

FEMALE PLUMAGE COLORATION IN THE BLUETHROAT: NO EVIDENCE FOR AN INDICATOR OF MATERNAL QUALITY¹

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Abstract. Sexual dimorphism in plumage coloration among passerines is believed to be largely the result of sexual selection, with males usually being more colorful than females. Yet in many species females also are brightly colored. Such "ornaments" are traditionally viewed as nonfunctional byproducts of selection for the same trait in the male, i.e., as genetic correlation. Alternatively, female coloration may have a signaling function in contexts such as male mate choice or intrasexual competition. The Bluethroat (*Luscinia svecica svecica*) is a species exhibiting strong sexual dichromatism and large variation in plumage coloration of females. In a recent aviary experiment, males associated more with colorful females which were both larger and heavier than dull females. These results could be interpreted as evidence for male preference for high quality females. Here we present correlational data from a two-year field study on Bluethroats in which we tested whether female plumage coloration is an indicator of female reproductive quality. Female coloration was positively, although weakly, related to skeletal size, but was not related to body mass during the nestling period. Clutch size, hatching dates, feeding rates, and nestling growth gave no indication that more colorful females were of superior phenotypic quality. The results suggest that plumage coloration does not reflect parental abilities in female Bluethroats. We discuss the implications of our results for the understanding of processes of sexual selection in passerine birds.

Key words: *Bluethroat, clutch size, Luscinia svecica, mate choice, parental care, sexual dichromatism, sexual selection.*

INTRODUCTION

Many passerine bird species show extreme sex differences in plumage coloration (Møller 1986). The evolution of this sexual dimorphism is believed to be largely an effect of sexual selection (Andersson 1994). The plumage of the male usually is more colorful than that of the female, and an increasing number of studies indicates that female choice acts as a directional selection pressure on male plumage coloration (Andersson 1994). The usually duller coloration of female plumage is believed to be mainly a result of natural selection and has been regarded as self-explanatory, not requiring explicit study. However, in many bird species, female plumage also is colorful, but the evolution of ornamental coloration in females has been studied much less (Muma and Weatherhead 1989, Hill 1993).

There are several hypotheses which may account for the evolution of colorful females, most of which were formulated initially to explain

sexual traits in males. Some hypotheses can be termed "indicator models" in which plumage color is a signal of phenotypic quality that may or may not have a genetic basis (Andersson 1994). According to the "good parent hypothesis," plumage coloration is an indicator of parental quality which influences immediate reproductive success (Hoelzer 1989, Hill 1993). In other indicator models, plumage color may signal immunocompetence (Potti and Merino 1996), general viability (Møller 1991), survival ability during migration (Fitzpatrick 1994), or social dominance over individuals of the same sex (Johnson 1988, Slagsvold and Lifjeld 1994). In contrast, the "Fisherian model" of sexual selection considers exaggerated sexual characters as the outcome of a self-reinforcing runaway process in which the preference for a trait and the trait itself are genetically linked, but there is no assumption of a link between the trait and the phenotypic quality of the bearer (Fisher 1930). Finally, the only nonfunctional hypothesis is the "genetic correlation hypothesis" which assumes that, because of genetic correlation between the sexes, the male sexual trait is partly expressed in the female, too (Lande 1980,

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Muma and Weatherhead 1989, Price and Langen 1992). Female coloration may then be neutral, or even slightly detrimental (Price and Burley 1994) with respect to female phenotypic quality. This genetic-correlation model is difficult to test directly and can gain support only through the rejection of all functional models (Cuervo et al. 1996).

The Bluethroat (*Luscinia svecica svecica*) is a suitable species for the study of female secondary sexual traits because of its highly variable plumage coloration. Moreover, a recent aviary experiment showed that male Bluethroats spent more time in association with the more colorful one of two stimulus females (Amundsen et al. 1997). In addition, body mass and tarsus length were both positively correlated with coloration, suggesting that female plumage coloration (FPC) may be an indicator of phenotypic quality. On the basis of these results, Amundsen et al. (1997) rejected the genetic correlation hypothesis and suggested that FPC is subject to direct sexual selection through male mate choice. Thus, if FPC in the Bluethroat were an indicator of general phenotypic quality, then this phenotypic superiority should be expressed in contexts which are closely related to fecundity (Hill 1993).

In the present study, we address the question whether FPC in the Bluethroat functions as an indicator of female parental quality (Hoelzer 1989) and of seasonal reproductive performance. Specifically, we predicted that timing of breeding (measured as hatching date), zygotic investment (measured as clutch size), maternal effort (measured as provisioning rates), and seasonal reproductive success (measured as nestling growth) should be related to the degree of female coloration.

METHODS

The Bluethroat is a predominantly monogamous, territorial, and migratory passerine that breeds in northern Europe. It shows strong sexual dimorphism in plumage coloration (Cramp 1988). The males have a glossy blue throat patch with a central chestnut spot and a chestnut band below, with a narrow band of white and black in between. Although females always are less colorful than males, they often show the same colors as males on their throat feathers. However, colors vary considerably more among females than among males, ranging from the complete

absence of blue and chestnut feathers to a very colorful throat patch, closely resembling that of the male (for color photographs see Amundsen et al. 1997).

The field study was conducted in Øvre Heimdalen (61°25'N, 8°52'E, altitude 1,100 m), Norway, in 1995 and 1996. For a more detailed description of the study area see Vik (1978) and Johnsen and Lifjeld (1995). Most females were mist-netted at their nests during the nestling stage, and standard measures (body mass, wing length, tarsus length) were taken following Svensson (1992). In order to reduce the effects of a possible seasonal variation in body mass, we caught females at similar nestling stages, i.e., days 2–4 post-hatch. The degree of FPC was scored according to a standardized scale ranging from 1 (dull) to 10 (very colorful). In this scoring procedure five components of the plumage ornament were scored separately (0 = absent, 1 = weakly developed, 2 = strongly developed) and the scores then summed to yield an overall score (Amundsen et al. 1997). Scoring was carried out by J. T. Lifjeld in 1995 and by all three authors in 1996. Four females bred in both seasons. To avoid pseudoreplication, the data for these females were excluded from the 1996 sample whenever data from both study years were pooled for analysis.

Most males were mist-netted and treated (see below) shortly after territory establishment. Variation in male plumage is difficult to quantify visually and therefore was not recorded. In both years the males were subject to experimental manipulation of their sexual attractiveness using three different techniques. In 1995, males were part of a color band experiment as described in Johnsen et al. (1997). In 1996, males were manipulated in two ways. In one part of the study area the throat patch of some males was blackened with nyanzol (Johnsen et al. 1998a), in another part of the study area the UV reflectance of the blue ornamental feathers was reduced (Johnsen et al. 1998b). Although male manipulation had significant effects on several indicators of male mating success (Johnsen et al. 1997, 1998a, 1998b), we were unable to find any significant effect on any of the measured variables in the present study (female ornamentation both years combined: $n_1 = 25$, $n_2 = 22$, Mann-Whitney U -test, $z = -0.59$, $P > 0.5$; hatching date both years, $n_1 = 25$, $n_2 = 22$, $z = -1.25$, $P > 0.2$; clutch sizes of 1995 and 1996, relative feed-

ing rates and absolute feeding rates per nestling measured in 1995, unpubl. data). Within the sample entering the analysis of nestling growth, male treatment did not systematically influence the occurrence of extra-pair paternity (unpubl. data). Belonging to the group of attractive or unattractive males, respectively, did not predict extra-pair paternity (1995: 2 out of 6 broods belonging to attractive males and 3 out of 11 broods belonging to unattractive males contained at least one extra-pair nestling; 1996: 3 out of 7 versus 4 out of 7; both years combined: 5 out of 13 versus 7 out of 18, $\chi^2_1 = 0.001$, $n = 31$, $P > 0.9$).

In 1996, we did not record feeding activity and assume that the experimental procedures did not affect parental behavior. We pooled the data on females of the experimental and control groups to look for effects of FPC on maternal quality. In all cases, the treatment of males did not affect territory acquisition because males were treated only after territory establishment.

Bluethroats are ground nesters. Nest building usually overlaps with the mate-guarding period, and we located nest sites by following females carrying nest material. Most nests were found during nest building or incubation, so that we knew the exact age of most of the clutches. Because most of the pairs were observed before the onset of breeding (during the mate guarding period), we can be reasonably sure that we did not miss early nesting attempts. In our study population, Bluethroats are single brooded and breeding takes place rather synchronously so that second nesting attempts are unlikely to occur, but likely to be recognized as such. Thus, in the two study years only one female was observed to re-nest at an early stage and in connection with mate switching. The nests were checked daily during the late part of incubation to record the exact day of hatching. In a few cases, however, nests were found during the nestling stage. In the analysis of nestling growth and feeding behavior, we included only those broods which were found on an estimated day-5 post-hatch or earlier, because at later nestling stages age estimation on the basis of growth curves becomes less reliable.

In 1995, provisioning rates (feedings hr^{-1}) of both males and females were recorded for a subsample of nests when the nestlings were 6, 7 ($n = 13$), and 8 ($n = 14$) days old. For this purpose, we placed video cameras on tripods 1–2 m away

from the nests which were recorded continuously for 3 hr. To habituate the birds to the presence of an unfamiliar object, the tripods were raised the day before (in two cases 1 hr before) the first filming took place and were removed only after the last recording. Because of frequent brooding on day 6, we excluded these data from the analysis. Recordings started between 09:00 and 17:30; there is no systematic relationship between feeding rates and time of day (Arheimer 1982, Reinsborg 1995). In the analysis of clutch size, we excluded nests that were found after hatching, because Bluethroats remove unhatched eggs and dead chicks from the nest (pers. observ.). We furthermore excluded data from renestings ($n = 1$) and nests of secondary females ($n = 1$).

We determined brood masses on days 7, 8, and 9 in 1995 and on days 6, 8, and 10 in 1996 using a 50 g Pesola spring balance. We did not record nestling mass after day 9 (1995) and 10 (1996), respectively, because from day 10 on, the nestlings become increasingly mobile and responsive to "predators." Disturbance may then lead to premature fledging and induce loss of nestlings. Because we were unable to determine nestling mass at fledging, we used nestling mass at the later stages as a substitute measure. In the European Blackbird (*Turdus merula*), a species with a nestling period of similar length (13 to 14 days), nestling mass on day 8 was shown to be predictive of nestling survival (Magrath 1991). In both years, measurements were taken between 18:00 and 23:00 except for day 9 in 1995. From these data we calculated average nestling masses. To correct nestling mass for brood size, we calculated the residuals from a regression of average nestling mass on brood size. Sample sizes vary for the different nestling ages because of predation (see Results). A few nests had to be excluded from the analysis because of disappearance or extremely low nest attendance by one parent as determined by direct observations or focal video recording of at least 1.5 hr (1995: $n = 1$; 1996: $n = 3$, FPC scores: 5, 5, 5). The actual reasons for reduced male parental care could not be determined. In the analysis of brood masses and feeding behavior, nests which were found after day 5 (1995: $n = 2$; 1996: $n = 4$, FPC scores: 2, 5, 5, 6, 8, 10, respectively), nests which suffered partial brood losses after day 3 (none in 1995; 1996: $n = 2$, FPC scores: 2, 7), and secondary nests (1995 only: $n = 1$, FPC score: 7) were excluded. How-

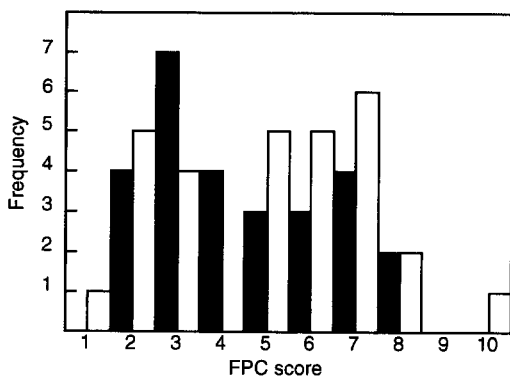


FIGURE 1. Frequency distribution of female plumage coloration (FPC) score. Solid bars: 1995 scores, open bars: 1996 scores.

ever, one case of renesting was included as it did not deviate from other nests with respect to hatching date. There was no obvious relation between FPC scores and the occurrence of extra-pair fertilizations. Within the sample entering the analysis of feeding rates and nestling growth, females with nests containing at least one extra-pair young and females with nests without extra-pair young did not differ with respect to FPC scores (Mann-Whitney U -test, $z = -0.88$, $n_1 = 12$, $n_2 = 19$, $P > 0.3$).

Statistical tests were computed using Statview 4.5 for the Macintosh. Significance level was set at $P \leq 0.05$. For sample sizes smaller than $n = 20$, P -values of nonparametric statistics were checked against P -values from statistical tables, following Mundry and Fischer (1998). Means are given with standard errors unless otherwise stated.

RESULTS

FEMALE AGE, BODY MEASURES, AND PLUMAGE COLORATION

In our study population, FPC scores ranged from 2 to 8 ($n = 27$) in 1995 and from 1 to 10 ($n = 29$) in 1996 (Fig. 1). Four females bred in both years. Two of these received the same scores in both years (7 and 8) and the other two were scored higher in the second year (7 versus 8, and 2 versus 4). In Figure 1, these females are represented only with their 1995 scores. The two age-classes (yearlings and older) differed significantly with respect to coloration (1995 and 1996 data combined, mean FPC scores: yearlings: 3.5 ± 0.5 , $n = 16$, older: 5.2 ± 0.4 , $n =$

39, Mann-Whitney U : $z = -2.45$, $P = 0.01$). The samples from 1995 and 1996 did not differ significantly with respect to tarsus length (Mann-Whitney: $z = -0.51$, $n_1 = 27$, $n_2 = 29$, $P > 0.5$), so the data sets were pooled. We found a nonsignificant positive correlation between FPC scores and tarsus length (1995: $r_s = 0.35$, $n = 27$, $P < 0.1$; 1996: $r_s = 0.28$, $n = 33$, $P > 0.1$; both years combined: $r_s = 0.23$, $n = 56$, $P < 0.1$). These results resemble those of Amundsen et al. (1997), who reported a significant correlation and an r_s of 0.28 ($n = 56$). Not all females could be measured at a fixed nestling stage, and a few were caught before the onset of the nestling period. Because female body mass tended to decrease with progressing nestling stage, we used residuals from a regression of female body mass over nestling stage at capture as a measure of female body mass. Again there were no differences between years (Mann-Whitney U -test, $P > 0.99$), so the two data sets were pooled. Residual female body mass was not correlated with FPC score ($r_s = 0.05$, $n = 50$, $P > 0.5$).

Because our study area is in immediate geographic vicinity of the area in which Amundsen et al. (1997) collected the females for their aviary experiment, the females of our 1996 data set and theirs (also from 1996) were collected from the same population. This makes it possible to compare directly the female body measures from Amundsen et al. (1997), which were taken during the prelaying period, with our own data, which were taken during the nestling stage. Regarding FPC scores, the descriptive statistics of our combined samples (both study years, the four females occurring in both samples represented with their 1996 scores only) are very similar to those of Amundsen et al. (1997) (means \pm SD = 4.8 ± 2.0 vs. 4.6 ± 2.2 , $n_1 = 56$, $n_2 = 56$, Mann-Whitney U , $z = -0.55$, $P > 0.5$; statistics from Amundsen et al. were calculated from their Fig. 1b). Thus, there is no evidence that more colorful females are more prevalent among breeding females than among prebreeding females.

The positive relationship between FPC score and body mass that existed during the prelaying period (Amundsen et al. 1997) had disappeared by the time the nestlings had hatched (see above). A comparison of the mean female body mass during the prelaying period (as taken from Fig. 4 in Amundsen et al. 1997) with the mean

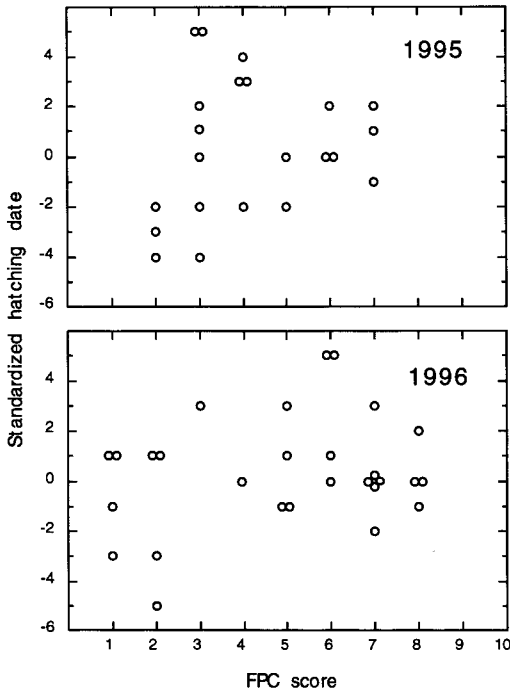


FIGURE 2. Standardized hatching date in relation to FPC score. Data from 1995 ($r_s = 0.26, n = 22, P = 0.24$), 1996 ($r_s = 0.15, n = 28, P = 0.44$).

body mass during the nestling period (our data from 1996 only) indicates that on average mothers were considerably heavier (mean = 18.6 g) than prebreeding females (mean = 15.7 g, $n = 54$) and even heavier than the most colorful (FPC score = 9) and heaviest prebreeding females (mean body mass = 16.4 g, $n = 2$).

HATCHING DATE AND CLUTCH SIZE

Timing of breeding often affects seasonal reproductive success in passerine birds. Reproductive success usually decreases as the season progresses, which may be because early breeding individuals are of higher quality and/or because breeding conditions deteriorate over time. Thus we used hatching dates to test the prediction that colorful females have a reproductive advantage over less colorful ones. Contrary to our prediction, female plumage score was not correlated with hatching date (standardized over the median hatching date for each year, $r_s = 0.22, n = 47, P = 0.14$). The Spearman correlation coefficients had a positive sign in both study years (Fig. 2).

Clutch size was not correlated with FPC

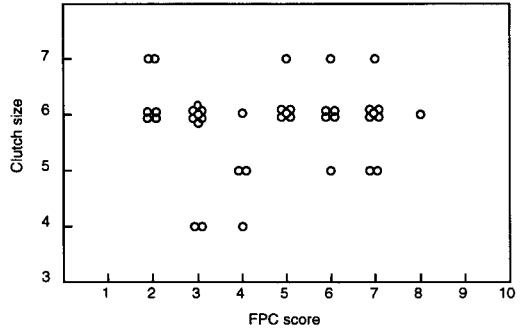


FIGURE 3. Clutch size in relation to FPC score for both years combined ($r_s = -0.01, n = 40, P > 0.5$). Multiple overlying data points are shown as clusters.

scores (Fig. 3). However, because clutch size showed a seasonal decline in 1995 ($r_s = -0.62, n = 18, P = 0.01$), although not in 1996 ($P > 0.5$), and colorful females tended to breed later than less colorful ones, a possible association between FPC and clutch size could be masked by seasonal effects. We therefore ran a multiple regression analysis of clutch size with FPC scores and standardized hatching date (square-root transformed) as independent variables: again there was no effect of FPC score on clutch size (standardized regression coefficient = 0.04, $P > 0.5$).

FEEDING BEHAVIOR AND NESTLING GROWTH

Male and female feeding rates were correlated with each other and with brood masses on day 8 (feeding rates per nestling: $r_s = 0.66, n = 14, P < 0.05$; combined feeding rates of male and female with average nestling mass: $r_s = 0.62, n = 14, P < 0.05$) but not on day 7 (feeding rates: $r_s = 0.30, n = 13, P > 0.3$; combined feeding rates of male and female with average nestling mass: $r_s = 0.36, n = 13, P > 0.2$). The time of day when feeding behavior was recorded was not related to FPC scores (day 8: $r_s = -0.03, n = 14, P > 0.5$) or feeding rates ($r_s = 0.17, n = 14, P > 0.5$).

Contrary to the prediction of the good parent hypothesis, female feeding rates per nestling were negatively correlated with FPC scores, but only significantly so on day 8 (day 7: $r_s = -0.22, n = 13, P > 0.4$; day 8: $r_s = -0.62, n = 14, P < 0.05$; Fig. 4). This relationship between FPC and feeding rates was not an effect of variable brood size (two to six nestlings), be-

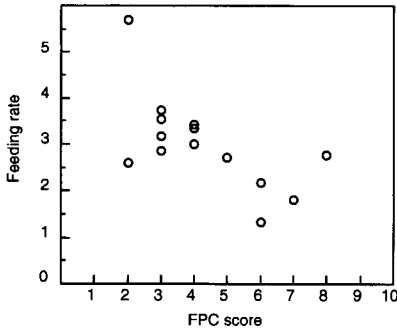


FIGURE 4. Female feeding rates per nestling (day 8) as a function of FPC score.

cause feeding rates per nestling on day 8 were not significantly correlated with brood size ($r_s = -0.36$, $n = 14$, $P > 0.19$). Controlling for brood size does not alter the conclusion that more colorful females fed their young with lower frequency ($r_s = -0.56$, $P < 0.05$). In this calculation, residuals from a regression of log-transformed feeding rates per nestling on day 8 on brood size were used. The reduced feeding rates of colorful females can not be explained by decreased food supply later in the season, because time of season did not affect parents' feeding rates per nestling on day 8 (male and female feeding rates combined: $r_s = -0.17$, $P > 0.5$). Males did not compensate for reduced parental care of their females as the combined feeding rates per nestling of males and females on day 8 were still negatively correlated with FPC scores ($r_s = -0.56$, $n = 14$, $P < 0.05$; corrected for brood size: $r_s = -0.47$, $P < 0.1$), and male relative feeding rates were not related to FPC scores ($r_s = 0.27$, $P > 0.3$).

In 1995, female coloration was negatively correlated with average nestling mass on day 8 ($r_s = -0.50$, $n = 18$, $P < 0.05$; corrected for brood size: $r_s = -0.56$, $P < 0.05$; Fig. 5). A similar trend was found on days 7 and 9 (corrected for brood size: day 7: $r_s = -0.52$, $n = 17$, $P < 0.05$; day 9: $r_s = -0.31$, $n = 17$, $P > 0.2$) and after combining and averaging nestling masses of day 7 to 9 (corrected for brood size: $r_s = -0.46$, $n = 15$, $P < 0.1$). In 1996, there was no relation between average nestling mass and female plumage coloration (corrected for brood size: day 6: $r_s = -0.06$, $n = 14$, $P > 0.5$; day 8: $r_s = -0.14$, $n = 17$, $P > 0.5$; Fig. 5; day 10: $r_s = 0.06$, $n = 12$, $P > 0.5$). Because the means of corrected nestling masses on day 8 did

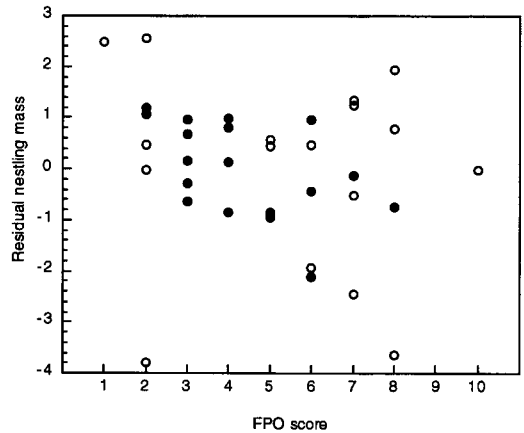


FIGURE 5. Average nestling mass on day 8 expressed as residuals of model I regressions of average nestling mass over brood size as a function of FPC score. Filled dots: 1995 data, open dots: 1996 data.

not differ between years (Mann-Whitney U -test: $z = -1.25$, 1995: $n = 18$; 1996: $n = 14$, $P > 0.2$), we combined the data sets and repeated the correlation with FPC score, yielding a nonsignificant negative correlation ($r_s = -0.14$, $n = 32$, $P > 0.5$).

DISCUSSION

In this field study we did not find any indication that female plumage coloration (FPC) in the Bluethroat was positively related to seasonal reproductive performance. There was no tendency for colorful females to breed earlier in the season, lay more eggs, feed their nestlings at a higher rate, or produce fledglings with higher body mass. To the contrary, in one of two study-years, colorful females tended to feed their nestlings at a lower rate, and there was a negative relationship between FPC and fledgling body mass.

Although yearlings were significantly less colorful than females of the older age class, we lack the necessary data to test the idea that females become gradually more colorful with age and that FPC is a reliable indicator of age. In the study of Amundsen et al. (1997), the two age-classes did not differ significantly with respect to coloration. Our results on nestling growth and feeding behavior, however, do not imply that more colorful females are more experienced or devoted parents. Similar to the results of Amundsen et al. (1997), female coloration was positively correlated with tarsus length,

but not significantly so. We are, however, reluctant to conclude that this superiority in body size necessarily indicates superiority in phenotypic quality. To be selected for, body size must translate into a reproductive advantage at some stage of the reproductive cycle, but as yet the available data fail to show this for the Bluethroat. Among passerines, the relation between female body size and female traits like fecundity and survival is not straightforward (Alatalo and Lundberg 1986, Bryant 1988, Møller 1991), and different selection pressures may be acting on male and female body size (Merilä et al. 1997). Although FPC scores correlated positively with body mass among prebreeding females (Amundsen et al. 1997), this pattern had disappeared by the time nestlings had hatched (this study). FPC might therefore reflect some form of female quality other than parental ability.

Our study adds to a relatively small number of studies exploring the evolution of female secondary sexual traits in birds (Muma and Weatherhead 1989, Irwin 1994, Tella et al. 1997). The small number of studies, their partly contradictory findings, and their diversity in focus do not allow for any general conclusions to be made at this stage. Among the species studied so far, there are only two others in which the relation between female provisioning behavior and female secondary sexual traits has been looked at. Cuervo et al. (1996), studying female Barn Swallows (*Hirundo rustica*), did not find the positive correlation predicted by the good parent hypothesis, whereas Linville et al. (1998) in their study of the Northern Cardinal (*Cardinalis cardinalis*) did. The latter study may be the one which compares best to ours because the female trait was plumage coloration and because Northern Cardinals, like Bluethroats, are territorial. However, in Northern Cardinals, FPC was positively correlated with absolute female provisioning rates, suggesting that males may benefit from mating with colorful females (Hoelzer 1989).

Although not the primary concern of our study, male mate choice is an important issue in relation to a possibly sexually selected female trait. Whether or not male mate choice is at all taking place in territorial passerine birds, is still not known, and the only field study specifically addressing this question is not supportive of this idea (Dale and Slagsvold 1994). Although male choice is likely to evolve in species with male

parental care (Trivers 1972), a territory-defense breeding system and short mating period are equally likely to counteract mutual mate choice, because there is a risk that a male may remain unmated if he rejects a low quality female. However, some evidence for male mate choice exists for the Bluethroat. Amundsen et al. (1997) performed an aviary mate choice experiment in which males associated more with the more colorful one of two stimulus females. The authors concluded that males prefer colorful females as mates and suggested that male mate choice may take place under natural conditions. However, it remains uncertain whether colorful females were recognized as females considering that Peiponen (1960) was unable to distinguish between the response behaviors of a male Bluethroat towards a male and a female dummy. Field studies on sex recognition in another territorial passerine species (Pied Flycatcher, *Ficedula hypoleuca*) have found males to have difficulties in distinguishing brown, female-like males from females (Slagsvold and Sætre 1991, Sætre and Slagsvold 1992) or heterospecific from conspecific females (Sætre et al. 1997). Such results suggest that in territorial species males are not strongly selected for mate choice mechanisms. Hence it is possible that the male preference for more colorful females reported by Amundsen et al. (1997) may be explained by nonadaptive genetic correlation (Hill 1993) which becomes evident in a situation of forced choice. There is clearly a need for further field studies concerning this issue (Dale and Slagsvold 1994).

Taken together, the current state of the evidence on the Bluethroat is reminiscent of Hill's (1993) study on House Finches (*Carpodacus mexicanus*). Here, too, a male preference for colorful females was found, but Hill was unable to find any indication of reproductive or phenotypic superiority of colorful females in an accompanying field study (Hill 1993), hence he concluded that the FPC in the House Finch is non-functional.

We conclude that, on the basis of existing knowledge, there is no indication that female plumage coloration in the Bluethroat is an indicator of female quality and that the nonadaptive genetic correlation hypothesis remains a viable hypothesis for this species. Functional hypotheses other than the good parent hypothesis (Hoelzer 1989), such as the immunocompetence-handicap hypothesis (Potti and Merino

1996), the good migration hypothesis (Fitzgerald 1994), and the Fisherian runaway process (Fisher 1930), remain untested in this species and require more research effort.

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