

Plumage coloration can be perceived as a multiple condition-dependent signal by Great Tits *Parus major*

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The evolution of multiple signals can be explained because they enhance the perception of a general message by recipients. Plumage coloration frequently acts as a condition-dependent signal, so that species displaying different colour patches have the potential to transmit information on condition through a multiple signalling system. The Great Tit *Parus major* exhibits plumage colour patches generated by the main types of colour production, some of which, particularly those based on melanins and carotenoids, are known to be related to body condition. However, the colour expressions of all of the different colour types have never been investigated simultaneously to determine whether they function as multiple signals of condition. In addition, visual perception models have never been applied to a multiple signalling system in a wild population of birds. Here I present information that links body condition with the colour expression of almost all of the different plumage patches of male Great Tits captured during the winter. Birds in better condition had greater reflectance values at short wavelengths in all plumage patches, and this was especially so in the white (i.e. structural) colour of the cheeks. Plumage colour characteristics were calculated by means of avian visual models, suggesting that Great Tits have the capacity to perceive information contained in the plumage coloration of conspecifics. These results show that short-wavelength reflectance has great potential to transmit biologically significant information on the body condition of birds, even in achromatic plumage patches.

Keywords: communication, multiple signals, visual perception.

Animal communication is commonly based on the use of multiple traits to transfer information to other species or to conspecifics (Johnstone 1996). These traits can belong to the same morphological or behavioural unit (like different plumage patches or colour components; Grether *et al.* 2004, Senar & Quesada 2006), or comprise different units (e.g. plumage and song; Andersson *et al.* 2002, Badyaev *et al.* 2002). In these multiple signalling systems, individual traits can all transmit the same type of information (redundant traits), or can signal multiple messages (Møller & Pomiankowski 1993, Johnstone 1996).

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The evolution of redundant signalling traits is hypothesized to ensure that recipients of the signals or cues better perceive a general message. However, the function of a redundant signalling system can only be revealed through consideration of all traits simultaneously while also considering the perceptual abilities of the recipients (Rowe 1999). Because of methodological difficulties, the study of the adaptive functions of animal communication can often be performed by considering only single traits, often without information on the perceptual ability of the animals involved. However, a more realistic model should consider the ability of receivers to integrate information from multiple signals (Scheuber *et al.* 2004). In this sense, birds offer unique opportunities to study multiple visual signals because information is available on the visual perception system for some

avian models (Cuthill 2006), and the mechanics of all known colour types have been explored in this group (Hill & McGraw 2006).

The Great Tit *Parus major* is a small passerine bird that uses three of the most common plumage colourants (structural colour, carotenoid and melanin pigments) to colour its feathers. Great Tits have yellow (carotenoid-based) and black (melanin-based) breast patches, olive green (carotenoid- and melanin-based) back patches, iridescent black (structural and melanin-based) crown patch, and white (structural) patches on their cheeks (Figueroa & Senar 2005, Hegyi *et al.* 2007, Galván & Sanz 2008). In addition, Great Tits present blue (structural) coloration in some wing feathers (Jenni & Winkler 1994). This diversity in plumage coloration makes the Great Tit a good model for the study of multiple colour signals. Because the degree of expression of all colour types (i.e. melanin-based, carotenoid-based, structural and achromatic) has been associated with body condition and mate choice in different species of birds (Hill 2006b, Hegyi *et al.* 2007), the different plumage colour patches of Great Tits are potentially redundant signals to confer information about the condition of individuals. Indeed, when considered separately, the colour intensity of the yellow breast and the black crown have been associated with body condition and mating success in this species (Senar & Quesada 2006, Hegyi *et al.* 2007, 2008, Dauwe & Eens 2008, Senar *et al.* 2008). Similarly, consideration of these traits together seems also to represent a condition-dependent signal (Hegyi *et al.* 2008). In Great Tits, however, associations between colour intensity and body condition have not been explored in relation to all colour traits (i.e. iridescent and non-iridescent black, yellow, green and white) simultaneously. In addition, the intensity of the non-iridescent black, green and white colours has never been measured and/or associated with body condition. Moreover, no studies have incorporated models of the avian visual perception system in assessment of the relationships between these colour traits and body condition considering their overall biological significance in the context of intraspecific signalling.

The aim of this study was to evaluate the correlations between multiple plumage colour traits displayed by Great Tits and body condition, which is generally a good predictor of survival probability (Møller & Szep 2001, Naef-Daenzer *et al.* 2001), in winter when food resources are limited (Orell

1989). Body condition values at moult (i.e. end of summer) and in winter are correlated in Great Tits (Gosler & Harper 2000), so any relationship between plumage coloration and body condition in winter may well reflect the strength of the relationship during the period in which the feathers grew, although this study does not consider body condition during moult. I use current models of avian colour vision (Vorobyev *et al.* 1998, Endler & Mielke 2005) to estimate plumage colour components that are perceived by birds and thus have the potential to be significant in signalling. Because previous studies have found the intensity of all colour types and body condition to be correlated (Hill 2006a), I predicted that all colour patches of Great Tits have the potential to transfer perceptually significant information on the body condition of birds and thus constitute redundant signals of quality. Therefore, the expectation was that the colour properties of all plumage patches should be related to some degree to body condition.

METHODS

The study was carried out in January–March 2006 in a deciduous forest of Pyrenean Oak *Quercus pyrenaica* in Miraflores de la Sierra, central Spain (40°49'N, 03°46'W). Feeders baited with husked peanuts were installed at different locations within the study area. A total of 44 Great Tits (36 males and eight females, representing 33 adults, 10 yearlings and one individual of unknown age) were captured at the feeders with funnel-traps (Senar *et al.* 1997), and classified as yearlings or older according to plumage (Jenni & Winkler 1994). However, seven Great Tits (five males and two females) escaped before colour measurements could be taken, and another three birds (two males and one female) escaped before morphometrics were taken. Individuals were uniquely marked with colour rings, weighed with a portable electronic balance and their tarsus length measured with a digital calliper. As approximately half the birds were captured more than once in the same funnel-traps during the course of the study (Galván & Sanz 2009, unpublished data), the birds caught appeared to be a representative sample of the wintering population of Great Tits at this site. The small number of females captured may be due to the low affinity of female Great Tits for artificial feeders or to an exclusion of females by dominant males at these sites (Senar *et al.* 1999). Therefore,

only males were included in all subsequent analyses.

Reflectance spectrometry

Plumage reflectance measurements were taken from five different patches: the yellow breast, the black breast stripe, the green back, the black crown and the white cheeks. Data were collected 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 fibre-optic probe (Ocean Optics, Dunedin, FL, USA). The fibre-optic probe both provided illumination and obtained light reflected from the sample, and had a reading area of *c.* 1 mm². The measurements were taken at a 90°

angle to the sample. The spectrometer measured reflectance in 0.36-nm increments. All measurements were relative to a white Spectralon[®] tablet (WS-1-SS; Ocean Optics), and the system was frequently calibrated. The spectral curves were generated using OOIBASE software. Three readings were obtained at different points of each plumage patch, moving the probe by at least 5 mm before taking each new reading, but always following the same order (from upper to lower patch) and taking each reading from approximately the same location in all birds. However, in the case of crown and cheek, because of the small size of the patches the three measures were recorded at the same point but removing the probe after each measure. The results of reflectance measurements for the five plumage patches are shown in Figure 1.

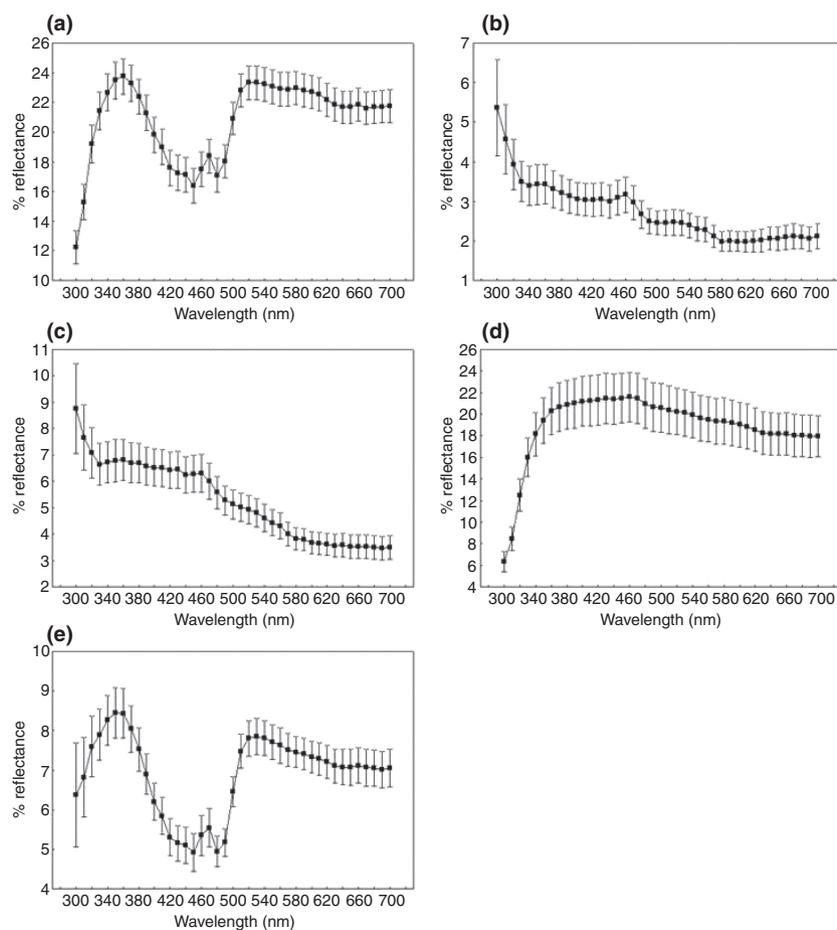


Figure 1. Reflectance spectra for the five plumage patches of male Great Tits considered in this study: (a) yellow breast, (b) black breast stripe, (c) black crown, (d) white cheek, (e) green back. Bars represent the standard error of the mean.

Visual modelling

Colour vision in diurnal birds is dependent upon four types of retinal cone cells which are sensitive to either very short (VS, ultraviolet (UV)), short (SWS, blue), medium (MWS, green) or long (LWS, red) wavelengths (Maier & Bowmaker 1993, Cuthill 2006). Spectral data were reduced into four quantal cone catches (Vorobyev *et al.* 1998) that quantify the amount of light captured by each of the single cones. By using the SPEC package (Hadfield & Owens 2006) implemented in R (R Development Core Team 2004), the four quantum cone catches (Q_i) were calculated by multiplying cone sensitivities by the reflectance spectrum, the irradiance spectrum and the transmission spectrum of the ocular media, as expressed by the formula:

$$Q_i = \frac{\int_{\lambda} R_i(\lambda)S(\lambda)I(\lambda)O(\lambda)d(\lambda)}{\int_{\lambda} R_i(\lambda)}$$

where λ indicates wavelength (nm), $R_i(\lambda)$ is the sensitivity (nm) of cone type i , $S(\lambda)$ is the percentage of light reflected from a patch compared with a white standard, $I(\lambda)$ is the irradiance spectrum ($\mu\text{mol}/(\text{m}^2/\text{s}/\text{nm})$) and $O(\lambda)$ is the transmittance spectrum of the ocular media.

As cone catches change with varying illumination, $I(\lambda)$, and this is discounted by animals through colour constancy, the von Kreis algorithm was used to normalize Q_i by the quantum cone catch for the irradiance spectrum. The irradiance spectral data used were obtained from a standard forest shade illumination provided by the SPEC package (Hadfield & Owens 2006), as this irradiance spectrum is the most appropriate for the present case (see habitat description above), and an achromatic adapting background (Hadfield & Owens 2006). I used the ocular media transmittance of a species closely related to the Great Tit (i.e. the Blue Tit *Cyanistes caeruleus*; Hart *et al.* 2000). Each cone catch was then standardized by dividing them by the sum of the four cone catches, and three of the standardized cone catches were divided by a fourth (that corresponding to LWS in this case) and their natural logarithm was then calculated. Thus, three log-contrasts were calculated to break the unit-sum of the four standardized cone catches (Hadfield & Owens 2006). In addition, these log-contrasts permit consideration of an

opponency model of colour vision where the exact opponency mechanisms are unspecified, as perception of chromatic variation occurs through a physiological mechanism that contrasts the relative outputs of the different cone types (Endler & Mielke 2005, Hadfield & Owens 2006).

Following Hadfield and Owens (2006), a principal components analysis (PCA) was performed on the three log-contrast colour variables to treat them as a multivariate response in a multivariate 'animal model'. In all plumage patches, the eigendecomposition showed a first axis that explained 69–90% of phenotypic variation; the other two axes explained 8–30% and 0.5–1% of variance, respectively (Table 1). Factor loadings for the first axis (PC1) were high and negative in all patches (except in the case of the crown patch, where they were high and positive), indicating that it is determined by the three first cone catches vs. LWS (Table 1). Thus, high PC1 scores indicate relatively more reflectance (or less reflectance in the case of the crown patch) at long wavelengths as compared with short/medium wavelengths. The second axis (PC2) was always determined by MWS vs. LWS cone catches (Table 1), and thus high PC2 scores indicate relatively more reflection at long wavelengths than at medium wavelengths, except in the case of the cheek patch, where PC2 was determined by VS vs. MWS cone catches. The variance explained by the third axis was too low to be biologically significant, and PC3 was thus not considered in the analyses.

As achromatic variation in birds is thought to be perceived not through the four single cones, but by double cones (Campenhausen & Kirschfeld 1998, Osorio *et al.* 1999), I calculated the double cone quantum catches from data on double cone spectral sensitivity of Blue Tits following the same procedure for the four single cones. The double cone quantum catch was used as a 'brightness index'.

Statistical analyses

As the aim of the study was to assess whether body condition influences some patterning of response on the plumage colour variables, I used multivariate analyses of covariance (MANCOVAs) in which PC1 scores, PC2 scores or brightness index values for each plumage patch were the dependent variables, and body condition (calculated as body mass divided by the cube of tarsus length) was introduced as a covariate. Although the use of this ratio presents some concerns like any other

Table 1. Factor loadings obtained from the principal components analysis (PCA) performed on the different log-contrasts (UVS, SWS and MWS) of five plumage patches in Great Tits.

	PC1	PC2
Yellow breast		
Colour	UV/blue/green vs. red	Green vs. red
Eigenvalue	2.73	0.25
% variance	90.88	8.30
UVS log-contrast	-0.97	0.21
SWS log-contrast	-0.98	0.18
MWS log-contrast	-0.91	-0.42
Black breast stripe		
Colour	UV/blue/green vs. red	Green vs. red
Eigenvalue	2.69	0.28
% variance	89.76	9.23
UVS log-contrast	-0.94	0.31
SWS log-contrast	-0.98	0.08
MWS log-contrast	-0.91	-0.41
Black crown		
Colour	UV/blue/green vs. red	Green vs. red
Eigenvalue	2.07	0.90
% variance	68.95	30.02
UVS log-contrast	0.86	0.50
SWS log-contrast	0.99	0.04
MWS log-contrast	0.59	-0.80
White cheek		
Colour	UV/blue/green vs. red	UV vs. green
Eigenvalue	2.16	0.82
% variance	71.92	27.46
UVS log-contrast	-0.72	0.69
SWS log-contrast	-0.99	-0.02
MWS log-contrast	-0.81	-0.58
Green back		
Colour	UV/blue/green vs. red	Green vs. red
Eigenvalue	2.72	0.26
% variance	90.72	8.77
UVS log-contrast	-0.99	0.10
SWS log-contrast	-0.95	0.28
MWS log-contrast	-0.91	-0.41

non-destructive measure of body condition (Green 2001), perhaps the most serious of them are related to the facts that the effect of the denominator may not be completely removed and that the distribution of ratios computed from normally distributed variables may be skewed and no longer normal (Blem 1984). However, in the present study there are no differences between localities and ages that could be affected by the first problem, and inspec-

tions of residuals from the models confirmed that the normality assumptions were fulfilled, thus avoiding problems related to the second concern. Furthermore, this measure of condition has successfully predicted several fitness-related variables in recent studies (e.g. Kleven *et al.* 2006, Morales *et al.* 2006), and was therefore used here.

Age was added as a fixed factor, but because it did not significantly explain variance in any of the dependent variables considered in either univariate or multivariate analyses, it was removed from the final models. In addition, plumage colour variables presented high intercorrelation values (PC1: $-0.55 < r < 0.48$; PC2: $-0.19 < r < 0.29$; brightness index: $-0.12 < r < 0.49$), which requires the calculation of a single, overall statistical test on these sets of variables instead of performing multiple individual tests that would inflate the chance of a Type I error and ignore the correlation among the multiple variables. MANCOVA is thus the best approach for testing this hypothesis. Nonetheless, univariate analysis of variance (ANOVA) was also used to identify responses that contributed to a significant multivariate response. The presence of outliers was determined on the basis of Cook's distances >2 and leverages $>2p/n$, where p is the number of parameters in the model and n is the sample size (Crawley 1993).

RESULTS

The MANCOVA for PC1 scores explained a high proportion of variance in the colour of the yellow breast ($R^2 = 0.15$, $F_{1,27} = 4.91$, $P = 0.035$), the black breast stripe ($R^2 = 0.15$, $F_{1,27} = 4.96$, $P = 0.034$) and the white cheek ($R^2 = 0.21$, $F_{1,27} = 7.05$, $P = 0.013$). In addition, the proportion of variance explained in the colour of the black crown and green back patches was close to significance ($R^2 = 0.11$, $F_{1,27} = 3.27$, $P = 0.082$; $R^2 = 0.12$, $F_{1,27} = 3.62$, $P = 0.068$, respectively). Body condition was significantly related to colour PC1 in all plumage patches (Wilks = 0.48, $F_{5,23} = 4.92$, $P = 0.003$), indicating that, although the magnitude of the correlation between body condition and PC1 scores differed between plumage patches (see below), overall plumage coloration covaried with body condition.

Univariate analyses showed that the correlation between body condition and PC1 scores was significant for the yellow breast patch ($F_{1,27} = 4.91$, $P = 0.035$; Fig. 2a), for the black breast stripe

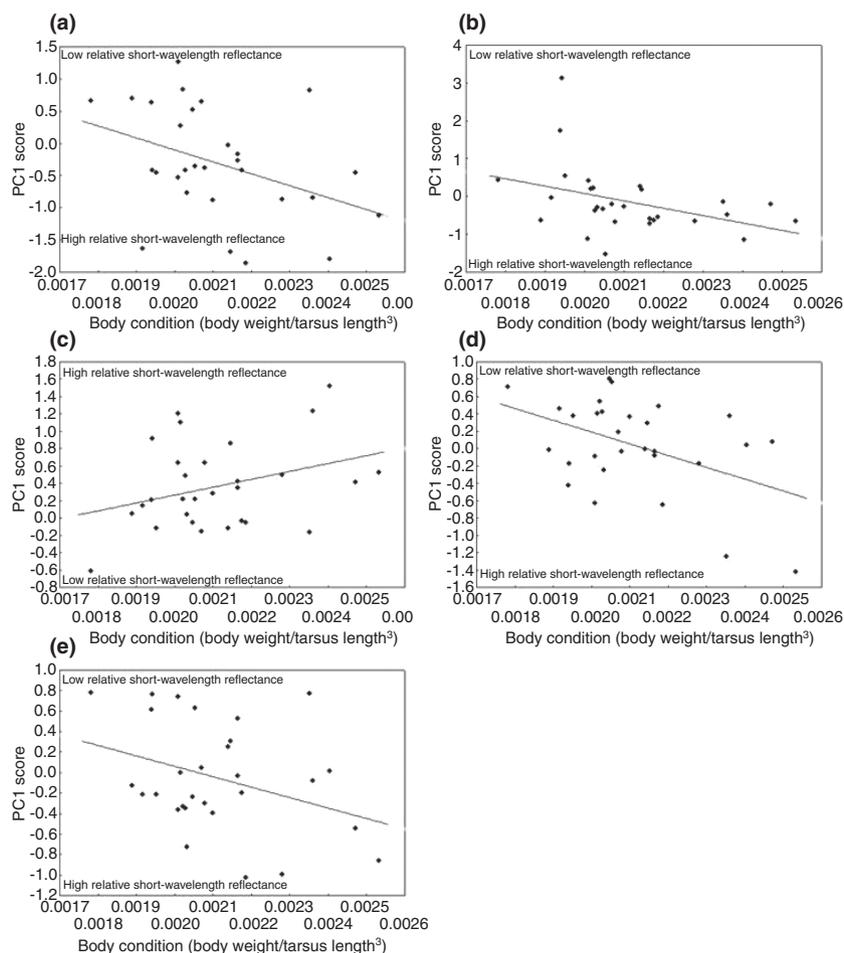


Figure 2. Relationship between body condition and PC1 plumage colour scores for the yellow breast (a), black breast stripe (b), black crown (c), white cheek (d) and green back (e) plumage patches of male Great Tits. PC1 scores indicate the relative contribution of short/medium vs. long wavelength reflectance as might be perceived by birds. Note that the sign of PC1 scores in the case of the black crown patch is reversed as compared with the other plumage patches. The lines are regression lines. Examination of Cook's distances and leverage values confirmed that no outliers were present.

($F_{1,27} = 4.96$, $P = 0.034$; Fig. 2b) and for the white cheek patch ($F_{1,27} = 7.05$, $P = 0.013$; Fig. 2d). A non-significant trend was observed for the black crown and green back patches (black crown: $F_{1,27} = 3.27$, $P = 0.082$, Fig. 2c; green back: $F_{1,27} = 3.62$, $P = 0.068$, Fig. 2e). In all cases except the black crown, the correlation between body condition and PC1 was negative ($\beta \pm \text{SE}$; yellow breast: -0.39 ± 0.18 , black breast stripe: -0.39 ± 0.18 , black crown: 0.33 ± 0.18 , white cheek: -0.45 ± 0.17 , green back: -0.34 ± 0.18), indicating that birds in better condition displayed shorter relative reflectance in all plumage patches.

By contrast, neither age nor body condition explained a significant proportion of variance in

PC2 scores or brightness index values for any plumage patch (results not shown). Thus, the only plumage characteristic that presents the potential to be perceived by birds as associated with body condition is the contrast between long and short wavelengths in plumage reflectance spectra.

DISCUSSION

The three main mechanisms leading to the production of colour traits in birds (i.e. melanin-based, carotenoid-based and structural) have all been associated with intraspecific condition-dependent (i.e. honest) and sexually selected signals (Hill 2006a, Hegyi *et al.* 2007). Several species, such as

the Great Tit, display many different colour traits, but the majority of studies that have explored the signalling function of colour traits have considered them individually because of obvious methodological difficulties (but see Senar & Quesada 2006, Hegyi *et al.* 2007). However, it is known that, in a mate-choice environment, females should integrate the information conferred by all traits displayed by males (Scheuber *et al.* 2004), which makes multi-coloured species candidates to display multiple reinforcing signals utilizing different coloured body parts.

This seems to be the case in the Great Tit, as the present study shows that body condition predicts the intensity of coloration when virtually all plumage patches are considered together. Although Great Tits obtain information about the quality of conspecifics from traits independent of colour (e.g. song repertoire or size of black breast stripe; McGregor *et al.* 1981, Senar & Quesada 2006), these results suggest that all colour traits with a potential to transmit information on quality in male Great Tits act as a multiple signalling system. In particular, it is the relative contribution of short vs. long wavelengths of the plumage reflectance spectra that is related to body condition in male Great Tits, with birds in better condition displaying colour patches that are more reflective at short wavelengths. As plumage colour variables were calculated on the basis of avian vision models with information on the visual system of a species closely related to the Great Tit (i.e. the Blue Tit), these results indicate that male Great Tits have the potential to perceive plumage colour as a whole trait related to body condition and thus could use this information in intraspecific communication. This appears to be the first time that the condition-dependence of all plumage patches in a multi-coloured species has been analysed by means of visual perception models. However, a proper demonstration that Great Tits actually perceive information on body condition through plumage colour should be provided by future behavioural studies.

Although there was an overall effect of body condition on the colour of plumage patches, the relationship was especially marked in the case of the white cheek patch. In Great Tits, uniform cheek patches (i.e. without black gaps due to feather loss) are indicative of a low number of aggressive acts from conspecifics and are thus associated with dominance (Galván & Sanz 2009),

which is translated into a higher mating success for high-quality birds that present large cheeks and thus amplify their dominance status (Galván & Sanz 2008). Differences in patch uniformity are generated by variations in the frequency of black gaps caused by conspecifics, so that irregularities in plumage might be associated with variation in the total reflectance of the cheeks and thus with the colour variable that has been measured in the present study. Stressful conditions seem to determine the brightness or the extension of white plumage in some species, which are in turn associated with individual quality (Qvarnström 1999, Hanssen *et al.* 2006, Ferree 2007, McGlothlin *et al.* 2007). Thus, it has been suggested that stressful conditions associated with diets of poor quality increase corticosterone levels and subsequently limit the capacity to synthesize proteins such as keratin needed for feather growth (McGlothlin *et al.* 2007). A protein-rich diet is thus necessary to develop both large and bright white plumage ornaments, as shown by McGlothlin *et al.* (2007) in Dark-eyed Juncos *Junco hyemalis*. Therefore, only high-quality individuals may have access to high-quality resources and thus a greater capacity to develop bright white ornaments. This is a likely explanation for the condition-dependence of the colour of white cheeks in male Great Tits, as dominant birds make more intense use of food resources during winter and thereby obtain and maintain better body condition than subordinates (Carrascal *et al.* 1998).

The relative short-wavelength reflectance of the other plumage patches also contributed to the overall effect of body condition on plumage coloration. The result obtained for the black crown has been previously reported by Hegyi *et al.* (2007), who found that the relative contribution of short wavelengths to the entire reflectance spectra of the melanin-based crown patch was positively related to an index of body condition during moult (i.e. end of summer; Jenni & Winkler 1994). It is noticeable, however, that the colour of another melanin-based trait (i.e. the black breast) greatly contributed to the condition-dependence observed in the plumage of male Great Tits, because the size of this trait is positively related to dominance and condition (Senar 2006 and references therein, Galván & Alonso-Alvarez 2008), but its colour characteristics have never previously been measured. The present study shows that short-wavelength reflectance may be important for the

signalling function of melanin-based traits even if total reflectance at those spectral regions is low.

Previous studies have also found that the body condition of Great Tits is associated with certain colour characteristics of the yellow breast patch, particularly with hue or chroma (a measure related to the carotenoid content of feathers; Senar & Quesada 2006, Hegyi *et al.* 2007, 2008, Dauwe & Eens 2008, Senar *et al.* 2008, but see Isaksson *et al.* 2008). This study confirms those results from an avian visual perception context. The mechanism leading to this condition-dependence might be related to a trade-off between using carotenoids for either antioxidants and immunological functions or for signalling tasks, as only high-quality individuals can use great amounts of these pigments for the latter function (Alonso-Alvarez *et al.* 2008).

The colour characteristics of the green back patch of male Great Tits, which is generated by a mixture of melanins and carotenoids (Figuerola & Senar 2005), also showed a tendency to be condition-dependent. As the use of melanins for the production of ornaments can also be limited to high-quality individuals because it requires a high antioxidant capacity (Galván & Alonso-Alvarez 2009), the green back patch of Great Tits may present higher production costs than other traits exclusively generated by melanins or carotenoids, such as the yellow or black breast plumage patches. Ideally, future studies will address the signalling potential of the green back patch and other plumage colours generated by mixtures of pigments.

In general, this study indicates that short-wavelength reflectance has the potential to signal condition not only with structural colours, but also with colour traits that are generated achromatically (i.e. white) or with pigments. Recent studies have reached the same conclusion (Hegyi *et al.* 2007, 2008, Penteriani *et al.* 2007, Galván *et al.* 2008), but the present study also indicates that the trait related to body condition can be actually perceived by birds. Dominance in winter is associated with breeding success in the subsequent season (Lambrechts & Dhondt 1986), indicating that displaying and assessing plumage characteristics that transfer information on body condition during winter, when getting access to food sources is especially important for survival (Orell 1989), is probably of great relevance for fitness.

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