

P.T. Smiseth · T. Amundsen

Does female plumage coloration signal parental quality? A male removal experiment with the bluethroat (*Luscinia s. svecica*)

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Abstract Females in several sexually dimorphic species with conventional sex roles possess ornamental traits that resemble those found in males. The evolution of such traits, however, is still poorly understood. Bluethroats (*Luscinia s. svecica*) are socially monogamous, sexually dichromatic passerine birds, in which female throat patch coloration varies from near absence to near full expression of male-like coloration. A recent study, demonstrating that male bluethroats prefer colourful females, suggests that female coloration is subject to sexual selection through male choice. However, the benefits males may gain from mating with colourful females have not yet been identified. In this study we tested the hypothesis that female coloration signals parental quality (the good-parent hypothesis). During the course of the same day, we recorded female care both in the presence and the absence of the male mate. The latter was done to eliminate the confounding effect of variable male care by removing the male temporarily. Female coloration did not correlate with female feeding rates either in the presence or in the absence of the male. Female feeding rates in the absence and the presence of the male were positively, although weakly, correlated. Female coloration did not correlate with female ability to compensate for the loss of male care, or with the change in brood mass during male removal. Therefore, there is no evidence for the good-parent hypothesis to explain female plumage coloration in bluethroats.

Key words Direct benefits · Female ornamentation · *Luscinia s. svecica* · Parental care · Sexual selection

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P.T. Smiseth (✉) · T. Amundsen
Department of Zoology
Norwegian University of Science and Technology
N-7491 Trondheim, Norway
e-mail: per.terje.smiseth@chembio.ntnu.no
Tel.: +47-73-590618, Fax: +47-73-591309

Introduction

In many bird species where males develop colourful ornaments during the breeding season and females tend to be more cryptic, females possess ornamental traits that resemble those found in the males (Darwin 1871; Andersson 1994). The presence of sexual ornaments in sexually dichromatic species has traditionally been explained as the result of sexual selection by female preferences for colourful males (Darwin 1871). Studies on sexual selection have focused on documenting female preferences for male coloration (e.g. Johnson 1988a; Hill 1990; Norris 1990a; Johnson et al. 1993; Andersson and Amundsen 1997) and potential benefits to females from choosing to mate with colourful males (Norris 1990b, 1993; Hill 1991; Sætre et al. 1995). Until recently, variation in female coloration, both between and within species, has received limited attention in empirical studies (Johnson 1988b; Muma and Weatherhead 1989; Hill 1993; Potti 1993; Irwin 1994; Martin and Badyaev 1996; Price and Birch 1996; Amundsen et al. 1997; Burns 1998; Linville et al. 1998; Amundsen 2000).

Nevertheless, several hypotheses have been proposed to explain the existence of visual ornaments in females. (1) The correlated-response hypothesis (Fisher 1930; Lande 1980, 1987) suggests that genetic correlations between the sexes can lead to the evolution of exaggerated traits in females. Thus, male-like coloration in females may be a by-product of sexual selection for colourful ornaments in males. (2) The female competition hypothesis (West-Eberhard 1983; Irwin 1994) states that female ornamentation signals social dominance in contests over limited resources, such as food or mates. (3) Finally, female coloration may be sexually selected through male mate choice. According to this hypothesis, both male and female visual ornaments are sexually selected but, in sexually dichromatic species, the intensity of sexual selection, relative to that of natural selection, is generally thought to be stronger in males than in females (Trivers 1972). The limited evidence presently available allows no consensus as to which hypothesis best explains the

existence of male-like coloration in females (Amundsen 2000). However, recent theoretical (e.g. Johnstone et al. 1996) and empirical (Jones and Hunter 1993; Amundsen et al. 1997) studies suggest that, in socially monogamous species, female ornamental traits may be subject to sexual selection by male choice.

Males may prefer to mate with colourful females to obtain indirect benefits if the offspring inherit the females' attractiveness as well as the male preference (Fisher 1930). Alternatively, female coloration may signal phenotypic quality to potential male mates (Andersson 1994), in which case males may obtain indirect benefit from mating with colourful females if coloration is an indicator of female genetic quality (Zahavi 1975; Hamilton and Zuk 1982; Fitzpatrick 1994), or direct benefits if coloration is an indicator of the females' ability to provide parental care (Searcy 1982; Heywood 1989; Hoelzer 1989). In species where parents provide care, direct benefits may be more important than the presumably slight indirect (genetic) benefits (Kirkpatrick and Barton 1997). The good-parent hypothesis (Heywood 1989; Hoelzer 1989) suggests that ornamental traits function as an indicator of parental quality. This hypothesis, which may be applicable to female as well as male ornaments, predicts that female coloration is positively correlated with both phenotypic quality and female parental quality. At present, some studies on socially monogamous birds have found a positive correlation between female ornamentation and female parental care (Møller 1993; Linville et al. 1998). However, it is unclear whether or not the males of these species actually choose among females to obtain direct benefits because a male preference for more ornamented females has not yet been documented (Cuervo et al. 1996).

In bluethroats (*Luscinia s. svecica*), males have been shown to prefer colourful females to drab ones in a controlled aviary experiment (Amundsen et al. 1997). Moreover, female coloration was weakly, but significantly, correlated with body size. Hence, there is evidence for male choice and some support for the suggestion that female coloration acts as an indicator of phenotypic quality in this species. However, it is still not known whether males benefit from mating with more colourful females and, if they do, what benefits they gain. The aim of the present study was to test the good-parent hypothesis (Heywood 1989; Hoelzer 1989) for the evolution of female coloration. The bluethroat is a suitable model species because it is predominantly socially monogamous (Rangbru 1994; Johnsen and Lifjeld 1995) and both sexes provide substantial amounts of parental care (Anthonisen et al. 1997; Smiseth et al. 1998). Moreover, female throat patch coloration varies from near absence to near full expression of male-like coloration (see Fig. 1 in Amundsen et al. 1997). A previous non-experimental study on bluethroats found no evidence for a relationship between female coloration and parental care measured as nestling provisioning and nestling growth (Rohde et al. 1999). In species with biparental care, each parent may adjust its amount of care to that provided by the mate

(Houston and Davies 1985; Wright and Cuthill 1989). Consequently, relationships between female coloration and parental care may be obscured by the confounding effect of variable male care. In the present experiment, we removed the male temporarily to avoid this confounding effect and, at the same time, stimulate females to provide care near their maximum capacity (see also Sætre et al. 1995). We focused on one aspect of parental quality, nestling provisioning, which was measured as female feeding rates, both with and without male assistance, as well as in terms of changes in brood mass. Nestling provisioning is a very important aspect of avian parental care and one that has been the main focus of many studies on male parental quality (e.g. Sætre et al. 1995; Wiehn 1997; Linville et al. 1998).

Methods

We performed the study in Øvre Heimdalen (61°25' N, 8°52' E), southern Norway, during June–July 1997. The study area is situated at an elevation of approximately 1100 m in the subalpine vegetation zone (Vik 1978), and has a density of around 20 breeding pairs/km² (Rangbru 1994). Bluethroats arrive at the area in the middle of May, and males establish territories immediately. Most females start egg-laying during the first half of June, and incubate for around 12 days (Rangbru 1994). Both parents feed the nestlings at similar rates, and feeding rates have not been found to vary with the time of day (Arheimer 1982; Reinsborg 1995). The young fledge 10–13 days after hatching (Anthonisen et al. 1997).

We quantified plumage coloration for 30 females. For 23 of these, we knew the exact hatching date of the first hatched nestling in their broods. The mean±SE hatching date for these nests was 26±0.6 (range: 21–32, $n=23$, day 1=1 June). For 7 females, we estimated the hatching date of their broods from nestling body masses, assuming normal growth of the nestlings (Rangbru 1994; see Ricklefs 1968 for a general description of growth rates in birds). Since parents may adjust their feeding rates to the number of nestlings in the brood (e.g. Wright and Cuthill 1990), we standardised brood size to six nestlings, which was identical to the average clutch size (6.0±0.1 eggs, range 5–7, $n=23$), and slightly above the average brood size in the year of study (5.3±0.2 nestlings, range 3–7, $n=23$). This was done on days 4–6 after hatching, by adding or removing intermediate-sized nestlings, so that the natural size difference within the brood was not altered.

On day 7 ($n=24$) or 8 ($n=5$) after hatching, we recorded female parental care both with and without male assistance. Before removing the male, we made a 3-h control video recording to obtain information on male and female feeding rates when both parents were present (median starting time: 0723 hours, range: 0647–1318 hours). We then caught the male (median removal time: 1116 hours, range: 1015–1610 hours) in mist nets placed at the nest site and weighed the nestlings to obtain initial brood mass, using a 50-g Pesola spring balance. Males were placed in individual and visually isolated cages at the field station and fed ad libitum with mealworms. To ensure that females were aware of the male's absence, we allowed some time (median: 5 h 6 min, range: 1 h 55 min–8 h 18 min) after the time of male removal before we started a 3-h video recording of the unassisted female (median starting time: 1740 hours, range: 1544–1908 hours). After completion of this recording, males were released near the nest site (median time removed: 10 h 4 min, range: 5 h 56 min–11 h 20 min). At the same time, nestlings were weighed again to obtain terminal brood mass. Because there was some variation in the time of day at which we recorded feeding rates, we tested for a potential relationship between time of day and parental feeding rates. We found no differences in feeding rates between early, intermediate and late recordings (female feeding rate before male removal; Kruskal-Wallis test:

$H=2.56$, $df=2$, $P=0.28$; male feeding rate: $H=1.18$, $df=2$, $P=0.56$; female feeding rate during male removal: $H=3.31$, $df=2$, $P=0.19$).

On day 8 ($n=22$), 9 ($n=6$) or 10 ($n=2$) after hatching, females were caught in mist nets at the nest site to obtain information on plumage coloration and condition. They were aged (1st year or older; Svensson 1992), and weighed to the nearest 0.1 g using a Pesola spring balance. Tarsus length was recorded to the nearest 0.1 mm using a slide calliper. To measure haematocrit values, we collected blood from the brachial vein in one or two 9- μ l capillary tubes that were centrifuged for 5 min in the field using a Compur M1100 portable centrifuge. Haematocrit level is a measure of the relative amount of red blood cells in the blood, and may be indicative of health status or nutritional condition (Gustafsson et al. 1994; Svensson and Merilä 1996; but see Dawson and Bortolotti 1997). Females were photographed using a standardised set-up (specially made photo stand, Nikon FM camera, Soligor AR-30 T auto ringlight, Kodak GPX film) to document variation in the extent of plumage coloration in the throat patch. These photographs were later used to score female coloration by dividing the throat patch into five parts (upper blue patch, central chestnut spot, lower blue patch, black band and chestnut band), which were scored according to the extent of coloration (0=no coloured feathers, 1=a few coloured feathers, 2=several coloured feathers). The five scores were then summed for each female to give an overall plumage score which could range from 0 to 10 (see Amundsen et al. 1997 for details). The scorings were performed by three persons (P.T.S., T.A. and L.T.T. Hansen), all of whom had previous experience with this procedure. The scores from each person were highly intercorrelated (Spearman rank correlation: $0.95 \leq r_s \leq 0.98$). In the statistical analyses involving female coloration, we used the median value of the three scorings. As a back-up procedure in case photographs were unsuitable for this purpose, P.T.S. also scored female plumage coloration in the field. For two females, photographs were either lacking or of poor quality and, therefore, we used the field scores in the statistical analyses. There was a highly significant correlation between field scores and median scores based on photographs (Spearman rank correlation: $r_s=0.96$, $n=27$, $P<0.0001$).

From each recording we noted the number of feeding visits by each parent and the time spent brooding or giving alarm calls. From control video recordings with both parents present, we determined the absolute feeding rates of females and males, as well as the proportions of all feedings to the broods that were provided by females. From video recordings following male removal, we determined the absolute feeding rate of unassisted females. We also estimated the ability of females to compensate for the loss of their mate. This was done by calculating the feeding rate of the female during male removal relative to the combined feeding rate for both parents during the control recording (100% means full compensation). Because load size or food quality may vary among parents and territories, the use of feeding rate to measure parental care has been questioned, and change in brood mass has been suggested to be a more reliable measure of parental care (Sætre et al. 1995). Accordingly, we calculated the change in brood mass per hour during male removal.

During the 180-min control video recording, females brooded for a mean duration of 13.7 ± 3.9 min (range: 0–77.3 min, $n=28$). Three of these females brooded for more than 30 min. Since females are unable to feed the nestlings while brooding and females only brood their young during or immediately after rainfall, brooding is more likely to reflect weather conditions at the time of video recording than female parental quality. We therefore excluded this period of time when calculating female feeding rate. There was no correlation between female feeding rate calculated in this way and the time spent brooding in the control video recording ($r=0.19$, $n=28$, $P=0.34$), suggesting that female feeding rate was not affected by the time spent brooding. For the second video recording, brooding was too infrequent to affect feeding rate (mean duration: 0.1 ± 0.1 min, range: 0–2.8 min, $n=28$). The difference in time spent brooding between the first and second recording was probably due to rainfall during the preceding night on 3 experimental days. Parents may also lower their feeding rate when hear-

ing or giving alarm calls. Therefore, we excluded occasional episodes of alarm calling when calculating both male and female feeding rate. Parents spent very little time giving warning calls both during the control video recording (mean duration: 1.5 ± 0.6 min, range: 0–14.1 min, $n=28$) and the second recording (mean duration: 0.1 ± 0.1 min, range: 0–2.8 min, $n=28$).

We calculated female body condition as residuals from a regression of tarsus length on body mass. In analyses involving brood mass at the time of male removal on day 7 (as a measure of nestling growth during days 0–7 after hatching), we only included cases where the exact hatching date was known and nestlings had not been removed or added at an intermediate stage ($n=9$). One female filmed on day 9 after hatching was not included in the statistical analyses on parental quality since parents may increase feeding rates with nestling age. We also excluded one control recording because the male gave alarm calls for more than 2 h. For one female, we failed to obtain female feeding rate during male removal due to technical problems with a video camera. In analyses involving the change in brood mass we excluded one extreme outlier that was probably due to measurement error. We used parametric statistics whenever the assumptions of such tests were met. Data on female ability to compensate for male removal were $\log_{10}(x+1)$ transformed before being used in parametric tests. When reporting descriptive data, we present means \pm SE. We used SPSS 4.0 for the Macintosh to test assumptions of parametric tests, and StatView 4.02 for the Macintosh in other statistical analyses. We calculated statistical power for the relations between female coloration and measures of female quality using GPOWER (Erdfelder et al. 1996). For the relationship between female ornamentation and measures of body size and condition, we used an effect size of $r=0.3$, which is close to that previously reported for bluethroats by Amundsen et al. (1997). For the relationship between female ornamentation and parental care, we used an effect size of $r=0.6$, which is the effect size obtained from Linville et al. (1998, Fig. 3); the only study from which comparable data are available. For other tests, where no previous information on effect sizes was available, we used the medium effect size ($r=0.3$) according to Cohen (1988).

Results

Female plumage coloration and condition

The mean plumage score for female bluethroats in our sample was 4.5 ± 0.4 (range: 1–10). There was no significant difference between 1st-year ($n=10$) and older ($n=20$) females in plumage coloration (mean plumage score for 1st-year and older females: 4.1 ± 0.6 and 4.8 ± 0.6 , respectively; $t=-0.71$, $df=28$, $P=0.48$). We obtained the following measures of female body size and condition: body mass (mean: 16.9 ± 0.2 g), tarsus length (mean: 29.8 ± 0.9 mm), body condition (mean: 0.0 ± 0.7), and haematocrit level (mean: $49.1 \pm 2.8\%$). We found no relationship between female plumage score and measures of female body size or condition (body mass: $r=0.08$, $n=27$, $P=0.68$, power=0.48; tarsus length: $r=-0.03$, $n=29$, $P=0.86$, power=0.50; body condition: $r=0.10$, $n=27$, $P=0.62$, power=0.48; haematocrit level: $r=-0.09$, $n=28$, $P=0.66$, power=0.49).

Female feeding rate with and without male assistance

With both parents present, the mean feeding rate was 14.0 ± 0.9 visits/h for females and 12.3 ± 0.7 visits/h for

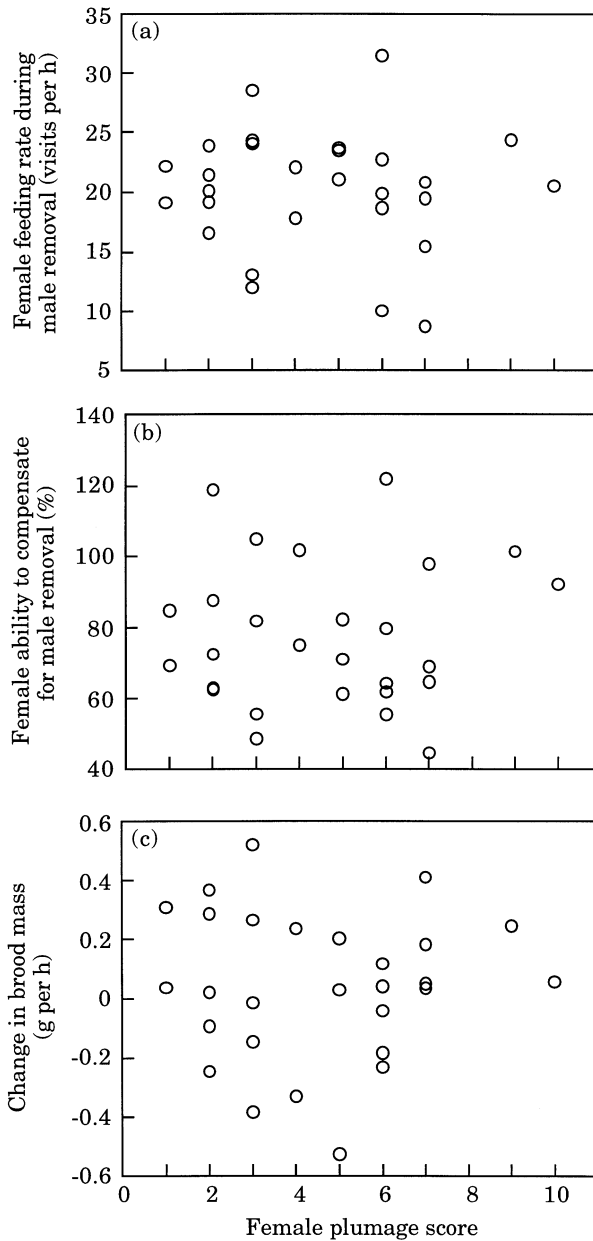


Fig. 1 Relationship between plumage score of female bluethroats and female feeding rate during male removal ($r=-0.06$, $n=28$, $P=0.78$, power=0.99) (a), female ability to compensate for male removal ($r=0.05$, $n=27$, $P=0.80$, power=0.98) (b), change in brood mass during male removal ($r=0.008$, $n=28$, $P=0.97$, power=0.99) (c)

males. For both parents combined, the mean feeding rate was 26.3 ± 0.9 visits/h. There was no statistical difference in the feeding rates of males and females (paired t -test: $t=-1.27$, $df=27$, $P=0.22$). On average, females provided $52.7 \pm 0.2\%$ (range: 32.0–80.0%) of all feedings. Male and female feeding rates were not correlated ($r=-0.32$, $n=28$, $P=0.10$). Females responded to the temporary removal of their mate by increasing the feeding rate to 20.2 ± 1.0 feeding visits/h (comparison of the feeding rate when females were unassisted and assisted;

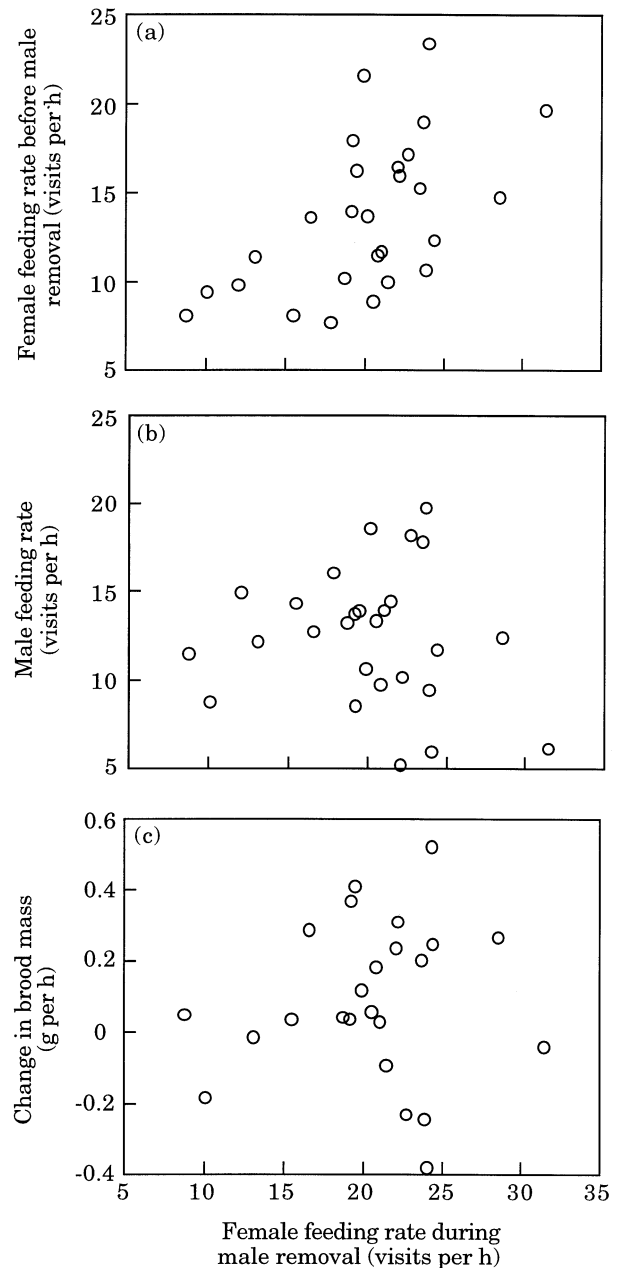


Fig. 2 Relationship between feeding rate of female bluethroats during male removal and female feeding rate when both parents were present ($r=0.56$, $n=27$, $P=0.002$, power=0.48) (a), male feeding rate when both parents were present ($r=-0.11$, $n=27$, $P=0.59$, power=0.48) (b), change in broods mass during male removal ($r=0.10$, $n=24$, $P=0.66$, power=0.44) (c)

paired t -test: $t=7.46$, $df=26$, $P<0.0001$). Unassisted females increased their feeding rate by $53.8 \pm 8.2\%$ (range: -7.9 – 131.5%) in comparison to their own feeding rate when assisted by their mate. Although unassisted females increased their feeding rate substantially, they did not fully compensate for the removal of their mate. During male removal, females delivered food at a rate which comprised $77.6 \pm 0.4\%$ (range: 44.7–121.9%) of the combined feeding rate when both sexes were present.

Female plumage coloration and parental care

Female plumage score was not significantly correlated with hatching date ($r=0.17$, $n=23$, $P=0.43$, $\text{power}=0.96$), clutch size ($r=-0.10$, $n=23$, $P=0.67$, $\text{power}=0.96$) or brood mass at the time of male removal on day 7 after hatching (Spearman rank correlation: $r_s=0.63$, $n=9$, $P=0.08$). Furthermore, female plumage score was not correlated with female feeding rate when the male was still present ($r=-0.22$, $n=28$, $P=0.27$, $\text{power}=0.99$), the proportion of feedings delivered by the female (Spearman rank correlation: $r_s=-0.18$, $n=28$, $P=0.34$), or with male feeding rate ($r=0.06$, $n=28$, $P=0.28$, $\text{power}=0.99$). Neither could we detect a relationship between female plumage score and female feeding rate during male removal (Fig. 1a), or female ability to compensate for male removal (Fig. 1b). During male removal, the mean change in brood mass was 0.045 ± 0.047 g/h. There was no correlation between female plumage score and the change in brood mass/h (Fig. 1c).

Female feeding rate during male removal was positively correlated with female feeding rate when both parents were present (Fig. 2a). This may either indicate a consistent effect of female parental quality, or that female feeding rate largely reflects territory quality. In the latter case, we would expect female feeding rate during male removal also to be correlated with male feeding rate, but this was not the case (Fig. 2b). Finally, we tested for a correlation between female feeding rate and the change in brood mass during male removal, but no such relationship was found (Fig. 2c). This may suggest that in nestlings that are large for their age less priority is given to body mass increment and more to feather growth than in smaller nestlings. However, there was a non-significant relationship between the change in brood mass and the total brood mass at the time of male removal ($r=-0.29$, $n=28$, $P=0.13$, $\text{power}=0.49$).

Discussion

Female coloration and parental care

When experimentally controlling for the confounding effect of variable male care, we found no evidence of a relationship between female plumage coloration and female parental care in bluethroats. However, we found an almost significant positive correlation between female coloration and brood mass at the time of male removal on day 7 after hatching. This trend was probably accidental because a previous non-experimental study on bluethroats in the same area with a larger sample found no relationship between female plumage coloration and brood mass (Rohde et al. 1999). We consider our results on the relationship between female plumage coloration and female parental care to be robust for the following three reasons. (1) The experimental design of temporary male removal ensured that female performance was not confounded by variation in male care (Houston and

Davies 1985; Sætre et al. 1995) and also stimulated females to provide nestling care at or near their maximum capacity. Thus, we probably obtained measures of female care that reliably reflected female parental quality. (2) When correlating female plumage score with measures of female parental quality during male removal, the observed effect sizes were close to zero ($-0.06 < r < 0.05$; see Fig. 1). Thus, there were no trends in either direction for a relationship between coloration and parental quality in females. (3) The statistical power at the effect size $r=0.6$ was high (approximately 98%; see Fig. 1), indicating that we had a good chance of detecting relationships between female coloration and female parental quality if present. We therefore conclude that our results do not support the hypothesis that female coloration signals parental quality (Heywood 1989; Hoelzer 1989) in this species. Our results are in agreement with those obtained in a previous non-experimental study on bluethroats from the same study area that reported no relationships between female coloration and parental quality measured as hatching date, clutch size, feeding rate and nestling growth (Rohde et al. 1999).

Male removal experiments may not provide information on the amount of care provided by females under natural conditions when the male mate is present. Therefore, we also recorded female care when the male was present. The lack of a significant correlation between female coloration and female feeding rate in the presence of the male confirms the finding that female coloration is not correlated with female care. The design used in this study allows comparison of the amount of care provided by individual females when they were and when they were not assisted by the mate. We found that female feeding rate when both parents were present was positively correlated with female feeding rate when the female was alone. This finding suggests that the amount of care provided by females when the mate is present reflects female parental ability, although it should be noted that female feeding rate when both parents are present explains relatively little of the variation in female feeding rate during male removal ($r^2=0.31$). Because both load size and food quality may differ between individual parents (e.g. Sætre et al. 1995), we also measured female care in terms of changes in brood mass during male removal. The finding that there was no significant correlation between female coloration and the change in brood mass confirms the finding that female parental care is not correlated with female coloration.

In this study, we focused mainly on nestling provisioning which is a very important aspect of avian parental care. Because female passerine birds also protect their nestlings from predators, female coloration could potentially be correlated, instead, with this aspect of care. However, a separate experiment on bluethroats in the same study area found no relationship between female coloration and anti-predator responses to adder dummies when the male was present or temporarily removed (M. Myklebust and T. Amundsen, unpublished data). Therefore, there is no evidence that female coloration signals

her ability to protect nestlings from predators in this species.

As stated in the Introduction, the aim of our study was to test the good-parent hypothesis (Heywood 1989; Hoelzer 1989). However, an alternative hypothesis for the relationship between attractiveness and parental care, the differential-allocation hypothesis (Burley 1986), states that attractive mates may provide *less* care than unattractive ones because their partners are willing to increase their contribution of care to obtain or maintain an attractive partner. The differential-allocation hypothesis, therefore, predicts a negative correlation between female coloration and female care as well as a positive correlation between female coloration and male care. This hypothesis also predicts that colourful females are better at compensating for the loss of their mate than drab females. This is so, because colourful females are expected to extract relatively more care from their mates than drab females so that drab females are closer to their maximum parental ability when both parents are present. We found no evidence of a relationship between female coloration and female feeding rate, male feeding rate, or female ability to compensate for the loss of male care. Therefore, there is also no support for the differential-allocation model in bluethroats. Recent modifications of this hypothesis (Kokko 1998; Møller and Thornhill 1998) do not predict such relationships and can, therefore, not be evaluated from our data. A recent theoretical model by Kokko (1998) suggests that the differential-allocation hypothesis requires a concave-shaped relationship between mating effort and mating success and, therefore, it seems not to apply to females in socially monogamous species.

Female ornamentation

Because we found no support for the hypothesis that female coloration signals parental quality, the existence of visual ornaments in female bluethroats has yet to be explained. The presence of a male preference for colourful females (Amundsen et al. 1997) supports the hypothesis that female coloration in bluethroats is sexually selected through male choice. Males may prefer to mate with colourful females to obtain indirect benefits, rather than direct benefits, if the offspring inherit the females' attractiveness as well as the male preference (Fisher 1930), or if coloration acts as an indicator of the females' genetic quality (Zahavi 1975; Hamilton and Zuk 1982; Fitzpatrick 1994). Indicator models of sexual selection suggest that ornaments can be honest signals of phenotypic or genetic quality if they are costly to produce or maintain (Grafen 1990a, 1990b). The blue colour of the throat patch in bluethroats is a structural colour, while the chestnut spot is probably melanin based (S. Andersson, personal communication). Because there is little evidence of production costs for structural and melanin-based colours, these colours have been considered as poor candidates for honest signals of phenotypic quality (e.g. Gray 1996; but see

Fitzpatrick 1998; Andersson 1999). There is some evidence suggesting that female coloration is correlated with phenotypic quality in bluethroats as Amundsen et al. (1997) found that female coloration was weakly, but significantly, correlated with body size. In this study, however, we found no evidence of a relationship between female coloration and female body size or condition. This apparent inconsistency is probably due to the lower statistical power in our study.

The most plausible alternative to the hypothesis that female coloration is sexually selected through male mate choice is that female coloration functions as a social badge in intrasexual competition over mates or in contests over limited resources, such as food (West-Eberhard 1983; Irwin 1994). In pinyon jays (*Gymnorhinus cyanocephalus*), for example, colourful females had higher success than less colourful females when competing for high-quality males (Johnson 1988b). Further experiments are needed to test whether or not female coloration in bluethroats signals dominance rank in contests with other females over male mates or other limited resources.

Female compensation

The male removal experiment also provides interesting information on female ability or willingness to compensate for the loss of male care. In most birds, both sexes provide substantial amounts of parental care (Lack 1968), and theoretical models predict that biparental care is evolutionarily stable when parents partially compensate for a reduction in care by their mate (e.g. Houston and Davies 1985). As predicted, we found that females increased their own feeding rates compared to when both parents were present, but that they did not fully compensate for the loss of their mate. This finding is in accordance with findings of some previous studies that have manipulated male parental care (Wright and Cuthill 1989; Wolf et al. 1990; Dunn and Hannon 1992; Meek and Robertson 1994; but see Wright and Cuthill 1990; Ketterson et al. 1992; Saino and Møller 1995).

Conclusion

We found no evidence for a relationship between female plumage score and parental care in bluethroats. Hence, there is no support for the good-parent hypothesis (Heywood 1989; Hoelzer 1989) in this species. Female bluethroats are in general less colourful than males, which suggests that selection acts against the development of male-like coloration in females. Nevertheless, there is a very high level of phenotypic variation in the plumage coloration of female bluethroats (see Fig. 1 in Amundsen et al. 1997). Assuming that the development or maintenance of conspicuous coloration is costly, the maintenance of a high level of phenotypic variation is difficult to explain from the genetic correlation hypothesis alone. Potential-

ly, female coloration could signal offspring attractiveness or viability to potential male mates, or dominance in female-female contests over mates or other limited resources. Further studies are needed to explain the presence and variation of female coloration in bluethroats and other sexually dichromatic species.

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