On the function of female ornaments: male bluethroats prefer colourful females

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SUMMARY

Female ornaments in animals with conventional sex roles have traditionally been considered non-functional, being merely a genetically correlated response to selection for male ornamentation. Alternatively, female ornaments may be influenced by selection acting directly on the females, either through female–female competition or male choice. We tested the latter hypothesis in mate choice experiments with blue-throats (*Luscinia s. svecica*), a passerine bird in which females vary considerably in coloration of an ornamental throat patch. In outdoor aviaries placed in prime breeding habitat, males were allowed to choose between a colourful and a drab female. We found that males associated more with, and performed more sexual behaviours towards, colourful females. Female coloration was not age-related, but correlated significantly with body mass and tarsus length. Thus, we have demonstrated both a male preference for female ornamentation, and a relationship between ornament expression and female body size, which may be indicative of quality. Our results refute the correlated response hypothesis and support the hypothesis that female ornamentation is sexually selected.

1. INTRODUCTION

In many animal species, males are extravagantly ornamented, while females typically are less conspicuous. This phenomenon has been attributed to sexual selection acting primarily on the male sex, and natural selection for cryptic appearance acting more strongly on females (Darwin 1871). However, in some species, females display male-like ornaments, although most often these are less developed than those of the males (e.g. plumage coloration in many birds: Johnson 1988; Muma & Weatherhead 1989; Hill 1993a; Stutchbury 1994). Two main hypotheses have been proposed to explain the existence of female ornamental traits. The correlated response hypothesis states that female ornaments are only the consequence of a genetic correlation with male ornamental traits, on which selection acts (Lande 1980, 1987; Lande & Arnold 1985). An alternative explanation is that female ornaments are influenced by sexual selection through male choice and/or female–female competition (Darwin 1871). The sexual selection hypothesis has received relatively little attention, and several recent studies have argued that female ornaments are mere results of a genetic correlation

between the sexes (Muma & Weatherhead 1989; Hill 1993b; Cuervo *et al.* 1996).

In species with conventional sex-roles, the traditional view has been that females are choosy and that males are indiscriminate. However, males are expected to be selective if female quality is highly variable (Parker 1983; Owens & Thompson 1994), or if mating is costly, for instance due to sperm depletion, time or energy expenditure, or loss of mating opportunities (e.g. Dewsbury 1982; Nakatsuru & Kramer 1982; Johnstone *et al.* 1996; Johnstone 1997). Mutual mate choice is likely to occur in predominantly monogamous species because the reproductive rates of males and females should be similar and benefits of choice are likely to be large for both sexes (Trivers 1972; Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Johnstone *et al.* 1996). In a variety of taxa, males have been shown to discriminate in favour of large and/or fecund females (e.g. Berven 1981; Johnson 1982; Sargent *et al.* 1986; Côte & Hunte 1989; Monaghan *et al.* 1996). However, few studies have addressed whether males select female mates based on ornamental traits. The strongest evidence comes from a study of monomorphic crested auklets (*Aethia cristatella*). Manipulating crest size of female and male mounts, Jones & Hunter (1993) showed that both males and females displayed more towards opposite-sex models with large crests. In dimorphic or dichromatic species (where males are the more ornamented and females possess some degree of

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Figure 1. (a) Schematic illustration of the throat patch of a female bluethroat. The coloration of each of five elements (A–E) was scored on a three-grade scale (0–2; drab–colourful), and female colour score (0–10) was calculated as the sum of these. (b–e) Variation in throat patch coloration of female bluethroats: (b) score 1, (c) score 4, (d) score 7, (e) score 10. (f) A typical male for comparison.

ornamentation), studies reported so far provide no general support for male choice of ornamented females (Burley & Coopersmith 1987; Johnson 1988; Muma & Weatherhead 1989; Hill 1993b; Møller 1993, 1994; Cuervo *et al.* 1996; Tella *et al.* 1997). It remains unknown whether female ornaments may act as quality indicators, but recent evidence suggests a potential relationship with body condition (Johnsen *et al.* 1996) and parasite resistance (Potti & Merino 1996).

Male bluethroats, *Luscinia s. svecica*, are conspicuously ornamented, bearing a bright blue and chestnut throat patch. Females are more drab, but extremely variable with respect to throat patch coloration (as judged by the human eye, much more variable than males) (figure 1). Assuming that a drab plumage would be equally beneficial to all females in terms of predator

avoidance, the high level of variation is surprising. The bluethroat therefore provides an excellent opportunity for testing hypotheses regarding the function and evolution of female ornaments. In the present study, we test whether female plumage ornamentation could be the result of sexual selection by male choice. In an aviary experiment conducted in the field, bluethroat males were allowed to choose between a colourful and a drab female. We found that males preferred colourful females, supporting the hypothesis that female ornamentation is sexually selected.

2. MATERIALS AND METHODS

(a) Study site and species

The experiment was carried out in Øvre Heimdalen (61°25'N, 8°52'E), southern Norway, during 22–29 May

1996. The study site is situated at 1100 m above sea level in the sub-alpine zone, with an open habitat dominated by low brush vegetation. Bluethroats are predominantly monogamous, but polygyny (e.g. Johnsen & Lifjeld 1995) and extra-pair paternity (Krokene *et al.* 1996) regularly occur in the study population. The female alone is responsible for nest-building and incubation, while both parents feed the nestlings at fairly equal rates (Reinsborg 1995). Birds to be used in the experiment were captured by mist-netting and immediately brought to the experimental site. They were placed indoors in individual, visually isolated, bird cages until used. Males and females were housed separately, and were fed mealworms *ad libitum*.

(b) Experimental design

We performed a total of 20 successful mate choice trials. In each of these, a new male was used as the respondent (i.e. 20 different males were used). A total of 25 different females were used as stimulus birds. Ten of these were used in one trial each, while the remaining 15 females were used in two trials. Females that were used twice were never matched with the same female in the two trials.

Female coloration was scored on a scale from 0–10 (figure 1). All scoring was made by the same person (T.A.). Fourteen of the 25 females used in the experiment were rescored before release, in order to check the repeatability of the scores. Twelve of these had identical scores on the two occasions, one differed by one point, and one by two points.

We arranged pairs of colourful and drab females that differed in colour score by three or more points (median five points, range 3–8). The drab females had a median score of 2.5 (range 1–4) and the colourful females had a median score of 7 (range 5–9). Whenever possible, we matched drab and colourful females of the same age (13 out of 20 trials). However, the colourful female was the older in four trials and the younger in three trials. The colourful female appeared a similar number of times in the left (11 trials) and right (9 trials) compartments. An equal number of yearling and older males (ten of each group) were used as response birds in the trials.

The trials were run in two identical, three-compartment outdoor aviaries, supplied with mealworms placed in Petri dishes (figure 2). Both males and females ate during trials. Stimulus females were not in visual contact, while the male could see both females. We marked off the inner 0.2 m of the male compartment with a thin white string on the ground, and considered this part to be the response area. When inside this area, the male could normally see only one of the females. We considered that a male showed interest in each female when he visited either the left or the right side of the response area (hereafter termed left and right response areas). Similarly, in the female compartments, we marked off the 0.2 m closest to the male compartment with string.

Males and females were released into the choice aviaries at least 1 h before observations started to allow them to get accustomed to the aviary. Thereafter, we observed the behaviour of the test birds for 1 h, from hides placed about 5 m away from the choice aviaries. Because of the potential disturbance caused by our entering of the hide, we waited for 5 min before initiating data recording.

(c) Recording behaviour

Males evidently responded to the presence of the stimulus females, and typically spent a high proportion of their time very close to the female compartments. Each time the male visited one of the response areas (left or right), we recorded

Figure 2. Plan of the outdoor mate choice aviary (measures in cm). The height of the aviary was 200 cm. Dashed lines indicate walls made of fine-mesh fish netting through which the birds could see. Solid lines indicate walls of translucent, white glass fibre fabric. The shading indicates the male response area, 20 cm deep. Circles indicate the position of Petri dishes with mealworms. Bars within the male compartment indicate a 'wall' of juniper branches that allowed the male to retreat to an area where none of the females were visible.

the time of entering and of leaving. The time spent in close proximity to each female was calculated as the cumulative time spent in each response area during a 60 min recording period. We further recorded male sexual behaviours directed at each of the two females. These were classified into three categories: (1) approach, (2) display, and (3) association. Approach included cases where the male was jumping or flying towards the netting, apparently trying to enter the female compartment. Displays were of various kinds: (i) the male approached the female with his head and breast in a lowered position, typically with the wings and tail somewhat spread; (ii) standing still, the male displayed his throat and/or tail to the female, with the bill pointing upwards and the throat patch exposed to its maximal extension; and (iii) the male uttered a song-like vocalization while sitting in the response area. Associations were of two different kinds: (i) the male and female sitting, or most often lying, quietly 5–30 cm from each other for extensive periods of time, normally facing each other, and (ii) the female moved back and forth along the net, with the male following at close range (but without any conspicuous display).

Potentially, differences in position or behaviour between stimulus females could influence the behaviour of the males, and therefore confound the experiment. All interactions between females and males (typically in the form of mutual displays or close associations, as described above) took place at very close range (within a zone less than 20 cm from the netting). When females were outside this zone, no displays or other behaviours that might be interpreted as sexual were observed. Therefore, a difference in behaviour between drab and colourful females that might influence male behaviour would most probably be reflected in the time spent within the zone close to the male. We recorded the time spent by each female 20 cm or less from the male compartment. We succeeded in keeping track of both females during the whole period in 14 of the trials, and during part of the trial (minimum 19 min 58 s) in three cases. On average, we

recorded the position of the female for 54 min 56 s out of the 60 min that trials lasted ($n = 34$ females in 17 trials). There was no difference in the proportion of time spent close to the male compartment between colourful ($36 \pm 29\%$) and drab ($38 \pm 29\%$) females (Wilcoxon signed-ranks test, $Z = 0.57$, $n = 17$, $p = 0.57$), suggesting that differences in female behaviour did not confound our results. The females spent $37 \pm 29\%$ of their time within the zone 20 cm or less from the male compartment, which was not significantly more than the 20% expected by chance (one-sample sign test, $n = 34$, $p = 0.12$).

Seven trials were unsuccessful and were not included in analyses. In five of these, the response male did not relate to any of the stimulus females, but instead seemed to attempt escape from the cage. We further rejected one trial in which the male spent less time within the response area than expected by chance (8 min 35 s), and one trial because of extreme weather conditions.

The right and left tarsus of each individual was measured using a digital calliper. The mean of the two values was used in analyses. Individuals were weighed (to the nearest 0.1 g, using a Pesola spring balance) at capture, and immediately before release. In addition, all birds were weighed once daily (in the afternoon) when in captivity. In analyses of male preference in relation to female body mass, we have used the last simultaneous recording of body mass for the two females before the trial (taken 0–3 days before the trial; median 1 day). The median number of days elapsing between capture and first use in a trial was one (range 0–4). In general, neither males (capture 16.6 ± 0.8 g versus release 16.8 ± 1.1 g; paired $t = 0.81$, d.f. = 19, $p = 0.43$) nor females (15.6 ± 0.8 g versus 15.5 ± 1.0 g; paired $t = 0.25$, d.f. = 23, $p = 0.80$) suffered from mass loss during the period in captivity (median duration: seven days). Analyses of coloration in relation to morphology were not restricted to females used in trials, but were performed on all females that had been scored and measured by T.A. in that season.

Results are presented as mean $\pm$ s.d. In order to obtain normality of data, proportions of time spent in front of the females were arcsin transformed. Statistical power ($1 - \beta$) was calculated using GPower 2.1.1 for Macintosh (Buchner *et al.* 1992; Erdfelder *et al.* 1996), assuming a 'medium' effect size (Cohen 1988). All tests are two-tailed.

3. RESULTS

(a) Male preference

The males clearly responded to the presence of stimulus females. Males spent on average $56 \pm 29\%$ of their time within the response area, about four times as much as expected by chance (14%). Out of the 20 trials conducted, 15 males spent more time in front of the colourful female and five spent longer in front of the drab female (binomial test, $p = 0.042$). On average, males spent $61 \pm 24\%$ of their time in the response area in front of the colourful female (figure 3a). The proportion of time in the response area spent in front of the colourful female was significantly higher than expected by chance (one-group t -test on arcsin transformed data versus expected value arcsin (50%): $t = 2.36$, d.f. = 19, $p = 0.029$).

The males performed sexual behaviours significantly more towards colourful than drab females (all three kinds of behaviours pooled; Wilcoxon signed-ranks test, $Z = 1.99$, $n = 16$, $p = 0.046$). The patterns for approaches, displays and associations were similar

Figure 3. Response of male bluethroats to colourful (filled bars) and drab (open bars) females (mean $\pm$ s.e.). (a) Time spent ≤ 20 cm from the female compartment during a trial lasting 1 h ($n = 20$). (b) Proportions of occurrences of three different kinds of male sexual behaviours directed towards colourful versus drab females (approach, $n = 9$; display, $n = 12$; association, $n = 11$).

(figure 3b). There was a strong positive correlation between the proportion of time spent with the colourful female and the proportion of sexual behaviours directed at this female ($r_s = 0.67$, $n = 16$, $p = 0.001$).

(b) Female ornamentation versus morphology

Old females were not significantly more colourful than yearlings (Mann–Whitney U -test, $Z = 0.99$, $n_{\text{old}} = 48$, $n_{\text{young}} = 16$, $p = 0.33$), but female coloration correlated positively with body mass at capture ($r_s = 0.34$, $n = 54$, $p = 0.016$; figure 4a) and tarsus length ($r_s = 0.28$, $n = 56$, $p = 0.041$; figure 4b). Potentially, then, experimental males might have based their choice on body mass or tarsus length, creating an apparent preference for female coloration. This was not the case. Ten out of 19 males spent more time with the heavier female, and nine spent more time with the lighter one. The proportion of time spent in front of the heavier female ($56 \pm 25\%$) was not significantly larger than the 50% expected by chance (one-group t -test on arcsin transformed data, $t = 1.36$, d.f. = 18, $p = 0.19$, $1 - \beta = 0.18$). Similarly, eight males preferred the female with the longer tarsi, and eight preferred the one with shorter tarsi. The proportion of time spent with the female with longer tarsi ($54 \pm 24\%$) was not significantly different from chance expectation (one-group t -test on arcsin transformed data, $t = 0.99$, d.f. = 15, $p = 0.34$, $1 - \beta = 0.16$).

Figure 4. The relationship between coloration and (a) body mass and (b) tarsus length of female bluethroats (mean $\pm$ s.e.). Numbers above error bars indicate sample sizes for each colour score.

4. DISCUSSION

Our data show that when male bluethroats are offered a choice between a colourful and a drab female, they spend more time in front of and show more sexual behaviours towards the colourful one. This strongly indicates a male preference for female coloration in the species. We also found a relationship between female coloration and size (body mass, tarsus length) that was not a function of age. Potentially, body size may reflect some aspect of female quality in the species.

Studies of barn swallows (*Hirundo rustica*; Cuervo *et al.* 1996), red-winged blackbirds (*Agelaius phoeniceus*; Muma & Weatherhead 1989) and pinyon jays (*Gymnorhinus cyanocephalus*; Johnson 1988) have looked for, but not found, any ornament-related male preference, while in zebra-finches (*Taeniopygia guttata*), males seem to prefer the less ornamented females (Burley & Coopersmith 1987). Only two previous studies (Hill 1993b; Jones & Hunter 1993) have demonstrated a male preference for female ornamental traits. The authors of these two studies came to quite different conclusions despite their similar findings. Jones & Hunter (1993) interpreted their demonstration of a male preference for female crest size in monomorphic and monogamous crested auklets as evidence for mutual sexual selection, whereas Hill (1993b) argued that the male preference for colourful female house finches (*Carpodacus mexicanus*) was due to a genetic correlation with the female preference for male ornamentation (Halliday & Arnold 1987). This conclusion

was reached because Hill (1993b) was unable to find any relationship between female coloration and quality. Among the few studies demonstrating male choice for female ornamentation, the present experiment with bluethroats is the first to demonstrate male choice for a female ornament that may reflect female quality.

Is the male preference for ornamented female bluethroats realized in male choice under natural conditions? Due to the short breeding season in the mountains, bluethroat females arrive quite synchronously at their breeding grounds and start searching for mates simultaneously by visiting advertising males in their territories. During encounters, the male plays the more active role, approaching the female at close range and often displaying his throat and tail in a conspicuous manner. Courtship, which may extend for several minutes, is usually followed by a chase flight in which the male follows the female. After such a flight, the female often disappears and the male resumes singing; sometimes, however, both birds terminate the chase by diving into the bushes where they may then copulate. As described, mating in bluethroats may seem quite similar to that of other territorial passerines where females are selective and males apparently indiscriminate (e.g. pied flycatcher, *Ficedula hypoleuca*; Dale *et al.* 1992; Dale & Slagsvold 1994). However, just as a female may select which of the advertising males to visit, and whether or not to accept a visited male, a male may choose whether to court and, provided he gets the opportunity, mate with a visiting female. The question is whether it would pay a male to be selective; i.e. to reject certain visiting females. The major cost of being selective is that of lost mating opportunities; at the extreme he may receive no further female visits and may remain unmated. However, mating with a poor female may also be costly. If a male accepts an inferior female mate, he may never get the opportunity of mating with better (more colourful) females. This is because once mated, the male is often escorted by his female, and his status as mated will probably be evident to any visiting female from this fact or from his own behaviour. If he attempts to court a second female, the resident female may be able to interrupt the act and prevent mating. Resident females respond very aggressively towards 'intruders' (playback of female song) at their territory (S. A. Sæther and T. Amundsen, unpublished data), suggesting that female-female competition over males does occur. Clearly then, a male should avoid mating with a poor female if the probability of achieving a better mating opportunity is high. Early in the breeding season, for instance, when many females are searching for mates simultaneously, high-quality males may afford to be choosy and should reject females of poor quality. Our results suggest that a drab coloration would be informative in this respect. Males of poor quality, or any male late in the season when fewer females are available, would probably not benefit from being choosy. It is generally hard to determine from field observations whether male choice (i.e. rejection of certain females) actually takes place. Conventionally, female visits not leading to mating have been interpreted as female rejection of the male. It is, however, possible that a

least in some instances males reject visiting females. Separating these two phenomena in the field represents a challenge for future studies.

In males, extravagant ornaments may function in attracting not only social but also extra-pair sexual partners (Hamilton 1990). Similarly, a female with a well-developed ornament may signal her quality to potential extra-pair mates. It is, however, questionable whether males should be choosy when it comes to extra-pair matings, unless reproductive benefits are more than offset by such costs as the transmission of parasites (for example venereal diseases) (Hamilton 1990; Sheldon 1993; Sheldon & Read 1997). Therefore, female ornaments are probably unimportant in extra-pair copulations.

What benefits could bluethroat males gain by being selective in their choice of mate? Female coloration was not age-related, but colourful females were heavier and had longer tarsi than drab ones. For a bluethroat male, it may be much easier to assess differences in female coloration than in size; therefore, ornamentation may act as a visual cue to body size. It seems reasonable to assume that body mass and skeletal size reflects female quality in one or another way. If this is true, males choosing ornamented females may gain either indirect genetic benefits resulting in viable offspring (Zahavi 1975; Hamilton & Zuk 1982; Andersson 1986; Pomiankowski 1988), or direct benefits through high female parental quality (Hoelzer 1989). Further studies are needed to investigate the relationship between female morphology and reproductive success in bluethroats.

In our experiment, the male preference for ornamented females was not accompanied by a statistically significant preference for larger females. If males base their choice on ornamentation, the lack of a significant preference for size is not surprising since ornamentation explained only a small part of the variation in female size. This might be sufficient for sexual selection on the trait, but very large samples would be required for experiments to demonstrate that a male preference for ornamented females also leads to a choice of large females.

In pied flycatchers, sexually inexperienced males have difficulty in distinguishing between females and female-like males (Slagsvold & Sætre 1991; Sætre 1993; Sætre *et al.* 1993). Could it be that male bluethroats are unable to distinguish between males and ornamented females, and that the response towards the latter was aggressive rather than reflecting sexual interest? We find this unlikely because none of the 'colourful' females in our experiment were even close to the ornamentation of the duller males, and all could easily be distinguished as females by a human observer. Furthermore, we did not detect any difference in the kinds of behaviours directed towards dull and colourful females; only in the number of occurrences. Many of the behaviours observed (e.g. close association) could hardly be interpreted as agonistic. It is also hard to imagine that females could gain any selective benefit from mimicking males, while males should be strongly selected to distinguish females from males without error.

According to the correlated response hypothesis, female ornaments have no function but exist because they are genetically correlated to male ornaments, which are sexually selected. Because most of the genome is shared between the sexes, any character in one sex could be a correlated response to selection on the same trait in the opposite sex. This idea has often been invoked to explain 'rudimentary' or 'vestigial male traits' in females (Darwin 1871; Lande 1980; Lande & Arnold 1985). Some authors have argued that even mating preferences in males, aggression in females, and female involvement in extra-pair copulations (EPCs), are correlated results of similar selected behaviours in the opposite sex (Halliday & Arnold 1987; Muma & Weatherhead 1989; Hill 1993*b*). It is doubtful whether this idea can be tested empirically. Regarding EPCs, recent studies suggest that female EPC behaviour is indeed adaptive, resulting from selection acting directly on females (Birkhead & Møller 1992; Kempenaers & Dhondt 1993). Similarly, we encourage serious investigation into the possibility that female ornaments are not merely due to a genetic correlation with male traits, but are influenced by sexual selection acting directly on females. In our view, this would be the more parsimonious conclusion when a male preference or a function in female-female competition has been established. The case would be particularly strong when the ornament is related to female quality, as may be the case in the present study, but female ornaments could also be selected through male choice in the absence of any relationship with quality, in a runaway process (Fisher 1930). The initial, genetically correlated, expression of a 'male ornament' in females may serve as the evolutionary basis for further exaggeration of the female trait through sexual selection. In fact, a genetic correlation between the sexes may provide an additional benefit for males choosing ornamented females: not only could they achieve high quality female mates, they may also get attractive sons.

Recent phylogenetically based comparative analyses suggest that the evolution of sexual colour dimorphism in passerine birds is unlikely to be constrained (Price & Birch 1996). In new-world blackbirds (Icterinae), most changes in plumage dichromatism seem to have resulted from changes in female coloration (Irwin 1994). Taken together, recent comparative studies suggest that selection acting on females is more important in the evolution of bird plumage coloration and dichromatism than previously thought (Björklund 1991; Irwin 1994; Martin & Badyaev 1996); selection on females for crypsis as well as signal elaboration need to be considered in order to understand avian dichromatism.

The existence of a male preference for female coloration does not preclude a potential role of ornamentation in female-female competition. Such competition could occur either over food or other resources during the non-breeding or breeding season (e.g. Wolf 1969; West-Eberhard 1983; Bleiweiss 1992, but see Stutchbury 1994), or directly over access to mates (Johnson 1988; Trail 1990). It remains to be tested whether female ornaments in bluethroats also serve a function in female-female competition.

In conclusion, female plumage ornaments in blue-throats are not functionless, but seem to be subject to sexual selection acting directly on females through male choice. Therefore, we refute the hypothesis that female ornamentation in bluethroats is a mere result of a genetic correlation with male traits (the correlated response hypothesis). Furthermore, female ornamentation in bluethroats is correlated with size, suggesting that males may obtain high quality mates by choosing to mate with colourful females.

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