

Age differences in blue tit *Parus caeruleus* plumage colour: within-individual changes or colour-biased survival?

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In many species of passerine birds yearlings display a less elaborate version of the adult secondary sexual traits, but the causes of such differences in ornamentation are not always well understood. We studied age-related changes in blue tit *Parus caeruleus* UV/blue structural crown coloration, a sexually selected trait. In our Austrian study population, older blue tits, irrespective of sex, displayed on average a more ultraviolet (lower hue, higher UV chroma), more chromatic and brighter crown coloration than yearlings. This age dichromatism was caused by within-individual changes in the expression of crown coloration between years since males and females became more UV, more chromatic and brighter as they aged. Colour biased survival did not contribute to the observed pattern of age dichromatism since crown coloration was largely unrelated to overwinter survival. Between-year repeatability of crown colour was significant for most colour variables but low in general, and lower for females than for males. In the blue tit, yearling males might benefit from being less ornamented by avoiding adult aggression but at the expense of sexual attractiveness. Adaptive explanations of blue tit age dichromatism should however take into account that age effects were of similar magnitude in males and females. This suggests that both male and female yearlings could benefit from being less ornamented and hence that sexual selection might be acting on both sexes simultaneously in this species.

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Older males (and sometimes females) of many species of passerine birds display more elaborate secondary sexual traits than juveniles and are often preferred as mates. The degree of age dimorphism in ornamentation shows great variability between species and according to Hill (1996), two main groups can be distinguished. In some species yearling males (first-time breeders born in the previous year) display a distinct “dull” female-like plumage, before acquiring the definitive adult plumage in a subsequent season. This particular type of age-specific variation in plumage pattern, known as “delayed plumage maturation”, has attracted a great deal of attention and several hypotheses have been formulated to explain its occurrence (reviewed in Lyon and Montgomerie 1986, Beauchamp 2003). In most species

however, age-related differences in ornamentation are not categorical but more a matter of degree with yearling birds displaying a similar but subdued version of the full adult plumage. This has been termed “age-related” plumage variation, in contrast to the “age-specific” differences in species with delayed plumage maturation (Hill 1996). In contrast to most cases of delayed plumage maturation, age-related differences in the expression of secondary sexual traits are not necessarily restricted to males, although they are usually more pronounced in males than in females (Møller 1991, Hill 1996).

While age-specific differences in plumage coloration are due to a relatively fixed schedule of within-individual changes, age-related differences in the expression of secondary sexual traits could be brought about by either

within-individual increases in ornamentation, by differential survival of more ornamented individuals, or by a combination of both. Indeed, often the most ornamented, presumably high quality individuals, show higher survival (see meta-analysis in Jennions et al. 2001), thus becoming over-represented in older age-classes (Forsslund and Pärt 1995). On the other hand, if investment in sexual ornaments is costly, ornament expression could correlate negatively with survival (Brooks 2000, Hunt et al. 2004), and this could obscure the effect of within-individual changes (Gil et al. 2001). Hence, to assess the contribution of these two mechanisms to the observed pattern of age-related differences it is necessary to perform a longitudinal analysis on ornament expression using individuals of known age, in combination with an analysis of the relationship between ornament expression and survival.

We studied age-related variation in structural plumage coloration in male and female blue tits *Parus caeruleus*. This species displays several conspicuous structurally coloured plumage patches which show pronounced sexual dichromatism in the near ultraviolet (UV), with males being more UV reflectant than females (Andersson et al. 1998, Hunt et al. 1998). The appeal of this "hidden" sexual dichromatism and the large amount of knowledge about blue tit life-history have made this species an increasingly popular model for the study of sexual selection on structural colours (Sheldon et al. 1999, Delhey et al. 2003, Griffith et al. 2003, Johnsen et al. 2003, Limbourg et al. 2004). However, despite our increasing understanding of blue tit sexually selected traits, basic questions like age-related colour expression are still largely unexplored. For some populations there is limited evidence suggesting that age differences in plumage coloration exist (Andersson et al. 1998, Örnborg et al. 2002), but its causes and consequences have not been studied. Interestingly, since more UV ornamented males show increased over-winter survival in a Swedish population (Sheldon et al. 1999, Griffith et al. 2003), some of these age differences could arise through differential survival. Here, we attempt to disentangle the relative importance of differential survival and within-individual changes to explain age-dependent colour signalling in our Austrian study population. Using a large data set collected over three years, we perform both cross-sectional and longitudinal analyses of age-related colour variation and assess the relationship between coloration and survival.

Methods

Study site and general methods

Fieldwork was carried out between March 2001 and December 2003, in a nestbox breeding, colour-banded blue tit population at Kolbeterberg, Vienna, Austria

(48° 13'N, 16° 20'E). The study site of 35 ha is part of a large mixed deciduous woodland and contains 250 nestboxes. Blue tits were captured at the nestbox either during the night while roosting (in winter), or while feeding 8-14 d old chicks (in spring). Unbanded birds were fitted with a metal band and a unique combination of plastic colour bands. A small (5-50 µl) blood sample was drawn from the brachial vein for genetic analyses, and colour measurements were performed (see below). Birds were aged as adults or yearlings based on the colour of the wing coverts (Svensson 1992) and sexed in spring by presence/absence of the brood-patch. If birds were only captured during winter we determined their sex by molecular analysis (see Johnsen et al. 2003). Since this blue tit population has been closely monitored since 1998 (Foerster et al. 2003), most birds present from 2001 onwards had been first banded as juveniles and thus their exact age was known. Some birds (12%) were captured for the first time as adults, and were assumed to be 2 years old then. This uncertainty did not bias the results however, since the patterns of age related colour variation remained qualitatively unchanged if these birds were excluded from the analyses (not shown). For the analyses, we classified birds as being first year (1 yr), second year (2 yr), or more than two years (> 2 yr) old. Older age classes were combined to obtain an adequate sample size.

Blue tits undergo only one moult per year. The first moult, which takes place at *circa* two months of age, is limited to the head, body and a variable number of tertials, tail feathers and secondary coverts (Cramp and Perrins 1993). Thus, the plumage worn during a blue tit's first breeding season (juvenile, or 1 yr birds) consists of a mixture of feathers grown in the nest (wing feathers and most tail feathers) and newly moulted feathers. After the first breeding season, blue tits undergo a complete post-breeding moult every year between late May and late August (Cramp and Perrins 1993).

Colour measurements

Coloration of the crown was measured in spring between mid-May and early June and in early winter between late November and early December. To measure feather reflectance we used a S-2000 spectrometer and a DH-2000-FHS deuterium halogen lamp (Ocean Optics, Eerbeek, The Netherlands). Spectrometer and lamp were connected through a bifurcated fiber optic probe, fitted at the end with a plastic cylinder to standardise measuring distance and shield out ambient light. The probe was held perpendicular to the surface of the feathers, and we took readings of five standardized spots (each 11.3 mm²). Reflectance (R) was calculated relative to a WS-2 white standard using the program Spectra-Win. Raw spectra were imported into a spreadsheet

program, smoothed using a running average calculated over a 10 nm interval, and the following variables were computed: (1) Brightness, which constitutes an estimate of the area under the curve or total light reflected by the feathers, was calculated as the average reflectance (R_{av}), between 300 and 700 nm. (2) Hue or spectral location was determined as the wavelength of peak reflectance (λR_{max}). (3) Chroma or spectral purity was calculated as the difference between peak and trough divided by total reflectance ($(R_{max} - R_{min})/R_{300-700}$). Finally, (4) The relative amount of UV reflectance or "UV chroma" was calculated as reflectance in the UV range (300-400 nm) divided by total reflectance ($(R_{300-400}/R_{300-700}) \times 100$) and expressed as a percentage (Andersson et al. 1998). We computed an estimate of measurement repeatability (Lessells and Boag 1987) using the five measurements taken per individual for a subsample of measured males. Repeatability estimates were moderate but highly significant for all colour variables (hue, $R = 0.50$, $F_{44,180} = 6.03$; UV chroma, $R = 0.64$, $F_{44,180} = 10.12$; chroma, $R = 0.56$, $F_{44,180} = 7.49$; brightness, $R = 0.40$, $F_{44,180} = 4.43$; all $P < 0.001$). These repeatability values are lower than previously reported for blue tit crown colour (see Örnberg et al. 2002). The difference is due to the fact that we measured five different spots on the crown to get an overall estimate of its colour, while Örnberg et al. (2002) repeatedly measured the same spot in the center of the crown. Hence our repeatability estimate combines variation from measurement error (estimated as 0.6 to 0.9 by Örnberg et al. 2002) and spatial variability within the crown. For a similar example focusing on repeatability of cell-mediated immune response see Granbom et al. (2005).

Data analysis

To assess whether coloration changes with age we performed both cross-sectional and longitudinal analyses. In the blue tit, crown feathers become progressively less UV reflectant as the plumage gets soiled and worn with use (Örnberg et al. 2002). Thus, age effects observed at the end of the breeding season might differ from those in freshly moulted plumage, especially if there is an age-related bias in the degree of seasonal change in colour. Therefore, we report the results of analyses using crown colour measurements taken both in early winter (late November to early December) and in late spring (May) when birds were feeding chicks. Changes in UV coloration are minimal during winter (Örnberg et al. 2002), and colour measurements during this period should thus provide an adequate estimate of colour after moult. For the cross-sectional analysis we used restricted maximum likelihood models (REML), with colour as dependent variable, age, sex, study year and the interaction between sex and age as fixed factors and individual

identity as a random factor. A different model was built for each colour variable. For the longitudinal analysis we used birds that had been measured in two consecutive years during the same period (i.e. either winter or spring). The change in colour between years was analysed using repeated-measures ANOVA, with colour in year_x and colour in year_{x+1} (measured on the same individual), as within-subjects factor. A significant within-subjects factor would indicate that individual crown coloration changed between consecutive years (i.e. whether the change differed from zero). To test whether changes in colour were influenced by initial age (i.e. age in year_x), sex or season (either 2001 to 2002, or 2002 to 2003), we included the interaction between these factors and the within-subjects factor (i.e. colour change) in the model. The interaction between the within-subjects factor and age reflects differences in the way colour changes during life (e.g. colour expression could increase more between the first and second year than later on in life). Similarly, the interactions with sex or season indicate whether colour changes are different between males and females or depending on the years when the colour was measured.

The relationship between survival and coloration (measured in spring) was assessed using logistic regression with survival (yes/no) as dependent variable, and year, age, and sex as factors and colour as a covariate. The models also included the interaction terms age x colour and sex x colour. Models were simplified using a backward elimination procedure, where factors or variables were excluded in order of decreasing significance until only terms with $P < 0.05$ remained in the model. Lack of significance of excluded terms was confirmed by including them one-by-one in the final model. Survival was estimated as the probability of recapture, where individual birds were assumed to have died if they were not recorded nesting in the next breeding season (Sheldon et al. 1999, Griffith et al. 2003). The accuracy of this survival estimate would depend on the incidence of dispersal in our population and on the relationship between crown colour and dispersal. In our study population females are more likely to disperse after having established a territory than males (24% of surviving females disperse vs. only 3% of the males, $\chi^2_1 = 16.74$, $P < 0.001$, $N_{females} = 102$, $N_{males} = 88$; M. Valcú and B. Kempenaers unpubl. data), and crown colour is unrelated to dispersal distance (for all colour variables: females, $P > 0.5$, $N = 40$; males $P > 0.2$, $N = 38$, M. Valcú et al. unpubl. data). Moreover if dispersal is biasing our survival estimate we would expect that females have a lower recapture probability than males which was not the case (see Results). Hence we believe that our survival estimate is reasonably accurate and, more importantly, unbiased with respect to the hypothesis being tested (i.e. correlation between crown colour and survival).

Results

Cross-sectional analysis

After controlling for sex and year, age had a significant effect on all four crown colour variables measured in spring (Table 1). The interaction between age and sex was non-significant in all cases, although for brightness it approached significance. This suggests that in general age effects on crown colour are similar for males and females (but see below). On average, yearlings (1yr) were less UV-coloured (higher hue and lower UV chroma), and had lower chroma and brightness than older birds (Fig. 1). Among adults, two-year old and older birds did not differ significantly in crown colour (Fig. 1), although the sample size for older birds was low.

The analyses based on colour measured in winter showed in general a similar pattern but with some differences. For hue and UV chroma, but not chroma or brightness, the interaction between sex and age was significant (sex \times age; hue, $P < 0.001$; UV chroma, $P = 0.028$; chroma, $P = 0.11$; brightness, $P = 0.21$). This reflects the fact that in these two variables age effects in winter were more marked in females than in males. Finally, age differences in winter brightness, although similar to spring differences, were not statistically significant ($P = 0.24$). Year effects were highly significant for all colour variables measured in winter (all $P < 0.001$).

Longitudinal analysis

The crown colour of individual blue tits became more UV (lower hue, higher UV chroma), and showed increases in chroma and brightness with age, as revealed by the significant effect of the within-subjects factor (colour change) on all colour variables (Table 2). The interaction between the colour change and age was significant for crown hue and UV chroma (Table 2),

indicating that changes with age are more pronounced between the first and second year than later in life (Fig. 2a, b). Chroma increased constantly irrespective of age (Fig. 2c), although changes were small. Brightness on the other hand seemed to increase earlier in life in males (transition between 1 yr to 2 yr), and later in females (Fig. 2d), as suggested by the significant interaction between the colour change, sex and age (Table 2). Overall however, there were no sex differences in the magnitude of age-related changes (Table 2, Fig. 2). Repeating the longitudinal analysis with winter colour confirmed that crown colour changes with age (within-subjects factor, $P < 0.001$ for all crown colour variables except brightness, where $P = 0.04$). However, there was no significant interaction with age for hue and UV chroma as with spring colour (both $P > 0.5$). All other interactions were non-significant (all $P > 0.10$), except for a significant effect of colour change \times year on brightness (colour change \times year, $P = 0.008$).

Crown colour within-individuals was generally correlated between years (Fig. 3, Table 3), but correlations were weak. If computed separately for each sex, repeatabilities (following Lessells and Boag 1987) were generally higher in males than in females, except for hue, which showed the lowest repeatability (Table 3, Fig. 3). Between year repeatabilities were generally lower for colour measured in winter than in spring (Table 3).

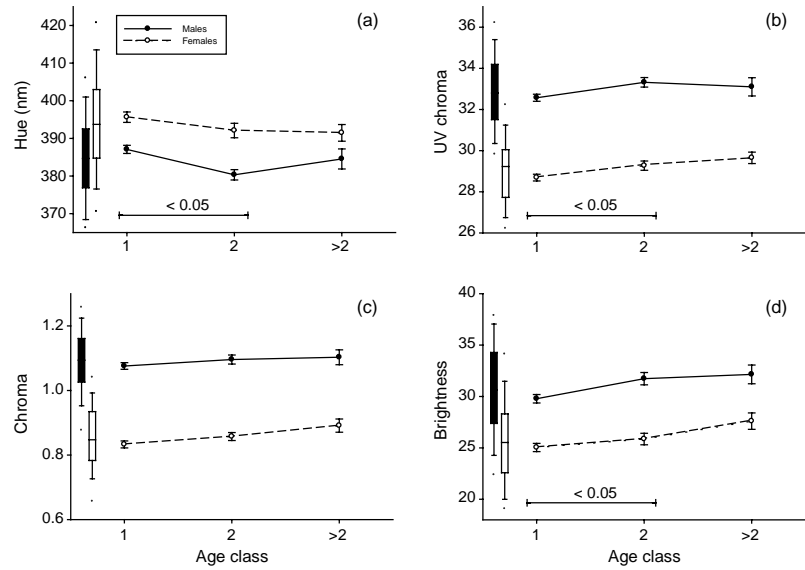
Colour and survival

Survival was independent of study year ($\chi^2_2 = 1.75$, $P = 0.42$), sex ($\chi^2_1 = 0.73$, $P = 0.39$), age ($\chi^2_2 = 4.51$, $P = 0.10$), or the interaction sex \times age ($\chi^2_2 = 1.18$, $P = 0.55$). Crown coloration was overall unrelated to survival, although there was a trend for brighter birds of both sexes to show higher over-winter survival (Table 4).

Table 1. Age, sex and year effects on blue tit crown spring coloration. Terms in bold were included in the final model. Effect size (β , relative to the last category in each factor) and their corresponding standard errors (\pm SE) are given for sex and age. Analysis carried out with restricted maximum likelihood models, based on 323 individuals, 11 measured in the three study years, 63 in two and the rest in only one.

	N	Hue			UV chroma			Chroma			Brightness		
		β (SE)	F	P	β (SE)	F	P	β (SE)	F	P	β (SE)	F	P
Intercept		385.3 (1.7)			30.2 (0.2)			0.91 (0.02)			27.7 (0.7)		
Year		–	56.17	<0.001	–	37.55	<0.001	–	28.22	<0.001	–	2.09	0.125
Sex			64.74	<0.001		504.1	<0.001		463.9	<0.001		113.0	<0.001
male	205	–9.9 (1.2)			4.0 (0.2)			0.24 (0.01)			5.1 (0.5)		
female	204	–			–			–			–		
Age			8.32	<0.001		7.89	<0.001		4.35	0.014		7.36	0.001
1 yr	229	3.3 (1.7)			–0.7 (0.2)			–0.04 (0.02)			–2.4 (0.7)		
2 yr	123	–1.5 (1.7)			–0.1 (0.2)			–0.02 (0.02)			–1.1 (0.7)		
>2 yr	57	–			–			–			–		
Sex \times Age		–	0.16	0.85	–	0.17	0.84	–	0.56	0.57	–	2.61	0.075

Fig. 1. The effect of age on male and female blue tit crown: (a) hue, (b) UV chroma, (c) chroma, and (d) brightness. Depicted are means and their corresponding standard errors. Significant differences between age classes based on post-hoc tests (sexes pooled, see Table 1) are indicated. Box plots on the left of each panel represent the degree of colour variability for each sex separately. Depicted are the 5th, 10th, 25th, 75th, 90th and 95th percentiles.



Discussion

The main conclusion from this study is that the observed age differences in blue tit crown coloration are due to within-individual changes and not to differential survival. Older blue tits in our study population had brighter, more chromatic and more UV (higher UV and lower hue) crown feathers than younger birds (Fig. 1 and Table 1). Age differences in crown colour were small compared to sexual dichromatism (Fig. 1) and differed somewhat from other published studies. In one of the first papers on blue tit crown coloration, Andersson et al. (1998) reported significant age effects on brightness (adult males being brighter than juveniles) but not on hue or UV chroma in a Swedish blue tit population (sample size $N=41$). This result was confirmed in a follow-up study, which also included blue tits from a different Swedish population and had a larger sample size ($N=339$, Örnborg et al. 2002). No age differences were found for crown chroma in a Spanish population (brightness and hue were not studied), although plumage colour was measured with a colorimeter that did not take reflectance in the UV into account (Figuerola et al. 1999). At the moment it is unclear whether between-populations differences in age dichromatism are common in the

blue tit and what is the cause for this discrepancies. One source of variation could be between-population differences in selection pressures on colour expression through either survival, male-male interactions or female choice. More studies are necessary to understand the extent and significance of between-populations differences in age dichromatism.

Age effects on structural colours have also been reported in other bird species. Adult males had more UV-chromatic feathers than juveniles in bluethroats *Luscinia svecica* (UV-blue throat patch, Johnsen et al. 2001) and in pied flycatchers *Ficedula hypoleuca* (iridescent-black dorsal coloration, Siitari et al. 2002). On the other hand, no age-related differences were found in the iridescent bluish-black dorsal coloration of barn swallows *Hirundo rustica* (Perrier et al. 2002).

Age changes in males and females

Age differences seemed to be similar for both sexes (Fig. 1), despite the pronounced sexual dimorphism in crown colour (Andersson et al. 1998, Hunt et al. 1998). However, in the winter sample, where colour was measured before the seasonal decline in UV reflectance

Table 2. Repeated measures ANOVA for age-related colour changes in the blue tit. The within-subject factor (i.e. the repeated measures) is coded as colour change (see Methods). Terms in bold are included in the final model.

	Hue			UV chroma			Chroma			Brightness		
	F	df	P	F	df	P	F	df	P	F	df	P
Colour change	22.97	1,69	<0.001	19.33	1,69	<0.001	18.81	1,70	<0.001	6.25	1,67	0.015
Colour change \times year	1.02	1,68	0.314	0.17	1,68	0.673	2.10	1,69	0.151	1.04	1,66	0.311
Colour change \times age	15.61	1,69	<0.001	6.90	1,69	0.011	0.00	1,69	0.988	0.14	1,67	0.709
Colour change \times sex	0.01	1,68	0.893	0.03	1,68	0.864	1.33	1,69	0.252	0.06	1,67	0.797
Colour change \times age \times sex	0.62	1,67	0.432	0.05	1,67	0.815	0.00	1,67	0.938	4.02	1,67	0.049

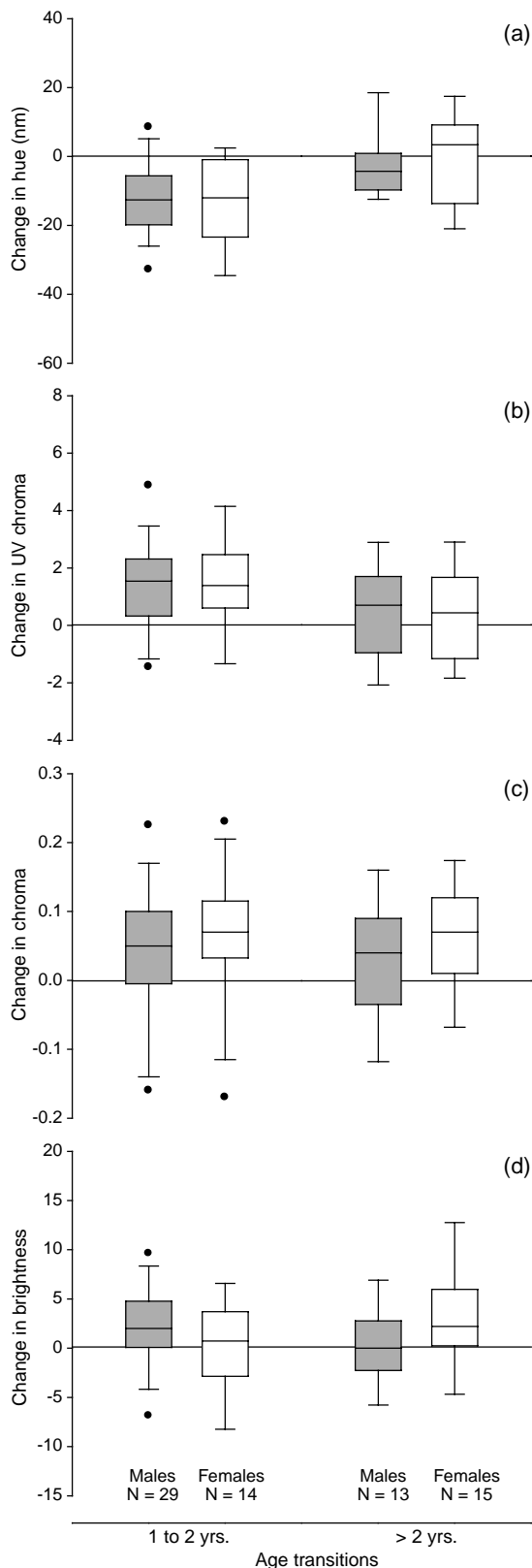


Fig. 2 (Continued)

(Örnberg et al. 2002), age dichromatism was more pronounced in females than in males. The reason for this is unclear, although it could be due to differences in the rate of crown colour decline between young and old males and females. However, the degree of decline in UV reflectance between winter and spring does not differ between sexes or between adult and juvenile males (Delhey et al. unpubl. data). This suggests that differential effects of feather wear or dirt accumulation are unlikely causes of age differences in colour, at least among males. The fact that age differences in crown coloration were at least as large in females as in males was confirmed by longitudinal analyses, which show for spring and winter, that sex had no effect on the magnitude of age-related colour change (Table 3). Thus, sexual dichromatism did not increase with age, in contrast to what is observed in most species with delayed plumage maturation (Lyon and Montgomerie 1986). Lack of sexual differences in the way ornamentation changes with age in addition to assortative mating (Andersson et al. 1998), and male preference for UV-reflectant females in captivity (Hunt et al. 1999) suggest that crown ornamentation may be selected through mutual mate choice in the blue tit.

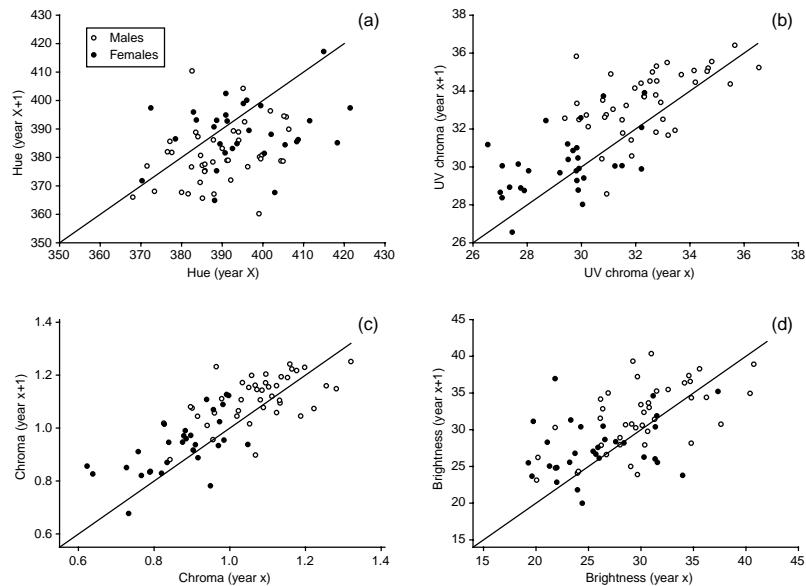
Age changes in juvenile and older birds

The magnitude of within-individual changes in coloration depended on individual age, except for crown chroma which increased steadily and irrespective of age. Hue and UV chroma followed the usual pattern of age-related ornamentation, where the greatest increase in ornamentation takes place between the first and second year (Møller 1991, Dale et al. 1999, Hegyi et al. 2002, Török et al. 2003). Age-related increases in brightness, on the other hand, showed a different timing in males and females: changes in this variable were more pronounced early in life in males and later in females (Fig. 2d).

What underlies the different ways in which colour variables respond to age remains unclear. Non-iridescent structural colours, like the crown of the blue tit, are created through coherent scattering of light by the internal microstructure of the feather (Prum et al. 2003). While chroma and UV chroma might depend on the regularity and number of scattering particles respectively (Shawkey et al. 2003), hue is probably determined by the size of these particles (Andersson 1999, Shawkey et al. 2003). Brightness on the other hand might depend on the thickness of the feather cortex or

Fig. 2 Within-individual changes ($\text{colour}_{(\text{year } x+1)} - \text{colour}_{(\text{year } x)}$) in crown: (a) hue, (b) UV chroma, (c) chroma, and (d) brightness of male and female blue tits due to age. Depicted are median changes and the 5th, 10th, 25th, 75th, 90th and 95th percentiles.

Fig. 3. Between-year repeatability of male and female blue tit crown: (a) hue, (b) UV chroma, (c) chroma, and (d) brightness. The diagonal line corresponds to $Y = X$; note that most data points lie only on one side of the line (below for hue, and above for the other variables), indicating significant changes in colour between years.



the amount of melanin deposited in the feathers (Shawkey et al. 2003). Thus, given that different mechanisms are responsible for different colour variables, it is possible that they change independently of each other with age. For example the regularity of the keratin rods could increase steadily as birds get older but their size may become fixed once a certain age is reached. Studies addressing the proximate mechanisms involved in the expression of structural ornaments in adult blue tits are needed to test this idea.

Between year repeatability of colour

Blue tit crown coloration seems to be a rather plastic trait able to change within a given year (Örnberg, et al. 2002) and also between years with individual age. Nonetheless the expression of crown colour in the same individual tended to be correlated in consecutive years (Fig. 3). Between year repeatability of crown coloration was slightly higher in males than in females, but low in general. Low repeatabilities are probably due

to a combination of different factors: (1) Repeatability of colour measurements of live birds using spectrometry is moderate (0.4-0.6) setting an upper limit to between-year repeatability (see Figuerola et al. 1999, Örnberg et al. 2002, Perrier et al. 2002, Materials and methods). (2) Changes in coloration due to age as described here (Fig. 2), especially between the first and the second year also contribute to lower repeatability. (3) Blue tit crown colour shows a high degree of within-year changes, with pronounced declines in UV reflectance, but also changes in chroma and brightness, after moult is completed (Örnberg et al. 2002). Thus, colour at the moment of measurement might differ to an unknown extent from the colour produced at moult. Surprisingly, however, repeatabilities of winter colour were lower than those for spring colour (Table 3), although winter and spring colour are positively correlated (Delhey et al. unpubl. data). (4) Structural colours show condition-dependence (Keyser and Hill 1999, Doucet 2002, McGraw et al. 2002, Johnsen et al. 2003), hence between-year differences in environmental and individual conditions at moult could affect the colour of the

Table 3. Between-year repeatability of male and female blue tit crown colour measured in spring or winter in consecutive years (see Methods).

	Spring colour						Winter colour					
	Males ¹			Females ²			Males ³			Females ⁴		
	R (± SE)	F _{42,47}	P	R (± SE)	F _{29,37}	P	R (± SE)	F _{34,46}	P	R (± SE)	F _{12,15}	P
Hue	0.18 (0.14)	1.47	0.099	0.25 (0.15)	1.76	0.053	-0.20 (0.12)	0.60	0.936	0.03 (0.23)	1.09	0.432
UV chroma	0.35 (0.12)	2.13	0.006	0.33 (0.14)	2.14	0.015	0.27 (0.13)	1.88	0.023	0.28 (0.22)	3.00	0.024
Chroma	0.41 (0.12)	2.74	<0.001	0.23 (0.15)	1.73	0.059	0.26 (0.13)	1.90	0.022	0.45 (0.19)	3.02	0.023
Brightness	0.54 (0.10)	3.53	<0.001	0.29 (0.15)	1.94	0.029	0.43 (0.12)	2.78	0.001	0.17 (0.23)	1.48	0.234

¹N = 39 measured in two years, N = 4 measured in three years; ²N = 27 measured in two years, N = 7 measured in three years; ³N = 24 measured in two years, N = 11 measured in three years; ⁴N = 11 measured in two years, N = 2 measured in three years.

Table 4. Blue tit crown colour and survival. Presented are means and standard errors (SE) for crown colour variables of male and female blue tits that did and did not survive to the next breeding season, and the results from the logistic regression models (see Methods for more details).

	Males-survived (mean \pm SE)		Females-survived (mean \pm SE)		Logistic regression
	No (N = 110)	Yes (N = 49)	No (N = 122)	Yes (N = 44)	
Hue	383.7 (1.1)	385.2 (1.6)	394.6 (1.3)	392.7 (2.1)	Hue, $\chi^2_1 = 0.17$, $P = 0.68$ Hue x sex, $\chi^2_1 = 1.08$, $P = 0.30$ Hue x age, $\chi^2_2 = 0.22$, $P = 0.89$
UV chroma	32.9 (0.2)	32.8 (0.2)	28.8 (0.2)	29.0 (0.2)	UV chroma, $\chi^2_1 = 0.50$, $P = 0.48$ UV chroma x sex, $\chi^2_1 = 0.68$, $P = 0.41$ UV chroma x age, $\chi^2_2 = 0.88$, $P = 0.64$
Chroma	1.08 (0.01)	1.09 (0.02)	0.84 (0.01)	0.85 (0.01)	Chroma, $\chi^2_1 = 1.20$, $P = 0.27$ Chroma x sex, $\chi^2_1 = 0.36$, $P = 0.55$ Chroma x age, $\chi^2_2 = 0.53$, $P = 0.77$
Brightness	30.4 (0.4)	31.0 (0.7)	24.4 (0.4)	26.6 (0.7)	Brightness, $\chi^2_1 = 3.22$, $P = 0.07$ Brightness x sex, $\chi^2_1 = 0.40$, $P = 0.53$ Brightness x age, $\chi^2_2 = 1.69$, $P = 0.43$

growing feathers. Indeed, study year had a significant effect on all crown colour variables except for brightness (Table 1). Relatively low between-year repeatability in the expression of condition-dependent plumage coloration has also been reported for carotenoid- or melanin-based ornamental plumage (Hill 1992, Veiga and Puerta 1996, Griffith and Sheldon 2001, Senar et al. 2002).

Age effects and survival

Previous studies on a Swedish blue tit population showed that more UV-chromatic males had a higher probability of survival (Sheldon et al. 1999, Griffith et al. 2003). However, in our population, survival was unrelated to the expression of crown colour in males or females, except for a very weak effect of brightness (Table 4). This suggests that, unlike Swedish blue tits, females in our study population cannot assess future survival prospects of males by their crown colour. Differences in the relationship between ornamentation and survival across populations have been reported for other intensively studied species like house sparrows *Passer domesticus* (Møller 1989, Griffith 2000), great tits *Parus major* (Hörak et al. 2001, Fitze and Richner 2002), and house finches *Carpodacus mexicanus* (Hill 1991, Badyaev et al. 2001). Current models of sexual selection, which take life history trade-offs into account, predict positive, no, or even negative relationships between survival and the expression of condition-dependent ornamentation depending on the intensity of sexual selection (Kokko et al. 2002). If the intensity of sexual selection is high (i.e. only the few most ornamented males sire most offspring), investing resources in the production of costly ornaments at the expense of future survival (negative correlation between survival and ornamentation) becomes the most successful strategy. On the other hand if mating skew is lower these models predict no, or even a positive correlation, between

viability and ornamentation. Differences in the intensity of sexual selection could be brought about by differences in the costliness of female choice, which could in turn be caused by different environmental or social conditions (Kokko et al. 2002). While it would be tempting to speculate that differences across blue tit populations in the attractiveness-survival relationship are due to differences in the intensity of sexual selection, we presently lack the necessary information to support this claim. Nonetheless, in the future the blue tit could become a suitable model to test some of the predictions of the “sexual selection continuum” model (Kokko et al. 2002). In this species, between-population differences in the incidence of extra-pair paternity and polygyny (Kempenaers 1994, Kempenaers et al. 1997, Krokne and Lifjeld 2000, Charmantier and Blondel 2003) may provide a gradient of mating skew, which could be related to the correlation between crown UV ornamentation and survival in each population.

The function of age-related colour expression in the blue tit

Adaptive explanations of age differences in ornamentation are mainly based on the idea that juvenile plumage, despite its lower sexual attractiveness, is advantageous by reducing adult aggressiveness (Lyon and Montgomerie 1986, Beauchamp 2003). This could indeed be the case in the blue tit since juvenile males might avoid male aggression by being less UV ornamented (Alonso-Alvarez et al. 2004), although they may then have lower breeding success as a result of female choice (Sheldon et al. 1999, Delhey et al. 2003, Griffith et al. 2003, Limbourg et al. 2004). However, even if on average yearlings could signal their lower status or age to adults, age-related differences in crown colour were small (Fig. 1), suggesting that the discriminative power of this trait might not be very high. Indeed, while discriminant

analysis functions based on crown coloration (including all four colour variables) correctly classified more than 95% of the birds according to sex, aging proved to be more difficult with only 70% of males and 60% of females being correctly identified as juvenile or adult (our unpubl. data). Thus, the degree of age-related differences in ornamentation in the blue tit does not provide receivers with an unambiguous signal of age as in species with true delayed plumage maturation.

Another important difference with delayed plumage maturation is that male and female blue tits display comparable levels of age-related changes in crown coloration (Figs. 1 and 2). This suggests that similar mechanisms are responsible for age differences in both sexes (Mountjoy and Robertson 1988), and argues against the idea that age-effects in females are just a correlated response to selection on males (Amundsen 2000). Whether female colour indicates attractiveness to males, as some studies suggest (Andersson et al. 1998, Hunt et al. 1999), or whether it could help mediate agonistic interactions between competing females (Kempenaers 1995), remains an open question. Little is known about the function of female coloration in the blue tit, and future studies focusing on the relationship between female crown coloration and breeding success might help to shed light on this issue.

Finally, an alternative, non-adaptive explanation for age differences in ornamentation is that juvenile birds are less ornamented simply because developmental constraints or lack of resources prevent them from acquiring full adult plumage (Landmann and Kollinsky 1995, Hill 1996). Experiments have shown that juvenile and adult birds attain similar levels of melanin- and carotenoid- based ornamentation if moulting in captivity under the same conditions (Hill 1996, Veiga and Puerta 1996). Given that the expression of blue tit structural coloration is partly condition-dependent (Johnsen et al. 2003), similar experiments using captive blue tits might provide insight into this possibility.

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