the day of manipulation (day 8 or 9 posthatch; Fisher's exact test: $P = 0.48$). Furthermore, the two treatment groups did not differ significantly in hatching date (t test: $t_{26} = -1.54$, $P = 0.14$) or in brood size during the feeding-rate recordings (Mann–Whitney U test: $U = 94.0$, $N_1 = 15$, $N_2 = 13$, $P = 0.87$), or during the nest defence observations ($U = 0.96$, $P = 0.94$). We conservatively included hatching date in the initial statistical models, to control for the weak tendency of broods of UV+ males to hatch earlier than those of UV− males. Molecular sexing of offspring, using a combination of a sex-linked microsatellite marker Phtr3 (Fridolfsson et al. 1997) and the sexing primers P2/P8 (Griffiths et al. 1998), showed that there was no significant difference between the treatment groups in brood sex ratio ($\overline{X} \pm$SE proportion of male offspring: UV+: 0.53 ± 0.03; UV−: 0.54 ± 0.04; t test: $t_{26} = -0.27$, $P = 0.79$).

Ethical Note

Adults and nestlings were captured in the nestboxes and transported in bird bags to the outskirts of the territory (day 14 nestlings) or a nearby field laboratory (day 19 nestlings and adults) for measurements and treatment. Nestlings were removed from the nestbox while the parents were absent from the vicinity of the box. For day 14 broods, we handled only half the brood at a time, while sitting at a sufficient distance from the nestbox to allow the parents to continue feeding the other half of the brood. Processing an entire brood took less than 20 min. For day 19 nestlings, we transported the whole brood to the laboratory, and measured and returned them to the nestbox within 45–60 min. All nestlings that were measured on day 19 fledged successfully. The crown colour manipulation and attachment of transponder added a few minutes to the usual handling time for adult birds (about 15 min) and the whole process from capture to release required no more than 30 min. During the application of markers and silicon paste, birds were held in a steady position and observed continuously for signs of treatment-related distress. No such behaviours were detected. Upon release in their territories after treatment, there were no indications of aberrant behaviour among treated birds compared with untreated ones. Furthermore, the treatment is unlikely to have affected the frequency of aggressive interactions between males, as we did not observe any interactions between males during the large amount of time we spent in the territories (collecting/measuring adults/nestlings and during the nest defence observations).

Three experimental broods failed, following female disappearance ($N = 2$) or abandonment by one or both parents ($N = 1$; this pair renested). When we became aware of the lack of sufficient parental care in these broods (containing 14, 10 and 8 chicks, respectively), it was already too late to relocate the chicks to other nests. Even if we cannot completely exclude the possibility that our handling of the birds had an influence on these desertions/disappearances, they seem unlikely to have been a direct result of our experimental protocol, for the following reasons. First, disappearance was unrelated to the colour manipulation itself, since the birds that disappeared were both females. Second, the 0.1-g

transponder added less than 1% to the total body mass of the birds and therefore seems unlikely to have been the cause of disappearance/abandonment. We used a transponder type and protocol for attachment of transponders that have been used in previous studies of small passerine birds, including blue tits (Råberg et al. 2000; Nilsson 2003). Third, there were no cases of brood abandonment after exposure to the artificial snake. Finally, the rate of nest failure among the experimental pairs (3/28 = 10.7%) was lower than the overall rate of nest failure in the study population in 2003, which was higher than in other years (in 2003 17.7% of the breeding attempts failed at some stage compared to 11.4% in 2001 and 7.9% in 2002, nest predation excluded). Our work was done under licence from the Magistrate of Conservation in Vienna and the Magistrate of Forestry and Agriculture.

Statistical Procedure

Parametric analyses were performed whenever the residuals of the response variables were normally distributed. We used general linear models (GLM) to test for treatment effects on feeding rate, nest defence and brood characteristics. Initial models included treatment, male and female age, hatching date, brood size, male yellow chroma and female crown hue. We also included interaction terms between treatment and male and female age, respectively, in the initial models. Final models were obtained by sequential removal of nonsignificant terms, starting with interaction terms. We confirmed the lack of significance of each eliminated term by re-entering it into the final model, and report these P values. We present effect sizes and 95% confidence intervals (CI) for parametric tests with nonsignificant treatment effects. All statistical tests are two tailed.

RESULTS

Effect of Treatment on Colour

As intended, UV+ males had lower hue and higher UV chroma than UV− males (Table 2). UV+ males also had somewhat higher crown brightness, but there was no significant difference in overall chroma (Table 2). For both treatments, the values were within the range of natural variation for each of the four colour variables (Table 2), with the exception of one UV+ male with a brightness (55.0) that was somewhat higher than the maximum of the natural range (52.6) and two UV− males with hues that were slightly more long-wave shifted (411 and 412 nm, respectively) than the extreme of the natural range (410 nm). The spectral shape of the UV− treatment differed slightly from the natural situation by being concave in the UV range of the spectrum (Fig. 1).

Comparisons of the pre- and post-treatment crown colour variables revealed significant changes to all four variables in both groups (paired tests; all $P < 0.005$). UV− males showed a 6.4% increase in hue and a 20.5 and 11.8% reduction in chroma and UV chroma, respectively. UV+ males showed a 5.1% decrease in hue, but also a reduction in chroma (18.2%) and UV chroma (4.4%). The reduction in chroma and UV chroma in both treatments is explained by the fact that these variables are calculated relative to brightness, which was increased in both treatments (UV+: 44.7%; UV−: 19.5%) because of the addition of the silicon overlay. Nevertheless, the main differences between the treatments occurred in the UV part of the spectrum, with UV− males displaying a more long-wave, less UV-reflective crown than UV+ males (Fig. 1, Table 2).

Treatment Effects on Feeding Rates

There was no significant treatment effect on absolute female feeding rate (effect size: 0.05; 95% CI: −6.2–2.5; Table 3, Fig. 2), but there was a significant interaction between treatment and female age. Post hoc tests within each age class indicated that yearling females tended to feed more per chick when paired to UV+ males than to UV− males ($t_6 = 2.12$, $P = 0.078$; effect size: 0.54; 95% CI: −0.08–1.17; Fig. 3a), whereas for older females there was no significant difference ($t_{10} = -0.83$, $P = 0.43$; effect size: −0.15, 95% CI: −0.55–0.26; Fig. 3a). Note that sample sizes are very low in these and other comparisons where the data are split in relation to female age. Female feeding rate was also related to brood size, with females feeding more frequently when they had bigger broods (Table 3).

UV+ males fed their chicks at a significantly lower rate than UV− males (Table 4, Fig. 2). The final model also retained male yellow chroma and brood size, showing that males with more chromatic yellow plumage and males with bigger broods fed at a higher rate (Table 4). Male feeding rate was not significantly predicted by female age or the interaction between treatment and female age (Table 4), but to test whether the age-dependent response found in females was mirrored in males, we performed tests within each female age class. Among males mated to yearling females, UV− males fed significantly more than UV+ males ($t_7 = -3.12$, $P = 0.017$; Fig. 3b), whereas there was no significant treatment effect among males mated to old females ($t_9 = -0.33$, $P = 0.75$; effect size: −0.05; 95% CI: −0.36–0.26; Fig. 3b).

In the analysis of relative female feeding rate, there was again a significant interaction between female age and treatment ($F_{1,14} = 14.61$, $P = 0.002$), whereas none of the other effects included in the initial model explained significant portions of the variation in this variable (all $P > 0.18$; effect size for treatment effect: 0.09; 95% CI: −0.10–2.95). Post hoc tests within each age class revealed that yearling females paired with UV+ males contributed a greater share of feeds than those paired with UV− males ($t_5 = 3.56$, $P = 0.016$), whereas there was no significant difference in old females ($t_9 = -1.26$, $P = 0.24$; effect size: −0.04; 95% CI: −0.10–0.03).

There was no significant difference in the total feeding rate between the two groups ($F_{1,15} = 2.33$, $P = 0.15$; effect size: 0.13; 95% CI: −6.8–1.1). The only significant predictor of total feeding rate was brood size, with bigger

Table 2. Summary of male crown colour variables after treatment for UV+ and UV− males, respectively

Colour component	UV+ (N=15)	UV− (N=13)	Test		Natural range (N=384)
			t_{26}/U	P	
Brightness	43.6±1.4	38.0±1.6	2.74*	0.011	18.8–52.6
Chroma	0.93±0.01	0.93±0.02	0.26*	0.80	0.77–1.39
UV chroma	0.327±0.002	0.302±0.003	8.16*	<0.001	0.28–0.40
Hue (nm)	357.2±1.9	404.4±1.6	0.00†	<0.001	341–410

The natural ranges are based on crown colour measurements of males caught during winter and spring in 2002 and 2003 (K. Delhey, A. Peters, A. Johnsen & B. Kempenaers, unpublished data). Values are means ± SE.
*t test.
†Mann–Whitney U test.

broods receiving more feeds ($F_{1,16} = 30.88$, $P < 0.001$; all other $P > 0.35$).

We compared the feeding rates of both sexes in the untreated control pairs from which we had provisioning observations (from 2002) with those in each respective treatment (Fig. 2), and found that UV− males tended to feed at a higher rate than control males, whereas there was no significant difference between UV+ and control males, or between females in each treatment and control females (see legend to Fig. 2 for test details).

Treatment Effects on Nest Defence Intensity

The treatment had a significant effect on the relative nest defence intensity of pair members (Table 5). In UV+ pairs, the female invested more in nest defence than the male, whereas the situation was opposite in UV− pairs (Fig. 4). None of the other variables explained significant portions of the variance in relative nest defence intensity (Table 5).

Univariate analyses of each of the four nest defence variables for each sex produced no statistically significant differences between treatment groups (Table 6). However, for both sexes, the difference was always in the predicted direction: higher average investment for females paired to UV+ males than those paired to UV− males, and higher average investment of UV− males compared to UV+ males.

Comparisons of the nest defence intensity of the 12 untreated control pairs with that of each treatment group (PC1 recalculated including all 39 pairs) revealed that UV− pairs had significantly more male-biased nest defence than control pairs, whereas there was no significant difference between UV+ pairs and control pairs (Fig. 4). To compare treatment groups and controls within each sex, we recalculated PC1 for males and females, separately. We found a significantly lower nest defence intensity of females mated to UV− males compared to control females ($t_{23} = 3.65$, $P = 0.001$) and also a significantly lower intensity of UV+ males compared to control males ($t_{24} = 2.82$, $P = 0.01$). Females mated to UV+ males and males in the UV− group did not differ significantly from their respective control group (controls versus

Table 3. Determinants of female feeding rate

	df	F	B*±SE	P
Treatment	**1, 0.97**	**0.25**	**−1.86±2.02**	**0.71**
Male age†		0.01		0.92
Female age†	**1, 0.99**	**0.06**	**2.83±2.36**	**0.85**
Brood size day 11	**1, 15**	**5.59**	**1.48±0.63**	**0.032**
Hatching date		0.01		0.92
Male yellow chroma		2.22		0.16
Female tail hue		0.25		0.62
Treatment× male age		0.44		0.52
Treatment× female age	**1, 15**	**5.21**	**7.39±3.24**	**0.037**

Variables in the final model are shown in bold.
*Unstandardized regression coefficient.
†Two age classes: yearling and older birds.

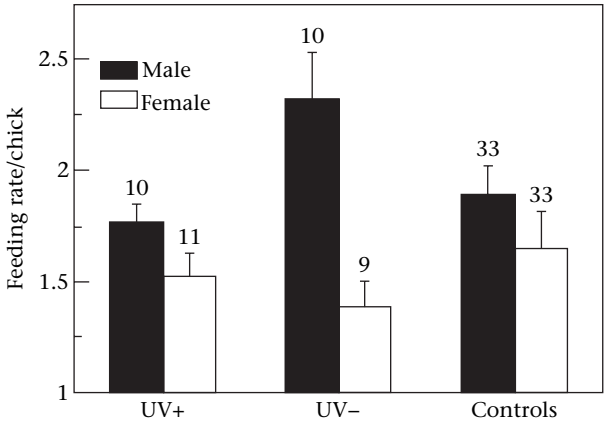

Figure 2. Average ± SE feeding rate/chick per h for males and females in pairs involving UV+, UV− and untreated control males, respectively. Feeding rates of the experimental pairs were obtained using transponders (in 2003) and those of control pairs by observation (in 2002); (see Methods for further details). Tests of sex-specific differences between untreated controls and each treatment group: control versus UV+ males: (Mann–Whitney U test: $U = 150.0$, $N_1 = 10$, $N_2 = 33$, $P = 0.67$), control versus UV− males ($U = 103.0$, $N_1 = 10$, $N_2 = 33$, $P = 0.075$), control versus UV+ females ($U = 173.0$, $N_1 = 11$, $N_2 = 33$, $P = 0.82$), control versus UV− females ($U = 122$, $N_1 = 9$, $N_2 = 33$, $P = 0.42$). Numbers refer to sample sizes.

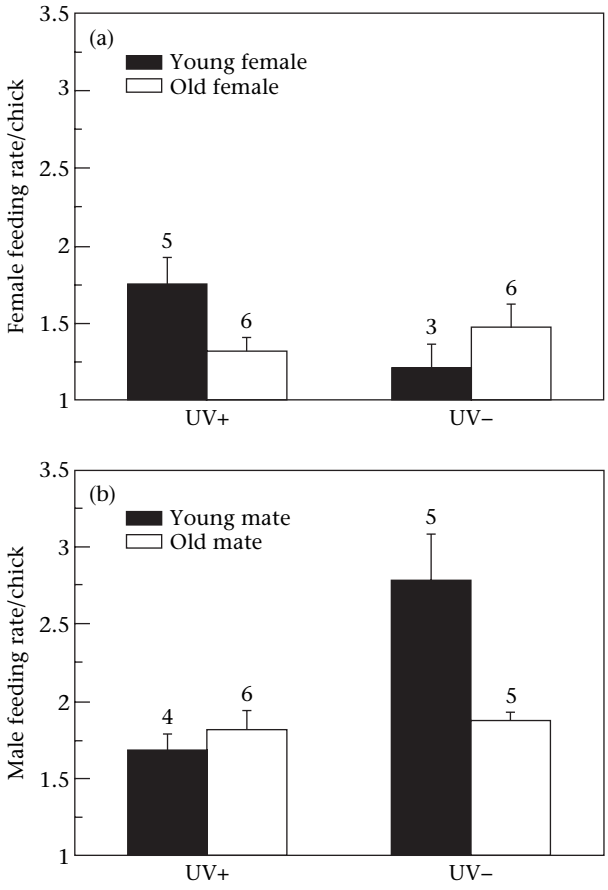

Figure 3. Average ± SE feeding rate/chick per h, for (a) females of each age class paired to males of each treatment group (UV+ and UV−), and (b) for males of each treatment group (UV+ and UV−) paired to females of each age class. Numbers refer to sample sizes.

females mated to UV+ males: $t_{21.4} = 1.69$, $P = 0.11$; effect size: 0.61; 95% CI: −0.14–1.35; controls versus UV− males: $t_{19} = 0.80$, $P = 0.43$; effect size: 0.30; 95% CI: −0.48–1.09).

Table 4. Determinants of male feeding rate

	df	*F*	*B** ± SE	*P*
Treatment	**1, 16**	**16.78**	**−7.99 ± 1.95**	**0.001**
Male age†		0.76		0.40
Female age†		2.58		0.13
Brood size day 11	**1, 16**	**4.50**	**1.52 ± 0.72**	**0.050**
Hatching date		0.32		0.58
Male yellow chroma	**1, 16**	**10.55**	**40.39 ± 12.44**	**0.005**
Female tail hue		1.64		0.22
Treatment × male age		0.82		0.38
Treatment × female age		2.61		0.13

Variables in the final model are shown in bold.
*Unstandardized regression coefficient.
†Two age classes: yearling and older birds.

Table 5. Determinants of relative nest defence (male minus female defence, see Methods for details of calculation)

	df	*F*	*B** ± SE	*P*
Treatment	**1, 25**	**6.22**	**−0.88 ± 0.35**	**0.020**
Male age†		2.81		0.11
Female age†		0.44		0.51
Brood size day 11		1.70		0.20
Hatching date		0.13		0.72
Male yellow chroma		0.02		0.91
Female tail hue		0.80		0.38
Treatment × male age		3.31		0.082
Treatment × female age		1.26		0.27

Variables in the final model are shown in bold.
*Unstandardized regression coefficient.
†Two age classes: yearling and older birds.

Treatment Effects on Reproductive Output

The treatment had no detectable effect on average nestling mass at day 14 (GLM: $F_{1,25} = 0.15$, $P = 0.70$; effect size: 0.01; 95% CI: −0.32–0.46; initial model also including male and female age, date of hatching, brood size, male yellow chroma, female crown hue, and the interaction between treatment and male and female age, respectively). Only date of hatching explained a significant proportion of the variance in brood mass, with early broods being heavier than late broods ($F_{1,25} = 13.7$, $P = 0.001$; all other $P > 0.29$). Similarly, no significant treatment effects were found for brood averages of day 14 tarsus length ($F_{1,25} = 1.45$, $P = 0.24$; effect size: 0.06; 95%

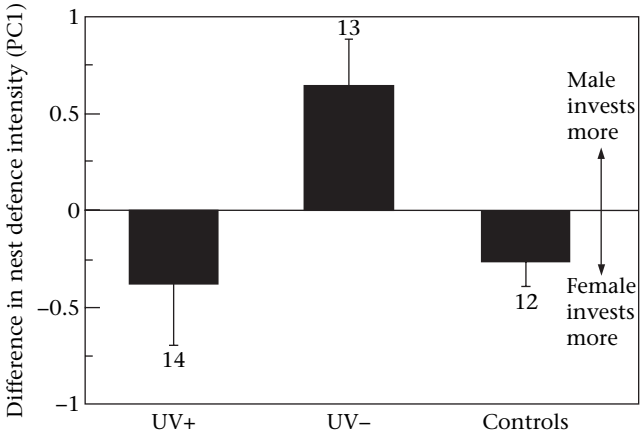

Figure 4. Average ± SE difference in nest defence intensity between the sexes in pairs involving UV+, UV− and untreated control males, respectively. The *Y* axis represents an index of relative nest defence intensity of the members in a pair, as estimated by the first principal component (PC1) from a factor analysis of differences between the sexes (male minus female) in four estimates of nest defence behaviour (see Methods for more details). Tests of differences between untreated controls and each treatment group: controls versus UV+: *t* test: $t_{24} = 0.33$, $P = 0.75$; controls versus UV−: $t_{23} = -3.20$, $P = 0.004$. Numbers refer to sample sizes.

Table 6. Summary of the four nest defence variables for birds subjected to the UV+ or the UV− treatment, shown separately for males and females

	Males		Test		Females		Test	
Nest defence variable	UV+ (N=14)	UV− (N=13)	t_{25}/U	P	UV+ (N=14)	UV− (N=13)	t_{25}/U	P
Proportion ≤5 m	0.11±0.03	0.17±0.05	79.5*	0.57	0.15±0.04	0.04±0.03	60.0*	0.10
Proportion ≤20 m	0.60±0.06	0.72±0.06	−1.40†	0.17	0.61±0.07	0.54±0.07	0.69†	0.50
Minimum distance (m)	4.7±1.2	3.8±1.1	81.5*	0.64	7.0±1.8	8.8±2.0	78.0*	0.53
Calling rate	0.60±0.06	0.75±0.06	−1.70†	0.10	0.64±0.08	0.57±0.08	76.0*	0.47

Values are means ± SE.
*Mann–Whitney U test.
†t test.

CI: −0.13–0.51), day 19 wing length ($F_{1,1.01} = 0.015$, $P = 0.92$; effect size: 0.02; 95% CI: −1.88–0.02) or day 19 mass ($F_{1,21} = 2.10$, $P = 0.16$; effect size: 0.09; 95% CI: −0.93–0.17).

There was no difference between the groups in the absolute number of fledged offspring ($\overline{X}$±SE number of fledglings: UV+: 9.93 ± 0.45; UV−: 9.91 ± 0.33; Mann–Whitney U test: $U = 80.0$, $N_1 = 15$, $N_2 = 11$, $P = 0.89$), or in the proportion of the clutch that fledged from those that were present at the beginning of the experiment (day 11; $\overline{X}$±SE proportion of fledged offspring: UV+: 0.994 ± 0.006; UV−: 0.967 ± 0.033; $U = 80.0$, $N_1 = 15$, $N_2 = 11$, $P = 0.78$). Two UV− broods that were partially and completely depredated, respectively, were excluded from these analyses.

DISCUSSION

Our manipulation of blue tit male phenotype had significant effects on male and female behaviour during the nestling phase. UV+ males fed their nestlings at a lower rate than UV− males, but there was no treatment effect on absolute or relative female feeding rate. There were, however, significant interaction effects between female age and treatment on absolute and relative female feeding rate, and post hoc tests indicated that yearling females paired to UV+ males fed more than those paired to UV− males, whereas there was no significant treatment effect in older females. Females mated to UV+ males invested relatively more in nest defence than their mates, whereas the opposite was true for females mated to UV− males. The experiment had no detectable effects on measures of reproductive success. In the following, we discuss these results in light of the differential allocation hypothesis, and address whether alternative explanations can account for the behavioural changes that we observed.

The chick-feeding data revealed a clear difference between males of the two treatment groups in feeding rate, but no overall difference between their females. According to Burley's original presentation of the differential allocation hypothesis, both an increase in the effort of females mated to attractive males and a reduction in the effort of such males are to be expected (Burley 1986). Given that our data set was large enough to demonstrate a highly significant treatment effect on male feeding rates, it seems unlikely that the lack of overall female response was entirely due to low statistical power. Rather, the significant interaction term between treatment and female age on absolute and relative female feeding rate indicates that there were age-related differences in female responses towards altered male attractiveness. Yearling females apparently responded to the treatment in the way predicted by the differential allocation hypothesis, whereas older ones did not. Sample sizes were low in these comparisons, so the results should be treated with caution. Nevertheless, there are reasons to expect differences between yearling and older females in their responses to the treatment. Old, more experienced females might base their decision about level of investment in feeding on more and/or different cues than yearling females and be less likely to be easily or quickly 'tricked' into believing that their mates' quality has changed. In particular, the fact that some ($N = 5$) of the older females in the experiment bred with the same partner in the year prior to the experiment might have reduced the likelihood that they would respond to the treatment. Furthermore, since we aged females as yearling and 2 years old or older, the group of yearling females was more uniform with respect to breeding experience and future reproductive value than the group of older females. In other words, the group of older females probably consisted of females with variable amounts of reproductive experience and differing residual reproductive value, and some females may have made their terminal reproductive investment (Williams 1966; Forslund & Pärt 1995). This increased level of noise might have concealed any patterns of differential allocation in this group.

A differential allocation explanation for the change in male feeding behaviour rests on the assumption that males received cues about their altered phenotypic attractiveness from their mates (Burley 1986). However, can this assumption be substantiated? If the males also interacted with neighbours and received feedback about an altered dominance/attractiveness from these, this could in theory result in a situation where UV+ males spent more time in territorial disputes and/or pursuing additional matings rather than on parental effort (Trivers 1972; Magrath & Komdeur 2003). While pursuit of additional matings is unlikely to have been important since there were few or no fertile females present at the time of our experiment, some evidence exists that the UV signal is involved in male–male aggression. Alonso-Alvarez et al. (2004) found

that during the egg-laying period, male blue tits behaved less aggressively towards a taxidermic mount presented within their territory when the UV reflectance of the crown feathers of the decoy was eliminated with sunblock. However, our experiment was carried out at a time when birds were busy feeding nestlings and interactions between neighbouring birds are likely to have been much rarer than in the study by Alonso-Alvarez et al. (2004), which was carried out at the time of egg laying. We therefore conclude that the female mate is the best candidate as a conveyer of cues about changes in male phenotypic attractiveness. Such cues could be transferred during brief moments of interaction between pair mates that occur frequently during the chick-feeding stage in blue tits (Cramp & Perrins 1993). These interactions are characterized by wing shivering of both sexes and raising of the crown feathers by the male, and may end with the transfer of food from the male to the female. These could be moments of (voluntary or nonvoluntary) information transfer. Alternatively, males may have used changes in the overall investment level of their mates as cues to their perceived attractiveness. Even though the interaction between female age and treatment did not have a significant effect on male feeding rate ($P = 0.13$; see Table 4), post hoc tests showed that the difference between UV+ and UV− males in feeding rate was almost entirely caused by UV− males feeding more than UV+ males when mated to yearling females (Fig. 3b), supporting the idea that males cued in on the investment level of their mates.

The effects of the treatment on nest defence behaviour are in accordance with the prediction from the differential allocation hypothesis: females mated to UV+ males invested more relative to their mates in nest defence whereas females mated to UV− males invested less relative to their mates. In univariate analyses on each of the four nest defence variables (within each sex), females paired to UV− males invested less in nest defence on average than females paired to UV+ males, whereas UV− males invested more than UV+ males. Even if none of these tests were significant, they collectively indicate that it was the combined effect of changes in both male and female behaviour that produced the overall difference in relative nest defence. Further evidence for this comes from the comparisons of sex-specific nest defence intensity between controls and each treatment group: both UV+ males and females mated to UV− males showed significantly reduced nest defence intensity compared to control males and females, respectively. The lack of a significant interaction effect between treatment and female age in the analysis of relative nest defence intensity further indicates that, for this measure of parental effort, the two female age classes did not show a significantly different response to the treatment. This result argues against the 'terminal investment' explanation for the lack of treatment effect on the feeding rate of older females. It seems that older females were slower to respond to the treatment than yearling females (intensity of nest defence was recorded 2 days later than feeding rate), and this supports the notion that they were not so easily or quickly 'tricked' into believing that the condition or attractiveness of their mate had changed.

As stated in the Methods, most of the birds involved in this experiment had received an identical treatment in the nest-building phase. The first experiment was performed to test whether the colour manipulation would influence patterns of extrapair paternity and other measures of reproductive success (K. Delhey A. Peters, A. Johnsen & B. Kempenaers, unpublished data). If the early treatment influenced patterns of paternity, then this could potentially be a confounding factor in the present experiment, since males might be expected to adjust their level of investment in a brood according to their perceived share of paternity (Whittingham et al. 1992; Westneat & Sherman 1993). However, this would influence the interpretation of our results only if UV+ males had a lower paternity than UV− males. A recent correlational study of the same blue tit population showed that males with a more UV-shifted hue and higher UV chroma were less likely to be cuckolded than males with a more long-wave shifted hue (Delhey et al. 2003); hence, if anything, the opposite pattern (UV− males losing more paternity) would be expected. Our results should therefore be conservative with respect to the potentially confounding effect of differences in paternity between the treatment groups. Besides, if females with UV− mates were able to adjust their paternity and thereby increase their perceived value of the brood, there would be little or no incentive to allocate less energy to such broods (Kempenaers & Sheldon 1997). In other words, our evidence that females apparently invested less in broods when mated to UV− males suggests that females were unable to compensate fully for any perceived reduction in mate quality (owing to the early treatment) in terms of paternity adjustments. Future paternity analyses will be able to resolve this issue.

There was a significantly positive relation between the natural carotenoid chroma of the yellow breast feathers of males and their feeding rate, when we controlled for the effects of treatment and brood size. This effect does not confound our evidence for a treatment effect since UV+ males were in fact feeding less frequently than UV− males, despite the accidental tendency for UV+ males to be more chromatic in the breast feathers (see Methods). Incidentally, this result supports the suggestion made by Senar et al. (2002) that aspects of the yellow plumage of blue tit males might signal their parental abilities (Hoelzer 1989), and it suggests that both processes of postcopulatory sexual selection (differential allocation and 'the good parent process') might be occurring simultaneously in this species.

Our data show that blue tit females pay attention to plumage characteristics of their mates at a time when they are busy feeding offspring, and that yearling females in particular respond quickly to changes in crown coloration, at least with respect to the magnitude of plumage changes created by our experiment. Our study provides support for the suggestion made by Örnborg et al. (2002), that the quality-revealing feature (signal content) of the crown ornament of male blue tits is the ability to maintain the colour of the ornament under stressful conditions. Comparisons of the relative nest defence behaviour of the treatment groups with that of an untreated control group indicated that the main change in behaviour occurred in

the pairs involving UV− males (but note that comparisons of sex-specific nest defence intensities showed a significant difference also between UV+ males and controls, see above). This was corroborated in comparisons between feeding rates of the treatment groups and the sample of 33 untreated pairs observed in 2002: UV− males tended to feed at a higher rate than untreated control males, whereas there was no difference between the latter and UV+ males nor between females of the two treatment groups and their respective control females (Fig. 2).

There are several possible reasons why there would be a stronger effect in UV− pairs. First, the relative change in UV coloration was greatest for UV− males, and their females might therefore be more likely to notice the change and respond accordingly. Second, since naturally occurring changes in blue tit male crown coloration over the breeding season consist of a decrease in the UV component of the signal (Örnborg et al. 2002), females might not respond towards the opposite, unnatural change (i.e. the UV+ treatment). Finally, even if the present treatment probably represents an improvement over previous manipulations of structural coloration in birds (e.g. Johnsen et al. 1998; Sheldon et al. 1999; Limbourg et al. 2004) because the resulting phenotypes more closely resemble the extremes of the natural plumage variation, we should consider the possibility that UV− males were nevertheless perceived as strange looking by their females. Results from the similar crown colour experiment that was performed earlier in the season, before the onset of egg laying, gave no indication of the presence of such a strange-male effect. If UV− males were perceived as unnatural, their mates would seem likely to abandon the breeding attempt more frequently or at least delay the start of egg laying compared to females paired to UV+ males or untreated males, but there was no evidence for this (K. Delhey, A. Peters, A. Johnsen & B. Kempenaers, unpublished data.). Hence, even if we cannot completely exclude the possibility of a strange-male effect, the present results seem best explained by a reduction of investment in parental care by females that are mated to males at the lower end of the attractiveness continuum.

The lack of treatment effects on measures of reproductive success suggests that UV− males were able to compensate for the reduction in female effort, but it should be borne in mind that our experiment was conducted in the second half of the chick-feeding period; hence, there might not have been enough time for differences in reproductive output to develop. Alternatively, the different investment levels of males in the two treatment groups might translate into differences in survival prospects (Gustafsson & Sutherland 1988), a possibility that we will explore further. Finally, we note that our results differ somewhat from those of Limbourg et al. (2004), who found strong evidence that female blue tits reduced their parental effort when their males' crown UV reflectance was removed by sunblock, but this did not have any detectable effect on male feeding behaviour. The lack of male compensation for reduced female feeding effort in Limbourg et al.'s study is surprising and might reflect real population differences in the importance of, or potential for, male compensatory parental investment. Nevertheless, despite the apparent differences, these studies collectively show that different levels of parental effort for birds of varying attractiveness have the potential to create directional selection pressures on the expression of the crown ornament of blue tit males.

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References

Alonso-Alvarez, C., Doutrelant, C. & Sorci, G. 2004. Ultraviolet reflectance affects male–male interactions in the blue tit (*Parus caeruleus ultramarinus*). *Behavioral Ecology*, **15**, 805–809.

Andersson, S. & Amundsen, T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proceedings of the Royal Society of London, Series B*, **264**, 1587–1591.

Andersson, S., Örnborg, J. & Andersson, M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society of London, Series B*, **265**, 1–6.

Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.

Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.

Burley, N. 1988. The differential-allocation hypothesis: an experimental test. *American Naturalist*, **132**, 611–628.

Cramp, S. & Perrins, C. M. 1993. Blue tit. In: *The Birds of the Western Palearctic* (Ed. by S. Cramp & C. M. Perrins), pp. 225–248. Oxford: Oxford University Press.

Cunningham, E. J. A. & Russell, A. F. 2000. Egg investment is influenced by male attractiveness in the mallard. *Nature*, **404**, 74–76.

Cuthill, I. C., Bennett, A. T. D., Partridge, J. C. & Maier, E. J. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *American Naturalist*, **153**, 183–200.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.

Delhey, K., Johnsen, A., Peters, A., Andersson, S. & Kempenaers, B. 2003. Paternity analysis reveals opposing selection pressures on crown colouration in the blue tit (*Parus caeruleus*). *Proceedings of the Royal Society of London, Series B*, **270**, 2057–2063.

Dhondt, A. A. 1989. Blue tit. In: *Lifetime Reproduction in Birds* (Ed. by I. Newton), pp. 15–33. London: Academic Press.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Forslund, P. & Pärt, T. 1995. Age and reproduction in birds: hypotheses and tests. *Trends in Ecology and Evolution*, **10**, 374–378.

Fridolfsson, A. K., Gyllensten, U. B. & Jakobsson, S. 1997. Microsatellite markers for paternity testing in the willow warbler *Phylloscopus trochilus*: high frequency of extra-pair young in an island population. *Hereditas*, **126**, 127–132.

Gil, D., Graves, J., Hazon, N. & Wells, A. 1999. Male at attractiveness and differential testosterone investment in zebra finch eggs. *Science*, **286**, 126–128.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998. A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.

Gustafsson, L. & Sutherland, W. J. 1988. The cost of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature*, **335**, 813–815.

Hailman, J. P. 1977. *Optical Signals*. Bloomington: Indiana University Press.

Hoelzer, G. A. 1989. The good parent process of sexual selection. *Animal Behaviour*, **38**, 1067–1078.

Hunt, S., Bennett, A. T. D., Cuthill, I. C. & Griffiths, R. 1998. Blue tits are ultraviolet tits. *Proceedings of the Royal Society of London, Series B*, **265**, 451–455.

Hunt, S., Cuthill, I. C., Bennett, A. T. D. & Griffiths, R. 1999. Preferences for ultraviolet partners in the blue tit. *Animal Behaviour*, **58**, 809–815.

Johnsen, A., Andersson, S., Örnborg, J. & Lifjeld, J. T. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. *Proceedings of the Royal Society of London, Series B*, **265**, 1313–1318.

Kempenaers, B. & Sheldon, B. C. 1997. Studying paternity and paternal care: pitfalls and problems. *Animal Behaviour*, **53**, 423–427.

Limbourg, T., Mateman, A. C., Andersson, S. & Lessells, C. M. 2004. Female blue tits adjust parental effort to manipulated male UV attractiveness. *Proceedings of the Royal Society of London, Series B*, **271**, 1903–1908.

de Lope, F. & Møller, A. P. 1993. Female reproductive effort depends on the degree of ornamentation of their mates. *Evolution*, **47**, 1152–1160.

Magrath, M. J. L. & Komdeur, J. 2003. Is male care compromised by additional mating opportunity? *Trends in Ecology and Evolution*, **18**, 424–430.

Nilsson, J.-A. 2003. Ectoparasitism in marsh tits: costs and functional explanations. *Behavioral Ecology*, **14**, 175–181.

Örnborg, J., Andersson, S., Griffith, S. C. & Sheldon, B. C. 2002. Sexually selected UV reflectance declines over the breeding season in blue tits, *Parus caeruleus*. *Biological Journal of the Linnean Society*, **76**, 237–345.

Petrie, M. & Williams, A. 1993. Peahens lay more eggs for peacocks with larger trains. *Proceedings of the Royal Society of London, Series B*, **251**, 127–131.

Råberg, L., Nilsson, J. A., Ilmonen, P., Stjernman, M. & Hasselquist, D. 2000. The cost of an immune response: vaccination reduces parental effort. *Ecology Letters*, **3**, 382–386.

Senar, J. C., Figuerola, J. & Pascual, J. 2002. Brighter yellow blue tits make better parents. *Proceedings of the Royal Society of London, Series B*, **269**, 257–261.

Sheldon, B. C. 2000. Differential allocation: tests, mechanisms and implications. *Trends in Ecology and Evolution*, **15**, 397–402.

Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J. & Sendecka, J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature*, **402**, 874–877.

Siitari, H., Honkavaara, J., Huhta, E. & Viitala, J. 2002. Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Animal Behaviour*, **63**, 97–102.

Svensson, L. 1992. *Identification Guide to European Passerines*. Stockholm: Lars Svensson.

Swaddle, J. P. 1996. Reproductive success and symmetry in zebra finches. *Animal Behaviour*, **51**, 203–210.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Westneat, D. F. & Sherman, P. W. 1993. Parentage and the evolution of parental behavior. *Behavioral Ecology*, **4**, 66–77.

Whittingham, L. A., Taylor, P. D. & Robertson, R. J. 1992. Confidence of paternity and male parental care. *American Naturalist*, **139**, 1115–1125.

Williams, G. C. 1966. *Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thoughts*. Princeton, New Jersey: Princeton University Press.