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Age-related differences in a carotenoid-based coloration trait are due to within-individual changes in Great Tits *Parus major*

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Adult birds usually display brighter plumage coloration than younger individuals. This difference may be either due to selection against less coloured yearlings or to an increase in coloration after their first complete moult. In this study, we examined age-related differences in carotenoid-based yellow ventral coloration of Great Tits *Parus major*. Cross-sectional analyses at the population level showed that older males are in general greener and more saturated in colour than yearling individuals. Longitudinal analyses using birds captured in subsequent seasons confirmed within-individual changes in coloration with age. Such increase in coloration might be the result of the development of better foraging skills with age- and hence, the individual ability to obtain enough carotenoid-rich sources at the time of moult-, or consequence of other factors indirectly associated with age. However, we cannot rule out the possibility that other factors (such as directional selection against less coloured individuals) operate additionally at the population level.

Key words: Great Tit, *Parus major*, carotenoid-based coloration, age-related differences in coloration, foraging experience

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In many passerine species, young birds display less elaborate plumage coloration than older individuals (Andersson 1994, Hill & McGraw 2006). These differences in ornamentation are often not categorical but more a matter of degree, with yearling birds displaying a similar but subdued version of the full adult plumage (Delhey & Kempenaers 2006). Previous studies show that age-related differences in coloration may be caused by within-individual increases in colour with age (e.g. Blue Tit *Cyanistes caeruleus*, Delhey & Kempenaers 2006), by colour biased survival against less coloured individuals, or by a combination of both (e.g. Tree Swallow *Tachycineta bicolor*, Bitton & Dawson 2008). To date, these alternative hypotheses have been only tested on species with iridescent and not-iridescent structural plumage, but similar studies on species with carotenoid-based coloration have not been developed so far.

In this paper, we describe age-related colour changes in ventral plumage of Great Tits *Parus major*, a small hole-nesting passerine (~19 g) widely distributed throughout the Palearctic region (Gosler 1993). The species displays a conspicuous carotenoid-based yellow ventral plumage, which has been shown to function as indicator of nutritional condition (Senar *et al.* 2003, Tschirren et al. 2003, Ferns & Hinsley 2008, Senar *et al.* 2008), foraging and parental ability (Isaksson *et al.* 2006, Senar *et al.* 2008), resistance to endoparasites (Dufva & Allander 1995, Hõrak *et al.* 2001) and survival (Hõrak *et al.* 2001). Yellow ventral colour in this species results from deposition of dietary lutein and zeaxanthin during feather development, apparently without any conversion of the molecules (Partali *et al.* 1987, Stradi 1998). Coloration has been shown to differ between sexes with males accumulating more carotenoids than females, and age-classes with adults being greener than first year birds (Cramp & Perrins 1993).

Similarly to previous works on structural coloration, our goal was to determine whether or not yellow ventral ornamentation changed with age in our Great Tit population and to discuss the underlying reasons for such variation. We performed both cross-sectional and longitudinal analyses on a large data set collected over nine years. As stated in other studies of age-specific relationships in wild populations, the combination of these two analyses avoids misleading 'age-effects' by confounding within-individual changes with age and changes in the composition of the population through time due to differential survival of more ornamented individuals (Desrochers 1992, Delhey & Kempenaers 2006, Bitton & Dawson 2008).

METHODS

Data collection

Great Tits were studied between 1997 and 2006 in a mixed forest close to Barcelona city (41°28'N, 2°09'E), Northeast Spain. The area (circa 80 ha) consists mainly of pure Oak (*Quercus ilex* and *Quercus cerrioides*) at the bottom of the valleys and pure Aleppo Pine *Pinus halepensis* on the hills, with mixed forest on the slopes covered by a dense understorey.

Birds were captured using special funnel traps baited with husked peanuts (Senar *et al.* 1997) and individually marked with numbered aluminium rings. Sex and age of birds were determined according to Svensson (1992) and Jenni & Winkler (1994). Yearlings with Euring codes 3 and 5 and adults with Euring codes 4 and 6 were included in the cross-sectional analysis (BTO 2006). The sample size for the longitudinal analysis comprised only yearling individuals recaptured as adults (Euring code 7) in the subsequent season. Breast coloration was measured using a Minolta CR200 portable colorimeter, which measured colour in standard conditions (Figuerola *et al.* 1999) and provided independent values of brightness, chroma and hue from the visible range (400–700 nm). Brightness (also called lightness) corresponds to physical light intensity on a scale from 0 for black to 100 for white. Chroma (also called saturation or intensity) corresponds to the colour purity on a scale from 0 for white to 100 for pure colour. Hue corresponds to the major wavelength of light in a colour spectrum, and is expressed in degrees of a circle starting with red, continuing through yellow, green and blue, and completing the circle again with red.

The yellow breast plumage of Great Tits presents a peak in the UV part of the spectrum (300–400 nm) (MacDougall & Montgomerie 2003, Quesada & Senar 2006). Although our colorimeter provided colour measurements within the visible range, this limitation is not problematic for our study since the reflectance of the UV peak is highly correlated with the peak of the yellow-red spectrum (Andersson & Prager 2006, Senar & Quesada 2006).

Statistical methods

For the cross-sectional analyses we used a sample of 1029 individuals. Three independent factorial ANCOVAs were performed, with the different colour descriptors (lightness, chroma and hue) as dependent variables. Age, sex and year were included as factors in the analyses due to the aforementioned sex-related differences and the significant between-year variation found in Great Tits yellow ventral coloration (Slagsvold & Lijfeld 1985, Hõrak *et al.* 2000). Further, we checked for interactions between age and year, age and sex, sex and year and all these three factors. The number of days from 1 September (end of moult) was introduced as covariable in order to standardize for seasonal effects on plumage coloration (Figuerola & Senar 2005).

For the longitudinal analyses we used 177 birds of which yellow ventral coloration had been measured both at yearling and adult age in consecutive years. In order to control for year and seasonal effects, colour data were first standardized by conducting GLM Factorial-ANOVAs, with year of moult and days from 1 September as independent variables. The residuals were calculated and summed to the average values of the whole population, obtaining standardized colour values for each individual. We then performed three independent repeated-measures ANOVAs with the standardized colour variables in year_x (yearling) and year_{x+1} (adult) measured in the same individual as within-subject factors, and sex as between-subjects factor. All statistical analyses were performed in Statistica 6.0 and data were considered significant at the 0.05 level.

RESULTS

Cross-sectional analysis

Great Tits showed a large variation in plumage colour characteristics. We found statistical significant differences in colour chroma and colour hue between yearling and adult birds (Table 1), with younger birds showing significantly lower chroma and hue values than older individuals (Table 2). Age, however, had no effect on colour lightness (Table 1). Sex had also a significant effect on yellow ventral coloration (Table 1). Males were significantly brighter and showed higher chroma and hue values than female Great Tits (Table 2).

Moulting year had important consequences for plumage-colour development in our population. Lightness, chroma and hue values were highly variable between years (Table 1). Moreover, the interactions among year and age revealed that the magnitude of the differences between age-classes in chroma and hue depended strongly on the year the data were collected (Fig. 1). Nevertheless, the interaction for hue did not remain significant after excluding 1998 from the analysis ($F_{8,893}$ = 1.49; P = 0.16).

Longitudinal analysis

Ventral coloration in Great Tits changed between consecutive years. Individual birds showed a significant increase in chroma after their second moult (first complete moult) as they aged from yearlings to adults (mean ± SE year$_x$ = 20.21 ± 0.35 vs. year$_{x+1}$ = 22.82 ± 0.36). Similar changes were observed in hue (year$_x$ = 93.26 ± 0.20 vs. year$_{x+1}$ = 95.45 ± 0.14). No age-related differences were found for plumage lightness (Table 3).

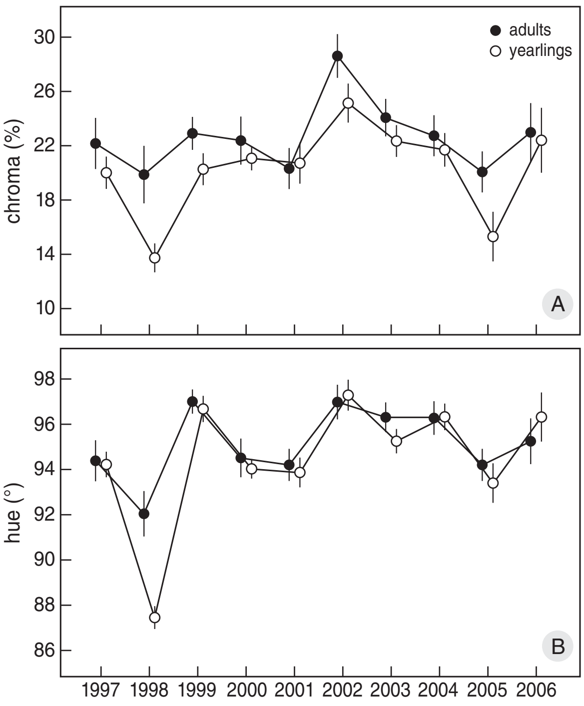

Figure 1. (A) Chroma and (B) hue of yellow breast coloration in adult and yearling Great Tits by year of moulting.

Table 1. Great Tit yellow breast coloration by age, year and sex. Presented are the results of factorial ANOVAs with days from 1 September as covariate (n = 1029). Significant results in bold.

	Lightness			Chroma			Hue		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Age	0.23	1,988	0.63	**43.76**	**1,988**	**< 0.001**	**13.67**	**1,988**	**< 0.001**
Sex	**156.88**	**1,988**	**< 0.001**	**105.92**	**1,988**	**< 0.001**	**96.84**	**1,988**	**< 0.001**
Year	**10.07**	**9,988**	**< 0.001**	**24.13**	**9,988**	**< 0.001**	**63.38**	**9,988**	**< 0.001**
Age × Year	1.17	9,988	0.31	**2.91**	**9,988**	**0.002**	**6.73**	**9,988**	**< 0.001**
Age × Sex	0.41	1,988	0.52	0.80	1,988	0.37	0.31	1,988	0.58
Sex × Year	0.80	9,988	0.61	1.30	9,988	0.24	0.44	9,988	0.92
Age × Sex × Year	0.85	9,988	0.57	0.90	9,988	0.53	0.74	9,988	0.68

Table 2. Ventral plumage characteristics by sex and age of Great Tits captured in a mixed forest close to Barcelona (1997–2006).

	Sex (mean ± SE)		Age (mean ± SE)	
	Females (n = 427)	Males (n = 602)	Yearlings (n = 614)	Adults (n = 415)
Lightness	59.02 ± 0.19	62.12 ± 0.16	60.51 ± 0.16	60.63 ± 0.19
Chroma	19.57 ± 0.27	23.26 ± 0.23	20.24 ± 0.23	22.59 ± 0.27
Hue	93.95 ± 0.13	95.62 ± 0.11	94.47 ± 0.11	95.10 ± 0.13

Table 3. Repeated-measures ANOVA showing changes in ventral coloration of individual Great Tits with age. Only birds captured as yearlings and recaptured as adults the following year were considered in the analysis (1997–2006; $n = 177$). Significant results in bold.

	Lightness			Chroma			Hue		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Age	1.08	1,175	0.30	**30.21**	**1,175**	**< 0.001**	**86.10**	**1,175**	**< 0.001**
Sex	**47.09**	**1,175**	**< 0.001**	**38.08**	**1,175**	**< 0.001**	**59.04**	**1,175**	**< 0.001**
Age × Sex	0.00	1,175	0.98	1.56	1,175	0.21	1.62	1,175	0.20

Sex again, had a significant effect on plumage coloration (Table 3). The non-significant interaction between sex and age suggests that the magnitude of age-related changes were similar between males and females (Table 3).

DISCUSSION

Cross-sectional analyses at the population level revealed that yellow underparts are less saturated and show lower hue values in yearling Great Tits than in older individuals. This pattern was also consistent in longitudinal analyses when comparing coloration of the same birds as they became older. Moreover, cross-sectional and longitudinal analyses confirmed that age-related changes in coloration occur in both sexes and are as large in females as in male Great Tits, suggesting that similar mechanisms may be responsible for age differences in both genders (Delhey & Kempenaers 2006).

Because birds cannot synthesize carotenoid pigments and must obtain them from food, it has been long suggested that carotenoid-based plumage coloration may serve as an honest signal of foraging ability and overall condition (Slagsvold & Lifjeld 1985, Hill & Montgomerie 1994, Hill 1999, McGraw & Hill 2000, Senar & Escobar 2002). Great Tits are principally insectivorous and feed on a wide range of invertebrate families, including moths and butterflies (especially larvae), beetles, bugs, wasps and allies, flies and spiders (Gosler 1993). They also consume a significant amount of seeds and fruits that constitute the main reserve food for the birds when the temperature drops and the invertebrates become less readily available (Gosler 1993, Cramp & Perrins 1993). Carotenoids are abundant in their diet, especially lutein and zeaxanthin (Slagsvold & Lifjeld 1985, Partali *et al.* 1987).

Foraging behaviour of Great Tits develops with age and experience, showing great flexibility and exploratory and learning ability (Cramp & Perrins 1993, Gosler 1993). Therefore, we suggest that the observed increase in plumage coloration with age might indicate, as in other species, that older Great Tits are more skilled foragers (Brandt 1984, Maccarone 1987, Enoksson 1988, Jansen 1990, Desrochers 1992, Heise & Moore 2003). They ingest larger quantities of carotenoids and hence are in better condition during moult. This assumption is supported by recent findings showing that different components of plumage coloration convey different units of information in Great Tits (Ferns & Hinsley 2008, Senar *et al.* 2008). Hue has been shown to be a good predictor of lutein content in feathers and as a consequence of individual's ability to locate and collect carotenoid-rich sources, whereas colour chroma seems to be more related to body condition (Senar *et al.* 2008)

However, age-related differences in coloration can also be brought about by other factors indirectly associated with age (Enoksson 1988). For example, adult Great Tits might exclude yearling individuals from the best foraging areas, the latter being at competitive disadvantage over food resources and hence, carotenoid pigments (Enoksson 1988, Desrochers 1992). Besides their role as integumentary colorants, carotenoids have also important functions in many physiological processes. They work as antioxidants, immunomodulators and photoprotectants or take part in vitamin synthesis and intercellular communications (reviewed in Møller *et al.* 2000). Therefore, another plausible explanation for age dimorphism in Great Tit ventral coloration might be that young birds require more carotenoids than adults for physiological functions and consequently, fewer pigments would be available for signalling purposes (Olson & Owens 1998). Furthermore, carotenoid availability may be significantly influenced by seasonal variation in food quantity and quality, becoming a limited resource at some times of the year (Hill 1995). Adult Great Tits moult their ventral feathers in early or mid-summer, during or immediately after the breeding season (Cramp & Perrins 1993). In yearling birds, however, feather replacement occurs in late-summer, at approximately two months of age (Cramp & Perrins 1993). At this period young birds could be confronted with potential constraints in environmental carotenoid availability that might restrict the development of the full adult plumage coloration (Hill 1995). Moreover, Great Tits that moult later in the season might be forced to moult faster and this has been shown to compromise feather quality and pigment deposition (Ferns & Hinsley 2008).

Finally, it is likely that the magnitude of the fluctuations in coloration between age-classes throughout the sampling period at the population level (Fig. 1) are directly related to differences among years in food availability and distribution (Slagsvold & Lifjeld 1985). When food is plentiful and the weather warm, even a less efficient forager may have few problems in finding enough food. However, inefficiency and lack of experience in yearlings could become crucial during harsher conditions (Enoksson 1988). This inter-annual food variability could also explain why in other works comprising a short sampling period colour differences between age-classes are not so apparent (Isaksson *et al.* 2008), emphasizing the need of large temporal series in studies of carotenoid-based plumage coloration.

In summary, our results demonstrate that the observed increase in carotenoid-based coloration in Great Tits is largely due to within-individual changes with age. However, other factors such as directional selection against less coloured individuals might additionally contribute to the observed changes in the colour composition of the entire population. To date, no study has demonstrated the role of survival on differences in carotenoid coloration between ages. In a recent study, Fitze & Tschirren (2006) showed that carotenoid-based plumage was not related to short- neither to long-term survival in a Swiss Great Tit population. Furthermore, Figuerola & Senar (2007) demonstrated that the selection direction in Serins *Serinus serinus* is stabilizing (and not directional), so that birds with low and high coloration quality had less survival probability.

For a better understanding of the underlying mechanisms of changes in colour with age, our hypotheses would need to be additionally tested in captivity, providing carotenoid-rich food sources to juveniles (before their pre-basic moult) and adult birds under experimental conditions. Interestingly, previous experiments have shown that juvenile and adult birds attain similar levels of carotenoid-based ornamentation if moulting in captivity under similar circumstances (Hill 1992, Veiga & Puerta 1996) and future studies in this direction would certainly contribute to determine the role of differential access to carotenoids on age dimorphism in Great Tits.

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SAMENVATTING

Het verenkleed is bij volwassen vogels over het algemeen feller van kleur dan bij jonge vogels. Dit verschil zou een gevolg kunnen zijn van een lagere overleving van de blekere vogels in de populatie. Het kan echter ook zijn dat het verenkleed na de eerste lichaamsrui intenser van kleur wordt. Bij Koolmezen *Parus major* hangt de gele kleur op de onderzijde van de vogel samen met de opname van carotenoïden (gele tot roodachtige kleurstoffen) in het voedsel. In dit onderzoek is nagegaan of de individuele verschillen in kleurintensiteit bij deze soort gerelateerd zijn aan de leeftijd van de vogels. Een vergelijking tussen de verschillende geslachten en leeftijden laat zien dat volwassen mannetjes over het algemeen groener en intenser geel van kleur zijn dan eerstejaars vogels. Een vergelijking tussen individuele mezen die in opeenvolgende seizoenen zijn gevangen, laat zien dat de kleurintensiteit inderdaad met de leeftijd toeneemt. Dit kan het resultaat zijn van een betere foerageertechniek op latere leeftijd, die de vogel beter in staat stelt om tijdens de rui voedselbronnen te benutten die rijk aan carotenoïden zijn. Het kan echter ook zijn dat andere factoren veranderen met de leeftijd, zoals een verandering in de aanwending van carotenoïden voor verschillende lichaamsfuncties. Dit neemt niet weg dat ook een gerichte selectie tegen bleke individuen of nog andere factoren kan bijdragen aan de leeftijdsgebonden toename van de kleurintensiteit op populatieniveau. (YIV)

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