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Brighter yellow blue tits make better parents

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Whether or not bird ornaments are a signal for direct (e.g. good parents) or indirect (e.g. good genes) benefits to prospective partners in sexual selection is controversial. Carotene coloration in *Parus* species is directly related to the ingestion of caterpillars, so that a brightly carotene-coloured tit may be signalling its ability to find caterpillars, a main high-quality food source for good fledgling development, and hence its parental abilities. If carotene-based plumage coloration is related to the good-parent hypothesis, we predict that yellow plumage brightness of tit fathers should be positively correlated to their investment in offspring provisioning. Here, we use cross-fostering experiments in blue tits (*Parus caeruleus*) to show that chick development (as measured by tarsus length) is related to yellowness of the foster father, but not to that of the genetic parents. Using these data, we were able to measure, for the first time to our knowledge, the separate contribution of genetic and environmental factors (i.e. parental plumage coloration) to chick development, and hence parental investment. Our data, which relate carotenoid coloration to models of good parents, and data from other authors, which relate ultraviolet coloration to good-genes models, stress that different kinds of coloration within an individual may provide different units of information to prospective females.

Keywords: parental investment; good parents; sexual selection; plumage coloration; blue tit

1. INTRODUCTION

There is considerable controversy as to whether bird ornaments act as signals to prospective partners for direct (e.g. good parents) or indirect (e.g. good genes) benefits in sexual selection (Andersson 1994). The good-genes hypothesis is widely recognized and supported by sources of data (Møller & Alatalo 1999), such as the proven heritability of several sexually selected plumage traits (Møller 1991; Slagsvold & Lifjeld 1992; Norris 1993; Alatalo *et al.* 1994; Sheldon *et al.* 1997; Roulin *et al.* 1998) and the fact that females adjust the primary sex ratio of their offspring according to the plumage ornamentation of their mate (Sheldon *et al.* 1999). The good-parent hypothesis, however, although widely accepted on theoretical grounds (Hoelzer 1989; Price *et al.* 1993; Møller & Thornhill 1998), has not been fully supported by empirical data. Typically, although an association has been found in several species between male plumage brightness and parental investment (Hoelzer 1989; Grafen 1990; Kirkpatrick & Ryan 1991; Price *et al.* 1993; Møller & Thornhill 1998), this is either based on feeding rates, which do not take into account the quality of prey items (Royama 1966; Saetre *et al.* 1995), or has failed to differentiate the environmental and genetic correlation between offspring and their parents. A good approach to overcome these difficulties may be to carry out cross-fostering experiments and to use the tarsus length of fully grown fledglings as an unbiased measure of parental investment; although tarsus length is genetically determined (Dhondt 1982), it has been shown to reflect accurately the body condition of the young in the nest and, hence, the quality of parental care (Garnett 1981; Alatalo *et al.* 1990; Merilä & Wiggins 1995; Riddington & Gosler 1995; Dufva & Allander 1996).

Secondary sexual coloration can be mainly categorized as structural or based on pigments such as carotenoids or melanin (Hill & Brawner 1998). In contrast to other kinds of coloration, carotenoids can only be obtained indirectly by animals through the food chain; as a consequence, it has been suggested that this coloration might serve as an honest signal of foraging (Endler 1980; Hill 1991; Gray 1996; Olson & Owens 1998; Grether *et al.* 1999) and, hence, provisioning ability (Hill 1999). This may be particularly the case in *Parus* species, for which the ingestion of caterpillars is the main source of carotenes (Slagsvold & Lifjeld 1985; Partali *et al.* 1987; Eeva *et al.* 1998). Because carotenes are deposited in the feathers of tits in an unmodified form (Partali *et al.* 1987; Stradi 1998), a brightly carotene-coloured tit may be signalling its ability to find caterpillars. Given that caterpillars are a main high-quality food source for good fledgling development (Blondel *et al.* 1993; Gosler 1993; Naefdaenzer 1994; Eeva *et al.* 1998), and that this is directly related to their survival (Garnett 1981; Alatalo *et al.* 1990), it would directly benefit the female to pair with a very yellow male. Blue (*Parus caeruleus*) or great tits (*Parus major*), which display carotene-based yellow coloration, therefore provide an ideal model species to test for the good-parent process of sexual selection.

If the good-parent hypothesis is related to carotene-based plumage coloration, we predict that yellow plumage brightness of tit fathers should be positively correlated to their investment in offspring provisioning. We tested this prediction in blue tits using the tarsus length of fully grown fledglings as an unbiased measure of parental investment. In order to separate the contribution of genetic versus environmental factors (i.e. parental investment) to chick development, we designed cross-fostering experiments.

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Table 1. Regression between the plumage coloration and tarsus length of mid-offspring–mid-parent, using data of foster and genetic parents.
(A dummy variable coding locality was added to the model.)

	full model			genetic parents			foster parents			locality		
	R	$F_{3,32}$	p	β	t	p	β	t	p	β	t	p
lightness	0.65	7.85	< 0.001	0.28	1.37	0.18	0.04	0.22	0.83	−0.87	3.51	0.001
intensity	0.63	6.90	0.001	−0.02	0.17	0.88	−0.07	0.47	0.64	−0.62	4.49	< 0.001
hue	0.66	8.06	< 0.001	−0.04	0.29	0.77	−0.22	1.49	0.15	−0.51	3.25	0.003
tarsus	0.58	5.54	0.004	0.43	2.99	0.005	−0.03	0.24	0.82	0.38	2.67	0.01

2. MATERIAL AND METHODS

Blue tits were studied during the spring of 1998 in two woodland areas in northeast Spain (Figuerola *et al.* 1999*b*). Once completed, whole clutches were swapped randomly within each locality ($n = 30$ in Barcelona and $n = 40$ in Vic), with others that were of similar size (a maximum of one egg difference) on similar dates (maximum of 2 days difference). When chicks were 14–17 days old, plumage coloration and tarsus length were measured. The plumage coloration was measured on the breast (averaging chest and belly measurements; Figuerola *et al.* 1999*b*) using a Minolta DR200 portable colorimeter. Colour was characterized according to the tri-stimulus variables of hue, intensity and lightness, showing high repeatability (computed from the mean squares of ANOVA on two repeated measures per individual (Falconer & Mackay 1983; Krebs 1989); lightness, $R_I = 0.85$, $p < 0.001$; intensity, $R_I = 0.87$, $p < 0.001$; hue, $R_I = 0.92$, $p < 0.001$; $n = 12$; Figuerola *et al.* 1999*b*). We do not consider our results are biased by the method used to estimate plumage colour (Bennett *et al.* 1994; Bennett & Cuthill 1994) because yellow coloration is largely lacking in emission in the ultraviolet portion of the spectra (Goodwin 1973; Gross 1987; Moss & Weeden 1999). Hue has normally been the parameter of interest when studying the relationship between plumage coloration and sexual selection (Hill *et al.* 1994; Hill 1995; Hill & Brawner 1998; Nolan *et al.* 1998; Wolfenbarger 1999), and hence it was initially the focus of our investigation. However, because colour intensity and lightness have also sometimes been found to have a degree of predictive value (Hill & Brawner 1998; Figuerola *et al.* 1999*a*), we also explored the relationship of these two variables to parental investment. Tarsus length was measured with a digital calliper (accuracy 0.1 mm) at 14–17 (most at 16–17) days, when considered fully grown (Björklund 1996). The same measurements were recorded for both genetic and foster parents. Complete data were collected from fledglings and both genetic and foster parents from a total of 36 pairs.

The effect of hatching date and clutch size on the growth of chicks (Merilä & Wiggins 1995) was standardized by introducing these variables into the regressions relating plumage colour to tarsus growth. The age of the parents was not taken into account because no age differences in yellowness of hue have been found in the blue tit breast plumage (Figuerola *et al.* 1999*b*). The power of our statistical analyses was tested using the GPOWER program (Erdfelder *et al.* 1996).

We additionally provide data from the winters of 1997–1999 to measure repeatability in plumage colour of adult birds ($n = 12$) between years; to control for seasonal variations in plumage colour we used colour measurements for each individual taken at the same (±1) month and included number of months from moult (August = 0) as a covariate.

3. RESULTS

As expected, a significant correlation was found between the tarsus length of fledglings and that of their genetic parents (table 1). However, no relationship between the yellow coloration of fledglings and that of foster or genetic parents was detected, either for hue, intensity or lightness colour parameters (table 1). A correlation as low as 0.27 should have been detected, considering our sample size and assuming a standard power of 0.80 and an α-value of 0.05. Yellowness of plumage in adult blue tits recaptured in different years showed a very low repeatability (R_I for lightness = −0.14, intensity = 0.39, hue = 0.04, $n = 12$, $p > 0.10$ in all cases). In order to investigate the relative value of coloration, we tested whether the yellowest males in year n were also the yellowest in year $n + 1$, by ranking the adult males within each year in relation to their yellowness and correlating these ranks. Results were inconclusive, probably because of small sample sizes, with a marginal effect for hue and lightness, and a marginally significant interaction to year, indicating that the maintenance of relative hue ranks from year to year may vary according to the pairs of years compared (general linear model analysis (GLIM); lightness n versus $n + 1$: $F_{1,1} = 5.49$, $p = 0.08$, interaction, $F_{1,3} = 0.12$, $p = 0.95$; intensity n versus $n + 1$: $F_{1,1} = 0.01$, $p = 0.91$, interaction, $F_{1,3} = 0.37$, $p = 0.78$; hue n versus $n + 1$: $F_{1,1} = 5.15$, $p = 0.09$, interaction, $F_{1,3} = 4.27$, $p = 0.10$, $n = 12$). Plumage brightness of adult birds was not correlated to tarsus length (r^2 for lightness = 0.05, $p = 0.25$; intensity = 0.03, $p = 0.35$; hue = 0.02, $p = 0.40$; $n = 72$; data corrected for locality effects).

The tarsus length of blue tit fledglings (standardized by the tarsus length of genetic mid-parents) was positively correlated with the plumage hue of foster fathers (figure 1). No correlation was detected with the plumage hue of genetic fathers (table 2). This result held when standardized by laying date, brood size and locality (table 2). The plumage coloration of the female, either foster or genetic, had no effect on the tarsus length of fledglings (table 2).

4. DISCUSSION

Because carotenoids are a limiting resource of great physiological importance, it is now widely recognized that carotene-based plumage coloration serves as a direct honest indicator of foraging ability and health status, and that females use this coloration to choose high-quality mates (Endler 1980; Hill 1991; Gray 1996; Grether *et al.* 1999;

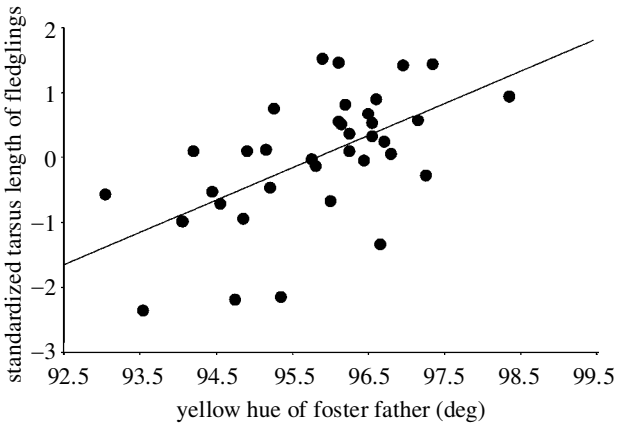

Figure 1. Relationship between tarsus length of fledglings (standarized by regression to the tarsus length of genetic mid-parents) and hue of foster-male yellow breast coloration. The relationship between the tarsus of fledglings and the two variables (see table 2) is described by $r = 0.69$, $F_{2,33} = 15.0$, $p < 0.000\ 02$; hue of foster male: $\beta = 0.54$, partial $r = 0.59$, $t_{33} = 4.21$, $p = 0.0002$; tarsus genetic mid-parents: $\beta = 0.33$, partial $r = 0.41$, $t_{33} = 2.56$, $p = 0.02$.

Olson & Owens 1998; Hill 1999; Møller *et al.* 2001). This relationship, between brightness of plumage coloration and foraging ability/health status, also seems to be the case for yellow-coloured tit species (Slagsvold & Lifjeld 1985; Dufva & Allander 1995; Svensson & Merilä 1996; Eeva *et al.* 1998; Harper 1999; Hörak *et al.* 2001). Hence, although there is at present no direct test of these birds for female preference to mate with the yellowest males, the general pattern already described for other species, and the close relationship between plumage yellowness and the ingestion of caterpillars (Slagsvold & Lifjeld 1985; Partali *et al.* 1987; Eeva *et al.* 1998), a main food source for chick development (see § 1), indicates a significant role for yellow coloration in mate choice, mainly in relation to the good-parent process of sexual selection.

Within this scenario, the good-parent model of sexual selection additionally predicts that, in a cross-fostering experiment, fledgling development should be related to plumage ornamentation of the foster parent. This is exactly what we found: the tarsus length of blue tit fledglings was positively correlated with plumage yellowness of foster fathers, but not with that of genetic fathers, or with genetic or foster mothers. This result held when standardized by laying date, brood size and locality. The lack of relationship between maternal yellowness and chick tarsus indicates that in this species sexual selection might be stronger in males.

The lack of relationship between the yellow coloration of blue tit fledglings and that of genetic parents, and the low repeatability in the yellowness of plumage colour in adult birds recaptured in different years, compared with that found in a given year (Figuerola *et al.* 1999*b*), stresses the reduced genetic basis of carotenoid-based coloration in comparison with environmental factors (see also Hörak *et al.* 2000). The low inter-year repeatability also stresses (i) the relative value of ornamental plumage, as carotene availability may fluctuate from year to year, and (ii) the relationship between plumage coloration and the current health status of a bird, which may also vary from year to year. Our results on ranked correlations comparing yellowness in adult males between year n and year $n + 1$ indicate that both instances may be operating, although more data on this topic are still needed. The lack of correlation between foster parents and chick plumage yellowness may be due to the fact that parents grow their feathers in the autumn of the previous year (Jenni & Winkler 1994), whereas the chicks develop their plumage coloration during the spring. Variability in the availability of caterpillars and other carotene sources in these two different periods, and between years, could therefore easily explain the lack of correlation (e.g. Hörak *et al.* 2000). In fact, Slagsvold & Lifjeld (1985) have already suggested that, for the great tit, yellow plumage coloration of chicks was more correlated to habitat availability of caterpillars than to the colour of their parents.

Because broods were cross fostered, we were able to demonstrate, for the first time to our knowledge, an effect of parental investment related to plumage coloration on

Table 2. Multiple-regression model of offspring's tarsus length against potential sources of variation related to plumage coloration (lightness, intensity and hue) of both foster and genetic male and female parents.
(Bonferroni correction sets significant p-values to 0.02. The model is based on 36 pairs of swapped broods. The tarsus length of the genetic mid-parents was included to standardize for genetic effects. The tarsus length of the foster mid-parents was also included for comparison. A dummy variable coding locality was also added to the model. Three different multiple regressions were carried out, according to the lightness, intensity and hue of foster and genetic males and females.)

	β	t_{26}	p
lightness			
laying date	−0.23	1.15	0.26
brood size	0.12	0.48	0.64
locality	0.03	0.08	0.94
foster parent tarsus	−0.12	0.69	0.49
genetic parent tarsus	0.36	2.09	< 0.05
foster male lightness	0.16	0.73	0.47
foster female lightness	0.14	0.63	0.54
genetic male lightness	−0.08	0.37	0.71
genetic female lightness	0.10	0.41	0.68
intensity			
laying date	−0.15	0.88	0.39
brood size	0.14	0.64	0.53
locality	0.27	1.32	0.20
foster parent tarsus	−0.06	0.33	0.74
genetic parent tarsus	0.42	2.58	0.02
foster male intensity	0.21	1.33	0.19
foster female intensity	−0.02	0.10	0.92
genetic male intensity	0.06	0.36	0.72
genetic female intensity	0.07	0.42	0.68
hue			
laying date	−0.05	0.32	0.75
brood size	0.10	0.54	0.60
locality	0.09	0.43	0.67
foster parent tarsus	−0.08	0.53	0.60
genetic parent tarsus	0.34	2.27	0.03
foster male hue	0.44	2.84	0.009
foster female hue	0.11	0.76	0.45
genetic male hue	0.04	0.29	0.77
genetic female hue	−0.04	0.28	0.78

chick development by separating genetic effects from those of the environment. The view of carotenoid-based coloration as a signal of good parents is not incompatible with the presence of other plumage badges that simultaneously signal other characteristics of an individual's suitability for choice as a mate. For instance, previous studies on the blue tit have shown that ultraviolet brightness of the crown is used by the female in mate choice (Andersson *et al.* 1998; Hunt *et al.* 1998, 1999; Sheldon *et al.* 1999), and the evidence indicates that it is related to good-gene models of sexual selection (Sheldon *et al.* 1999). It has recently been recognized that different kinds of coloration within an individual may provide different units of information to prospective females (Gray 1996; Hill & Brawner 1998; Badyaev & Hill 2000; McGraw & Hill 2000, Senar & Escobar 2001). The challenge in future studies will be to understand how females may trade off between the different individual characteristics.

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