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Seasonal changes in carotenoid- and melanin-based plumage coloration in the Great Tit *Parus major*

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Plumage coloration plays an important role as a signal of individual quality. We studied plumage coloration in two Great Tit *Parus major* populations to test the hypothesis that coloration changes during the year without moult. As expected, the coloration of 'yellow' and 'dark green' areas in the breast and back changed with time but not the colour characteristics of the 'black' crown. This suggests that colours based on carotenoids could be more exposed to abrasion or fading than melanin-derived colours, although other factors could affect the patterns of change found. Our results show that effects of colour alteration could be important to the understanding of the potential for reliable signalling of different colours. Seasonal changes in plumage colour should be considered in future analysis of intraspecific variation in coloration.

The diversity of colours and patterns in avian plumage results from two, often opposing, forces. Natural selection is thought to favour concealing coloration to mislead predators (Wallace 1889, Götmark 1999), whereas sexual selection favours the development and maintenance of plumage ornaments and bright colours that facilitate mating opportunities (Darwin 1859, 1871, reviewed in Andersson 1994, Zahavi & Zahavi 1997, Hill 1999, Espmark *et al*. 2000, Hill 2002).

Bird colours can be produced by the microstructure of the feather itself, or by pigments, mainly carotenoids and melanins (Fox 1976, Brush 1978). Carotenoids are responsible for bright red, orange and yellow colours, cannot be synthesized by birds and must be incorporated through the diet (Olson & Owens 1998). Melanin produces the black and earth tones of feathers, can be synthesized by birds from amino acid catabolism (Fox 1976, Jawor & Breitwisch 2003) and confers greater resistance to abrasion than do carotenoids (Burtt 1986, Bonser 1995). Feathers are subject to biochemical degradation by feather-eating bacteria (Clayton 1999, Burtt & Ichida 1999, Burtt 1999) and to mechanical abrasion (Averill 1923 (cited in Burtt 1986), Burtt 1986, Willoughby *et al*. 2002). We should therefore expect plumage coloration to change through the season with more easily abraded feathers changing more than less easily abraded feathers. Although feathers are only grown during the restricted period of moult, field ornithologists have been aware for a long time that plumage colour might, nevertheless, change seasonally (e.g. see Jenni & Winkler 1994). Some species appear adaptively to take advantage of abrasion to increase plumage brightness without any intervening moult (Newton 1972, Bogliani & Brangi 1990, Møller & Erritzøe 1992, Veiga 1996, Willoughby *et al*. 2002). However, most behavioural biologists studying plumage coloration assume in their analyses that colour remains constant through the season, and quantify coloration only once during the year (but see Sundberg 1994, Örnborg *et al*. 2002, McGraw & Hill 2004).

Taking advantage of improved methods and technology to study bird coloration, we analyse seasonal variation in plumage brightness in the Great Tit *Parus major*. We test the assumption that plumage coloration changes through the year, and that the amount of change is related to the characteristics of the pigments present in the feathers. Our results imply that researchers should not assume that plumage coloration is a fixed trait once the bird has moulted, but that it can change seasonally.

MATERIALS AND METHODS

Great Tits were trapped at approximately weekly intervals in baited funnel traps (Senar *et al*. 1997) in

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Table 1. Eigenvectors and variance explained by the first axis of a PCA of colour characteristics of the crown, back and breast of Great Tits. For the crown and breast, higher values for the first axis correspond to high coloration scores for lightness, saturation and hue. For the back, high scoring corresponds to colorations more saturated, higher hue but lower lightness.

	Crown	Back	Breast
Lightness	0.62727	−0.52804	0.45972
Saturation	0.41605	0.60578	0.63308
Hue	0.65835	0.59516	0.62279
Variance explained	61	70	62

Sarria, a suburban area of orchards and small forests in Barcelona, and at more irregular intervals in Can Catà (Cerdanyola), a mixed forest close to Barcelona with a composition ranging from pure evergreen oak at the bottom of the valleys to pure pine forest in the hills. Coloration in the visible human spectrum was measured with a Minolta CR200 colorimeter, on a three-variable scale of lightness, saturation and hue. Hue corresponds to the wavelength of the colour, and is expressed in degrees of a circle starting with red, continuing through yellow, green and blue and completing the circle again with red. Lightness corresponds to the physical light intensity on a scale from 0 (black) to 100 (white). Saturation (also called chroma or intensity) is positively correlated with colour monochromatism, to colour purity on a scale of 0 for white to 100 for pure colour (Minolta Company 1994). Measurements of colour were taken at the crown, breast, belly and back (repeatability 0.67–0.94, Figuerola *et al.* 1999). Measurements of the breast and belly were averaged prior to analyses because they correspond to the same plumage tract. A Principal Components Analysis (PCA) was performed with lightness, saturation and hue values separately for each body area, and the first component was used as an overall estimator of colour brightness (Table 1). The principal components were calculated using the correlation matrix because the variables analysed were measured in different units. The results obtained analysing factor scores did not differ significantly from those obtained when using each variable separately, but only results for principal components are presented in order to simplify the presentation and interpretation of the results.

In the Great Tit, the colour of the crown is derived from melanin, the yellow of the breast results from the deposition of carotenoids, mainly lutein and zeaxanthin (see Partali *et al.* 1987, Stradi 1998), and the green of the back is derived from both melanin and carotenoid (I.M. García and J.J. Negro unpubl. data).

To test the occurrence of seasonal changes in plumage coloration, we conducted repeated-measures ANOVAs comparing the coloration during the first and last recapture of an individual ($n = 40$ individuals in Sarria and 32 in Can Catà). Only birds captured at least twice in the same intermoult interval, and with at least 1 month between captures, were included in the analyses (days elapsed between first and second measurement: mean 95.0, se±6.0, range 33–279 days). The first axis of the PCA of crown colour characteristics was not distributed normally, so ANOVA was calculated using ranked data (see Conover & Iman 1981, Marden & Muyot 1995). The relationship between changes in colour scores and number of days elapsed between measurements was tested separately for each feather-tract using Spearman regression, because the number of days between measurements was not normally distributed.

Quantification of bird coloration has been fraught with methodological problems (Endler 1990). An important problem concerns the subjectivity of colour appreciation, and variation in perception, of different observers, and under different light conditions. Recently, this has been solved by the application of field colorimeters, which allow a quantitative approach to the study of colour (Hill 1998, Villafuerte & Negro 1998, Figuerola *et al.* 1999). A drawback of this approach is that bird perception extends into the ultraviolet range, undetectable to humans (Hunt *et al.* 1998, Andersson *et al.* 1998), and current colorimeters cannot measure in this range of the spectrum. However, given that we are interested in detecting changes in plumage coloration, we think that our approach, based on the use of colorimeters, is valid for the human-visible portion of the spectrum.

RESULTS

Differences in coloration between localities occurred for the breast ($F_{1,64} = 9.87$, $P = 0.003$, Table 2) and the back ($F_{1,64} = 8.64$, $P = 0.005$), with birds in the forest area (Can Catà) being more brightly coloured; no differences in crown coloration occurred between the study areas ($F_{1,64} = 0.07$, $P = 0.80$). A significant interaction between age and sex was detected for the breast ($F_{1,64} = 4.62$, $P = 0.04$), because age differences in breast coloration occurred in males ($F_{1,64} = 8.00$, $P = 0.006$) but not in females ($F_{1,64} = 0.50$, $P = 0.48$). In the same way, first-year individuals did not differ in breast colour according to sex ($F_{1,64} = 0.06$,

Table 2. Results of a repeated-measures ANOVA comparing the first axis of a PCA of colour characteristics during the first and last capture of each individual. Principal components for the crown were not distributed normally and analysis was performed on the ranked variable. Between-individual factors test for variation between sexes, ages and localities or their interactions. Within-individual factors test for variation with time between repeated measurements taken from the same individuals. Variation with time was significant for breast and back but not for crown, while the lack of any significant interaction with time suggests similar rates of change across sexes, ages and localities.

	Crown			Back			Breast		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
All between	0.66	7.64	0.70	2.54	7.64	0.02	4.75	7.64	0.0002
Intercept	2.34	1.64	< 0.001	0.46	1.64	0.50	0.06	1.64	0.80
Sex	1.16	1.64	0.29	0.003	1.64	0.96	3.57	1.64	0.06
Age	0.73	1.64	0.40	0.99	1.64	0.32	0.93	1.64	0.34
Sex * Age	0.18	1.64	0.68	0.73	1.64	0.40	4.62	1.64	0.04
Locality	0.07	1.64	0.80	8.64	1.64	0.005	9.87	1.64	0.003
Sex * Locality	2.31	1.64	0.13	1.07	1.64	0.31	0.42	1.64	0.52
Age * Locality	0.06	1.64	0.80	0.72	1.64	0.40	2.40	1.64	0.13
Sex * Age * Locality	2.61	1.64	0.11	1.19	1.64	0.24	0.06	1.64	0.81
All Within	0.80	7.64	0.59	0.47	7.64	0.85	0.39	7.64	0.91
Time	0.08	1.64	0.78	4.45	1.64	0.04	9.34	1.64	0.003
Time * Sex	1.88	1.64	0.18	0.84	1.64	0.36	0.59	1.64	0.45
Time * Age	0.49	1.64	0.49	0.47	1.64	0.50	0.48	1.64	0.49
Time * Sex * Age	3.06	1.64	0.09	1.63	1.64	0.21	1.81	1.64	0.18
Time * Locality	0.11	1.64	0.74	0.18	1.64	0.67	0.10	1.64	0.75
Time * Sex * Locality	0.99	1.64	0.32	0.67	1.64	0.42	0.005	1.64	0.95
Time * Age * Locality	0.85	1.64	0.36	1.53	1.64	0.22	0.52	1.64	0.47
Time * Sex * Age * Loc	1.42	1.64	0.24	1.93	1.64	0.17	0.03	1.64	0.87

$P = 0.81$), but sexual differences in breast colour occurred in adult birds ($F_{1,64} = 5.75$, $P = 0.02$).

A significant effect of time was detected on breast ($F_{1,64} = 9.34$, $P = 0.003$) and back ($F_{1,64} = 4.45$, $P = 0.04$, Table 2) coloration, but no change was detected in crown coloration ($F_{1,64} = 0.08$, $P = 0.78$, Fig. 1). These changes in principal component scores with time indicate that breast coloration became less brightly yellow as the season advanced (reduction in light, saturation and hue), and back coloration became darker, less saturated and greenish. None of the interactions between time and sex, age and/or locality was significant (Table 2), suggesting that rates of change in back and breast coloration for males and females, and first-year and adult birds were similar in both study areas.

The amount of change in breast and back coloration was positively correlated with the number of days elapsed between the first and second captures of the birds (breast: $R_s = 0.35$, $P = 0.003$; back: $R_s = 0.34$, $P = 0.003$).

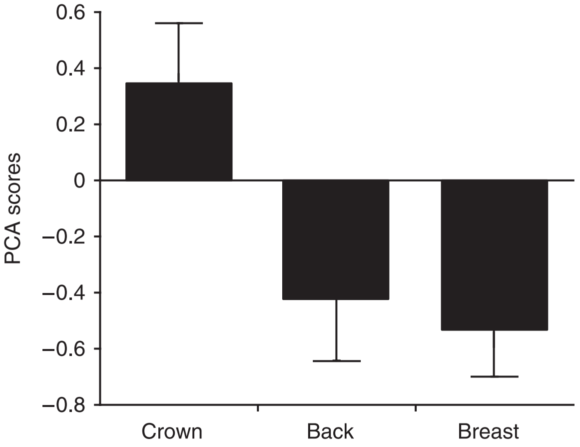

Figure 1. Mean change in principal component scores (± se) for the coloration in the different plumage tracts between the first and last capture within the same season. Seasonal changes are statistically significant for the back and breast coloration ($P < 0.05$).

DISCUSSION

Changes in coloration due to abrasion have typically been reported for finches, in which the grey tips of the feathers of some body regions disappear by wearing away at the start of the breeding season, thereby increasing the general brightness of the plumage (Newton 1972, Svensson 1984, Willoughby *et al.* 2002). This strategy has also been reported for the House Sparrow *Passer domesticus* (Bogliani & Brangi

1990, Møller & Erritzøe 1992, Veiga 1996). However, the seasonal change we describe in the Great Tit results in the fading of plumage coloration and a reduction in brightness with time. This has only been described very recently for the House Finch *Carpodacus mexicanus* (McGraw & Hill 2004; we exclude from here changes due to plumage soiling, e.g. Montgomerie *et al.* 2001). However, our results on changes in overall coloration are very robust because they have been analysed by a comparison of repeated measurements obtained from different individuals under completely standardized measuring conditions using detailed colorimetry. This design excludes possible biases such as differential mortality or emigration associated with bird coloration that could have affected the results if the analyses were not based on capture and recapture data.

Changes in Great Tit coloration were clearer in the carotenoid-pigmented area studied, a barely significant change was detected for the more melanin-derived back coloration and no change occurred in the crown, which is only pigmented by melanin. Although different areas of the body are exposed to different degrees of abrasion (Jenni & Winkler 1994), this cannot explain the differences in rates of change between breast, back and crown. Crown and back areas are more exposed to abrasion from airborne particles (Burtt 1986) and ultraviolet light than the breast, but nevertheless the breast showed the greatest change in coloration. Abrasion could also take place when birds enter cavities for nesting or roosting (see Cramp & Perrins 1993), but it is unclear why the breast would be more exposed to abrasion than the back. Furthermore, no differences in abrasion between back and crown areas are expected according to this hypothesis, contrary to our results. We therefore favour the view that different body regions differed in the extent of plumage coloration change because they were coloured with different pigments, as non-melanin-pigmented feathers have already been shown to differ from melanin-pigmented feathers in susceptibility to abrasion and change (Burtt 1986, 1999, Bonser 1995, Goldstein *et al.* 2004).

The reasons for differences in the exposure of melanin- and carotenoid-pigmented areas to seasonal changes in coloration could be diverse. First, melanin is more resistant to abrasion, enhancing plumage colour integrity (Burtt 1986); secondly, carotenoids may be subjected more easily to photobleaching and hence to plumage colour change (Mortensen & Skibsted 1999); thirdly, light colours could fade more easily than dark colours, irrespective of their chemical origin.

However, irrespective of the real origin of the differences, our results challenge the view that plumage could only signal the quality of the individual during the previous moult period, because the signal is modified after the moult. Consequently, factors affecting the degree of colour change will determine the conditions of plumage coloration during the mating season. Much work must be done to identify which factors are associated with colour change because, for example, individual differences in oil production by the uropygial gland, ectoparasite load (e.g. see Møller 1994), the abundance or distribution of feather-degrading micro-organisms (Burtt & Ichida 1999), habitat use or migratory patterns could be suitable candidates to affect the rate of colour change.

If the different rates of colour change are related to the type of pigment producing the colour, melanin-free areas could function as signal amplifiers of plumage quality in birds (Fitzpatrick 1998). Signal amplifiers increase the perceptibility of quality (Hasson 1991), and clearly melanin-free areas will make abrasion more visible. Consequently, the quality of a feather will be more clearly evident for feathers lacking melanin.

In conclusion, our results are of importance for two reasons. First, changes in plumage coloration through the year could be an important factor in any study dealing with intraspecific variation in coloration, and we strongly encourage researchers to control for this seasonal factor in their analyses (see also McGraw & Hill 2004). Secondly, and more importantly, carotenoid-pigmented areas seem to be more susceptible to colour change, supporting the hypothesis that melanin and carotenoids may play different roles in the evolution of bird communication (see Hill & Brawner 1998, Badyaev & Hill 2000, McGraw & Hill 2000, Fitze & Richner 2002, Parker *et al.* 2003, Senar *et al.* 2003).

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