



Plumage yellowness predicts foraging ability in the blue tit *Cyanistes caeruleus*

VICENTE GARCÍA-NAVAS*, ESPERANZA S. FERRER and JUAN JOSÉ SANZ

Área de Zoología, Facultad de Ciencias Ambientales y Bioquímica, Universidad de Castilla-La Mancha, Avenida Carlos III s/n 45071 Toledo, Spain

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Carotenoid-based coloration in adult birds has been often regarded as an honest signal of individual quality. However, few studies have demonstrated a link between carotenoid display and the quantity or quality of resources provided to the offspring. The present study investigated the expression of a carotenoid-based ornament, the breast plumage yellowness of the blue tit *Cyanistes caeruleus*, in relation to the level of parental provisioning effort and the amount of carotenoid-rich prey provided to the young. The study was conducted in two forest types (evergreen and deciduous), which also allowed an exploration of the possible existence of habitat effects on the coloration of breeding birds. It was found that plumage colour intensity (carotenoid chroma) correlated positively with nestling provisioning rates of both males and females, supporting the good parent hypothesis. In addition, carotenoid chroma was positively related with the proportion of Lepidoptera larvae brought to the nest in both sexes. Female but not male coloration was positively linked to breeding success (proportion of fledged young). Nestling coloration did not correlate with that of their parents, nor the frequency with which they were fed. Hue and lightness of nestling's plumage correlated positively with body mass and tarsus length, respectively. The results obtained in the present study indicate that ventral plumage coloration in blue tits may advertise the ingested carotenoids (carotenoid foraging ability) and also their overall parental quality in terms of nestling provisioning rates. This suggests that plumage yellowness can be used as an indicator of foraging ability in this species. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 418–429.

ADDITIONAL KEYWORDS: carotenoids – coloration – feeding effort – good parent – nestling diet – Paridae.

INTRODUCTION

Over the last 15 years, evolutionary and behavioural biologists have become increasingly interested in carotenoid-based coloration as an honest signal of individual quality (Lozano 1994; Olson & Owens, 1998; Møller *et al.*, 2000). Carotenoids cannot be synthesized *de novo* by birds but must be obtained from the diet. Thus, the concentration of carotenoids in feathers depends on foraging efficiency, the availability of carotenoid-rich prey and the ability to shunt carotenoids into feathers (McGraw, 2006). Regarding the former, few studies have reported a link between the expression of carotenoid-based ornament and the bearer's ability or willingness to provision chicks (i.e. foraging efficiency). Hill (1991, 1992) found that the

plumage colour of male house finches *Carpodacus mexicanus* correlated with their rate of nestling provisioning. In a study with siskins *Carduelis spinus*, Senar & Escobar (2002) reported a relationship between male coloration and two behavioural indexes of foraging skills. Most studies have reported no relationship between plumage colour and male provisioning effort (Sundberg & Larsson, 1994; Lozano & Lemon, 1996; Kappes, Stutchbury & Woolfenden, 2009). The unique evidence of the role of female ornamentation as an indicator of foraging ability comes from studies with northern cardinals *Cardinalis cardinalis*. In this species, female underwing colour as well as the darkness and size of the mask have been shown to be correlated with their level of provisioning effort (Linville, Breitwisch & Schilling, 1998; Jawor *et al.*, 2004). Unexpectedly, few studies to date have tested directly the relationship between

*Corresponding author. E-mail: vicente.garcianavas@uclm.es

carotenoid-based pigmentation (plumage yellowness) and parental food provisioning to nestlings in parids (Fitze, Kolliker & Richner, 2003; Johnsen *et al.*, 2005). According to the good parent hypothesis, elaborate ornaments such as plumage yellowness may indicate a high level of parental care by the bearer (Hoelzer, 1989; Price, Schluter & Heckman, 1993). Hence, females should benefit directly through their choice of highly ornamented males by mating with those that invest more in parental care than would other potential mates. In addition, ornaments may act as signals to prospective partners for indirect benefits ('good genes') that result in healthier or more attractive offspring (Searcy, 1982; Møller & Alatalo, 1999). Both hypotheses are thus not mutually exclusive and plumage ornamentation may act as an indicator of both direct and heritable resources (Iwasa & Pomiankowski, 1999).

Concerning the role of the availability of carotenoid-rich items on plumage coloration, several studies have performed feeding experiments with captive birds to investigate how dietary carotenoid access can influence colour expression (Tscharren, Fitze & Richner, 2003; Isaksson, Delhey & Andersson, 2006; Peters *et al.*, 2008; for a review, see Hill 2006). For example, Hill (1992) found that the extent of ventral carotenoid pigmentation in house finches was dependent on carotenoid intake; carotenoid-supplemented males expressed significantly larger patches than males in the carotenoid-deficient group. However, field studies linking plumage coloration and carotenoid intake in wild bird populations (i.e. if birds are 'what they eat') are scarce. Hill, Inouye & Montgomerie (2002) studied the gut contents of moulting house finches and found positive correlations between the concentration of carotenoids ingested by birds and the ornamental coloration of growing feathers. Slagsvold & Lifjeld (1985) showed that nestling great tits *Parus major* more frequently fed with carotenoid-rich items (greenish-coloured Lepidoptera larvae) developed a yellower plumage. However, Slagsvold & Lifjeld (1985) did not relate the nestling diet with the coloration of adult birds; in other words, whether more chromatic parents brought a higher proportion of carotenoid-rich prey to the nest compared to paler individuals.

Habitat characteristics can also influence the expression of carotenoid-based coloration (Arriero & Fargallo, 2006). It has been reported that great tits from deciduous forests and rural areas are more yellow than those from coniferous forests and urban areas, respectively (Slagsvold & Lifjeld, 1985; Hørak *et al.*, 2000; Isaksson & Andersson, 2007). This pattern has been ascribed to differences in food quality (i.e. carotenoid concentration) between habitat types (Isaksson & Andersson, 2007). On the

other hand, intraspecific variation in plumage coloration has also been related to variation in ambient lights (Gómez & Théry, 2004). According to the maximal conspicuousness hypothesis plumage colour is adapted to provide maximum chromatic contrast against backgrounds (Endler, 1983). For example, individuals living in relatively closed habitats should have generally brighter plumage compared to those from relatively open habitats because the overall level of luminescence is lower in the former. However, a more reflective or brighter plumage may imply in turn, a major vulnerability to predation (Dale & Slagsvold, 1996). Thus, according to the matching background hypothesis, natural selection should favour darker (more cryptic) plumages in closed habitats and brighter plumages in open habitats (Baker & Parker, 1979).

In the present study, we employed the blue tit *Cyanistes caeruleus*, a small passerine with biparental care, as model species. Both sexes have similar appearance to human eyes. Specifically, sexual dimorphism in ventral carotenoid-based coloration of blue tits is very small and probably at or below the discrimination threshold of bird vision (Delhey, Roberts & Peters, 2010). In a first step, we tested whether adult blue tit plumage coloration reflects their level of effort in provisioning nestlings as predicted by the good parent hypothesis. This measure of parental quality has been found to be relatively stable in time (Dor & Lotem, 2010). Thus, if the level of parental care is related to plumage ornamentation, such a trait may be used as a consistent indicator of parental quality. Secondly, we test whether plumage coloration is related to the proportion of caterpillars in the nestling diet. If adult coloration reflects some basic quality of the bearer, one might expect a positive relationship between plumage colour and quantity/quality of resources provided to the offspring. We also examined whether plumage coloration predicts reproductive performance of adult blue tits and the possible influence of forest type (evergreen and deciduous) on the expression of this ornament. Finally, we explored additional causes of variation in colour expression in nestling blue tits (body condition, parental plumage coloration, parental provisioning effort).

MATERIAL AND METHODS

GENERAL FIELDWORK

The present study was conducted over two consecutive breeding seasons (2007–2008) on two nearby (2 km) nestbox plots at the Cabañeros National Park (Ciudad Real Province, central Spain). The first plot ('El Brezoso', 100 nestboxes) is located in a deciduous

forest dominated by Pyrenean oak *Quercus pyrenaica* and heather *Erica* spp. The second plot ('Anchurones', 150 nestboxes) consists of an evergreen forest (composed of scattered holm oaks *Quercus rotundifolia* and cork oaks *Quercus suber*) interspersed with areas of open grassland and Mediterranean scrublands (gum cistus *Cistus ladanifer* and rosemary *Rosmarinus officinalis*). Nestboxes were erected at a height of 2 m and protected from predators with wire mesh and a pipe fixed to the hole-entrance.

Nests were visited routinely to estimate the laying date, clutch size, number of hatched young, and number of fledged young. Adults were captured with nestbox traps when feeding chicks at 8 days old. All birds were sexed based on the presence/absence of a brood patch and aged (yearling versus adult) by the colour of the wing coverts. Adult body mass and tarsus length were measured with an electronic balance (accuracy: ± 0.1 g) and a digital calliper (accuracy: ± 0.01 mm), respectively. All breeding birds were identified with metal rings and equipped with a passive integrated transponder attached to one of their legs (see below). On day 13 post-hatching, nestlings were ringed and similarly measured. We did not include in our data set individuals that bred in both years (seven females and five males). We randomly chose one year of data for that parent to include in the analyses.

COLOUR MEASUREMENTS

The coloration of the breast plumage of adult (2007: 28 males and 27 females; 2008: 34 males and 35 females) and nestling (2007: 250 from 34 broods) blue tits was measured in the field using an Ocean Optics USB2000 spectrophotometer (range 250–800 nm) with ultraviolet (tungsten halogen) and visible (deuterium) lamps and a bifurcated 400- μ m fibre-optic probe. All measurements were relative to a white standard 'Spectralon' tablet, and reference measurements were made before each scan. For each bird, we computed the mean of three readings obtained on different points of the breast plumage, but always following the same order (i.e. from upper to lower patch) and taking each reading from approximately the same location in all birds. Reflectance curves were obtained by calculating the median of the percentage reflectance in 10-nm intervals, covering the full spectral range (320–700 nm) that can be detected by birds (Cuthill *et al.*, 2000). We used tristimulus scores because this technique has been suggested as effective to capture pigment-based colour variation in carotenoid-containing ornaments (Evans *et al.*, 2010; Butler, Toomey & McGraw, 2011) and has been employed in a large number of studies providing useful insights (Montgomerie, 2006). From the spec-

tral reflectance data, for each individual, we calculated the objective colourimetrics: hue, lightness (also called brightness) and carotenoid chroma. Hue (spectral location) is a correlate of the shape of the reflectance spectrum, measured in degrees, around a circular spectrum (colour wheel). This indice was estimated with an algorithm provided in Saks, McGraw & H6rak (2003). Lightness (spectral intensity) was estimated as the average reflectance in the range 320–700 nm. Finally, we calculated carotenoid chroma (or spectral purity) as the relative difference in reflectance between the wavelengths of minimum (700 nm) and maximum (450 nm) absorbance of the two main carotenoids (lutein and zeaxanthin) in parid plumage (Andersson & Prager, 2006). It has been demonstrated that this index (higher values = greater colour saturation) is positively correlated with the amount of carotenoids deposited in feathers in the great tit (Isaksson *et al.*, 2008; Eeva, Sillanp6 & Salminen, 2009) and other species (Butler *et al.*, 2011). Carotenoid chroma negatively correlated with both hue ($r = -0.49$, $P < 0.001$, $N = 158$) and lightness ($r = -0.17$, $P = 0.03$, $N = 158$), although the latter two were not correlated ($r = -0.13$, $P = 0.09$, $N = 158$). The intra-individual repeatability of colour measurements was high (adults, lightness: $r = 0.95$, chroma: $r = 0.97$, hue $r = 0.96$, all $P < 0.001$; nestlings, lightness: $r = 0.95$, chroma: $r = 0.93$, hue: $r = 0.96$, all $P < 0.001$).

FORAGING ABILITY

Feeding frequency (number of provisioning events detected over a 24-h period) was used as an indicator of the parents' ability to hunt or gather food. This measure of parental care has been employed in a large number of studies focused on testing the relationship between epigamic traits (e.g. plumage coloration) and parental quality (M6ller & Thornhill, 1998). Brood-size manipulation studies have shown that parents may increase their visit rate but to some extent (i.e. a ceiling effect), resulting in fewer visits per chick as brood size increases (Rytk6nen, Koivula & Orell, 1996). According to this general pattern, only those individuals with better foraging skills (or access to better territories) may be able to fully compensate for the increase in brood demand. Thus, provisioning chicks at high rates over a considerable period of time may carry significant costs for adults (Nur, 1984) and only high-quality individuals (or individuals breeding in high-quality territories) may be able to maintain such work rates. Besides provisioning rates, the size and type of food items are also important components of provisioning effort. For example, a higher number of feeding visits to the nest does not necessarily imply a higher amount of carotenoid-rich items provided to the young (see Results), although, in our study area,

as well as most of the distribution range of this species, caterpillars make up the bulk of the nestling diet (Cabañeros National Park: 65–70%, see Supplementary Material in García-Navas & Sanz, 2011). Thus, we analyzed both the number and the type of food item brought to the nest during a short time period in a subsample of nests aiming to link the plumage coloration of adult blue tits with the proportion of caterpillars in the nestling diet (see more below).

A total of 124 adult birds (62 males and 62 females) were fitted with a small cylindrical micro-transponder (Trovan ID 103, length 11.6 mm, mass 0.1 g; Trovan Ltd) glued to two plastic bands and wrapped in a piece of black duct tape. These microchips produce a unique amplitude modulated code signal in the presence of an electromagnetic field providing individual identification of each bird. Upon capture (day 8 post-hatching), the front of the nestbox was replaced by another one with an antenna connected to a stationary data logger placed on the ground. By means of this device, we recorded the timing of the visits by each individual parent to the nest. The efficiency and reliability of the estimates obtained with this method was validated with feeding data collected from video recordings (García-Navas, Ortego & Sanz, 2009). From these data, we also examined the correlation between male and female feeding effort to test for the existence of an assortative mating between high-quality individuals (Andersson, 1994).

In a subsample of nests (2008; $N = 14$), the provisioning behaviour of parents was monitored by means of infra-red handy cams (SONY DCR-SR290, Sony Corp.) placed at the back of the nestbox. This device was installed 1 day before filming (days 9–10). All videotaping sessions started in the morning between 09.00 and 11.00 h and lasted 90 min. The first 30 min of recording was discarded because birds take time to resume feeding activity after the disturbances that the camera installation entails. The next 60 min of film were played and analyzed in detail on a computer. Males and females could be identified from ringing details (females were marked with coloured plastic bands upon capture). The sexes could also be identified by behaviour because only females brood the young and perform nest-sanitation activities. For each sex, we calculated the proportion of caterpillars delivered to the young (i.e. the number of caterpillars provisioned to the chicks divided by the total number of provisioning trips). In this way, we were able to relate the total amount of caterpillars caught per unit of time with the ventral-plumage coloration of the forager allowing us to ask if the breast yellowness of blue tits reliably reflects the parents' ability to collect their main food source of carotenoids, primarily lutein (Isaksson & Andersson, 2007; Arnold *et al.*, 2010).

STATISTICAL ANALYSIS

We used generalized linear models (GLMs) to test the effect of sex, age (yearling versus adult), inter-year variability, and study plot (i.e. forest type: deciduous versus evergreen) on adult coloration measures (hue, lightness and carotenoid chroma for both the male and the female). In a second step, we tested for relationships between adult coloration and (1) their provisioning ability (daily feeding rates) and (2) the share of the pair's total provisioning rates (i.e. relative feeding effort). Study plot, calendar date, and brood size on day 8 were entered in the initial models as potential influencing variables. We also explored whether the proportion of fledged young (as a measure of reproductive success) varied with adult coloration when controlling for other explanatory variables. To investigate predictors of nestling condition (body mass and size), we constructed models with study plot, calendar date, brood size on day 13, nestling tarsus length, and nestling colour measurements as potential predictor variables. We always began GLMs by including all the explanatory variables in the full model and then running backward selection procedures. We removed one by one the least significant factors until we ended with only the statistically significant variables in the final model. Spearman's correlations were used to test for relationships between adult coloration and the amount (%) of carotenoid-rich items (caterpillars) delivered to the young. We also explored the relationship between adult plumage coloration and that of their offspring. Because provisioning rates differed significantly between years ($P < 0.001$ for both males and females), we standardized such variables to a mean of zero and a SD of 1. In this way, we were able to investigate whether, within a particular environmental and social regime, more colourful individuals provisioned chicks at a higher rate than less colourful individuals. Model assumptions were fulfilled with variables being transformed to achieve normality when required. The results report the F , d.f. and P -values of nonsignificant predictors, immediately before they were removed from the model. Analyses were conducted with STATISTICA, version 6 (StatSoft). Data are given as the mean \pm SE.

RESULTS

COLOUR VARIATION IN ADULTS: EFFECTS OF SEX, AGE, AND FOREST TYPE

Adult coloration did not differ significantly between years (hue, lightness and chroma; all $P > 0.05$). We found sex differences in the expression of carotenoid-based plumage coloration and structural size of blue tits. Males had longer tarsi and presented a more

Table 1. Sex differences (mean \pm SE) in plumage colour characteristics of adult blue tits at the Cabañeros National Park, central Spain

Variable	Males ($N = 62$)	Females ($N = 62$)	$F_{1,122}$	P
Hue	75.52 \pm 6.55	72.37 \pm 8.83	5.07	0.03
Carotenoid chroma	53.28 \pm 0.02	46.38 \pm 0.02	6.78	0.01
Lightness	12.21 \pm 0.55	11.41 \pm 0.55	1.04	0.30

Significant results are shown in bold.

chromatic and greenish (higher values of hue) yellow breast plumage coloration than did females (Table 1). The mean lightness and carotenoid chroma of the yellow breast colour did not differ significantly between age groups (i.e. between 1- and >2-year-old adults) or forest types (all $P > 0.2$). Hue did not predict adult age (both $P > 0.5$) but differed significantly (in the case of males) and marginally (in the case of females) between study plots (males: $F_{1,59} = 4.24$, $P = 0.04$; females: $F_{1,60} = 3.69$, $P = 0.06$). Individuals from the evergreen forest showed a greener shade of yellow ('Anchurones', males: 77.76 ± 1.32 , females: 75.03 ± 1.76) compared to those of the deciduous forest ('El Brezoso', males: 74.19 ± 1.02 , females: 70.69 ± 1.40). There was no significant assortative mating on the basis of any of the colourimetric variables (all $P > 0.25$).

FORAGING ABILITY

Parental feeding effort, measured as the number of provisioning visits per chick over a 24-h period, correlated with the ventral plumage coloration of adult blue tits. Carotenoid chroma of both males and females correlated with the rate at which they provisioned nestlings; more chromatic parents fed their young more often (Fig. 1) (Females: chroma: $F_{1,52} = 8.22$, $P < 0.01$, estimate: 50.36 ± 17.55 ; Males: chroma: $F_{1,49} = 5.16$, $P = 0.027$, estimate: 38.72 ± 17.05). Neither hue, nor lightness was correlated significantly with the number of provisioning events in either sex (all $P > 0.25$). There was no effect of study plot, calendar date or brood size on parental provisioning effort (all $P > 0.1$).

On average, the male was responsible for 57% of the provisioning events to offspring (SD 14%, range 21–80%). The relative contribution of the male to the care of the young was unrelated to their colour measures (study plot: $F_{1,36} = 0.53$, $P = 0.47$; calendar date: $F_{1,36} = 0.93$, $P = 0.34$; brood size: $F_{1,36} = 0.64$, $P = 0.43$, chroma: $F_{1,36} = 0.04$, $P = 0.84$; lightness: $F_{1,36} = 0.42$, $P = 0.52$; hue: $F_{1,36} = 1.28$, $P = 0.26$). Moreover, we did not find an association between the female proportion

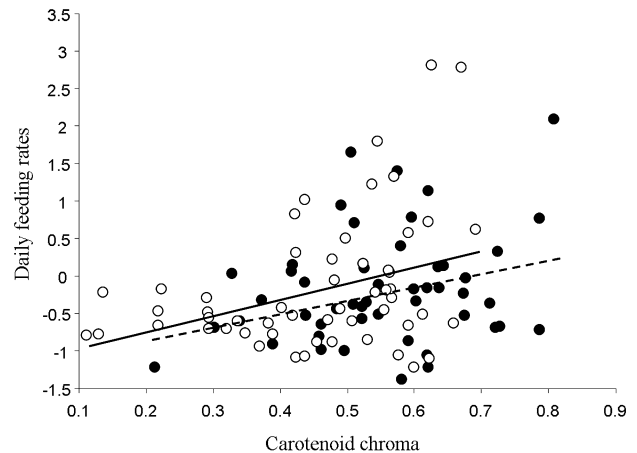


Figure 1. Relationship between daily feeding rates (feedings per chick over a 24-h period) and adult plumage coloration (carotenoid chroma) for male (black dots, dotted line) and female (empty dots, solid line) blue tits. Daily feeding rates were standardized to control for year effects.

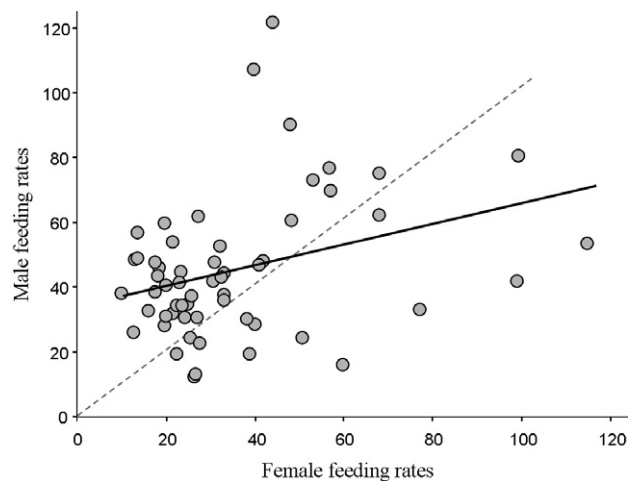


Figure 2. Relationship between male and female provisioning effort on day 8 post-hatching (Pearson: $r = 0.32$, $P = 0.013$, $N = 57$). Daily feeding rates (number of feeding events per chick over a 24-h period) are shown. The dotted line indicates the slope of the relationship if both sexes contribute equally to the care of the young.

of feedings and any of their colour measures (study plot: $F_{1,39} = 0.85$, $P = 0.36$; calendar date: $F_{1,39} = 1.43$, $P = 0.23$; brood size: $F_{1,39} = 1.33$, $P = 0.25$; chroma: $F_{1,39} = 0.22$, $P = 0.64$; lightness: $F_{1,39} = 0.52$, $P = 0.47$; hue: $F_{1,39} = 0.80$, $P = 0.37$). Within pairs, we found a significant, positive correlation between male and female feeding effort (Fig. 2). Individuals that fed nestlings at higher rates had mates that did the same.

Carotenoid chroma was positively related with the proportion of caterpillars delivered to the young by both males and females (Fig. 3). Neither hue, nor

lightness was significantly correlated with the parents' ability to obtain this prey type (Spearman: Males: hue: $r = -0.16$, $P = 0.59$, lightness: $r = -0.40$, $P = 0.16$; Females: hue: $r = 0.01$, $P = 0.97$, lightness: $r = -0.36$, $P = 0.20$). The number of provisioning events detected over a 24-h period was not correlated with the proportion of caterpillars delivered to the young over a 1-h period (Spearman: $r = -0.09$, $P = 0.77$, $N = 12$).

REPRODUCTIVE OUTPUT

To investigate the relationship between adult plumage coloration and the proportion of fledged young, we constructed a model in which we included study year, forest type, adult coloration, clutch size, and calendar date as potential predictor variables.

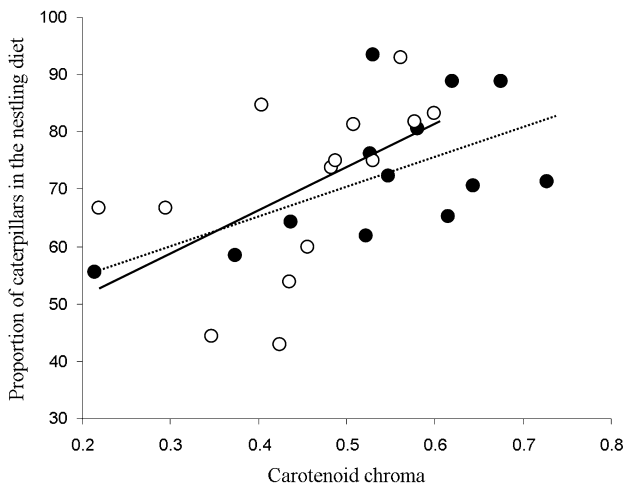


Figure 3. Relationship between the proportion (%) of caterpillars delivered to the young and adult plumage coloration (carotenoid chroma) for male (Spearman: $r = 0.58$, $P = 0.036$, $N = 13$; black dots, solid line) and female (Spearman: $r = 0.63$, $P = 0.015$, $N = 14$; empty dots, dotted line) blue tits.

Maternal but not paternal yellow coloration explained a significant proportion of the variance in fledgling success. Breeding females with hue shifted towards shorter wavelengths and more chroma had higher fledgling success (Final model: calendar date: $F_{1,57} = 6.25$, $P = 0.01$, estimate: -0.82 ± 0.32 ; hue: $F_{1,57} = 3.74$, $P = 0.05$, estimate: 0.80 ± 0.41 ; chroma: $F_{1,57} = 4.94$, $P = 0.03$, estimate: 53.48 ± 24.04).

NESTLING CONDITION AND PLUMAGE COLORATION

No measure of adult coloration (hue, carotenoid chroma or lightness) was correlated with that of their offspring (all $P > 0.07$). More chromatic parents did not raise more chromatic nestlings. There was no relationship between the plumage coloration of adults and the mean body condition of their young (all $P > 0.1$), after controlling for other influencing variables (calendar date). That is, more chromatic parents did not raise nestlings in better condition. There was also no association between parental provisioning effort and nestling condition (Body mass: male feeding rates $F_{1,51} = 0.05$, $P = 0.82$, females feeding rates: $F_{1,51} = 0.03$, $P = 0.86$; Tarsus length: male feeding rates: $F_{1,51} = 1.25$, $P = 0.27$, females feeding rates: $F_{1,51} = 0.10$, $P = 0.75$). To determine which variables influenced the condition of nestlings (body mass and size), we constructed two models in which we included potential predictor variables as brood size or forest type (Table 2). We found a positive correlation between nestling body mass and plumage hue after controlling for nestling size and seasonal effects (Fig. 4, Table 2), whereas nestling tarsus length was positively correlated to plumage lightness (Fig. 5, Table 2). All other relationships between colour measures and nestling condition were nonsignificant (all $P > 0.1$).

DISCUSSION

Ventral plumage coloration (more precisely, the carotenoid chroma) of adult blue tits predicted their

Table 2. Models indicating relationships between body condition and size of nestling blue tits

Variable	Nestling body mass			Nestling tarsus length		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Study plot	0.55	1.26	0.46	2.01	1.27	0.17
Calendar date	16.75	1.31	< 0.001	0.80	1.27	0.37
Brood size on day 13	0.07	1.26	0.79	3.80	1.31	0.06
Tarsus length	8.37	1.31	< 0.01	–	–	–
Hue	7.86	1.31	< 0.01	< 0.01	1.27	0.99
Carotenoid chroma	0.02	1.26	0.88	0.23	1.27	0.63
Lightness	0.39	1.26	0.53	4.98	1.32	0.03

Significant results are shown in bold.

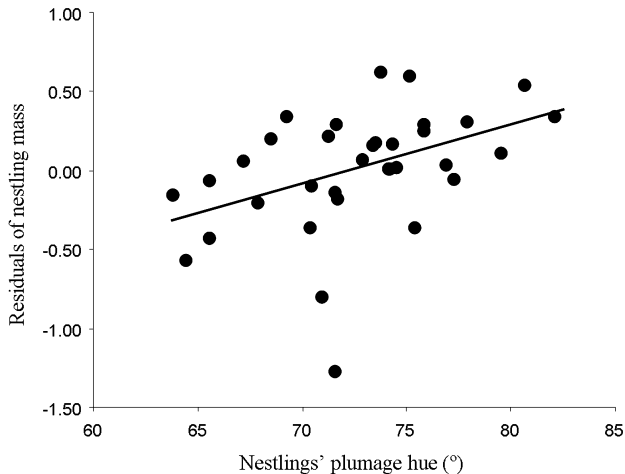


Figure 4. Residual of nestling body mass in relation to plumage hue after controlling for other influencing variables (nestling tarsus length and calendar date). Mean values per brood are represented (estimate: 0.04 ± 0.01).

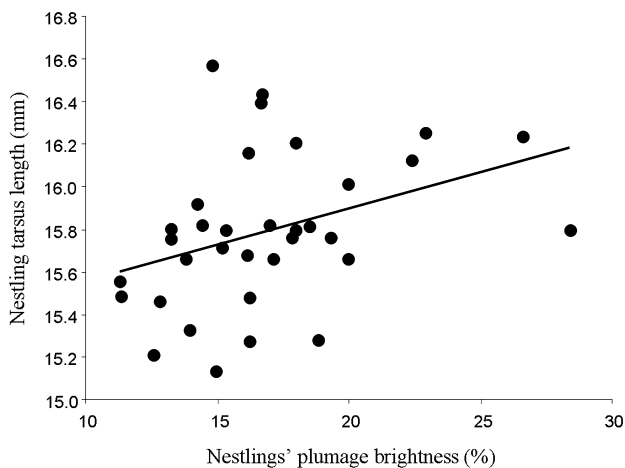


Figure 5. Nestling tarsus length in relation to plumage lightness. Mean values per brood are represented (estimate: 0.03 ± 0.01).

foraging ability, estimated using two surrogates: number of provisioning events detected over a 24-h period (daily feeding effort) and the percentage of caterpillars delivered to the young per hour (although in this latter case our sample size was lower). Both males and females with higher carotenoid chroma values fed their young more frequently and provided them a greater amount of caterpillars than less chromatic individuals, which is in agreement with the good parent model (Hoelzer, 1989). These two measures (daily feeding rates and percentage of caterpillars in diet) were not correlated and can be interpreted as two different estimates of the parents' ability to deliver food to the nest. With regard to the

former, it has been suggested that provisioning effort is highly repeatable across both broods and years (i.e. individuals are consistent in their parental contributions irrespective of yearly conditions or their mate's contribution) (Dor & Lotem, 2010). This suggests that yellow ventral plumage coloration of adult blue tits may operate as a relative signal (*sensu* Senar & Quesada, 2006) of the innate provisioning ability of each individual. A positive association between parental feeding effort and the expression of a carotenoid-based ornament has been documented by only a few studies (Table 3). On the other hand, the relationship between adult coloration and the percentage of caterpillars gathered per unit of time is intuitively reasonable because this prey type is the main source of carotenoids for tits (Arnold *et al.*, 2010). As far as we know, no other studies have related the expression of carotenoid-based ornaments to a direct measure of the bearer's ability to collect carotenoid-rich food items. We assume that this specific measure is not a highly fluid attribute, although no studies have examined whether birds are consistent in their diet features across seasons. The proportion of caterpillars in the diet was not correlated with the frequency with which parents fed their young. That is, those individuals that visited the nest at higher rates do not necessarily provided a greater amount of carotenoid-rich items to their young. Our result thus implies a nonlinear relationship between plumage coloration, food quality (percentage of caterpillars in diet), and provisioning effort. This apparent puzzling relationship could be partially explained by considering that plumage coloration is likely to depend on several proximate factors including carotenoid-availability (diet) and genetic effects (Tschirren *et al.*, 2003). Thus, from our point of view, ventral plumage coloration may advertise the ability of the bearer to incorporate carotenoids in their diet in the short-term and also their overall quality as foragers in terms of provisioning effort, a less stochastic trait that has been related to the genetic quality of the individual (García-Navas *et al.*, 2009). Thus, individuals exhibiting a more colourful plumage may be those able to gather a greater amount of carotenoid-rich items (or those with access to better territories) and in turn, more colourful individuals may be those able to cope with non-optimal conditions (food shortage or low availability of the preferred prey type, high brood demand) by increasing their feeding frequency.

Moreover, Senar *et al.* (2008) predicted that hue coloration may provide information on the ability of the signaller to collect carotenoids whereas carotenoid chroma may be more related to body condition. We failed to find an association between hue and parental provisioning ability. The reason why carotenoid chroma but not hue correlated positively with the

Table 3. Studies testing the relationship between parental feeding effort and carotenoid-based pigmentation (green-yellow, yellow, orange, red) in birds

Species	Plumage trait	Colour measure	Response variable	Effect (sex)	Reference
Northern cardinal <i>Cardinalis cardinalis</i>	Underwing	Rank scores	Feeding effort	+ (♀); NE (♂)	Linville <i>et al.</i> (1998)
	Breast	Rank scores	Feeding effort	NE (♀); NE (♂)	
Northern cardinal <i>Cardinalis cardinalis</i>	Male breast	PCA (HSB)	Feeding effort	-	Jawor and Breitwisch (2004)
	Male bill	Rank scores	Feeding effort	NE	
	Female underwing	PCA (HSB)	Feeding effort	NE	Jawor <i>et al.</i> (2004)
	Female bill	Rank scores	Feeding effort	NE	
Siskin <i>Carduelis spinus</i>	Male wing	Stripe length	Foraging skills	+	Senar & Escobar (2002)
House finch <i>Carpodacus mexicanus</i>	Male plumage	Rank scores	Feeding effort	+	Hill (1991)
Yellowhammer <i>Emberiza citrinella</i>	Male plumage	PCA (patch size)	Feeding effort	NE (♀); NE (♂)	Sundberg & Larsson (1994)
Yellow warbler <i>Dendroica petechia</i>	Male breast	Rank scores	Feeding effort	NE	Lozano & Lemon (1996)
Common yellowthroat <i>Geothlypis trichas</i>	Male bib	PCA (HSB)	Feeding effort	NE	Mitchell <i>et al.</i> (2007)
	Male mask face	Size	Feeding effort	NE (♀); - (♂)	
Blue tit <i>Cyanistes caeruleus</i>	Breast	HSB	Feeding effort	+ (♀); + (♂)	Present study
Rock sparrow <i>Petronia petronia</i>	Throat	Patch size	Feeding effort	NE (♀); + (♂)	Griggio, Zanollo & Hoi (2010)
European roller <i>Coracias garrulus</i>	Head	PCA (HSB)	Feeding effort	NE (♀); + (♂)	Silva <i>et al.</i> (2008)
	Scapulars	PCA (HSB)	Feeding effort	NE (♀); + (♂)	
	Back	PCA (HSB)	Feeding effort	+ (♀); NE (♂)	
American redstart <i>Setophaga ruticilla</i>	Male wing	HSB	Feeding effort	NE	Kappes <i>et al.</i> (2009)
	Male flank	HSB	Feeding effort	-	
	Male tail	HSB	Feeding effort	NE	
American redstart <i>Setophaga ruticilla</i>	Male flank	HSB	Feeding effort	NE (♀); + (♂)	Germain <i>et al.</i> (2010)
	Male tail	PCA	Feeding effort	- (♀); NE (♂)	
Blackbird <i>Turdus merula</i>	Male bill	Rank scores	Residual visit rates	+ (♀); + (♂)	Préault <i>et al.</i> (2005)
Eurasian kestrel <i>Falco tinnunculus</i>	Male tail and back	Rank scores	Hunting effort	+	Palokangas <i>et al.</i> (1994)
Eurasian kestrel <i>Falco tinnunculus</i>	Male tail and back	Rank scores	Hunting effort	-	Tolonen and Korpimäki (1994)
American kestrel <i>Falco sparverius</i>	Male tail	Band width	Feeding effort	-	Wiehn (1997)
	Male plumage	Rank scores	Feeding effort	NE	

+, positive effect; -, negative effect; NE, no effect; PCA: principal components analysis; HSB, three tristimulus colour variables (hue, saturation or chroma and brightness). When the measured trait is not preceded by male or female, it means that this ornament was measured in both sexes.

parents' ability to gather food and carotenoid-rich prey is not clear. Recent studies with finches and great tits have found that carotenoid chroma but not hue correlated with the amount of carotenoids in feathers (Saks *et al.*, 2003; Isaksson *et al.*, 2008). This reinforces the view that the mechanism by which feather carotenoid content is reflected by these colour attributes may be different (Saks *et al.*, 2003; Andersson & Prager, 2006). More research on this topic is required for in-depth understanding of the underlying pathways linking different colour parameters to feather carotenoid concentration.

We found evidence of assortative mating by provisioning effort such that the daily feeding rates of males and females were significantly correlated within pairs. This suggests that in our population mate selection is not random but that pairing of similar males and females is more likely than expected by chance (Linville *et al.*, 1998; Pr eault *et al.*, 2005), which is compatible with the good parent hypothesis. Alternatively, this pattern could arise as a consequence of the fact that males and females within a pair are faced with similar opportunities to provide food for chicks (i.e. effects of territory quality). On the other hand, we found that female but not male coloration was positively linked to breeding success. A similar finding has been reported by Doutrelant *et al.* (2008) in an experimental study in which they forced female blue tits to produce a replacement clutch. However, as far as we are aware, no study has shown that male blue tits prefer more yellow females or that male blue tits strategically allocate their parental investment in relation to female ornamentation; therefore, the influence of sexual selection as a driving/evolutionary force on this character remains unclear.

When looking for the effect of forest type on plumage coloration, we found that individuals from the evergreen forest had larger hue angles in comparison to those of the deciduous forest. Ferns & Hinsley (2008) reported that blue and great tits from large woods were a significantly greener shade of yellow (i.e. larger hue angles) than those from small woods, and they argued that such a result may be a result of differences in caterpillar abundance between the habitat types. In our case, we did not find significant differences in the proportion of caterpillars in the diet between the evergreen and deciduous forest (Anchurones: 69%, El Brezoso: 68%; V. Garc a-Navas and J. J. Sanz, unpubl. data). This result, together with the fact that hue was not correlated with the percentage of caterpillars or the number of provisioning events, leads us to conjecture that this is a less dynamic colour attribute and probably more dependent on the rearing environment than carotenoid chroma. On the other hand, our results may provide

support for the crypsis or matching background hypothesis because individuals living in the deciduous forest exhibited higher hue values than those from the evergreen forest. This result is noteworthy because both nestbox plots are only 2 km apart. However, we are cautious of such an interpretation because we did not perform specific measurements of backgrounds and forest ambient light in both sites. Thus, further work on these populations should consider the importance of light environments when investigating within-species variation in plumage coloration (Moyen *et al.*, 2006; Delhey *et al.*, 2010).

Regarding nestling coloration, none of the three measures of the nestling plumage coloration correlated significantly with the values of their parents, which is in accordance with a previous study on this species (Arriero & Fargallo, 2006). Nor did the level of parental provisioning effort predict the plumage coloration of blue tit nestlings. On this matter, Fitze *et al.* (2003) found a positive correlation between nestling plumage coloration and that of their rearing father, although they failed to find an association between male coloration and male provisioning effort; therefore, they suggested that more chromatic fathers would provide chicks with a more carotenoid-rich diet. Isaksson *et al.* (2006) reached a similar conclusion; it is food quality rather than quantity that determines variation in offspring plumage coloration. However, to our knowledge, only one study has related the carotenoid content of food provided to nestlings with the coloration of feathers grown by them (Slagsvold & Lifjeld, 1985). Regrettably, we have no data on nestling diet corresponding to the 2007 breeding season in which nestlings' coloration was measured. In the present study, we have shown a link between the amount (%) of caterpillars gathered per hour and adult coloration. However, it has been suggested that nestling plumage coloration may have evolved under different selection pressures than adult coloration (H orak *et al.*, 2001). In this sense, there is evidence that environmental conditions have a strong effect on nestling plumage (Hill, 1992; H orak *et al.*, 2000; Senar, Figuerola & Pascual, 2002; Fitze *et al.*, 2003). In addition, maternal effects via transference of carotenes through deposition in the egg yolk may contribute to origin-related variation in nestling coloration (Blount, Houston & M oller, 2000). In a similar vein, Isaksson *et al.* (2008) reported that carotenoid chroma of nestling great tits did not reflect their feather carotenoid content. Thus, the role of carotenoid acquisition as an important source of variation for nestling plumage coloration is considered controversial and a matter of ongoing debate (Hadfield & Owens, 2006; Jacot *et al.*, 2010).

On the other hand, the absence of correlation between adult coloration and nestling condition is not

unexpected because higher feeding rates or a higher proportion of caterpillars in the diet do not always guarantee heavier nestlings (Nour *et al.*, 1998; Mägi *et al.*, 2009; García-Navas & Sanz, 2011). Meanwhile, we found that nestling condition was correlated with some colour parameters. Nestling body mass was positively associated with hue (but not with carotenoid chroma; Eeva *et al.*, 2009; but see also Johnsen *et al.*, 2003) of nestlings' plumage. Body size (nestling tarsus length) was correlated with lightness, a result also reported by Hegyi *et al.* (2007) in a study on great tits. Lightness is a colour parameter that has been suggested to be more dependent on feather structure (i.e. physical properties of feathers) and, thus, plumage development than others (Saks *et al.*, 2003; Montgomerie, 2006); therefore, plumages with higher values of this parameter may indicate better growth conditions (faster growth rates) resulting in larger chicks. Finally, studies testing the condition-dependence of carotenoid-based coloration have provided mixed results (Isaksson *et al.*, 2008) and it is likely that the relationship between nestling plumage colour and condition is not causal and in turn, depends largely on local conditions.

To conclude, the results obtained in the present study indicate that ventral plumage coloration may act as a consistent indicator of foraging ability in blue tits. As far as we know, the present study is the first to report a relationship between feeding effort and carotenoid-based coloration in a parid species (Table 3). Our findings are in line with previous studies on this species in which it has been suggested that plumage yellowness may indicate individual quality (father quality: Senar *et al.*, 2002; mother quality: Doutrelant *et al.*, 2008). However, no other study on this species has reported an association between plumage coloration and some measure of parental quality in both males and females. The possibility that such information can be used by the two sexes to assess potential partner quality mutually should be tested by means of mate-choice experiments, in which the influence of other well-known sexual characters (blue crown) should be controlled.

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