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# Carotenoid plumage hue and chroma signal different aspects of individual and habitat quality in tits

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We hypothesized that Blue tits *Cyanistes caeruleus* and Great Tits *Parus major* from low quality habitat (small woods) would have less yellow ventral plumage than those from high quality habitat (large woods) because they moult faster and/or their diet contains fewer carotenoids. They moult faster because they moult later in the season and are subject to more rapidly shortening daylengths. We tested this using a database of the plumage coloration (chroma, hue and lightness) of birds breeding in woods of different sizes, by manipulating the speed of moult in captive Blue Tits, and by counting the abundance and size of caterpillars (the major source of dietary carotenoids) in the diet of nestlings. In accordance with our hypothesis, juveniles of both species (which moult about three weeks later than adults) were about 8% less saturated in colour (lower chroma) than adults, but there was no significant difference in chroma between habitats. However, both species did differ significantly in hue in large and small woods. Blue Tits forced to moult faster in captivity, at a rate similar to that caused by a month's delay in the start of moult, had yellow flank feathers that were 32% less saturated in colour than those allowed to moult more slowly. Blue Tit nestlings in large woods

consumed 47% more caterpillar flesh (per gram of faecal material voided) than those in small woods, and Great Tit pulli 81% more. When habitat effects were controlled in ANOVAs, Blue Tits mated assortatively on the basis of flank hue and Great Tits on the basis of flank lightness. Flank colour therefore has the capacity to provide information about the potential quality of both habitats and individual birds to potential colonists and sexual partners.

The expression of carotenoid-based plumage coloration reflects the food provisioning rates of the males of several species, including the Blue Tit *Cyanistes caeruleus* (Hill 1991, Linville *et al.* 1998, Senar & Escobar 2002, Senar *et al.* 2002, Isakson *et al.* 2006). The yellow feathers of the underparts of Blue Tits and Great Tits *Parus major* are paler in a range of habitats assumed to be of poorer quality than deciduous woodland. For example, this is the case in coniferous forest (Slagsvold & Lifjeld 1985), mixed forest (Figuerola *et al.* 1999, Figuerola & Senar 2005), and both polluted and urban habitats (Eeva *et al.* 1998, Hõrak *et al.* 2000). One cross-fostering study in Great Tits has shown that such colour differences are phenotypic in nestlings and therefore reflect habitat quality rather than genetic quality (Hõrak *et al.* 2000), whilst others have demonstrated both environmental and genetic effects in both species (Fitze *et al.* 2003a, Johnsen *et al.* 2003). The colour is assumed to be subject to sexual selection because it is correlated with male parental quality in Blue Tits (Senar *et al.* 2002, Johnsen *et al.* 2005).

We know that habitat quality affects both breeding success (Hinsley *et al.* 1999) and the timing of moult (Hinsley *et al.* 2003) in both Blue Tits and Great Tits in our study area. Individual tits breeding in small woods start laying eggs later, produce fewer chicks and moult later. Great Tits that moult later after the summer solstice, when daylengths are shortening, moult faster (Bojarinova *et al.* 1999) and this is known to compromise feather quality (Nilsson & Svensson 1996, Dawson *et al.* 2000, Hinsley *et al.* 2003, Dawson 2004).

We therefore predicted that tits breeding in unfavourable habitats (small woods) would be paler in colour because they breed later and consequently they and their offspring would moult later and faster, depositing less pigment per unit mass of feather

than they would in high quality habitats (large woods). We tested this possibility in two ways. Firstly, we examined field data to determine whether the size of the wood in which Blue and Great Tits bred was correlated with the colour of their underparts, using our database of tit plumage coloration measured by reflectance spectrometry collected over a six-year period in woods of different sizes in Cambridgeshire, UK. Secondly, we decreased the daylength of moulting Blue Tits in captivity, which is equivalent to forcing them to moult later in the year (as they do in small woods), and then measured the colour of their plumage. Thirdly we examined the quality of the diet in different habitats by counting the number, and measuring the size, of caterpillar jaws found in the droppings of nestlings. Finally, we tested for assortative mating by measuring the colour of male and female parents caught at the same nest, and controlling for the effects of age and habitat in ANOVAs.

We are concerned here solely with the yellowness of the ventral plumage, caused mainly by the carotenoids lutein and zeaxanthin, since this colour has been found to be correlated with habitat and breeding parameters by previous workers. The UV reflectance of these carotenoids may be indicators of other qualities (Bleiweiss 2004).

## **MATERIAL AND METHODS**

Colour measurements were made in the field on Blue Tits and Great Tits caught in nestboxes feeding chicks in large (26.9-156.8 ha,  $n = 4$ ) and small (0.1-7.5 ha,  $n = 21$ ) woods located in arable farmland in East Anglia, UK (Hinsley *et al.* 1999). These were all caught within a relatively short time window each year (between April and June) and so seasonal changes in colour (Figuerola & Senar 2005) should have been minimal.

Measurements were made with a Minolta CR221 Chroma Meter which records colour

in the region 400-700 nm, with a spectral response matching that of the CIE 1931 Standard Observer curves. Six measurements were made of the colour of the flank feathers of each individual bird, moving the bird away from the sensor between each reading. The measuring area was a circle of 3 mm diameter, illuminated at 45°. The instrument was calibrated using a certified standard white plate (CRA45) prior to the measurement of every bird. The repeatability of individual measurements was moderate (e.g. Blue Tit, chroma,  $R = 0.647$ ,  $F_{19,120} = 11.99$ ; hue,  $R = 0.549$ ,  $F_{19,120} = 8.32$ ; lightness,  $R = 0.748$ ,  $F_{19,120} = 18.79$ ;  $P < 0.0005$  in all cases), whilst that of the mean of the six measurements we used in all analyses was high ( $R = 0.815-0.938$ ,  $P < 0.0001$ ).

Birds were aged using the criteria in Svensson (1992) and females identified by the presence of a wrinkled brood patch. Every one of the 77 pairs captured in this study comprised one individual with a wrinkled brood patch and one without. Three colour parameters were recorded – chroma (higher values = greater colour saturation), hue (0° = red, 90° = yellow, 180° = green) and lightness (black = 0%, white = 100%). These three parameters were significantly correlated with one another in both species, but the largest covariance (between lightness and chroma in Great Tits) was 27%, and the average of the others was only 10%, so the three parameters were clearly worth analysing separately. ANOVAs were therefore used to test for relationships between these three colour parameters and the sex and age of the birds concerned, and the year and size of woodland in which they were caught. Only main effects and first order interactions were included in these analyses. Since three colour parameters were analysed, we applied a standard Bonferroni correction and only relationships significant at  $P < 0.017$  were considered further. A total of 227 Blue Tits were caught (and 36 recaptured) in the six years from 1996 to 2001, and 114 Great Tits caught (and 15

recaptured) in the three years from 1996 to 1998. The recaptures were not included in the analyses.

For the moult trials, adult Blue Tits (at least one year old) were captured in Monk's Wood (good habitat) under licence in July and early August, at a time when they had just started primary and body feather moult. They were housed in individual cages in one of two identical rooms with different artificial daylengths (Dawson *et al.* 2000). Equal numbers of birds ( $n = 5$ ) were included in both groups, and all were female except for a single male in the long daylength group. In one room, the daylength was a constant 18 hours, in the other it decreased by one hour each week until it reached 12 hours and was then kept constant. Each bird was provided with food (mealworms, "Prosecto", egg biscuit, peanuts and fresh green lettuce) and water *ad libitum*. The rate of feather moult was recorded at approximately weekly intervals by scoring all the primaries of one wing (Newton 1966). We used wing moult as an index of moult speed because it is possible to record its rate of progression with greater precision than is the case with the body feathers (Dawson 2004). In individual corvids, the timings of feather moult in the primary and ventral tracts were found to be quite consistent relative to one another (Seel 1976), and the same was true of our Blue Tits. In tits, the ventral tract is the first part of the body plumage to commence moult (Dhondt 1973, Rymkevich & Bojarinova 1996) and is thus concurrent with most of primary moult, though it lasts several weeks longer (Cramp & Perrins 1993). We analysed the moult scores in a repeated measures ANCOVA in which subject (individual birds) constituted a random variable nested within treatments, time was a covariate, and subject was used as the error sum of squares for the main effect (daylength). Plumage colour was measured as soon as the flank feathers had finished moulting, which was about a month later in the

long daylength group. The single male bird in the latter group was not included in the analysis of flank colour because captive males have been found to deposit more carotenoid in their feathers when maintained on the same diet as females in the American Goldfinch (McGraw *et al.* 2002).

Droppings were collected from 11-day old chicks and stored in 70% alcohol for 4-8 months before being analysed. Excretory and faecal materials were separated, caterpillar jaws were removed and their lengths (base to tip of longest tooth, at right angles to the base) measured, before oven-drying the faeces. The jaws were counted, measured and converted into the equivalent dry mass of caterpillar flesh per gram dry mass of nestling faeces using a logarithmic regression derived from 96 caterpillars (size range 1-238 mg dry mass) collected from both habitats in 1998-2000. Caterpillars were combined for this purpose regardless of family or species since it was not possible to identify most of them (c.f. Gosler 1987).

Parental flank colour was corrected for the effects of the significant variables identified in Table 1 (other than sex) by ANOVA, and major axis regression performed on male and female residuals to test for assortative mating. This correction had to be made to avoid spurious correlations arising from common environmental influences, notably wood size. As before, only those relationships significant after Bonferroni correction ( $P < 0.017$ ) were considered further. Forty five pairs of Great Tits were trapped for this purpose in 1996-1998, and 32 pairs of Blue Tits in 1999-2001.



## RESULTS

### Flank colour in the field

Although both Blue Tits and Great Tits were more saturated with colour in high quality habitat in the field, in neither case was this effect statistically significant. However, Blue Tits breeding in different habitats differed significantly in hue, those in high quality woods being a significantly greener shade of yellow ( $F_{1,200} = 10.38$ ,  $P = 0.001$ ) (Table 1). The size of this difference was small, amounting to  $0.33^\circ$  in males and  $0.59^\circ$  in females. Males had a significantly larger hue angle than females ( $F_{1,200} = 86.65$ ,  $P < 0.0005$ ), and females were significantly lighter than males ( $F_{1,200} = 20.05$ ,  $P < 0.0005$ ). There was no significant sexual difference in saturation (chroma,  $F_{1,200} = 1.90$ ,  $P = 0.169$ ).

Individual Great Tits from high quality habitat were, like Blue Tits, a significantly greener shade of yellow than those from poor habitat ( $F_{1,97} = 10.01$ ,  $P = 0.002$ ). Unlike Blue Tits, they were also significantly lighter ( $F_{1,97} = 7.99$ ,  $P = 0.006$ ). Males had a significantly larger hue angle than females ( $F_{1,97} = 42.79$ ,  $P < 0.0005$ ), and were also significantly lighter ( $F_{1,97} = 14.75$ ,  $P < 0.0005$ ) and more fully saturated with colour ( $F_{1,97} = 8.03$ ,  $P = 0.006$ ).

The original hypothesis was supported in relation to age, since adults moult earlier than juveniles, and adults were more saturated in colour in both species (Blue Tit,  $F_{1,200} = 10.81$ ,  $P = 0.001$ ; Great Tit,  $F_{1,97} = 11.75$ ,  $P = 0.001$ ). It was not upheld in relation to habitat quality, however, since the colour was not significantly more saturated in better habitat.

The only significant interaction in all of these ANOVAs (for full details see *supp mat*) was the year versus wood interaction in Blue Tit lightness ( $F_{5,200} = 4.30$ ,  $P = 0.001$ ). In

two years of the study, birds from large woods were lighter, and in the other four, birds from small woods were lighter.

### **Moult in captivity**

Blue Tits subjected to short daylengths in captivity moulted their primaries and body feathers significantly faster than those on long daylengths (repeated measures ANCOVA,  $F_{1,8} = 5.92$ ,  $P = 0.041$ ). The fitted regression lines showed rates of increase in moult score per day that were nearly twice as fast in the short daylength group (mean  $\pm$  SE =  $0.48 \pm 0.03$ ) as they were in the long daylength group ( $0.25 \pm 0.02$ ). This contrasted with a rate of about 0.65 per day for birds in the field (Ginn & Melville 1983), indicating that taking Blue Tits into captivity reduced the rate of moult, even in the birds subjected to shortening days.

There was no significant difference in the lightness or hue of the flank feathers of these two groups of birds after they had moulted. However, the flanks of the birds on short daylengths (Fig. 1, mean chroma  $\pm$  SE =  $19 \pm 6$ ) were significantly less saturated with yellow pigment than those on long daylengths ( $28 \pm 2$ ). The original expectation was thus upheld. The birds on long daylengths did not differ significantly in saturation from adults measured in the field (Table 1,  $t_{152} = 0.88$ ,  $P > 0.100$ ). Short daylength birds did differ from adults in the field ( $t_{151} = -2.10$ ,  $P = 0.020-0.050$ ), but not from juveniles ( $t_{116} = -0.68$ ,  $P > 0.100$ ).

### **Diet**

Faecal pellets were collected from 171 Blue Tit and 142 Great Tit broods in 1998-2004 and the size of over 3,000 caterpillars estimated from jaws contained therein. Both

species fed a greater mass of caterpillars to their young in high quality habitat than they did in small woods, though only in Great Tits was the difference significant (one-tailed paired *t*-test on yearly means (Fig. 2). The droppings of nestlings from large woods contained caterpillar jaws representing 47% greater dry mass of caterpillars per gram dry mass of faeces in Blue Tits and 81% greater in Great Tits.

### **Assortative mating**

When significant age and habitat effects were controlled in ANOVAs, there was no significant assortative mating on the basis of residual chroma in either species, but there was on the basis of residual hue in Blue Tits (Fig. 3a,  $F_{1,30} = 12.42$ ,  $P = 0.001$ ,  $R^2 = 0.293$ ) and residual lightness in Great Tits (Fig. 3b,  $F_{1,43} = 6.41$ ,  $P = 0.015$ ,  $R^2 = 0.130$ ). Lightness is a measure the total amount of light reflected, regardless of hue or chroma, and so this means that Great Tits that appeared brighter tended to be paired together. The effect size, and statistical significance, of this assortative mating was very similar when the actual colour scores were used rather than the residuals ( $R^2 = 0.287$  and  $0.184$  respectively).

## **DISCUSSION**

The largest differences in colour observed in the field were those between the chroma of adults and juveniles, with adults being more saturated. This difference was consistent in both sexes and habitats. This is in accordance with our original hypothesis, since juvenile body feathers are moulted about three weeks later than those of adults (present results, Flegg & Cox 1969, Ginn & Melville 1983, Cramp & Perrins 1983). As well as moulting faster than adults, juveniles may also be less efficient at absorbing or utilising

dietary carotenoids (Hill 2002). The flanks of male Great Tits, but not Blue Tits, were also more saturated with colour than those of females.

As expected, Blue Tits forced to moult quickly grew feathers that were less fully saturated with yellow pigment, but they did not differ significantly in hue or lightness. Hue is a measure of the dominant wavelength of the reflected light and would not be expected to differ in birds fed an identical diet, and in which the carotenoids responsible for the yellow coloration are deposited in an unmodified form in the feathers (see below).

Although there were significant differences in colour between tits breeding in high and low quality habitats, the differences did not correspond to those induced in the laboratory, since they involved hue and lightness, but not chroma. The different response of birds in the field and in captivity was probably due to the fact that our short daylength regime forced the birds to moult at a rate almost twice that of controls, which was a much larger differential than occurs between birds in large and small woods in the field. Moult was only delayed by a week on average in small woods (Hinsley *et al.* 2003), and a delay three times greater than this only reduced body moult duration in juvenile Great Tits and primary moult in starlings by about 12% (Bojarinova *et al.* 1999, A. Dawson unpublished data). In retrospect, therefore, we accelerated the moult of our short daylength birds (relative to controls) more than would have resulted from the difference in timing between habitats of different quality. Although we could not have predicted it in advance, we accelerated the body moult of short daylength birds to approximately that of juveniles in the field, and consequently fast moulting captives and juveniles from the field did not differ significantly in chroma. Forcing birds to moult faster than normal, by subjecting them to daylengths that are too short may be one of

the factors that leads to the loss of normal carotenoid coloration in captive birds (see Hudon 1994).

High quality habitat did, however, contain birds with larger hue angles. Thus dominant wavelengths closer to green (though still much closer to yellow than green) are characteristic of individuals from better quality habitats (present study and Figuerola *et al.* 1999). This suggests a difference in deposited (and therefore ingested) carotenoids. The yellow colour of the underparts of these two species is due to the presence of the carotenoids  $\beta$ -carotene, lutein and zeaxanthin in the feathers (Partali *et al.* 1987). Adding lutein and zeaxanthin to the diet of nestling Great Tits when they were growing their juvenile plumage in the nest, increased the intensity of the yellow coloration of their breast plumage (Fitze *et al.* 2003b). Partali *et al.* (1987) also found that the body feathers of nestling Great Tits from deciduous woods contained more carotenoids by weight than those from coniferous woods. According to the latter authors, the carotenoids are derived unmodified from the diet of the birds. Caterpillars provide a major source of these carotenoids, especially lutein, which is preferentially absorbed from the leaves on which the caterpillars feed. The ratio of lutein to zeaxanthin is higher in the plumage of chicks reared in deciduous woodland than it is in coniferous woodland (Partali *et al.* 1987) and the proportion of caterpillars in the diet is higher (Cramp & Perrins 1983). Moreover, birds with greater access to caterpillars have a high ratio of lutein to zeaxanthin in the diet, since this is what caterpillars themselves contain (Partali *et al.* 1987). Lutein has peak absorbances at shorter wavelengths (422, 445 and 473 nm in acetone) than zeaxanthin (425, 450 and 476 nm), and thus a higher ratio of lutein to zeaxanthin should result in slightly shorter absorbed wavelengths. This, in turn, would decrease the dominant reflected wavelength, shifting it slightly towards

the green. This is exactly what occurred in both species of tits in our large deciduous woods.

Caterpillar abundance declines throughout the course of the birds' breeding season as the larvae mature and pupate (Lack 1966). However, it seems reasonable to assume that birds that have access to more and larger caterpillars during chick rearing, have similarly improved access (despite reduced caterpillar numbers), during the moult. Reduced caterpillar availability as the season progresses may also account for the successively smaller hue angles (less green shade of yellow) recorded in Great Tits compared with Blue Tits; and in both species, of females compared with males (Table 1). Great Tits are known to moult slightly later than Blue Tits, and females slightly later than males (Ginn & Melville 1983).

Although the above interpretation is consistent with the few existing measurements of the carotenoid content of the flank feathers of these species and their caterpillar diet in different habitats, it remains a tentative one until more complete measurements are made of the carotenoid content of the feathers of birds of different ages, sexes, and with different diets. Simulations have shown, for example, that an increasing concentration of lutein alone (without any change in lutein to zeaxanthin ratio), should produce a shift in yellow away from green towards red i.e. lower hue angles (Andersson & Prager 2006). Moreover, the presence of small amounts of melanin could be responsible for shifting the yellow of carotenoids towards the green to varying extents (Andersson & Prager 2006). The carotenoid content of caterpillars, as well as their numbers, may also differ between habitats.

The yellow colour of individual resident males (i.e. local moulters), provides dispersing females searching for mates with information about the potential quality of

their woods, and provides each party with information about the other's foraging abilities. The latter is supported by Senar *et al.*'s (2002) finding that male foster parent Blue Tits with larger hue angles reared young with longer tarsi, and that our Blue Tits paired assortatively on the basis of flank hue. Hidalgo-Garcia (2006) found that Blue Tits in Spain paired assortatively on the basis of both chroma and lightness, and that the lightest birds raised heavier young with a stronger immune response. The fact that our Great Tits paired assortatively on the basis of lightness may be because, all other things being equal, it is best to select the mate with the cleanest, least worn or least faded (and therefore brightest) plumage. Figuerola & Senar (2005) found that fading was the main factor effecting seasonal changes in the breast colour of individual Great Tits. More generally, flank colour provides all individuals, searching for suitable sites in which to settle, with two sorts of information about individual and habitat quality. Firstly, the average colour saturation (chroma) of residents' flanks provides potential information on the local timing of breeding and moulting, such as that associated with woodland type e.g. coniferous versus deciduous (Slagsvold & Lifjeld 1985), whilst the saturation of particular individuals reflects their likely parental quality within the local area (especially the lack of breeding experience in juveniles). Secondly, the hue of residents' flanks may provide information on the quality of the local food supply e.g. caterpillar abundance, and each individual bird's capacity to exploit it.

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## **Supplementary material**

**Table 2.** Mean  $\pm$  SD flank colour parameters in different groups of Blue and Great Tits, regardless of whether these groups differed significantly or not (sample size in round brackets, range in square brackets).

**Table 3.** ANOVAs of flank colour parameters.

**Table 1.** Statistically significant differences in flank colour parameters between different groups of Blue and Great Tits, based on ANOVAs (see text for significant test results, and *supp mat* for all tests and a complete breakdown by age, sex and habitat). Categories that do not differ significantly have been combined in this table (sample size in brackets).

Species	Parameter	Age	Sex	Habitat quality	Mean $\pm$ SD (n)	
Blue Tit	Chroma	Adult			25.5 $\pm$ 4.3 (115)	
		Juvenile			23.3 $\pm$ 4.5 (112)	
	Hue			Male	Large woods	102.4 $\pm$ 1.1 (59)
				Small woods	102.1 $\pm$ 1.1 (4350)	
		Female	Large woods	100.8 $\pm$ 1.3 (75)		
			Small woods	100.2 $\pm$ 1.1 (56)		
	Lightness			Male		51.7 $\pm$ 2.1 (101)
				Female		53.1 $\pm$ 2.3 (124)
Great Tit	Chroma	Adult	Male		36.6 $\pm$ 4.5 (24)	
			Female		34.5 $\pm$ 2.7 (30)	
		Juvenile	Male		33.5 $\pm$ 4.4 (25)	
			Female		31.8 $\pm$ 3.6 (33)	
	Hue			Male	Large woods	100.1 $\pm$ 1.0 (28)
				Small woods	99.2 $\pm$ 1.2 (21)	
		Female	Large woods	98.4 $\pm$ 1.0 (32)		
			Small woods	97.8 $\pm$ 1.2 (31)		
	Lightness			Male	Large woods	64.1 $\pm$ 3.0 (28)
				Small woods	62.0 $\pm$ 3.3 (21)	
Female		Large woods	61.3 $\pm$ 2.3 (32)			
		Small woods	60.1 $\pm$ 2.5 (31)			

## FIGURE CAPTIONS

**Figure 1.** Degree of saturation (chroma) of the yellow flanks of Blue Tits that moulted at different speeds in the laboratory (means with se bars). Fast moulters were significantly less colourful than slow moulters ( $t_7 = -4.75$ ,  $P < 0.010$ ).

**Figure 2.** Dry weights of caterpillar flesh (means with se bars) represented by the number of pairs of measured caterpillar jaws per gram dry weight of nestling faeces collected from Blue and Great Tit nests in habitats of different quality. More caterpillar flesh was consumed in large woods in both species, but the difference was only significant in Great Tits (one-tailed paired  $t$ -tests on yearly means, Blue Tit,  $t_6 = 1.10$ ,  $P > 0.200$ ; Great Tit,  $t_6 = 2.54$ ,  $P = 0.010-0.025$ ).

**Figure 3.** Significant assortative pairing on the basis of flank coloration in Blue and Great Tits (after removing the significant age and wood effects in Table 1). The major axis regression line is shown (slope = 1.08 in Blue Tits, and 0.86 in Great Tits).

**Table 2.** Mean  $\pm$  SD flank colour parameters in different groups of Blue and Great Tits, regardless of whether these groups differed significantly or not (sample size in round brackets, range in square brackets).

Species	Parameter	Age	Sex	Habitat quality	Mean $\pm$ SD (n) [range]
Blue Tit	Chroma	Adult	Male	Large woods	25.1 $\pm$ 4.2 (31) [13.6-33.1]
				Small woods	26.2 $\pm$ 3.9 (24) [17.9-32.6]
		Female	Large woods	25.0 $\pm$ 4.5 (36) [14.1-32.2]	
			Small woods	26.3 $\pm$ 4.5 (24) [16.4-35.5]	
		Juvenile	Male	Large woods	23.9 $\pm$ 4.7 (28) [13.3-35.3]
				Small woods	24.9 $\pm$ 4.2 (19) [17.7-34.9]
	Female	Large woods	22.9 $\pm$ 3.6 (39) [15.4-30.0]		
		Small woods	21.8 $\pm$ 5.3 (26) [14.0-29.8]		
	Hue	Adult	Male	Large woods	102.7 $\pm$ 1.1 (31) [100.0-104.8]
				Small woods	102.2 $\pm$ 1.2 (24) [100.5-104.1]
		Female	Large woods	100.8 $\pm$ 1.3 (36) [97.5-102.6]	
			Small woods	100.2 $\pm$ 1.1 (24) [98.3-102.5]	
		Juvenile	Male	Large woods	102.2 $\pm$ 1.0 (28) [100.3-104.3]
				Small woods	102.0 $\pm$ 1.1 (19) [100.2-103.9]
	Female	Large woods	100.8 $\pm$ 1.3 (39) [98.5-104.9]		
		Small woods	100.3 $\pm$ 1.2 (26) [97.7-104.0]		
	Lightness	Adult	Male	Large woods	51.5 $\pm$ 2.0 (31) [47.8-56.5]
				Small woods	51.3 $\pm$ 1.6 (24) [47.9-54.2]
Female		Large woods	53.8 $\pm$ 2.1 (36) [48.9-57.2]		
		Small woods	53.1 $\pm$ 2.6 (24) [48.0-57.9]		
Juvenile		Male	Large woods	51.4 $\pm$ 1.9 (28) [47.5-55.8]	
			Small woods	52.4 $\pm$ 2.5 (19) [47.3-57.0]	
Female	Large woods	52.8 $\pm$ 2.2 (39) [47.2-57.5]			
	Small woods	52.7 $\pm$ 2.4 (26) [48.3-57.5]			
Great Tit	Chroma	Adult	Male	Large woods	37.3 $\pm$ 4.4 (16) [27.4-44.2]
				Small woods	35.2 $\pm$ 4.7 (8) [28.9-44.3]
		Female	Large woods	35.5 $\pm$ 2.6 (19) [30.9-39.9]	
			Small woods	32.8 $\pm$ 1.9 (11) [29.4-35.5]	
		Juvenile	Male	Large woods	33.7 $\pm$ 4.3 (12) [29.7-45.9]
				Small woods	33.3 $\pm$ 4.7 (13) [25.3-42.4]
	Female	Large woods	31.4 $\pm$ 3.5 (13) [25.8-37.1]		
		Small woods	32.0 $\pm$ 3.7 (20) [24.7-38.2]		
	Hue	Adult	Male	Large woods	100.0 $\pm$ 1.1 (16) [97.3-102.3]
				Small woods	99.4 $\pm$ 1.1 (8) [97.4-100.6]
		Female	Large woods	98.3 $\pm$ 0.8 (19) [96.6-100.3]	
			Small woods	97.6 $\pm$ 0.8 (11) [96.2-98.9]	
		Juvenile	Male	Large woods	100.2 $\pm$ 1.0 (12) [98.4-101.7]
				Small woods	99.1 $\pm$ 1.3 (13) [97.4-102.1]
	Female	Large woods	98.6 $\pm$ 1.1 (13) [96.6-100.0]		
		Small woods	98.0 $\pm$ 1.4 (20) [96.6-101.6]		
	Lightness	Adult	Male	Large woods	64.3 $\pm$ 2.7 (16) [59.8-69.3]
				Small woods	62.2 $\pm$ 3.3 (8) [58.3-68.7]
Female		Large woods	61.8 $\pm$ 2.3 (19) [58.2-66.7]		
		Small woods	58.9 $\pm$ 2.6 (11) [55.7-62.5]		
Juvenile		Male	Large woods	63.7 $\pm$ 3.4 (12) [60.3-69.8]	
			Small woods	61.8 $\pm$ 3.4 (13) [56.5-66.2]	
Female	Large woods	60.7 $\pm$ 2.4 (13) [56.9-64.6]			
	Small woods	60.8 $\pm$ 2.1 (20) [57.2-64.5]			

**Table 3.** ANOVAs of flank colour parameters. The maximum value of *P* indicating significance = 0.017 after Bonferroni correction.

Species	Colour parameter	Explanatory variable	<i>F</i>	df	<i>P</i>
Blue Tit	Chroma	Year	1.52	5, 200	>0.100
		Sex	1.90	1, 200	>0.100
		Age	10.81	1, 200	0.001
		Wood	0.29	1, 200	>0.100
		Year × Sex	1.25	5, 200	>0.100
		Year × Age	2.10	5, 200	0.067
		Year × Wood	1.48	5, 200	>0.100
		Sex × Age	2.72	1, 200	0.100
		Sex × Wood	0.43	1, 200	>0.100
		Age × Wood	0.94	1, 200	>0.100
	Hue	Year	1.36	5, 200	>0.100
		Sex	86.65	1, 200	<0.0005
		Age	0.29	1, 200	>0.100
		Wood	10.38	1, 200	0.001
		Year × Sex	0.46	5, 200	>0.100
		Year × Age	0.30	5, 200	>0.100
		Year × Wood	0.86	5, 200	>0.100
		Sex × Age	1.76	1, 200	>0.100
		Sex × Wood	0.31	1, 200	>0.100
		Age × Wood	0.12	1, 200	>0.100
	Lightness	Year	2.36	5, 200	0.041
		Sex	20.05	1, 200	<0.0005
		Age	1.02	1, 200	>0.100
		Wood	0.06	1, 200	>0.100
		Year × Sex	0.86	5, 200	>0.100
		Year × Age	2.21	5, 200	0.054
		Year × Wood	4.30	5, 200	0.001
		Sex × Age	2.04	1, 200	>0.100
Sex × Wood		1.56	1, 200	>0.100	
Age × Wood		1.15	1, 200	>0.100	
Great Tit	Chroma	Year	0.26	2, 97	>0.100
		Sex	8.03	1, 97	0.006
		Age	11.75	1, 97	0.001
		Wood	2.97	1, 97	0.088
		Year × Sex	1.53	2, 97	>0.100
		Year × Age	1.08	2, 97	>0.100
		Year × Wood	1.47	2, 97	>0.100
		Sex × Age	0.03	1, 97	>0.100
		Sex × Wood	0.21	1, 97	>0.100
		Age × Wood	3.06	1, 97	0.083
	Hue	Year	0.03	2, 97	>0.100
		Sex	42.79	1, 97	<0.0005
		Age	0.51	1, 97	0.002
		Wood	10.01	1, 97	0.002
		Year × Sex	0.38	2, 97	>0.100
		Year × Age	0.72	2, 97	>0.100
		Year × Wood	1.66	2, 97	>0.100
		Sex × Age	0.22	1, 97	>0.100
		Sex × Wood	0.38	1, 97	>0.100
		Age × Wood	0.21	1, 97	>0.100
	Lightness	Year	0.78	2, 97	>0.100
		Sex	14.75	1, 97	<0.0005
		Age	0.06	1, 97	>0.100
		Wood	7.99	1, 97	0.006
		Year × Sex	0.04	2, 97	>0.100
		Year × Age	1.33	2, 97	>0.100
		Year × Wood	1.73	2, 97	>0.100
		Sex × Age	0.55	1, 97	>0.100
Sex × Wood		0.51	1, 97	>0.100	
Age × Wood		1.39	1, 97	>0.100	



Figure 1

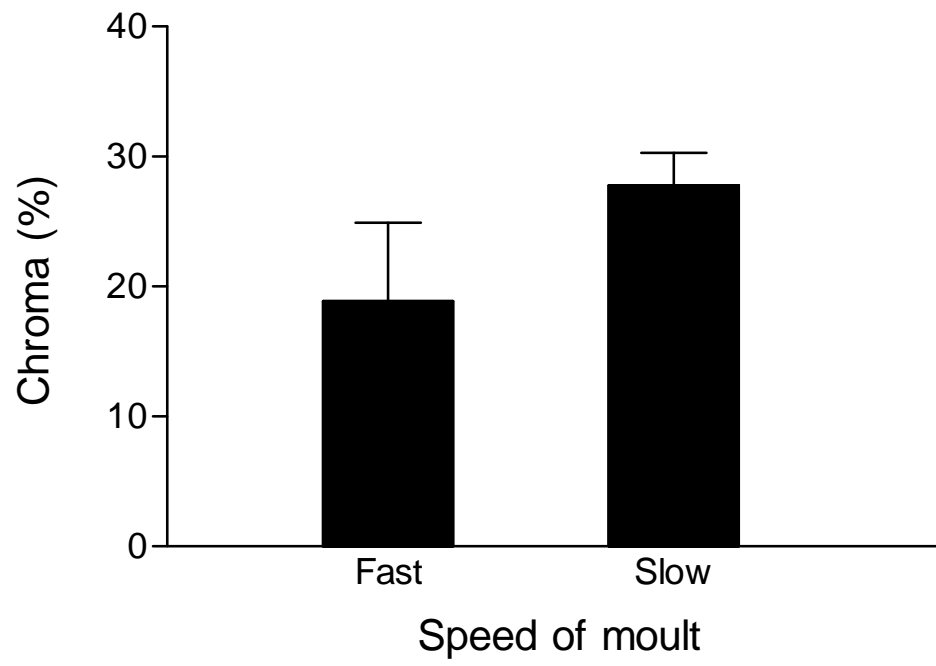


Figure 2



Figure 3

