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Plumage coloration and nutritional condition in the great tit *Parus major*: the roles of carotenoids and melanins differ

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Abstract The size and coloration of some body characters seem to influence mate choice in many species. Most animal colours are either structural or based on melanin or carotenoid pigments. It has recently been suggested that carotenoid-based or structural coloration may be a condition-dependent trait, whereas melanin-based coloration is not; a difference that may be highly relevant when studying the evolution of multiple mating preferences. We tested this hypothesis in the great tit (*Parus major*). The size of the melanin breast band was not correlated to nutritional condition as estimated by the rate of tail growth (ptilochronology), controlling for locality, age, sex, year and season effects. However, the correlation was significant for the hue of yellow breast (carotenoid-based coloration), and the slopes of the regressions of the two pigments to growth bars differed significantly. These results suggest that the expression of the two traits may be regulated by different mechanisms.

Introduction

Most plumage coloration results either from structural feather properties (e.g. white, blue or UV) or from pigment molecules, mainly carotenoids and melanins, embedded in the feathers (e.g. red, yellow or black, Brush 1978). A current debate on the evolution of mate choice through plumage coloration centres on whether different shades of colour convey different kinds of information (Gray 1996; Badyaev and Hill 2000). Since birds cannot

synthesize carotenoids they must be ingested (Fox 1976), and since they play an important role as precursors of vitamins (Olson and Owens 1998) and in the neutralisation of potentially harmful secondary metabolites (Von Schantz et al. 1999), it is widely recognised that carotenoid-based plumage coloration may confer information on the nutritional, parasitic and general body condition of the bearer (Hill 1999; Møller et al. 2000). Structural plumage coloration has also been shown to be condition-dependent (Gustafsson et al. 1995; Qvarnström 1998) and to be related to nutritional and parasitic condition (Potti and Merino 1996; Keyser and Hill 1999, 2000).

Data from melanin-based plumage coloration, however, is more controversial, since different studies on different species either support (Møller et al. 1996; Veiga and Puerta 1996; González et al. 1999; Poiani et al. 2000; Fiske and Richner 2002) or reject (Hill and Brawnner 1998; Figuerola et al. 1999a; McGraw and Hill 2000; Hill 2000; Senar and Escobar 2002) the view that melanin coloration signals body condition. Further support for the lack of condition dependence comes from the fact that melanin pigments may be synthesised from several common dietary components (Fox 1976) and that no physiological link of melanin to general body condition has yet been described (Hillgarth and Wingfield 1997; Olson and Owens 1998).

The aim of this paper was to explore the potential value of melanin-based coloration as an indicator of nutritional condition by analysing the relationship between the size of the great tit's (*Parus major*) central black breast-stripe and the rate of tail feather growth (ptilochronology). Previous studies have shown that the central black breast-stripe of the great tit is related to the quality of male parental care (Norris 1990a, 1993) and to female investment in reproduction (Norris 1990b). We used ptilochronology as a measure of nutritional condition because of its straightforward interpretation and its previously proven usefulness (Grubb 1995), but most importantly because it has already been found to be related both to carotenoid-based (Hill and Montgomerie

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1994) and structural (Keyser and Hill 1999) colorations; this would thus allow, for the first time, a comparison of the three kinds of coloration within the same frame of reference.

Materials and methods

Great tits were captured in baited funnel traps from 1997 to 2000, in two contrasted areas near Barcelona, north-eastern Spain, situated approximately 10 km apart but with no exchange of birds. Age was determined according to the method of Jenni and Winkler (1994).

The size of the melanin-based black breast band was measured on digital photographs ($n=144$) with Image Tool software (for more technical details see Figuerola and Senar 2000). Measurement repeatability (measured as intra-class correlation) was $r_1=0.98$, $P<0.001$, $n=12$ (see Figuerola and Senar 2000). General yellowish plumage coloration on the breast was measured with a Minolta CR200 colorimeter (Minolta Corporation 1994) using a standard D65 light flash ($n=221$, see Figuerola et al. 1999b). Colour was characterised according to the tri-stimulus variables of hue, chroma and lightness. The repeatability of the three colour variables was high (lightness, $r_1=0.85$, $P<0.001$; chroma, $r_1=0.87$, $P<0.001$; hue, $r_1=0.92$, $P<0.001$; $n=12$; Figuerola et al. 1999b). Two data point outliers were discarded from analyses because of a very low value of hue ($<75^\circ$) which was probably due to an error in measurement, although the results still hold if they are retained. We did not measure the extent of yellow coloration in the breast because the whole area is generally covered in yellow, rendering this measurement impractical.

We used tail ptilochronology to estimate the conditions of food availability and nutritional condition experienced by birds during feather growth (Grubb 1995). The second pair of rectrices was plucked for further measurement in the laboratory, where the same observer measured the width of the first ten measurable distal growth bars to the nearest 0.1 mm (see Carrascal et al. 1998). This value was transformed by dividing by ten to obtained daily growth rate (mm/day) and averaging the values for the left and right rectrices. Measurement repeatability was $r_1=0.99$, $P<0.001$, $n=15$. We measured the first ten measurable growth bars rather than following the standard technique (Grubb 1989) because the length of the great tit feather very often would not allow for measuring ten bands. Since great tits only moult in the autumn (Jenni and Winkler 1994), rectrices and contour feathers were moulted during the same period. Since yellow and black breast feathers belong to the same feather tract, they are moulted within the same time period (Gosler 1993).

Results

Breast band size was not correlated to the tri-stimulus variables of yellow breast coloration (lightness, $r=0.07$, $P=0.43$; chroma, $r=0.07$, $P<0.45$; hue, $r=0.002$, $P<0.98$; $n=144$; standardising by age, sex and locality).

Width of tail growth bars was positively correlated with hue of the yellow coloration of the breast (Table 1, Fig. 1). However, width of growth bars was not correlated with the melanin-based breast band size (Table 1, age, sex, locality, year and months from moult controlled in a MANCOVA with the three colour variables and breast band size as dependent variables and width of the growth bars and months since moult entered as covariates).

The two regressions of growth bars to either hue of the yellow breast and size of the black breast band significantly differed in slopes (parallelism test, $F_{1,352}=4.42$,

Table 1 MANCOVA analysing the relationships of tail feather growth rate as measured from ptilochronology (i.e. nutritional condition) to lightness, intensity and hue of the carotenoid-derived yellow coloration of the breast and size of the melanin-derived black breast band of great tits, controlling for the effects of age, sex, locality, year and months since moult. Multivariate tests: overall regression Wilks' $\lambda=0.84$, $P=0.01$; fixed effects: age Wilks' $\lambda=0.78$, $P<0.001$, sex Wilks' $\lambda=0.35$, $P<0.001$, locality Wilks' $\lambda=0.85$, $P=0.01$, year Wilks' $\lambda=0.36$, $P<0.001$. Slopes are standardized to mean = 0 and SD=1

| | Slope (beta) | t_{115} | P |
|---------------------------|--------------|-----------|--------|
| <i>Ptilochronology</i> | | | |
| Yellow lightness | -0.12 | 1.25 | 0.21 |
| Yellow intensity | 0.00 | 0.02 | 0.98 |
| Yellow hue | 0.20 | 2.22 | 0.03 |
| Black breast band size | 0.05 | 0.51 | 0.61 |
| <i>Months since moult</i> | | | |
| Yellow lightness | -0.16 | 1.70 | 0.09 |
| Yellow intensity | -0.22 | 2.42 | 0.02 |
| Yellow hue | -0.18 | 1.99 | 0.05 |
| Black breast band size | -0.13 | 1.36 | 0.18 |
| Fixed effects | | | |
| <i>Age</i> | | | |
| Yellow lightness | | 0.67 | 0.41 |
| Yellow intensity | | 14.14 | <0.001 |
| Yellow hue | | 15.37 | <0.001 |
| Black breast band size | | 8.23 | <0.01 |
| <i>Sex</i> | | | |
| Yellow lightness | | 12.44 | <0.001 |
| Yellow intensity | | 0.64 | 0.42 |
| Yellow hue | | 0.25 | 0.62 |
| Black breast band size | | 207.54 | <0.001 |
| <i>Locality</i> | | | |
| Yellow lightness | | 0.11 | 0.74 |
| Yellow intensity | | 7.35 | <0.01 |
| Yellow hue | | 12.18 | <0.001 |
| Black breast band size | | 0.11 | 0.74 |
| <i>Year</i> | | | |
| Yellow lightness | | 3.25 | 0.02 |
| Yellow intensity | | 3.18 | 0.03 |
| Yellow hue | | 25.28 | <0.001 |
| Black breast band size | | 12.96 | <0.001 |

$P=0.04$, controlling for age, sex and locality, including the whole data set). This shows that melanin-based coloration is less important than carotenoid-based coloration in relation to growth.

Discussion

Condition dependence is critical to the understanding of ornament evolution (Pomiankowski 1987). Ptilochronology (Grubb 1995) is a robust approach to testing the condition-signalling role of plumage, since it directly links foraging success to the expression of plumage coloration (Hill and Montgomerie 1994). Here we have shown that the width of the great tit melanin-based breast stripe was not related to feather growth rates. However, yellow carotenoid coloration (hue) of the breast was

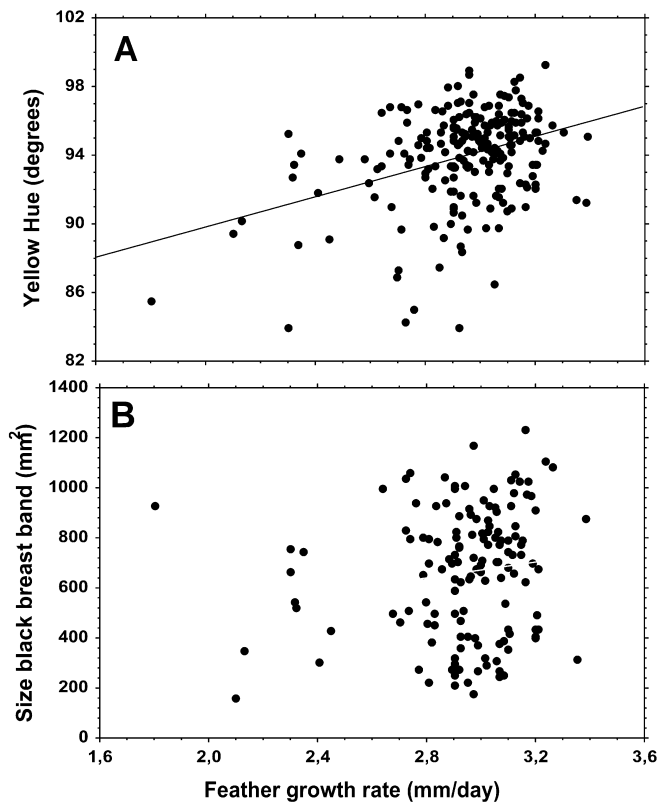


Fig. 1 Relationship between tail feather growth rate, as measured from width of growth bars (ptilochronology) and **A** hue of the yellow carotenoid-based coloration of the breast as obtained from colorimetry, and **B** size of the melanin-based breast band of the great tit, as obtained from digital photography

significantly related to feather growth rates. The discrepancy between our results and those of Eeva et al. (1998) is probably related to the greater repeatability and precision of our colour measurements, where the slopes of the two regressions (carotenoid and melanin) differed significantly. This supports the hypothesis that melanin-based coloration is not a good candidate for signalling nutritional condition, and that melanin- and carotenoid-based colorations might serve fundamentally different functions (Gray 1996; Badyaev and Hill 2000).

The main source of carotenes for tits are caterpillars (Slagsvold and Lifjeld 1985). Once ingested, carotenes are deposited unmodified in the feathers of tits (Partali et al. 1987). A brightly carotene-coloured great tit may therefore be directly signalling its ability to find caterpillars, a main food source for both adults and fledglings (Gosler 1993). Our data relating width of tail growth bars to yellow hue supports this higher foraging efficiency of more brightly coloured tits. Hence, it would be of direct female benefit to pair with a very yellow great tit male (see Senar et al. 2002). The study of tits could therefore neatly solve the missing link in other bird studies in relation to the question of why finding carotenes may be difficult but nevertheless highly advantageous in order to acquire a mate.

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References

- Badyaev AV, Hill GE (2000) Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biol J Linn Soc* 69:153–172
- Brush AH (1978) Avian pigmentation. In: Brush AH (ed) *Chemical zoology*, vol. X: Aves. Academic Press, New York, pp 141–161
- Carrascal LM, Senar JC, Mozetich I, Uribe F, Domènech J (1998) Interactions among environmental stress, body condition, nutritional status, and dominance in great tits. *Auk* 115:727–738
- Eeva T, Lehikoinen E, Rönkä M (1998) Air pollution fades the plumage of the great tit. *Funct Ecol* 12:607–612
- Figuerola J, Senar JC (2000) Measurement of plumage badges: an evaluation of methods used in the great tit *Parus major*. *Ibis* 142:482–484
- Figuerola J, Muñoz E, Gutiérrez R, Ferrer D (1999a) Blood parasites, leucocytes and plumage brightness in the circl bunting *Emberiza circlus*. *Funct Ecol* 13:594–601
- Figuerola J, Pascual J, Senar JC (1999b) The use of a colorimeter in field studies of blue tit *Parus caeruleus* coloration. *Ardea* 87:269–275
- Fiske PS, Richner H (2002) Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behav Ecol* 13:401–407
- Fox DL (1976) *Animal biochromes and structural colours*. University of California Press, Berkeley, Calif.
- González G, Sorci G, Lope F (1999) Seasonal variation in the relationship between cellular immune response and badge size in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 46:117–122
- Gosler AG (1993) *The great tit*. Hamlyn, London
- Gray DA (1996) Carotenoids and sexual dichromatism in North American passerine birds. *Am Nat* 148:453–480
- Grubb TC (1989) Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106:314–320
- Grubb TC (1995) Ptilochronology: a review and prospectus. *Curr Ornithol* 12:89–114
- Gustafsson L, Qvarnström A, Sheldon BC (1995) Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature* 375:311–313
- Hill GE (1999) Mate choice, male quality, and carotenoid-based plumage coloration. In: Adams N, Slotow R (eds) *Proceedings of the 22nd international ornithological congress*, Durban. BirdLife South Africa, Johannesburg, pp 1654–1668
- Hill GE (2000) Energetic constraints on expression of carotenoid-based plumage coloration. *J Avian Biol* 31:559–566
- Hill GE, Brawnner WR (1998) Melanin-based plumage coloration in the house finch is unaffected by coccidial infection. *Proc R Soc Lond B* 265:1105–1109
- Hill GE, Montgomerie R (1994) Plumage colour signals nutritional condition in the house finch. *Proc R Soc Lond B* 258:47–52
- Hillgarth N, Wingfield JC (1997) Parasite-mediated sexual selection: endocrine aspects. In: Clayton DH, Moore J (eds) *Host-parasite evolution: general principles and avian models*. Oxford University Press, Oxford, pp 78–103
- Jenni L, Winkler R (1994) *Moult and ageing of European passerines*. Academic Press, London
- Keyser AJ, Hill GE (1999) Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc R Soc Lond B* 266:771–777
- Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav Ecol* 10:202–209

- McGraw KJ, Hill GE (2000) Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proc R Soc Lond B* 267:1525–1531
- Minolta Corporation (1994) Precise color communication: color control from feeling to instrumentation. Minolta Corporation, Osaka, Japan
- Møller AP, Kimball RT, Erritzoe J (1996) Sexual ornamentation, condition, and immune defence in the house sparrow *Passer domesticus*. *Behav Ecol Sociobiol* 39:317–322
- Møller AP, Biard C, Blount JD, Houston DC, Ninni P, Saino N, Surai PF (2000) Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? *Avian Poult Biol Rev* 11:137–159
- Norris KJ (1990a) Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. *Behav Ecol Sociobiol* 26:129–138
- Norris KJ (1990b) Female choice and the quality of parental care in the great tit *Parus major*. *Behav Ecol Sociobiol* 27:275–281
- Norris KJ (1993) Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* 362:537–539
- Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol* 13:510–514
- Partali V, Liaaen-Jensen S, Slagsvold T, Lifjeld JT (1987) Carotenoids in food chain studies. II. The food chain of *Parus* spp. monitored by carotenoid analysis. *Comp Biochem Physiol* 87B:885–888
- Poiani A, Goldsmith AR, Evans MR (2000) Ectoparasites of house sparrows (*Passer domesticus*): an experimental test of the immunocompetence handicap hypothesis and a new model. *Behav Ecol Sociobiol* 47:230–242
- Pomiankowski A (1987) Sexual selection: the handicap principle does work – sometimes. *Proc R Soc Lond B* 231:123–145
- Potti J, Merino S (1996) Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proc R Soc Lond B* 263:1199–1204
- Qvarnström A (1998) Sexual selection in the collared flycatcher (*Ficedula albicollis*): a life-history perspective. PhD thesis, Uppsala University, Sweden
- Senar JC, Escobar D (2002) Carotenoid-derived plumage coloration in the siskin *Carduelis spinus* is related to foraging ability. *Avian Sci* 2:19–24
- Senar JC, Figuerola J, Pascual J (2002) Brighter yellow blue tits make better parents. *Proc R Soc Lond B* 269:257–261
- Slagsvold T, Lifjeld JT (1985) Variation in plumage colour of the great tit *Parus major* in relation to habitat, season and food. *J Zool* 206:321–328
- Veiga JP, Puerta M (1996) Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proc R Soc Lond B* 263:229–234
- Von Schantz T, Bensch S, Grahn M, Hasselquist D, Wittzell H (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proc R Soc Lond B* 266:1–12