Ultraviolet-blue reflectance of some nestling plumage patches mediates parental favouritism in great tits *Parus major*

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The colouration exhibited by nestling birds is generally cryptic, but in some species it has a conspicuous appearance. The adaptive function of these nestling displays is poorly known, especially in altricial species. We performed an experimental study in which the ultraviolet-blue reflectance of the carotenoid-based plumage of great tit *Parus major* nestlings was reduced in order to find possible evidence of parental favouritism. Tarsus length increment in a three-day period was significantly lower in manipulated nestlings than in their control siblings. As tarsus length may be a good predictor of survival, the parents may increase their fitness return by investing more in those nestlings reflecting more in the UV-blue spectral region. Interestingly, this effect was only found in a yellow patch located at the nape of nestlings that has been previously overlooked, as all the studies on plumage colouration in this species have focused on the breast plumage. Some quality indicators are proposed for the colour of nestling plumage, though the possibility exists that selection may operate through aspects of signal efficacy instead of aspects of signal content.

Many bird species exhibit conspicuous plumage colouration, frequently with a signaling role towards individuals of the opposite sex or competitors from the same or different species (reviewed in Hill and McGraw 2006). However, most colour signal functions are between adults, and thus, young individuals exhibit more cryptic colouration, probably because they usually need to communicate only with their parents and the consequences of the receivers' responses to these displays are not as important in determining fitness as in adulthood (Kilner 2006).

However, juveniles can also exhibit coloured plumage patches and other integumentary parts, as well as mouth colourations, especially in precocial species (Kilner 2006). Conspicuous plumage colouration in altricial birds, such as in the great tit *Parus major*, is rare, and its function is poorly known (Tschirren et al. 2005, Kilner 2006). In this species, nestlings exhibit a plumage pattern that closely resembles that of their parents (Cramp and Perrins 1993). This socially monogamous hole-nesting passerine has a carotenoid-based yellow plumage on the breast, which has been a classic model in studies of bird colouration (e.g., Slagsvold and Lifjeld 1985, Eeva et al. 1998). Nestlings moult their feathers about two months after they leave the nest (Jenni and Winkler 1994), and plumage colour as nestlings is not correlated with colour later as breeders, which discards the role of sexual selection in nestling colouration (Fitze et al. 2003a). The hypothesis that carotenoids may be costly to obtain and to incorporate into feathers (Tschirren et al. 2003, McGraw et al. 2004, McGraw and Parker 2005) raises the question of why growing nestlings invest in generating this colour before their first moult. Together with the rarity of conspicuous colours in altricial nestlings, this suggests a signaling role of the nestlings' colour towards their parents or siblings.

Evidence for parental favouritism in relation to plumage colour (i.e., that parents preferentially feed the chicks with the strongest signal expression) has been looked for in great tits, without success (Tschirren et al. 2005). Since the yellow colour of this species is carotenoid-based (feathers contain lutein and zeaxanthin obtained from food; Partali et al. 1987), the above authors experimentally provided nestlings with carotenoids and found that, though the intensity of the colour increased with treatment and reflected nestlings' quality (expressed as body mass gain; Tschirren et al. 2003), they did not receive more food from their parents. However, Tschirren et al. (2003) did not measure or take into account the ultraviolet (UV) component of yellow breast colouration in this species which could arguably have an effect on parental responses.

On the other hand, the only colour patch that has been studied in great tit nestlings is the yellow breast (Hõrak et al. 2000, Fitze et al. 2003a,b, Tschirren et al. 2003, 2005). However, this is not the only carotenoid-based colour patch exhibited by these nestlings. In this species a coloured plumage area can be observed on the nape, which is yellow like the breast in nestlings and turns to white with the first moult, maintaining this colour during the rest of the life of birds (Cramp and Perrins 1993). After this first

moult, the relative size of the nape patch also seems to decrease. Thus, the change in colour and size suggests that this patch could have a signaling role in nestling great tits.

In this study we investigate the signaling role of both carotenoid-based plumage patches (nape and breast) exhibited by great tit nestlings. To examine whether carotenoid-based colouration of nestlings may be mediating parental favouritism, we experimentally reduced the UV-blue part of the reflecting spectra in the nape or in the breast of nestlings. In unsaturated (but not for saturated) colours like that treated here, relative long wavelength but not UV reflectance is likely to be positively related to carotenoid content (Shawkey et al. 2006). If nestlings' plumage has a signaling role mediated by the UV-blue (i.e. structural) component of its colour, we expected that parents should decrease the feeding rates of manipulated nestlings. Therefore, we expected to find lower growing rates in nestlings with reduced UV-blue reflectance.

Methods

The study was carried out in May–July 2006 in two deciduous forests of Pyrennean oak *Quercus pyrenaica* in Sierra de Guadarrama, Central Spain. The nape colour manipulation was carried out in 19 nests (172 nestlings in total) in Miraflores de la Sierra (40° 49′N, 03° 46′W, 1,352 m a.s.l..), and the breast colour manipulation was carried out in 14 nests (128 nestlings in total) near Navacerrada (40° 43′N, 03° 55′W, 1,300 m a.s.l.). These localities are separated by only 10 km and belong to the same population of great tits. Frequent checks of nest-boxes allowed us to collect data on dates of clutch initiation and clutch size for all breeding pairs.

In each nest we manipulated half of the nestlings by applying a Edding 4500 yellow marker pen (Ahrensburg, Germany; colour code 0.05) at the nape or breast. In some nests (Miraflores de la Sierra population) we manipulated the nape colouration of half of the nestlings and in other nests (Navacerrada) we manipulated the breast colouration of half of the nestlings. In both cases, the other half of nestlings was control, in which the pen was applied on the inferior surface of flight feathers. Nestlings were randomly assigned to one of these treatments. Similar type of marker pens have been previously used by other authors to manipulate the UV-blue reflectance of adult blue tits *Cyanistes caeruleus* (Johnsen et al. 2005). In addition to the pen, these authors also applied a silicone paste in order to impermeabilize the feathers and thus securing the durability of the effect. As we applied the pen to nestlings inside protected nest boxes and we only needed to obtain a durability of three days, the use of additional products was not necessary here. Birds can preen breast but not nape, though it is unlikely that the effect of marker pens can be removed by preening.

The manipulation was made on day 12 after hatching (hatching date = day 0), date at which nestlings were also ringed, weighed with a portable electronic balance to the nearest 0.1 g and their tarsus length measured with a calliper to the nearest 0.01 mm. These measures were taken again on day 15 after hatching. Experimental and control nestlings did not differ in initial tarsus length ($\bar{x} \pm$ SE,

paired t-test: nape colour experiment: experimentals: 19.68 ± 0.10 mm, controls: 19.73 ± 0.11 mm, $t_{18} = 1.08$, $P = 0.295$; breast colour experiment, experimentals: 19.71 ± 0.16 mm, controls: 19.70 ± 0.15 mm, $t_{13} = 0.53$, $P = 0.607$) or body mass (nape colour experiment, experimentals: 16.84 ± 0.27 g, controls: 16.75 ± 0.30 g, $t_{18} = 0.05$, $P = 0.962$; breast colour experiment, experimentals: 17.03 ± 0.31 g, controls: 17.12 ± 0.31 g, $t_{13} = 0.82$, $P = 0.425$).

Plumage colour was measured in the field using an Ocean Optics USB2000 spectrophotometer (range 250–800 nm) with ultraviolet (deuterium) and visible (tungsten-halogen) lamps and a bifurcated 400 μm fiber-optic probe (Dunedin, Florida, USA). The measurements were taken at a 90° angle to the sample and with the 'Coincident Normal' configuration (Andersson and Prager 2006). All measurements were relative to a white "Spectralon" tablet (WS-1-SS, Ocean Optics, Dunedin), and reference measurements were frequently made (after 5–6 plumage measurements). An average spectrum of three readings on different points of the upper part of the right side of the yellow breast was obtained for each great tit nestling, moving the probe by at least 5 mm before taking each new reading, but always following the same order (from upper to lower breast). The same was done for the nape patch, but due to its small size the three measures were recorded at the same point but removing the probe after each measure. Plumage colour could be only measured in the population in which the nape patch was manipulated. Measures were taken in both control and experimental nestlings on day 12 after hatching. In experimental birds, colour measures of the nape patch were taken before and immediately after the application of the pen. However, due to time constraints colour measures could not be taken in all nestlings, particularly after manipulation. Measurement anomalies forced us to remove some colour measures from the analyses.

Following Montgomerie (2006), spectral data were summarized as measures of brightness (differentiating between UV-blue brightness ($R_{300-475}$) and long wavelength brightness ($R_{475-700}$)), chroma (differentiating between UV-blue chroma ($R_{300-475}/R_{300-700}$), and long wavelength chroma ($R_{475-700}/R_{300-700}$)), and hue (wavelength corresponding to maximum reflectance in the UV spectral region). High carotenoid contents (mainly lutein in the case of great tits) are reflected by low values of chroma at the blue region and high values at long wavelengths (Shawkey et al. 2006). Mean values for each treatment group in each nest were used, except to find relationships between nape and breast colour variables in individual nestlings.

In unsaturated pigmentary colours, some absorbance of carotenoids occurs in spectral regions different from those of maximal absorbance, which makes long wavelength chroma the best indicator of pigment content (Andersson and Prager 2006). Thus, our manipulation simulates an increase in the carotenoid content of feathers, so that any effect found in experimental nestlings should be assigned to a decrease in the structural properties of feathers and an increase in their carotenoid content (Pearson's correlation test between UV-blue chroma and long wavelength chroma using control nestlings only: r = −0.95, P < 0.001, n = 18). However, an

increment in the content of carotenoids would not decrease UV chroma, as this colour variable is not affected by the content in carotenoids (Shawkey et al. 2006). Since our treatment significantly decreased the UV-blue chroma of nestlings' plumage colour (see Results), we interpret our results as caused, at least in part, by a reduction in the structural components of plumage.

We used paired t-tests to compare the mean increment in tarsus length and body mass between experimental and control nestlings in each nest and to compare colour variables of nestlings before and after treatment. Wilcoxon matched pairs tests were used instead when data were not normally distributed. Relationships between colour variables and increments in tarsus length and body mass were explored through single Pearson's correlation tests, as colour variables were intercorrelated. As carrying out multiple tests inceases the probability of committing type I statistical errors, the sequential-Rice correction (Rice 1989) was used. The relationships between colour variables taken for nape and breast were also investigated with Pearson's correlation tests, although Spearman's correlations were used in the case of hue due to violations of normality assumption. Means are showed with the corresponding standard error.

Results

Manipulation effects on colour

Reflectance curves of the nape patch of nestlings with and without the UV-blue reduction treatment are shown in Fig. 1. Considering those nestlings in which the nape colour could be measured before and after the treatment ($n = 17$ nestlings belonging to 10 nests), UV-blue brightness was considerably reduced after manipulation (before treatment: 123.10 ± 16.42; after treatment: 48.20 ± 7.91; $t_{16} = 4.54$, $P < 0.001$), while long wavelength brightness was not modified (before treatment: 224.28 ± 26.98; after treatment: 213.65 ± 21.63; $t_{16} = 0.39$, $P = 0.699$). The same applied to UV-blue chroma (before treatment: 0.45 ± 0.02;
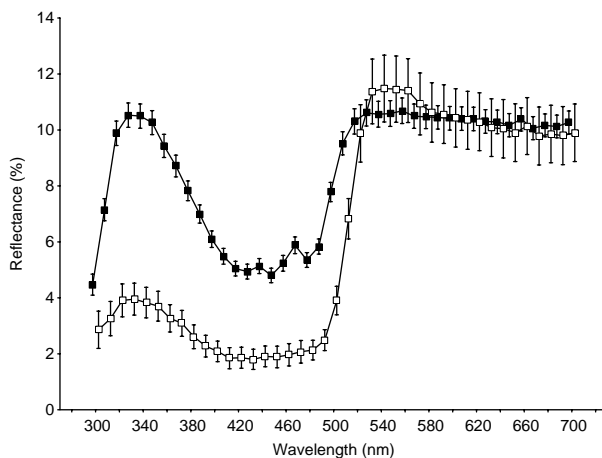

Figure 1. Spectral reflectance ($\pm$ SE) of the yellow nape patch of great tit nestlings before (black squares) and after (white squares) experimental manipulation. Data are provided in 10 nm intervals and correspond to measures from 128 unmanipulated and 21 manipulated nestlings.

after treatment: 0.19 ± 0.02; $t_{16} = 11.04$, $P < 0.001$) and, as a consequence, long wavelength chroma was significantly increased after the treatment (before treatment: 0.85 ± 0.01; after treatment: 0.94 ± 0.01; $t_{16} = 11.18$, $P < 0.001$). UV hue did not change with the manipulation ($Z = 1.56$, $n = 17$, $P = 0.120$).

Considering all the nestlings from which we had measured the nape colour before the treatment, the range of the different colour variables were as follows: UV-blue brightness: 13.61 ± 349.03, UV-blue chroma: 0.22 ± 0.67, long wavelength brightness: 36.82 ± 575.79, long wavelength chroma: 0.76 ± 0.95. Therefore, colour values obtained after the treatment (see above) were inside the natural range of this trait.

On the other hand, although the colour of the breast was not measured after the manipulation, the similarity of the breast spectrum to that of the nape (see Galván and Sanz 2006) leads us to assume that the manipulation effect is the same in both experiments.

Manipulation effects on nestling growth

The increment in tarsus length in those nestlings in which the UV-blue reflectance of the nape patch had been reduced was much lower than in control nestlings ($t_{18} = 5.43$, $P < 0.001$; Fig. 2a). However, body mass did not differ between experimental and control nestlings ($t_{18} = 0.44$, $P = 0.664$; Fig. 2b). By contrast, no significant differences were found between experimental and control birds in the population in which the UV-blue reflectance of the breast patch was reduced (tarsus length increment: $t_{13} = 0.53$, $P = 0.607$; body mass increment: $t_{13} = 0.75$, $P = 0.466$; Fig. 2c, d).

None of the colour variables of the nape patch were correlated with the increment in tarsus length or body mass in control nestlings ($-0.26 < r < 0.33$, all $P > 0.18$).

In contrast, UV-blue brightness and long wavelength brightness of the breast were negatively correlated with body mass increment of control nestlings ($r = -0.71$, $n = 18$, $P = 0.001$ for both variables). No breast colour variables were significantly correlated with tarsus length increment after sequential-Rice correction ($-0.46 < r < 0.56$, all $P > 0.015$).

Although the shape of spectral curves was similar for nape and breast colour (see Galván and Sanz 2006) and the majority of colour variables were correlated between the two patches (UV-blue brightness: $r = 0.27$, $P = 0.003$, $n = 123$; UV-blue chroma: $r = 0.30$, $P = 0.001$, $n = 123$; UV hue: $r_s = 0.31$, $P = 0.001$, $n = 123$; long wavelength chroma: $r = 0.30$, $P = 0.001$, $n = 123$), a non-significant relationship was found for long wavelength brightness ($r = 0.05$, $P = 0.605$, $n = 123$).

Discussion

The results of this experimental study suggest that parental favouritism in great tits may be mediated by the short wavelength reflectance of the nestlings' plumage. We suggest that the signaling area is not the yellow breast patch, which has been traditionally studied in great tits
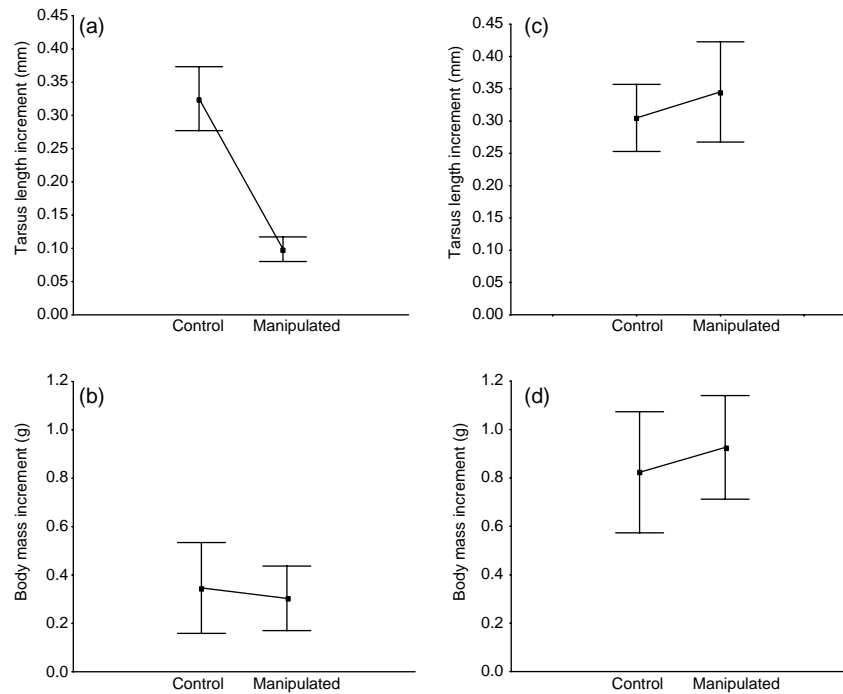
Figure 2. Tarsus length and body mass increments between days 12 and 15 after hatching in great tit nestlings with manipulated (UV-), and unmanipulated (UV+) nape (a and b; n = 19 nests), and breast (c and d; n = 14 nests) colour.

(e.g., Slagsvold and Lifjeld 1985, Eeva et al. 1998, Fitze et al. 2003a,b, Tschirren et al. 2003, 2005), but the yellow nape patch. Thus, altricial nestlings could use other visual traits in addition to mouth or skin colour (e.g., Heeb et al. 2003, Bize et al. 2006, Kilner 2006) to communicate with their parents.

The nestlings in which the UV-blue reflectance of the nape patch was reduced had lower gains in tarsus length than control birds, indicating that they were limited to allocate resources to skeletal growth because the parents fed them at lower rates than their siblings, but there was no difference in body mass. The fact that we found significant differences in only three days makes it compelling. Although we did not find a relationship between increments in tarsus length and UV-blue reflectance among control nestlings, this should be investigated more in detail in the future with a larger data sample, as our relatively small data set and the limited range of patch colour variation among control nestlings could prevent us to find such a relationship. Thus, the possibility exists that adult great tits use the UV-blue reflectance properties of the nape patch to assess the quality of their nestlings. Directional selection seems to act on tarsus length, as nestlings with long tarsi have advantages in survival and competitive terms (Garnett 1981, Alatalo and Lundberg 1986, Alatalo et al. 1990, Moreno et al. 1997). By contrast, the body mass of nestlings is under stabilizing selection pressures, with optimal intermediate values leading to the highest survival later in life (Lindén et al. 1992). The adaptive value of this could be that, at least in great tits, nestlings need to have a high maneuverability to leave the nest, which cannot be done with a high body mass (Lindén et al. 1992). No evidence for parental favouritism was found when the breast colour was manipulated instead. The possibility that parents could

perceive experimental and control nestlings as individuals of different sex and this has caused the observed effect is unlikely, as there are no sex-related differences regarding the UV chroma of yellow feathers in the closely related blue tit (Johnsen et al. 2003).

The degree of expression of structural plumage colour is associated with individual condition (e.g. Keyser and Hill 1999, 2000, McGraw et al. 2002, Siefferman and Hill 2005a,b,c). Thus, the same could be applied to structural components (UV-blue reflectance) of carotenoid-based colour, though the mechanisms generating the underlying structural colour in carotenoid-based plumage is still unknown (Shawkey and Hill 2005). Nestlings with highly developed structural colour components could be thus favoured by signaling their genotypic or phenotypic quality to their parents, or to their siblings as a signal of social dominance (Mock and Parker 1998).

For honest signals to evolve, it is necessary that they are costly to produce or maintain (Hasson 1997). In that respect, possible costs could be those associated with incorporating carotenoids into feathers (Tschirren et al. 2003, McGraw et al. 2004, McGraw and Parker 2005), as the nape patch of great tits turns to white after the first moult, indicating that they do not incorporate carotenoids to this patch after that moment. Although the UV-blue reflectance of carotenoid-based plumages is generated by an underlying white structure (Shawkey and Hill 2005), carotenoids are needed to create the contrast of the UV-blue portion of the spectrum against that corresponding to the long wavelength range (Shawkey et al. 2006), which probably enhances its perceptibility.

An alternative and non-exclusive hypothesis is that parents could use plumage UV-blue reflectance to locate nestlings inside dark nests, instead of (or in addition to)

assess nestlings' quality (Kilner 2006). This could be possible because UV light strongly contrasts against the background in these nests, as shown for nestling skin, and mouth colour and for the colour of blue-green eggs (Heeb et al. 2003, Hunt et al. 2003, Jourdie et al. 2004, Avilés et al. 2006). On the other hand, an innate preference by parents for a specific colouration is also possible without implying a functional adaptiveness for this trait.

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