

Effects of nestling condition on UV plumage traits in blue tits: an experimental approach

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Intraspecific sexual and social communications are among the most important factors shaping costly color traits in birds. Condition capture models assume that only animals in superior condition can develop and maintain a colorful plumage. Although there is good evidence that carotenoid-based components of plumage colors show condition dependence, the situation is more controversial with the underlying UV-reflecting structural component. We conducted a brood size manipulation in blue tits (*Parus caeruleus*) to investigate condition-dependent effects on plumage coloration in male and female offspring. Carotenoid chroma and UV reflectance of the yellow breast plumage showed condition-dependent expression in male and female fledglings. However, only males that were raised in reduced broods had higher UV reflectance in the UV/blue tail feathers, whereas female tail coloration did not differ between treatments. Our data suggest that there is a sex-specific effect on the blue but not the yellow plumage and that this is related to differences in the signaling function of both plumage traits. Although sexual selection may already act on male nestlings to develop colorful tail feathers for the next breeding season, the UV/yellow breast feathers are molted during the postjuvenile molt, and their signaling value is likely to be important for both sexes during the extended postfledgling phase. *Key words:* carotenoids, condition dependence, *Cyanistes caeruleus*, *Parus caeruleus*, plumage color, UV. [*Behav Ecol* 18:34–40 (2007)]

Intraspecific variation in plumage coloration is a widespread phenomenon in many bird species. Most variation is explained by sexual dichromatism, but substantial variation exists within gender and among immature birds. Although the evolution of colorful male plumage is best explained through sexual selection processes, immature and female birds may benefit from costly plumage signals in intra- and interspecific interactions (Andersson 1994; Owens and Hartley 1998; Maynard-Smith and Harper 2003). Indicator and condition capture models assume that plumage colors are costly to produce or maintain and that color expression is positively related to an individual's quality (Zahavi 1977; Nur and Hasson 1984; Grafen 1990; Cotton et al. 2004). Hence, only individuals in prime condition are able to produce or maintain intense coloration, which thereby guarantees the honesty of the signal.

To understand the costs associated with variation in plumage coloration, knowledge about the anatomical and physical mechanisms of plumage color expression is required. However, despite extensive research, these mechanisms are still not fully understood. Feather colors are generally divided into pigment-based (e.g., melanin- and carotenoid-based colors) and structural colors. This is somewhat misleading, in the sense that most plumage colors result from a combination of light reflection by the feather or its structural components and light absorption by incorporated pigments (Shawkey and Hill 2005). For example, structural UV/blue colors, which show a single pronounced reflectance peak in the short wavelengths, result from a combination of coherent, constructive light reflectance at a complex keratin microstructure and light absorption by the underlying melanin granules (Prum et al. 1998, 2003; Prum and Torres 2003). Yellow to red feather colors, on the other hand, result from light reflectance at the feathers' structure in combination with carotenoid-specific light absorption (Cuthill et al. 1999;

Bleiweiss 2004a, 2004b). Carotenoid spectra thereby typically exhibit a bimodal profile with a peak in the UV part (between 300 and 400 nm) and a plateau in the longer wavelengths (between 500 and 700 nm). The UV portion of carotenoid colors is probably produced by an entirely different mechanism (i.e., incoherent scattering) as it does probably not have a microstructure specialized to reinforce (via coherent scattering) particular wavelengths (for details see Prum 2006). Recent studies demonstrated that the carotenoid content of yellow, orange, and red plumage colors confers reliable information about an individual's overall growing conditions (Hill 2000; Horak et al. 2000; Tschirren et al. 2003), parasitic infection (McGraw and Hill 2000; Fitze et al. 2004), and immune status (Hill 2002; Blount et al. 2003). The causes of variation in UV/blue, violet, or green plumage colors and the information conveyed by this variation are more controversial. It has been suggested that variation in saturation of these colors is caused by variation in the regularity of a feather's microstructure (Andersson 1999; Shawkey et al. 2003, 2005). Because feather synthesis is a long-lasting, continuous, and physiologically costly process, any developmental stress during this period may alter feather characteristics. Only individuals in prime condition are expected to grow feathers with a regular microstructure that translates into more saturated structural colors and thereby enhanced signaling value. McGraw et al. (McGraw et al. 2002) showed that the non-UV-reflecting iridescent green plumage of cowbirds honestly reflected nutritional condition during molt. Additionally, the iridescent plumage of turkeys was negatively affected by coccidial infection (Hill et al. 2005), and recent correlational studies suggest that UV/blue colors are partially condition dependent (Bennett et al. 1996, 1997; Keyser and Hill 1999, 2000; Johnsen et al. 2003; Siefferman and Hill 2003) and correlate with levels of male paternal care (Siefferman and Hill 2003; Siefferman et al. 2005). To date, there is only one experimental study showing the condition dependence of UV plumage traits. Siefferman and Hill (2005) demonstrated that female eastern bluebirds that were given ad libitum access to food developed more ornamented structural coloration than females on a food-restricted diet.

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Received 25 January 2006; revised 3 August 2006; accepted 12 August 2006.

Here, we investigate the effects of a brood size manipulation on the UV-reflecting yellow carotenoid-based breast coloration and the UV/blue tail coloration in male and female nestling blue tits (*Parus caeruleus*). It is important to note that the body feathers (e.g., breast and crown) are molted during the postjuvenile molt, whereas most tail feathers are only replaced after the first breeding attempt in the following year (Cramp and Perrins 1993). This difference in feather development and molting pattern might affect the selection pressures acting on the different feather colors and thereby their condition dependence and signaling value. The juvenile's breast coloration might have a signaling function during the extended postfledging phase, whereas the male tail coloration is expected to be a signal in the next breeding season. Thus, nestling condition and its consequences on plumage coloration may have important consequences for an individual's first-year breeding success through male-male competition (Alonso-Alvarez et al. 2004), female choice (Hunt et al. 1998, 1999; Delhey et al. 2003), and female reproductive investment (Limboung et al. 2004; Johnsen et al. 2005; Korsten et al. 2006).

A previous study on blue tits already suggested the condition dependence of the blue and yellow plumage coloration in blue tits (Johnsen et al. 2003). However, that study is based on correlative evidence only, and the authors did not investigate the UV part of the carotenoid-based double-peaked spectra. An experimental approach as presented in this paper is needed, because most, if not all, traits show positive relationships with mass or body condition. Only an experimental study can reveal whether the color traits reported by Johnsen et al. (2003) show treatment effects that are above that associated with changes in absolute or residual body mass. Blue tit nestlings seem ideal model system because males and females possess UV/blue and UV/yellow plumage coloration, both colors with higher degree of elaboration in males. This offers the opportunity to investigate key predictions of handicap models, that ornaments will show stronger condition dependence in males compared with females, and that condition dependence should increase as ornaments become more exaggerated, that is, sexually dichromatic (Cotton et al. 2004).

METHODS

General methods

The study was conducted in 2004 in a color-banded blue tit population breeding in nest-boxes in a mixed deciduous forest at Kolbeterberg, Vienna, Austria (48°13'N, 16°14'E). Nest-boxes were checked regularly for start of egg laying, start of incubation, and hatching.

Nestling body mass was measured on days 2 and 18 after hatching, with day 0 as day of hatching. On day 14, nestlings were banded, tarsus length and wing length were measured, and a small blood sample was collected for molecular sexing. On day 18, shortly before fledging, we measured body mass and breast coloration following the procedures described in Johnsen et al. (2003). We used a handheld spectrometer (AvaSpec-2048, Avantes, Eerbeek, The Netherlands) connected to a deuterium-halogen light source (AvaLight-DHS, Avantes) through a bifurcated fiber optic probe. The probe was fitted at the end with a plastic cylinder to standardize measuring distance and exclude ambient light. We measured 5 different spots on the breast (2 on each side and 1 in the middle). In addition, we plucked a tail feather (third from the right) to measure variation in the UV/blue tail feather coloration. The measured feather is expected to be representative because the outer vanes of all 4 outer rectrices show a UV-reflecting blue coloration. Johnsen et al. (2003) measured

tail coloration of 19-day-old chicks in the field (compared with day 18 in our study) and obtained similar values for tail colour scores. In the laboratory, the tail feather spectra were measured against a black velvet background with uniform, low reflectance across all wavelengths. Reflectance spectra were measured at 3 different spots along the erupting tail feather. Total feather length and the length of the erupted part of the feather were measured with slide calipers. The fledglings' grayish crown coloration was not measured because fledged birds acquire the adult UV/blue crown during postjuvenile molt in autumn (Cramp and Perrins 1993).

Feather reflectance was calculated between 300 and 700 nm relative to a WS-2 white standard (Avantes). As described in detail in Johnsen et al. (2003), we computed the objective indices of the 3 main dimensions of color perception: brightness (spectral intensity), hue (spectral location of peak reflectance), and chroma (spectral saturation). Brightness of tail and breast feathers was estimated by calculating the average reflectance between 300 and 700 nm. Due to the double-peaked spectra of the carotenoid-based breast feathers, hue (R_{\max}) was only calculated in tail feathers. Chromatic information was assessed using a general measurement of chroma ($R_{\max} - R_{\min}$)/ R_{average} (tail feathers only) and specific measures of carotenoid and UV chroma. For the yellow breast feathers, we calculated carotenoid chroma [$(R_{700 \text{ nm}} - R_{450 \text{ nm}})/R_{700 \text{ nm}}$], which represents relative reflectance around peak absorbance of carotenoids. Two different methods were used to calculate UV chroma. In the UV/blue tail feathers, we measured the proportion reflecting in the UV waveband ($R_{300-400 \text{ nm}}/R_{300-700 \text{ nm}}$; Andersson and Amundsen 1997; Andersson et al. 1998). For the breast feathers, the intensity of the UV peak depends on the amounts of carotenoids (correlation between UV chroma and carotenoid chroma: $r = 0.847$, $N = 368$, $P < 0.001$) as they absorb highly at wavelengths between 400 and 500 nm, creating a dip in what would otherwise be a sharply increasing curve followed by a plateau (Shawkey and Hill 2005). Despite the strong correlation between both measures, different physiological mechanisms are involved in producing both color traits and they may potentially act as multicomponent signals, revealing different aspects of an individual's quality or condition (Candolin 2004). Thus, to get a measure of UV chroma at the maximum reflectance in the UV waveband [$(R_{\text{UV peak}} - R_{450 \text{ nm}})/R_{\text{UV peak}}$; Bleiweiss 2004a], we need to control for carotenoid chroma. In the subsequent statistical models analyzing treatment effects on UV components in the breast plumage, we do this by incorporating carotenoid chroma as a covariate.

Brood size manipulation

The brood size manipulation was implemented among 22 pairs of nests with the same hatching date and a similar brood size (± 1 chick). On day 2, chicks were partially cross-fostered between nests, creating reduced (-2 chicks) and enlarged broods ($+2$ chicks) remaining in the natural brood size range. Nestlings were ranked according to their body mass in the nest of origin. The heaviest nestling was randomly assigned to stay in the nest of origin or to be exchanged to the partner nest. Cross-foster treatment (exchange/stay) was then alternated through the mass-based rank list. To keep within-brood variance in nestling body mass equal between experimental treatments, we increased experimental broods by randomly selecting 2 nestlings, except the lightest and the heaviest chick. Following this procedure, increased and decreased broods had on average the same number of original and foster chicks. Prior to brood size manipulation, reduced and enlarged broods did neither differ in clutch size (reduced: 12.1 ± 0.36 and enlarged: 12.4 ± 0.39 ; $F_{1,33} = 0.31$, $P = 0.58$)

nor in brood size (reduced: 11.3 ± 0.39 and enlarged: 11.2 ± 0.37 ; $F_{1,33} = 0.03$, $P = 0.86$). After the brood size manipulation treatments differed significantly in chick number at day 2 (reduced: 9.3 ± 0.39 and enlarged: 13.2 ± 0.37 ; $F_{1,33} = 50.85$, $P < 0.001$) and day 18 (reduced: 9.1 ± 0.53 and enlarged: 12.6 ± 0.21 ; $F_{1,33} = 30.03$, $P < 0.001$). We measured nestling coloration in 35 out of 44 cross-fostered nests (15 enlarged, 20 reduced). Four enlarged broods were predated, either by greater spotted woodpeckers (*Picoides major*, $N = 2$) or by aesculapian snakes (*Elaphe longissima*, $N = 2$), whereas all chicks in 2 reduced nests died because of female depredation or desertion. Additionally, 3 enlarged broods had to be excluded from further analyses because they were used in another experiment.

Statistical analyses

Statistical analyses were performed with the freeware R 2.1.1 (R Development Core Team 2005). Mortality was analyzed with a general linear mixed effect model with binomial error distribution that included survival until fledging (yes/no) as dependent variable, the brood size manipulation as fixed factor, and the brood of rearing as random factor. To analyze the effects of the experimental treatment on juvenile body mass, structural size, and plumage coloration, we performed mixed effect models (sequential tests) with crossed random effects as described in detail by Pinheiro and Bates (2000, p. 163). These types of models are known to perform well for unbalanced data sets and/or with complex random structures. All models a priori included the sex of the nestlings and the brood size manipulation as fixed factors and box of origin and rearing as random factors. To analyze treatment effects on tail coloration, we included the length of the erupted feather as covariate (see Johnsen et al. 2003). For model simplification, we used a stepwise backward procedure and tested the significance of predictor variables in a hierarchical fashion, retaining lower order effects in the analyses in case a higher order term was significant. Model assumptions were fulfilled in all analyses. In mixed models with a complex random structure (i.e., more than one random level and in-

dependent cross random effects), the test statistics only approximate an F distribution. Therefore, the denominator degrees of freedom (df) cannot be computed accurately, and Tables 1 and 2 present denominator df at their upper bound (default in R 2.1.1). However, the most important part of a mixed model is the unbiased estimation of the F statistic and therefore is the correct test of the hypothesis. Note that changes in the denominator degrees of freedom have only a small influence on P values.

RESULTS

Treatment effects on nestling survival, body mass, condition, and structural traits

Nestling mortality between day 2 (day of cross-fostering) and day 18 was not different between experimentally reduced and enlarged broods (logistic regression: $\chi^2 = 0.001$, $P = 0.97$). Mean nestling survival was 0.94 ± 0.03 and 0.94 ± 0.02 for the reduced and enlarged groups, respectively.

The brood size manipulation significantly affected nestling body mass, tarsus length, and body condition (body mass controlled for tarsus length; Table 1). Chicks from reduced broods were heavier, had longer tarsi, and were in better body condition compared with chicks from enlarged broods. In contrast, the experimental treatment did not affect wing length or tail feather development (Table 1). In all analyses, nestling sex was included. We found that males were heavier and larger than females, but the treatment effect was independent of sex (Table 1).

Treatment effects on plumage coloration

The brood size manipulation did neither affect tail brightness nor tail hue, but nestlings from reduced broods had more chromatic tail feathers compared with chicks from enlarged broods (Table 2). There was a tendency that UV reflectance of the tail feathers showed a sex-specific expression pattern (sex \times brood size manipulation: $F_{1,348} = 3.46$, $P = 0.063$). To corroborate this result, we analyzed the sexes separately. Males

Table 1

Effects of the brood size manipulation on male and female nestling body mass, body condition, and structural traits

	Factor	Estimates	SE	df	F	P
Body mass 18 (g)	Sex ^a	-0.63	0.06	1,362	98.18	<0.001
	Brood size manipulation ^b	0.291	0.11	1,362	7.06	0.008
	Brood size manipulation \times sex	-0.043	0.06	1,361	0.46	0.50
Tarsus length (mm)	Sex ^a	-0.437	0.06	1,366	48.83	<0.001
	Brood size manipulation ^b	0.11	0.04	1,366	6.74	0.010
	Brood size manipulation \times sex	-0.05	0.06	1,365	0.67	0.42
Body condition 18 (g)	Tarsus length	0.316	0.05	1,361	90.90	<0.001
	Sex ^a	-0.485	0.07	1,361	55.47	<0.001
	Brood size manipulation ^b	0.250	0.11	1,361	5.66	0.018
Wing length (mm)	Brood size manipulation \times sex	-0.027	0.06	1,360	0.20	0.66
	Sex ^a	-0.89	0.24	1,362	14.07	<0.001
	Brood size manipulation ^b	0.46	0.31	1,362	2.20	0.14
Feather length (mm)	Brood size manipulation \times sex	0.002	0.24	1,361	<0.01	0.99
	Sex ^a	-0.09	0.27	1,355	0.14	0.71
	Brood size manipulation ^b	0.53	0.35	1,359	2.31	0.13
Erupted feather (mm)	Brood size manipulation \times sex	-0.11	0.27	1,354	0.17	0.68
	Sex ^a	0.43	0.29	1,355	2.20	0.14
	Brood size manipulation ^b	0.33	0.37	1,359	0.82	0.37
	Brood size manipulation \times sex	-0.086	0.288	1,354	0.09	0.77

All analyses are controlled for brood of origin and brood of rearing as random factors. For statistical details see Methods. SE = standard error.

^a Estimates are relative to males.

^b Estimates are relative to enlarged broods.

Table 2

Estimates and test statistics for feather color traits in relation to the brood size manipulation while controlling for feather length (tail color only) and the sex of the nestlings

	Factor	Estimates	SE	df	F	P	
Tail feathers	Brightness	Feather length	0.20	0.03	1,350	38.82	<0.001
		Sex ^a	0.50	0.20	1,350	6.45	0.012
		Brood size manipulation ^b	0.09	0.11	1,349	0.64	0.42
		Brood size manipulation × sex	-0.07	0.20	1,348	0.14	0.71
	Hue	Feather length	-0.01	0.12	1,349	<0.01	0.96
		Sex ^a	1.36	0.69	1,357	3.93	0.048
		Brood size manipulation ^b	-0.28	0.49	1,356	0.31	0.58
		Brood size manipulation × sex	0.68	0.69	1,348	0.99	0.32
	Chroma	Feather length	0.01	0.002	1,349	28.68	<0.001
		Sex ^a	-0.14	0.01	1,349	176.59	<0.001
		Brood size manipulation ^b	0.02	0.01	1,349	4.65	0.032
		Brood size manipulation × sex	-0.02	0.01	1,348	2.45	0.12
	UV chroma	Feather length	0.14	0.02	1,349	33.64	<0.01
		Sex ^a	-1.20	0.24	1,349	227.49	<0.01
Brood size manipulation ^b		0.47	0.18	1,349	4.26	0.039	
Brood size manipulation × sex		-0.20	0.11	1,348	3.46	0.063	
Breast feathers	Brightness	Sex ^a	-1.08	0.29	1,364	13.82	<0.001
		Brood size manipulation ^b	0.04	0.25	1,363	0.03	0.87
		Brood size manipulation × sex	-0.04	0.29	1,362	0.02	0.88
Carotenoid chroma	Sex ^a	Brood size manipulation ^b	-0.02	0.005	1,363	23.18	<0.001
		Brood size manipulation × sex	0.01	0.003	1,363	8.53	0.004
		Brood size manipulation × sex	0.002	0.005	1,362	0.12	0.73
UV chroma	Carotenoid chroma	Sex ^a	0.65	0.02	1,363	1165.1	<0.001
		Sex ^a	-0.002	0.002	1,360	0.93	0.33
		Brood size manipulation ^b	0.01	0.004	1,363	6.48	0.011
		Brood size manipulation × sex	-0.002	0.002	1,359	1.09	0.30

All analyses are controlled for brood of origin and brood of rearing as random factors. For statistical details see Methods. SE = standard error.

^a Estimates are relative to males.

^b Estimates are relative to enlarged broods.

from reduced broods developed more UV-reflecting tail feathers compared with males from enlarged broods (feather length: $F_{1,164} = 33.89$, $P < 0.001$; treatment: $F_{1,164} = 6.73$, $P = 0.01$), whereas the brood size manipulation had no effect on UV reflectance of female tail feathers (feather length: $F_{1,185} = 30.83$, $P < 0.001$; treatment: $F_{1,185} = 0.45$, $P = 0.50$; Figure 1). In a next step, we analyzed whether variation in male tail feather coloration could be explained through treatment-induced changes in body mass or whether the treatment affected coloration independent of body condition. When entering body mass ($F_{1,165} = 5.55$, $P = 0.019$) into the analysis, the treatment effect is still significant ($F_{1,165} = 5.20$, $P = 0.024$). Thus, variation in UV reflectance is partly related to body mass (as has already been shown in correlational studies), but the brood size manipulation had additional effects on tail coloration, independent of body mass. Males had brighter, more chromatic feathers, and the hue was shifted toward shorter wavelengths (Table 2).

The brood size manipulation did not affect the brightness of the yellow breast feathers (Table 2). Yet, the treatment significantly affected carotenoid chroma and UV chroma of breast feathers (Table 2). Chicks in reduced broods had more carotenoid-rich and UV-chromatic breast feathers than chicks in enlarged broods (Figure 2), independent of nestling sex (both interactions: $P > 0.25$). Again, when entering body mass on day 18 as covariate into the model (both $P < 0.001$), the main treatment effect remained significant (for UV chroma: $F_{1,362} = 5.89$, $P = 0.02$) or very close to significance (for carotenoid chroma: $F_{1,361} = 3.47$, $P = 0.06$). Thus, the brood size manipulation affected the UV reflectance of the breast

plumage independent of changes in body mass. Additionally, there were significant differences between male and female breast plumage coloration. Males had brighter and carotenoid richer plumages, whereas UV reflectance was not sexually dichromatic (Table 2).

DISCUSSION

This experimental study demonstrates that UV-reflecting structural components are condition-dependent plumage traits that reliably reflect juvenile growing conditions during the period of feather development and affect plumages of different coloration. Interestingly, the treatment effects were most pronounced in the color traits with the highest sexual dichromatism (tail: UV chroma; breast: carotenoid chroma), and the effects were always independent of changes in body mass. Thus, body mass and plumage colour traits independently responded to the brood size manipulation, and there was no evidence that both traits are causally related. Whether receivers are able to discriminate against low-quality individuals on the basis of the observed variation in UV-reflecting plumage traits remains to be shown. Colour discrimination is limited by noise in the photoreceptors and neural mechanisms (Vorobyev and Osorio 1998), but sensitivity in the UV wavelengths is expected to be very high (Goldsmith and Butler 2003). Proof that variation in plumage coloration is actually perceived by the receiver, ultimately requires behavioral experiments under natural light conditions (e.g., Limbourg et al. 2004; Johnsen et al. 2005; Korsten et al. 2006).

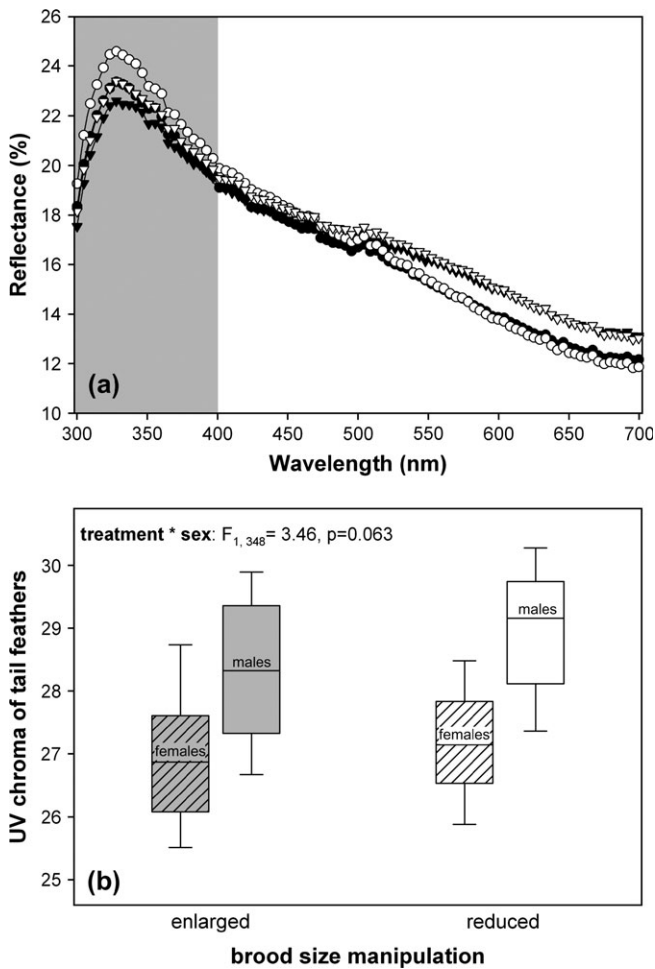


Figure 1
 Reflectance spectra from the tail feathers of blue tit nestlings across the range of spectral sensitivity (a). The shaded region indicates the UV waveband (300–400 nm). The spectra with the open symbols indicate chicks from reduced broods, whereas the spectra with the solid symbols indicate chicks from enlarged broods. Triangular symbols specify female spectra, whereas male spectra are indicated with circular symbols. (b) Effect of the brood size manipulation on the UV chroma of tail feathers of male and female blue tit nestlings on day 18 (sex \times brood size manipulation: $P = 0.063$). Note that the graph shows box plots of the raw data, whereas the statistics in the Results are based on restricted maximum likelihood mixed models.

Feathers are energetically expensive to produce (Lindström et al. 1993; Klaassen 1995), and malnutrition impairs feather growth and quality (Murphy et al. 1988). In our study, feather length was unaffected by the brood size manipulation and did not explain the observed treatment effects on plumage coloration. However, aspects of the feather quality that translate into color differences might be altered by the brood size manipulation. Even small changes in the 3-dimensional arrangement pattern or size of the feather's microstructure can cause variation in the UV/blue plumage color (Shawkey et al. 2003). In enlarged broods, suboptimal growing conditions and developmental stress during feather growth may have impaired the production or arrangement of microstructural feather elements required for maximum coloration. Alternatively, variation in feather coloration could have been caused by abrasion of the feather's microstructure or by the accumulation of dirt or specific chemical compounds during the nestling phase. A study by Neuenschwander et al. (2003) has demonstrated that chicks in experimentally enlarged broods

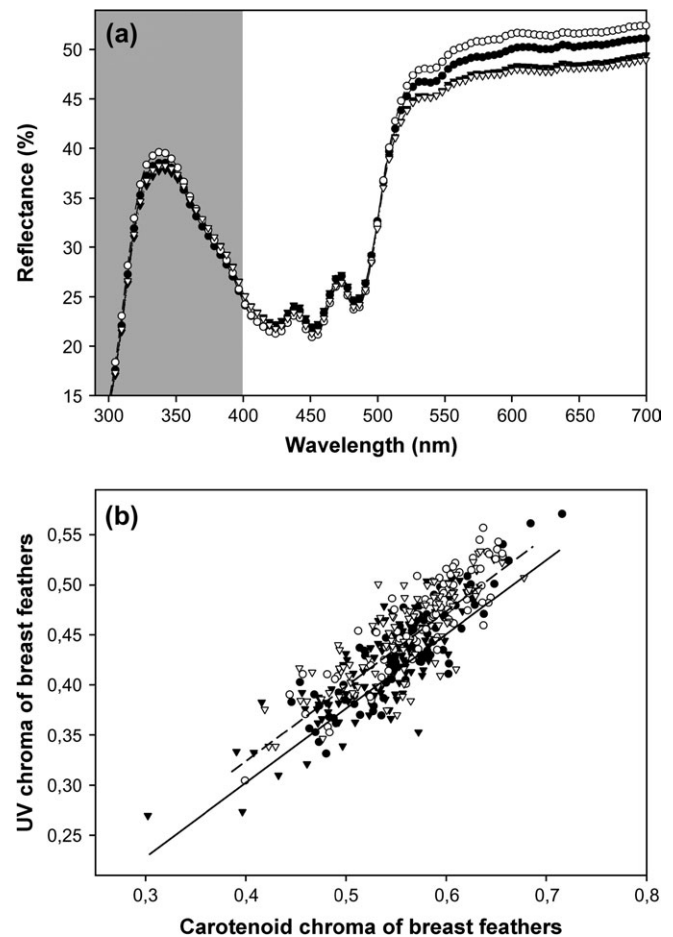


Figure 2
 (a) Reflectance spectra from the breast feathers of blue tit nestlings across the range of spectral sensitivity. The spectra with the open symbols indicate the mean spectra of chicks in reduced broods, whereas the solid spectra indicate the mean spectra of chicks in enlarged broods. Triangular and circular symbols indicate females and males, respectively. (b) Relationship between carotenoid chroma and UV chroma of breast feathers in relation to the brood size manipulation. Chicks in reduced broods (dashed regression line) had relatively more UV-chromatic breast feathers than chicks in enlarged broods (solid regression line).

show an increase in begging rates and mobility. Thus, this increase in overall activity (i.e., scramble competition) and the tight squeezing of nestlings in enlarged broods could affect feather wear and hygienic conditions, which could ultimately reduce UV reflectance of the plumage coloration. Örnborg et al. (2002) suggested that dirt and fat mostly absorb at short wavelengths, which would mainly affect UV coloration. In budgerigars, it has recently been shown that individuals that were prevented from preening showed a reduced coloration mainly in the UV waveband, which translated into reduced sexual attractiveness (Zampiga et al. 2004). Such mechanisms might explain why the brood size manipulation affected the UV reflectance independent of treatment-induced changes in nestling body mass.

These mechanisms, however, do not explain why only males would show a condition-dependent expression of the UV/blue tail feathers. A study on great tits (Oddie 2000) suggests that the males as the more competitive sex should do relatively better under stressful conditions (i.e., in enlarged broods). Our data do not support this hypothesis, and the discrepancy in coloration is probably related to different

selection pressures acting on male and female plumage colors. Male tail coloration might have coevolved with the female preference for more chromatic feathers, which are more costly to produce and thereby show stronger condition dependence. In contrast, female blue tits showed no significant condition dependence of the UV/blue tail coloration, which indicates that the coloration may approximate the ancestral state where no directional selection has led to a costly exaggeration of the trait. As already mentioned in the introduction, outer UV/blue tail feathers are not molted during the postjuvenile molt (Cramp and Perrins 1993) and are likely to have a signaling function in inter- or intraspecific sexual selection for the next breeding season. Plumage color scores from previous years (1999–2003) revealed that nestling tail coloration is positively related to the tail coloration ($r^2 = 0.16$) and the UV/blue crown coloration ($r^2 = 0.34$) in the first breeding attempt in the subsequent year (our unpublished data). Sexual selection might therefore already act on male nestlings to develop a colorful plumage that will enhance male sexual attractiveness in the following year. Despite the nonsignificance of the interaction (sex \times brood size manipulation: $P = 0.064$), our results support an important prediction of sexual selection theory, which states that ornaments will have increased condition dependence as they become more exaggerated and thereby more costly (Cotton et al. 2004). Further research is clearly needed to confirm these findings and to investigate the condition-dependent expression patterns of sexual ornaments in relation to the degree of sexual dichromatism.

In contrast to the tail feathers, both male and female fledglings show condition-dependent expression of their UV/yellow breast coloration. Body feathers (e.g., breast and crown) are replaced during the postjuvenile molt in late summer/autumn, and intense plumage coloration might serve as a signal to the feeding parents and/or indicate social dominance to the siblings during the extended postfledging phase. In great tits, parental feeding allocation rules during the nestling stage were not affected by the experimentally altered carotenoid content of the nestlings' yellow plumage (Tschirren et al. 2005). However, plumage traits may have an important signaling function to the parents during the extended postfledging phase, and parents may enhance their fitness via differentially allocating resources to their offspring via assessing nestling "value" according to phenotypic plumage traits (Lyon et al. 1994). Interestingly, only blue tit nestlings show pronounced sexual dichromatism in the UV/yellow breast coloration, whereas adults are mainly monochromatic and show higher levels of carotenoid chroma (Johnsen et al. 2003). However, a higher degree of elaboration in adults does not necessarily imply heightened condition dependence (Fitze and Richner 2002) because the relative costs to produce a colorful plumage might be higher for nestlings than for adults. Additionally, the signaling value of the color might change between life stages, and future research is urgently needed to understand the ultimate function of plumage colors in social and sexual interactions.

We thank May Seet, Mihai Valcu, Kristine Kasparian, Irene Kopetz, Agnes Türk, Kees van Oers, and Kim Teltscher for assistance in the field and Jim Dale and 3 anonymous referees for valuable comments on an earlier version of the manuscript. The study received financial support from the Max Planck Society and from the Swiss National Science Foundation through a research grant (PBBEA-105034) to A.J.

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