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Negative relationship between plumage colour and breeding output in female great tits, *Parus major*

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ABSTRACT

Hypothesis: A higher carotenoid content of the plumage has usually been considered an indicator of superior individual quality in birds. Therefore, we expected a positive relationship between breeding output and plumage yellowness of male and female parents.

Organism: Great tit (*Parus major*).

Field site: Deciduous and coniferous forests in Estonia.

Search method: We examined whether basic breeding parameters were related to the plumage hue of male and female breeding partner in this monogamous species. We conducted our study in two years, differing markedly from each other in weather conditions during the breeding season and overall breeding success.

Results: Contrary to our expectation, more yellow females had on average lower fledging success and fewer fledglings than less yellow females in the year when breeding conditions were unfavourable. Colourful females were in better body condition than dull females during the nestling period. Breeding output was not significantly related to male plumage yellowness.

Keywords: body mass, breeding success, carotenoids, conditional strategy, good parent hypothesis, *Parus major*, plumage hue.

INTRODUCTION

Carotenoid-based ornaments in birds have been found to correlate with aspects of individual quality such as ability to find high-quality food, immunocompetence, parasite resistance, parental ability, and general health and vigour (for reviews, see Olson and Owens, 1998; Møller *et al.*, 1999, 2000; Pryke *et al.*, 2002), although there is also considerable variation in effects among studies (for reviews, see Møller *et al.*, 1999; Hõrak *et al.*, 2001). Because such traits are usually believed to be subject to sexual selection, most studies have been focused on males. However, females of many species, especially those with biparental care, are also extravagantly adorned (Amundsen, 2000). Recent theoretical and empirical research has indicated that both female and male

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ornaments may reflect phenotypic quality (Jones and Hunter, 1993; Cuervo *et al.*, 1996, 2003; Johnstone *et al.*, 1996; Amundsen *et al.*, 1997; Linville *et al.*, 1998; Amundsen, 2000; Smiseth *et al.*, 2001; Massarro *et al.*, 2003), although several studies have failed to provide such evidence. Few studies have tested simultaneously for the effects of ornaments of both sexes on reproductive success or breeding behaviour (Møller, 1993, 1994; Cuervo *et al.*, 1996; Linville *et al.*, 1998; Hill, 2002; Massarro *et al.*, 2003).

The great tit (*Parus major*) is a socially monogamous bird species in which males and females have similar parental roles. Both sexes also have quite similar appearance, although the black breast stripe is remarkably larger (Norris, 1989) and the yellow ventral plumage is more brightly coloured in males than in females (Slagsvold and Lifjeld, 1985; Hõrak *et al.*, 2001). This yellow coloration of the plumage is carotenoid-based (Partali *et al.*, 1987; Hõrak *et al.*, 2001; Tschirren *et al.*, 2003), and therefore it is possible that plumage coloration of both males and females reflects phenotypic or parental quality. The sex difference in coloration suggests that plumage colour is under sexual selection, although this assumption remains to be tested, as in most species studied to date.

The aim of the present study was to explore whether breeding output in great tits is related to plumage colour of either breeding partner. We conducted our study in two years, differing markedly from each other in terms of weather conditions during the breeding season, nestling growth rate and overall breeding success (Tilgar *et al.*, 2004; see also Methods). Since physiological trade-offs often appear only under unfavourable conditions [e.g. food stress (Stearns, 1992; Thessing and Ekman, 1994)], we expected the relationship between reproductive output and plumage colour as a putative indicator of individual quality to be more clearly expressed during the unfavourable breeding year.

METHODS

We analysed data collected in an earlier research project conducted in the surroundings of Kilingi-Nõmme (58°7′N, 25°5′E), south-west Estonia, in 2000–2001. The size of the study area, containing both deciduous and coniferous forest plots, was approximately 50 km^2 [see Mänd *et al.* (2005) for the scheme of the study area]. Great tits bred in nest-boxes mounted on tree trunks at a height of about 1.5–2.0 m. The internal size of nest-boxes was approximately $11 \times 11 \times 30$ cm and the diameter of the entrance hole was 3.5–4.0 cm. Old nest material was removed every year in March, before territory establishment by tits. The nest-boxes were checked regularly to record clutch size, date of hatching and number of fledglings. At the expected hatching time (day 12 after completion of clutch), the nests were visited daily until first chicks hatched. In some nests, all chicks were not hatched by inspection time and therefore the sample size for hatched young is smaller than that for fledglings. Depredated or deserted nests were omitted from the analysis when calculating average number of fledglings per brood, and this is unlikely to have biased the results since they only accounted for 6% of the nests. Adults were trapped during the second half of the nestling period and their sex and age class (yearling or older bird) were determined from plumage characteristics (Svensson, 1984). They were weighed with a Pesola spring balance to the nearest 0.1 g and their tarsi were measured with a sliding caliper to the nearest 0.1 mm. Chicks were weighed 15 days after hatching. Body mass corrected for tarsus length was used as an indicator of body condition of adults.

The two study years differed markedly from each other by breeding conditions. In 2001, it was very cold during the nestling period at the end of May (Fig. 1) and also in April (emergence time of caterpillars, which constitute the main food for great tits during that

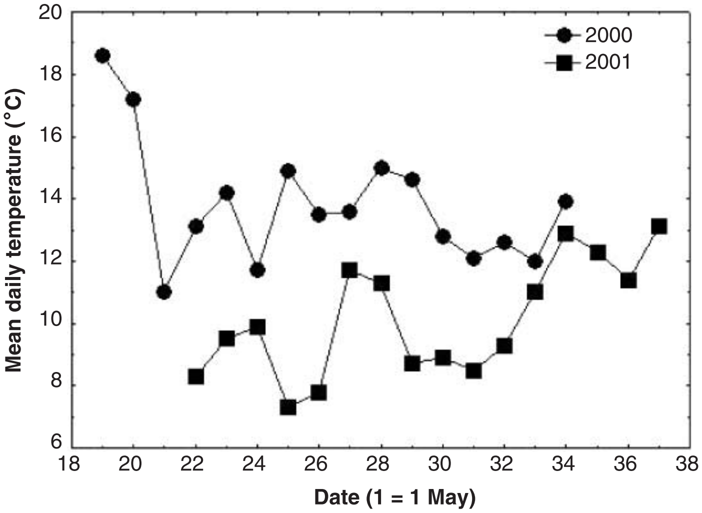

Fig. 1. Mean daily temperature during the nestling period of the great tit in 2000 and 2001. For both years, the first point on the figure corresponds to the median date of hatching in that year and the last point corresponds to day 15 after hatching.

part of the year). Nesting conditions were much more favourable in 2000. Accordingly, the average number of young fledged per nest was significantly lower in 2001 (mean ± standard deviation: 6.91 ± 2.38) than in 2000 (8.50 ± 1.95) (*t*-test; $t_{102} = 3.44$, $P = 0.001$). When comparing the data from these two study years with long-term breeding data from the same study area (Tilgar *et al.*, 2004; Mänd *et al.*, 2005), it is evident that 2000 was an average year and that 2001 was a worse than average year.

Analysis of plumage colour was performed on two feathers, plucked from a standard position on the breast. Feathers were subsequently placed in a plastic bag and stored in darkness until measurements were made. Colour was measured blindly with respect to other information about the individual in an area of the visible surface of the feather of approximately 1 mm^2 using a spectrometer (Ocean Optics S2000). Two feathers from each bird were placed one on top of the other during measurement. The mean of two separate measurements was used in further analysis. Data from the spectrometer were converted to digital information with a DAQ Card 700 and passed into a computer with appropriate software (Spectrawin 3.1), which automatically transformed the spectra into numerical values. Additional details about the measurement procedure are described in Hõrak *et al.* (2001) and Saks *et al.* (2003). The hue values obtained from the process (for calculation details, see Saks *et al.*, 2003) were used as the measure of plumage 'yellowness'. Hue has been shown to be associated with feather carotenoid content (Saks *et al.*, 2003). Repeatability (Lessells and Boag, 1987) of hue measurements was 0.75 in 2000 ($F = 7.1$, $n = 133$, $P < 0.0001$) and 0.70 in 2001 ($F = 5.7$, $n = 177$, $P < 0.0001$).

The statistical package Statistica 6.0 (Statsoft, Inc., 1984–2001) was used for data analyses. Parametric statistical methods [general linear models (GLM), Pearson correlation analysis] were used. To avoid pseudo-replication, in all cases when an individual bird was sampled in both study years, we selected randomly one value, so that no bird was entered twice into the analyses. Preliminary analysis showed that the plumage colour of tits was significantly related to sex, year and habitat, but not to age class or time of egg-laying (GLM; sex: $F_{1,274} = 26.3$, $P < 0.001$; age: $F_{1,274} = 0.2$, $P = 0.7$; year: $F_{1,274} = 19.3$, $P < 0.001$; lay-date: $F_{1,274} < 0.1$, $P = 0.99$; habitat: $F_{1,274} = 4.3$, $P = 0.039$; year × habitat: $F_{1,274} = 7.2$, $P = 0.008$). More specifically, males had on average more yellow plumage than females, tits breeding in 2000 had on average more yellow plumage than those breeding in 2001, and tits breeding in coniferous habitat were more brightly coloured than those breeding in deciduous habitat in 2000. Therefore, sex (male, female), year (2000, 2001) and habitat type (deciduous, coniferous) were considered in all models testing the effect of adult plumage colour on breeding parameters. All significance levels are for two-tailed tests.

RESULTS

No significant relationship was found between plumage hue of either parent and clutch size, number of hatchlings, or mass of fledglings (Table 1). However, female plumage hue was significantly negatively related to number of fledglings (Table 1). Inclusion of parent age class or lay-date in the model did not change the above result. Female age (but not male age) was also positively related to the number of fledglings ($F_{1,84} = 7.59$, $P = 0.007$; larger broods in older age class), but this was not the case for male age. The only significant interaction was between female plumage hue and year. A more detailed study revealed that there was a strong negative correlation between female hue and number of fledglings in 2001 (habitat: $F_{1,62} = 0.01$, $P = 0.9$; lay-date: $F_{1,62} = 0.04$, $P = 0.8$; female hue: $F_{1,62} = 7.68$, $P = 0.007$, $\beta = -0.33$; male hue: $F_{1,62} = 1.11$, $P = 0.3$), but not in 2000 (habitat: $F_{1,31} = 0.04$, $P = 0.8$; lay-date: $F_{1,31} = 2.98$, $P = 0.094$; female hue: $F_{1,31} = 0.27$, $P = 0.6$, $\beta = -0.09$; male hue: $F_{1,31} = 1.05$, $P = 0.3$) (Fig. 2). Since no relationship was found between clutch size or number of hatchlings and female plumage colour (Table 1), we supposed that the smaller breeding output of brighter females in 2001 was mainly caused by lower fledging success of their broods. Indeed, after correcting for brood size at hatching, the number of fledglings remained negatively correlated with female plumage hue in 2001 (habitat: $F_{1,56} = 0.05$, $P = 0.8$; lay-date: $F_{1,56} = 0.09$, $P = 0.8$; number of hatchlings: $F_{1,56} = 0.92$, $P = 0.3$; female hue: $F_{1,56} = 8.03$, $P = 0.006$, $\beta = -0.35$; male hue: $F_{1,56} = 2.38$, $P = 0.13$), but not in 2000

Table 1. The effects of plumage hue of parents, habitat type (deciduous, coniferous) and year (2000, 2001) on clutch size, number and body mass of fledglings in great tits (GLM, in all groups $\text{d.f.}_{\text{effect}} = 1$)

	Clutch size ($\text{d.f.}_{\text{error}} = 104$)		Number of hatchlings ($\text{d.f.}_{\text{error}} = 84$)		Number of fledglings ($\text{d.f.}_{\text{error}} = 98$)		Body mass of fledglings ($\text{d.f.}_{\text{error}} = 93$)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Year	0.09	0.8	0.01	0.9	4.88	0.029	1.50	0.22
Habitat type	0.63	0.4	0.29	0.6	0.04	0.9	0.87	0.35
Female hue	0.08	0.8	1.92	0.17	8.02*	0.006	0.07	0.79
Male hue	0.12	0.7	0.58	0.45	1.79	0.18	0.42	0.52
Year × female hue	0.04	0.9	<0.01	0.99	5.64	0.019	1.65	0.20

* $\beta = -0.29$.

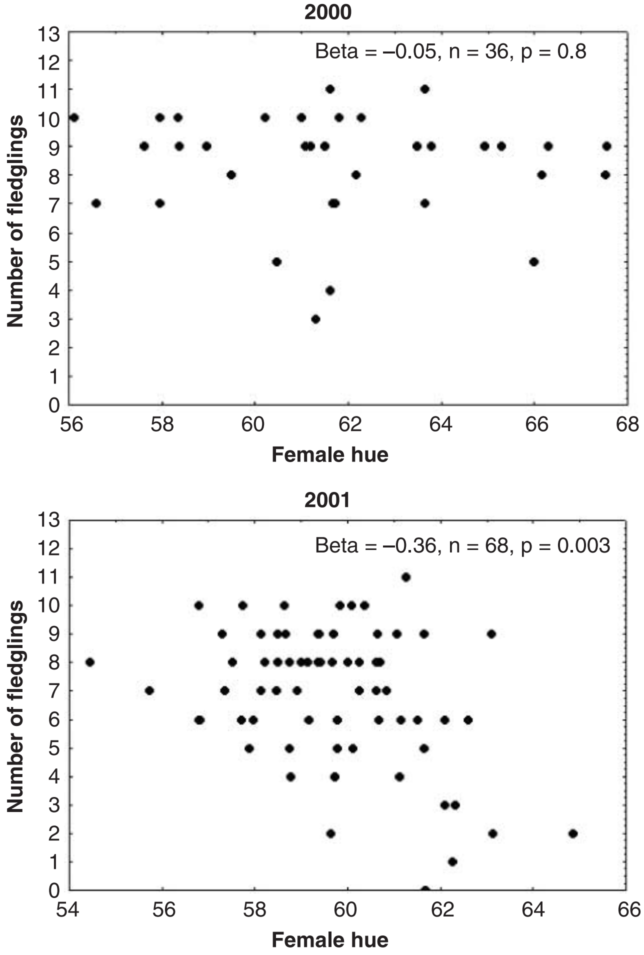

Fig. 2. Relationship between hue of yellow ventral plumage of adult females and number of fledglings in broods of the great tit in two different years. Beta values derived from GLM models.

(habitat: $F_{1,15} = 0.44$, $P = 0.5$; lay-date: $F_{1,15} = 1.57$, $P = 0.23$; number of hatchlings: $F_{1,15} = 0.90$, $P = 0.4$; female hue: $F_{1,15} = 0.04$, $P = 0.8$; male hue: $F_{1,15} = 0.01$, $P = 0.96$).

There was a significant positive relationship of female plumage hue with body mass and mass after controlling for tarsus length, but not with tarsus length (Table 2). Females were heavier in deciduous than coniferous habitat (mean ± standard error: 17.91 ± 0.1 vs. 17.56 ± 0.12 g; Table 2). When brood size at fledging was included in the model as a covariate, the positive relationship between female plumage hue and both mass ($F_{1,98} = 6.6$, $P = 0.01$) and mass controlled for tarsus length ($F_{1,97} = 6.7$, $P = 0.01$) remained significant. No significant relationship between plumage colour and any body parameter was found in males. Also, no significant correlation was detected between plumage hue of either sex and body parameters of their partners, nor was there a significant correlation between plumage hue of pair-members (ANCOVA; $r = -0.03$, $n = 111$, $P = 0.8$; corrected for year and habitat), indicating that mating in great tits is not assortative with respect to plumage hue.

Table 2. The effects of plumage hue, habitat type (deciduous, coniferous) and year (2000, 2001) on body mass, tarsus length and body mass corrected for tarsus length in female great tits during the nestling period (GLM, in all groups $\text{d.f.}_{\text{effect}} = 1$)

	Female mass ($\text{d.f.}_{\text{error}} = 107$)		Female tarsus length ($\text{d.f.}_{\text{error}} = 106$)		Female mass corrected for tarsus length ($\text{d.f.}_{\text{error}} = 105$)	
	F	*P*	*F*	*P*	*F*	*P*
Year	1.77	0.19	2.47	0.12	1.28	0.26
Habitat	6.49	0.012	0.14	0.7	7.07	0.009
Plumage hue	5.40*	0.022	0.41	0.5	5.14**	0.025
Tarsus length	–	–	–	–	$3.99^{\#}$	0.048

* $\beta = 0.24$, ** $\beta = 0.23$, $^{\#}$ $\beta = 0.19$.

Although number of fledglings was related to plumage hue of the female parent, and the latter trait in turn was related to female body mass, there was no significant correlation between number of fledglings and female body mass in either year (2000: $r = -0.14$, $n = 36$, $P = 0.4$; 2001: $r = -0.08$, $n = 68$, $P = 0.5$).

DISCUSSION

As a higher carotenoid content of the plumage is usually considered to be an indicator of superior individual quality (for reviews, see Møller *et al.*, 1999, 2000; Pryke *et al.*, 2002), one would expect a positive rather than a negative relationship between plumage yellowness and breeding output. For example, in a recent paper, Massarro *et al.* (2003) reported a positive correlation between long-term breeding success and saturation of eye colour in both male and female yellow-eyed penguins (*Megadyptes antipodes*). However, in our study, more yellow female great tits had on average lower fledging success and a smaller number of fledglings than less yellow females in the year when breeding conditions were harsh and overall reproductive output of great tits was low. To our knowledge, this is the first time that a negative relationship between a carotenoid-based trait and current breeding success has been observed in female birds. This finding is unlikely to be a chance event, since the sample sizes were large, and hence the statistical power of the tests was strong, compared with many other studies in this area.

Due to the correlative nature of the present study, we can only hypothesize about possible causes for our observations. Since no significant relationship between plumage hue of parents and clutch size was observed, the relationship between reproductive success and female plumage colour was most likely related either to maternal effects via egg quality or to parental behaviour. Egg quality is an important maternal effect (Bernardo, 1996), and carotenoids have been hypothesized to be responsible for maternal effects of egg quality in wild birds (for reviews, see Blount *et al.*, 2000; Møller *et al.*, 2000). Thus, if a trade-off exists between allocation of carotenoids by the female to own plumage and eggs, this could indeed result in low-quality eggs/chicks being produced by more colourful females. However, we have reason to doubt this explanation because, first, growth of feathers and production of eggs are temporally separated from each other in this species (Cramp and Perrins, 1993), and, second, recent studies have indicated that carotenoid content of female integument and their eggs is positively correlated (e.g. Blount *et al.*, 2002; Hõrak *et al.*, 2002). An alternative explanation for such a maternal effect lies in the probable detrimental influence of carotenoids, suggested recently by Nowak (1994) and Olson and Owens (1998). However, no evidence for detrimental effects of carotenoids on growth pattern, mortality and local recruitment rate of nestlings was found in an experimental study of great tits (Tschirren *et al.*, 2003).

Regarding parental behaviour as a possible cause of the relation between reproductive success and female plumage colour, our results appear not to support the 'good parent hypothesis', according to which the expression of the secondary sexual trait reflects parenting ability (Kirkpatrick, 1985; Heywood, 1989; Hoelzer, 1989; Møller and Jennions, 2001). Colourful females did not perform better than dull females. On the contrary, in the year when overall fledging success was relatively low, more brightly coloured females produced less young than dull females, and the fledging mass of the young of colourful females was not significantly greater than that of dull females. The physical condition of females during the nestling period (assessed from their body mass and mass corrected for tarsus length) was related to their plumage colour – brightly coloured females tended to be in a better condition than dull females. Unfortunately, since we have no data on body condition of adults from the pre-laying and pre-hatching periods, we cannot determine whether the superior condition of brightly coloured females during the nestling period was due to their low investment in parental care or to possible differences in their initial condition. However, the second explanation is more likely, because the positive correlation between female hue and mass persisted even when controlling for brood size.

In light of these findings, it is probable that female great tits adopt a conditional strategy depending on their own characteristics as well as on current breeding conditions. More specifically, colourful females appear to allocate less effort to the current reproductive attempt than dull females, especially when breeding conditions in that particular year are difficult. If yellow coloration of the breast plumage in our tits indeed reflects their phenotypic quality (for instance, their resistance to parasites), our findings are consistent with the differential allocation hypothesis (Burley, 1986) in its extended sense (Kokko, 1998; Møller and Thornhill, 1998; Sheldon, 2000; Badyaev and Qvarnström, 2002). According to this, the life-history traits of individuals (e.g. residual reproductive value) should be taken into account when females make reproductive decisions. For example, when future breeding prospects of an individual are good (e.g. birds with high parasite resistance, as reflected by their colourful plumage), it may be more advantageous for them to invest relatively less in parental care in the current breeding attempt than birds with low health status, who run a high risk of dying before the next breeding season. In small passerine birds, including the great tit, the existence of a cost of reproduction in terms of lowered future survival or fecundity is well documented (e.g. Bryant, 1979; Smith *et al.*, 1987; Gustafsson and Sutherland, 1988; Verhulst and Tinbergen, 1997; Tinbergen and Verhulst, 2000; Visser and Lessells, 2001). More colourful males generally live longer than less colourful males in birds in general (Jennions *et al.*, 2001), and such males generally provide little parental care when indirect fitness benefits are important (Møller and Thornhill, 1998; Møller and Jennions, 2001). If the first of these facts holds also for female great tits, they may trade current reproductive investment against investment in the next breeding attempt. This could explain why broods of colourful females experienced lower fledging success than broods of dull females in the year with poor breeding conditions, when the overall probability of nestling survival was low. On the other hand, such a strategy may not apply to dull coloured females, who cannot be certain that they will be able to successfully re-nest (due to low body condition). Therefore, the best tactic of such females may be to invest in the current breeding attempt rather than to postpone reproduction to a later stage. Note also that the adults breeding in 2001 were on average less yellow than those breeding in 2000 (see Methods), perhaps indicating that the overall condition of the breeding cohort was worse in 2001 than in the previous year. This could be an additional reason why the trade-off between reproduction and survival was relatively strong in the harsh breeding year, but not in the benign year.

Does such a flexible strategy pay in our region? A long-term study in the same study area has shown that due to the unstable climatic conditions, reproductive success is highly variable between years in great tits, and that a ‘bad’ year is usually followed by a ‘good’ year (Mänd *et al.*, 2005). Hence, the probability that the next season will be more favourable than the current ‘bad’ season is greater than random. Therefore, it may indeed pay for birds in prime body condition to postpone their breeding investment until the next season, when the conditions of the current season are unfavourable. In this context, the results of studies by other researchers in the same region are noteworthy. First, Hõrak *et al.* (1999) found that female great tits that deserted their broods were on average in a better nutritional condition than non-deserters. Second, Hõrak (2003) showed experimentally that females, but not males, reduce their investment in the current brood when the expected reproductive value of the brood is low. These findings provide additional evidence that female tits in good condition may adopt tactical reproductive restraint when the prospects of the current breeding attempt are unfavourable.

Our observation that a negative relationship between plumage yellowness and breeding output occurred in females but not in males, together with the above findings by Hõrak and colleagues (1999), suggest that the previously mentioned strategy is unlikely to be used by males. If so, why is that the case? We suggest that the association between parental behaviour and residual reproductive value may in general be stronger in females than in males, because egg production, incubation and early brooding place additional costs on females (e.g. Visser and Lessells, 2001). In particular, the total investment in egg carotenoids and other antioxidants by females is of a considerable magnitude, a cost that is not paid by reproducing males. There is also evidence that brood rearing imposes a greater workload and exerts greater stress on female than male great tits (Hõrak *et al.*, 1998a,b). Furthermore, in a study of house martins (*Delichon urbica*), Bryant (1979) found that breeding twice during the same breeding season diminished survival prospects in females, but not in males. Finally, some data indicate that brood-reduction may primarily be initiated by females, because chick mortality mainly occurs during the early stages of the nestling period when the contribution of males is marginal (see Hõrak *et al.*, 1999, for references).

It is noteworthy that breeding success was related to the hue of yellow ventral plumage in females, but not to female mass. Empirical studies on birds have focused on parental performance by using body mass to characterize individual condition. However, several authors (see review in Hõrak *et al.*, 1999) have cautioned against using body mass as the only index of condition. Indeed, the results of our study indicate that the reproductive tactics of birds may depend on a component of individual condition reflected by variation in carotenoid-based coloration of plumage, but not by body mass.

Most studies on carotenoid coloration in birds have treated this trait in the context of sexual selection, including yellow ventral plumage colour in great tits (Hõrak *et al.*, 2001; Tschirren *et al.*, 2003). However, our data indicate that, unlike some other bird species (e.g. Massarro *et al.*, 2003), at least social mating in the great tit is not assortative with respect to carotenoid-based plumage coloration. Differential allocation of parental care can also be characterized as a form of cryptic mate choice (Møller and Thornhill, 1998; Sheldon, 2000; Colegrave, 2001). According to this hypothesis, selection may favour individuals that allocate parental effort depending on the characteristics of their mate, especially their attractiveness. Unfortunately, we lack observational data that would allow a test of this hypothesis in our study population. However, it is unclear how differential allocation of parental care could lead to a higher breeding output by less coloured females. It is unlikely that males try to increase the number of offspring, especially when mated to unattractive partners.

Although we cannot exclude the possible role of either sexual selection or maternal effects via egg quality, it appears that the adoption of a conditional parental strategy by the female, depending on the characteristics of herself and the environmental conditions of the particular breeding season, is the most plausible explanation for the relation between female coloration and breeding success observed in this study. If this is the case, it is not at odds with the good parent hypothesis, as in unfavorable breeding conditions more colourful females use tactical restraint of their contribution to the current breeding attempt to increase their long-term reproductive success. However, experimental research is needed to adequately address this hypothesis.

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