

**INFORMATION CONTENT OF PLUMAGE
COLOURS
IN TWO TIT SPECIES**

Abstract of the thesis

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1. INTRODUCTION AND OBJECTIVES

Sexual dimorphism and individual variation found in many animal species may be the result of sexual selection. During this process, competition is going on for mates. If mate choice is influenced by the expression of the chosen individual's secondary sexual ornaments, that is, preference is operating, the choosing individual may receive direct or indirect benefits. Direct benefits include the avoidance of parasites, an increased contribution to nestling care or increased fertility of the mate. Indirect benefits may arise from "good genes" that increase the fitness of offspring.

In iteroparous species, the differential allocation hypothesis posits that if the actual mate of an individual is attractive, i.e. it may provide benefits, it is worthy to the individual to invest more in current reproduction than if its mate was unattractive. This hypothesis can readily be tested in birds focusing on decisions taken both before egg laying, as clutch size, egg size or the amount of bioactive egg components, and after laying, as the intensity of feeding the young. Because in blue tits (*Cyanistes caeruleus*), several sexually selected traits are already known, we investigated (1) whether differential allocation in egg size and yolk carotenoids occur in this species. Studied traits included plumage colours since the production of plumage colours of different origin - melanin based, carotenoid based and structural colours - has been shown to be costly to birds, therefore, these may provide honest information on the individual quality of their bearers to the choosing individuals.

In the closely related great tit (*Parus major*), it has not been known whether the crown colour – a sexually selected trait in blue tits – is a signal during mate choice. Since birds, unlike humans, can see light in the near ultraviolet (UV) range, and the crown colour of blue tits show the greatest variation in this range, we investigated (2) whether sexual dimorphism occurs in great tits too in their crown and breast colour as well as in the size of their black breast stripe. Because the honesty of signals may be ensured by the costs of their production, we examined whether these traits are condition-dependent signals. Finally, we were interested in the presence of assortative mating based on these traits which would indicate mutual sexual selection.

In general, mate choice is based on more than one trait. According to the "multiple message hypothesis", every signal provides information on a different aspect of the quality of its bearer to the choosing individual. The "redundant message hypothesis", however, posits that every signal provides information on the same aspect of individual quality.

As some parameters of the crown and breast colour of great tits proved to be condition-dependent and under sexual selection, we investigated (3) whether these signals show

correlated variation. If so, this would give support to the redundant message hypothesis. Since the plumage of great tits is grown during the annual autumn moult but mate choice takes place only after some feather abrasion, i.e. in spring, we also questioned whether the correlated variation between the colour of the two plumage regions persists from autumn to spring. And in addition, whether the common colour axes arising from this correlation are also condition-dependent. Finally: is there an assortative mating based on these common colour axes?

2. METHODS

All three studies were performed on the nestbox-plot in Pilis mountains, from 2003 to 2006. For the study of differential allocation (*1*), we collected the firstly laid three eggs from blue tit nests, measured their size, and calculated egg volume. Digital photographs were taken of egg yolks, then yolk hue was computed with Photoshop for assessment of yolk carotenoid concentration. Parent birds were captured during chick feeding. Age, tarsus length and body mass were recorded, then feathers were plucked from standard points on the crown and the breast. We obtained reflectance spectra of feathers in the laboratory with an USB-spectrometer between 320 and 700 nm, from which the following colour variables were calculated: average reflectance, UV contrast and UV chroma of the crown; and yellow chroma of the breast.

For the study of plumage signals of great tits (*2,3*), birds were captured after moult in autumn, and during chick feeding in spring. Then, after recording their age and morphometrics, we fixed them in a box designed for this purpose, and took digital photographs from their ventral side. Finally, we plucked feathers from standard points in the crown and the breast. Photographs were further used to calculate the area of the breast stripe; and feathers were measured with the spectrometer used in blue tits for obtaining reflectance spectra. In autumn, we also collected two defined tail feathers from every individual in order to calculate feather growth rate from the width of growth bars (ptilochronology). This was used to estimate body condition during moult for the investigation of the condition dependence of signals.

From reflectance spectra of crown and breast feathers, principal components of coloration were calculated using principal component analysis (PCA). The advantage of this method comes from the condensation of the information contained in spectra into several principal components (the axes). In addition, it can be used to quantify the differences in spectral shape measured from diverse colours which is not always possible with traditional colour variables. Also, the principal components maximize the proportion of variation

explained. To examine the information content of the two plumage regions (2), we performed separate PCAs for yellow and black feathers and for autumn and spring samples but we included males and females in the same analysis. However, when investigating the common information contained in the two plumage regions (3), we entered spectra of both types of feathers in the same analysis. We used GLM as statistical method.

3. RESULTS

In blue tits (1), yolk hue showed a significant relationship with male plumage colour (crown UV contrast), clutch initiation date and yolk mass. These results indicate that eggs richer in carotenoids were laid by females mated to males with more chromatic blue/UV plumage and which started laying later in the breeding season, and that larger yolks had a higher carotenoid concentration. We could rule out the possibility that the relationship with male plumage colour was due to an underlying correlation between male colour and female phenotype.

Egg size showed a positive relationship with female crown brightness but in contrast to our expectations, neither morphological traits, nor breast colour of females were connected to investment in egg quality.

As expected, breast stripe of great tits was larger for males than females (2), and for old birds compared to first-years. However, no relationship with feather growth rate could be detected. As for plumage colours, both yellow and black PC1 reflected brightness, and PC2 showed yellow chroma and UV chroma, respectively. Factor loadings of autumn and spring PCs were highly correlated, indicating that feather abrasion did not affect our results. Yellow PC1 was related to tarsus length and yellow PC2 with body mass but neither was influenced by feather growth rate. PC1 and PC2 of the black crown, however, were strongly related to feather growth rate. In addition, black PC2 showed a marked sex-dependence and assortative mating was positive with respect to spring values.

Common PCs calculated from breast and crown spectra of great tits (3) reflected variance in brightness and differed strongly in spring and autumn. This means that the direction of variation in reflectance of the two plumage regions differed between seasons. Therefore, we did not analyse condition-dependence and mating patterns for these raw PCs. Instead, we conducted new PCAs using brightness-standardized spectral data. The two PCs obtained this way were consistent between the two seasons. In both seasons, common PC1 reflected the proportion of long and short wavelength reflectance both for the black crown and the yellow breast. However, the contribution of crown reflectance to this PC increased greatly

from autumn to spring. Common PC2 was highly correlated with UV chroma of the black crown and with yellow chroma of the yellow breast. In contrary to common PC1, common PC2 was dependent on sex and feather growth rate. Assortative mating was not found based on common PC1, but was significantly positive for common PC2.

4. DISCUSSION AND CONSLUSIONS

Since yolk colour reflects carotenoid concentration, our results indicate that blue tit females invest carotenoids in eggs depending on the attractiveness of their mate (**1**) which corroborates the differential allocation hypothesis. Although this is a correlative finding, we could rule out alternative explanations. Thus, to my knowledge, it is the first demonstration of differential allocation into eggs in free-living birds. We could show no relationship between yolk colour and breast yellowness of the parents. The lack of differential allocation based on this trait is not surprising given that in the closely related great tit, neither this work (**2**), nor other studies have found sexual dimorphism or condition-dependence in breast yellowness, therefore, breast colour is not likely to be a sexually selected trait.

Egg size of blue tits was only predicted by female crown brightness: females with a brighter crown laid larger eggs. In addition, these birds started laying earlier in the season which indicates that crown brightness may signal individual quality in females too.

Our study on great tits (**2**) showed that the small reflectance of black crown feathers in the UV range contains information on sex and individual quality, and may be used in the context of mutual mate choice. These data, combined with previous findings, suggest that more attention should be paid to the spectral attributes of dark plumage areas. Black crown PC1 of great tits reflected achromatic brightness, and we found that birds in better condition grew darker crown feathers. This result is in line with previous findings on other species with black plumage areas. Black crown PC2 corresponded to UV chroma. Increased UV reflectance was also related to increased body condition during moult. Since this colour attribute depends on the amount of keratin deposited in the spongy layer of feather barbs, it may convey information about nutrition during moult. We also found an assortative mating pattern with respect to crown PC2 which may indicate that this trait could be used by both sexes during mate choice.

Neither the size of the breast stripe, nor the colour of the yellow area surrounding it were related to body condition during moult but they reflected age and body size, respectively. In other study populations, equivocal results were found about the condition-dependence of breast stripe size and breast coloration which, together with our results, may indicate

population differences in the information content of plumage ornaments. In the context of the reliability of plumage coloration of different types, our results support the pattern that carotenoid-based colours are not consistently better signals of body condition than melanin-based colours, and that structural colours are particularly reliable indicators of individual quality.

In reference to sexual selection acting on multiple signals (3), these findings corroborate the multiple message hypothesis, i.e. great tits in this population may choose a mate by assessing several plumage signals of different information content during mutual mate choice. However, signals also contain shared axes of information which may convey information more reliably or more efficiently than independent signals, as by using common PCA, we found significant and seasonally consistent correlated variation in yellow breast and black crown spectra. Several mechanisms may cause correlation between the expression of ornaments with different metabolic background, i.e. carotenoid- and melanin-based colours. First, feather microstructure should be similar in the whole plumage of an individual. Second, metabolic and physiological constraints act on the deposition in feathers of both melanins and carotenoids, e.g. both pigment types have antioxidant functions. Finally, their expression may also correlate if both colour types are condition-dependent and reflect the common phenotypic and genetic basis of body condition.

We show that overall plumage colour PC2 was significantly related to body condition during moult, irrespectively of sex and age. This means that great tits in better condition simultaneously developed higher UV chroma on the crown and more intense yellow colour on the breast than those in worse condition. Furthermore, this colour PC correlated positively between social mates which may indicate mutual sexual selection with respect to overall coloration but an experimental approach is needed to establish the exact causal mechanism. To conclude, we cannot rule out that sexual selection based on visual cues acts on the combination of correlated signals which supports the redundant signal hypothesis.

5. PAPERS INCLUDED IN THE THESIS

- (1) **Szigeti B**, Török J, Hegyi G, Rosivall B, Hargitai R, Szöllösi E, and Michl G, 2007. Egg quality and parental ornamentation in the blue tit *Parus caeruleus*. *J Avian Biol* 38: 105-112.
- (2) Hegyi G, **Szigeti B**, Török J, and Eens M, 2007. Melanin, carotenoid and structural plumage ornaments: information content and role in great tits *Parus major*. *J Avian Biol* 38: 698-708.

(3) Hegyi G, **Szigeti B**, Laczi M, Eens M, and Török J, 2008. Correlated variation of colour between melanin and carotenoid pigmented plumage areas in great tits. *Evol Ecol Res* 10: 559-574.

6. OTHER PUBLICATIONS

Hargitai R, Török J, Tóth L, Hegyi G, Rosivall B, **Szigeti B**, and Szöllősi E, 2005. Effects of environmental conditions and parental quality on the inter- and intraclutch egg size variation in the collared flycatcher (*Ficedula albicollis*). *Auk* 122: 509-522.

Herényi M, Török J, Garamszegi LZ, Hargitai R, Hegyi G, Michl G, Rosivall B, **Szigeti B**, and Szöllősi E, 2004. Másodlagos nemi jellegek és utódszám kapcsolata a hím örvös légykapóknál. *Állattani Közlemények* 89: 31-41.

Laczi M, Cserepes TM, Hegyi G, Michl G, **Szigeti B**, and Török J, 2006. A tollazat UV-reflektanciája és a táplálkozás kapcsolata vízimadaraknál. *Állattani Közlemények* 91: 117-126.