Symmetry: attractive not only to females

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Fluctuating asymmetry in bilateral traits has been proposed to reflect aspects of individual quality, and has hence been suggested to act as a cue in mate choice. Since sexual selection generally acts more strongly on males, numerous studies have focused on female preferences for symmetrical partners, while very little is known about potential male symmetry preferences. In the present experiment, we tested whether bluethroat males are sensitive to symmetry in an artificial ornament. Using different combinations of blue and orange leg bands, females were made symmetrical or asymmetrical. In outdoor aviaries placed in breeding habitat, males were allowed to choose between a symmetrical and an asymmetrical female. We found that males associated more with symmetrical than asymmetrical females, indicating a preference for symmetry. The magnitude of the symmetry preference of bluethroat males was similar to that of females of the same species.

Keywords: male mate choice; artificial ornament; fluctuating asymmetry; developmental stability; sexual selection; *Luscinia s. svecica*

1. INTRODUCTION

Fluctuating asymmetry refers to small random deviations from perfect bilateral symmetry in morphological characters (Ludwig 1932). The degree of fluctuating asymmetry expressed in a trait reflects the bearer's ability to withstand stress during the development of the trait (reviewed in Møller & Swaddle 1997), and may hence be a reliable indicator of phenotypic and genotypic quality (Møller 1990, 1992; Allen & Simmons 1996; Møller & Thornhill 1997; but see Clarke 1998). The degree of fluctuating asymmetry is greater in secondary sexual characters than in other characters (Møller & Thornhill 1998), probably because such traits impose a higher cost on the bearer. Hence, an individual could potentially determine another individual's quality by the symmetry of its secondary sexual characters, information that is highly valuable in a mate choice situation. Whereas female preferences for symmetrical males have been demonstrated in many species (reviewed in Møller & Thornhill 1998), including bluethroats (*Luscinia s. svecica*, Fiske & Amundsen 1997), it is generally unknown whether males exhibit similar symmetry preferences.

The current knowledge of male mate choice and female ornamentation is quite limited (Amundsen 1999). The main reason for this is probably that sexual selection in species with conventional sex roles generally acts more strongly on males than females (Darwin 1871). Thus, most studies have focused on selection acting on males. It has convincingly been shown that, in general, females choose

mates, while males compete to be chosen. In consequence, males often carry extravagant ornaments while females of the same species have a relatively drab appearance (reviewed in Andersson 1994). However, females of species with conventional sex roles may also be ornamented, often carrying a less striking version of the male ornament. The bluethroat represents such a system (Amundsen *et al.* 1997).

We have previously shown that bluethroat males in a mate choice situation prefer colourful to drab females (Amundsen *et al.* 1997). The present study investigates if males of this species also take symmetry into account when given a choice between a symmetrical and an asymmetrical mate. In general, male choosiness is expected if female quality is highly variable (Owens & Thompson 1994) or if mating is costly for the male (Dewsbury 1982; Johnstone *et al.* 1996). Recent empirical studies have shown that males of species with conventional sex roles can be choosy (Jones & Hunter 1993; Hill 1993; but see Cuervo *et al.* 1996), and that female ornamentation may signal quality (Johnsen *et al.* 1996; Potti & Merino 1996; Linville *et al.* 1998; but see Hill 1993). Hence, in some species with conventional sex roles, sexual selection may maintain female ornaments.

A recent meta-analysis by Møller & Thornhill (1998) confirmed the general prediction that the mating success of males is more affected by fluctuating asymmetry than the mating success of females. They found that female success in this respect was not significantly related to fluctuating asymmetry, but their sample size highlights the need for more studies focusing on females. Møller & Thornhill (1998) report only seven species with data on fluctuating asymmetry in females, as opposed to 41 in males. Most of these studies on

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Figure 1. Schematic illustration of the experimental treatments. (a) The symmetrical treatment. The left (L) and right (R) leg had two blue bands above two orange bands. (b,c) The two asymmetrical treatments. One leg had three blue bands above one orange band, while the other leg had one blue band above three orange bands. The use of treatments (b) and (c) was balanced.

females are observational and deal with natural variation in ordinary morphological characters (i.e. not secondary sexual characters).

In the present experiment, we employ an artificial ornament (coloured leg bands; see Burley *et al.* 1982; Johnsen *et al.* 1997) to investigate if male bluethroats prefer symmetrical females. Ornaments coloured leg bands have previously proven successful in demonstrating female preferences for male symmetry (e.g. Swaddle & Cuthill 1994a; Bennett *et al.* 1996; Fiske & Amundsen 1997; but see Jennions 1998). In this study, male sexual preferences are judged by male association with a symmetrical or an asymmetrical female in a specifically designed aviary. Mate preferences expressed under such conditions seem to reflect real mate choice, since previous experiments in the same bluethroat population have shown that males favoured by females in aviary experiments (Andersson & Amundsen 1997) are also favoured in the field (Johnsen *et al.* 1998). To our knowledge, the present study is the first to experimentally manipulate the symmetry of live females to test if symmetry in an artificial ornament is preferred by males (for manipulations and ratings of human images, see Singh 1995; Swaddle & Cuthill 1995). The bluethroat is a highly suitable model species to test the hypothesis of a male symmetry preference, since a male preference for colourful females (Amundsen *et al.* 1997) and a female symmetry preference (Fiske & Amundsen 1997) have been found in previous studies. The experimental design is essentially the same as that employed by Fiske & Amundsen (1997), thus allowing a comparison of the strength of symmetry preferences in the two sexes.

2. MATERIAL AND METHODS

The experiment was carried out in Øvre Heimdalen (61°25' N, 8°52' E; elevation 1100 m) in south-central Norway during 20–31 May 1997. Bluethroats are small, sexually dichromatic passerines (e.g. Amundsen *et al.* 1997). Females are responsible for nest building, while the feeding of young is shared equally between the parents (Reinsborg 1995; Smiseth *et al.* 1998). Bluethroats arrive at the study site in mid-May, and the experiment was conducted during the mate acquisition period (second half of May). The study population is mainly monogamous, though polygyny occurs (Johnsen & Lifjeld 1995) and as much as 20% of the chicks are sired by extra-pair males (Krokene *et al.* 1996).

Bluethroats were caught in mist-nets, weighed and ringed with plastic bands for individual recognition. On the day of

capture, five distinct elements of each female's ornamental throat patch (see Amundsen *et al.* 1997) were scored separately on a three-point scale (0–2), and these scores were added to give a total score ranging from 0 (drab) to 10 (colourful). Females were rescored before release. There was a strong positive correlation between the score and rescore ($r_s = 0.95$, $n = 27$, $p < 0.0001$). Captive birds were kept in individual, visually isolated cages and fed meal worms *ad libitum*. Males and females were housed in separate rooms. We weighed all captive birds daily.

We used an experimental design virtually identical to that adopted by Fiske & Amundsen (1997) to test for symmetry preferences. Females were given a symmetrical or an asymmetrical treatment by adding ornamentally coloured (transparent blue and orange) 'hobby beads' (Hill 1992; Johnsen *et al.* 1997) to their legs (figure 1). Four such bands were added to each leg. The symmetrical and asymmetrical treatments had the same total amount of orange and blue (figure 1). Since previous studies have found no effect of which band colour is positioned closest to the body (e.g. Swaddle & Cuthill 1994a; Fiske & Amundsen 1997), we did not double the number of treatments by swapping the position of the leg-band colours. Thereby, we avoided applying asymmetrical and symmetrical combinations twice to the same individual.

In addition to allowing the comparison with female mate preferences previously established using the same leg-band design, this design has the advantage of mimicking naturally occurring asymmetry more closely than alternative designs (Swaddle & Cuthill 1994a; discussed in Rohde *et al.* 1997). On the other hand, it has been argued that the design does not completely rule out the possibility that any apparent symmetry preference only reflects a preference for a particular leg-band arrangement (Swaddle 1997). We elaborate on the advantages and limitations of our specific design in § 4.

We matched pairs of females with respect to coloration (score difference: 0.4 ± 0.6 , range 0–2, $n = 14$) and age (same-age pair-members in ten pairs, age difference of one year or more in four pairs), before giving them the symmetrical or asymmetrical treatment. The pair-member which was first assigned to the symmetrical and to the asymmetrical treatment was determined randomly. The two pair-members were then let into two adjacent stimulus compartments of an aviary (figure 2) situated in typical breeding habitat. After acclimatization of the females, a male was let into the response compartment of the aviary (figure 2). Within their compartments, all birds could move freely. Females were visually isolated from each other, but could see the male, while the male could see both females (figure 2). Observations were made from a hide placed 5 m away from the front of the response compartment.

Figure 3. Mean $\pm$ s.e. proportion of time males spent ≤ 20 cm from aviary compartments containing females with leg bands arranged symmetrically or asymmetrically, including (a) all accepted trials ($n=28$), and (b) only trials where males showed a marked preference ($\geq 70\%$) for either female ($n=15$).

the male spending $68 \pm 34\%$ of the time with the symmetrical female (figure 3b; one-sample $t=2.67$, d.f. = 14, $p=0.018$). Males did not direct significantly more sexual behaviour patterns towards symmetrical ($66 \pm 41\%$) than asymmetrical females (Wilcoxon signed-ranks test, $Z=1.31$, $n=22$, $p=0.19$; all accepted trials with such male behaviour included).

Symmetrical and asymmetrical females spent a similar amount of time close to the male compartment ($11 \pm 22\%$ versus $13 \pm 25\%$; Wilcoxon signed-ranks test, $Z=0.12$, $n=28$, $p=0.90$), and did hence not bias the male choice by showing different degrees of interest in the male when wearing the two treatments. They also exposed their legs for a similar proportion of time (symmetrical, $83 \pm 26\%$ versus asymmetrical, $85 \pm 19\%$, $Z=0.02$, $n=28$, $p=0.99$).

4. DISCUSSION

Our results demonstrate that male bluethroats are sensitive to the symmetry of artificial ornaments, since they preferred to associate with females wearing symmetrically arranged leg bands. Furthermore, in cases where the male showed a pronounced preference (spending more than 70% of the time with one female), the result is even stronger in favour of symmetrical females. This is

reassuring, since it is uncertain whether males exert mate choice when they spend a similar amount of time with both females. Males did not perform significantly more sexual behaviour patterns towards symmetrical than asymmetrical females, although the difference was in the predicted direction. However, there were vast differences between males in the tendency to engage in sexual behaviour, and the failure to detect a significant difference in this parameter may hence be owing to an insufficient sample size.

Pioneering symmetry studies employing leg bands (Swaddle & Cuthill 1994a; Bennett *et al.* 1996; Swaddle 1996) used a design where asymmetrical zebra finch (*Taeniopygia guttata*) males either had different colours on each leg or different relative positions of two colours on each leg (termed 'asymmetric' and 'cross-asymmetric', respectively, in Swaddle & Cuthill (1994a)). Such asymmetries are rarely encountered in naturally occurring traits where bilateral symmetry is 'normal'. In contrast, the treatments of the present design differ only in the relative amount of each band colour on each leg, with both colours represented on both legs (figure 1). Although still artificial and exaggerated, the latter design structurally mimics asymmetry as it appears in nature (see also Fiske & Amundsen 1997; Rohde *et al.* 1997; Jennions 1998). Swaddle (1997) criticized this design, pointing out that an apparent preference for symmetry in fact could be a preference for a particular leg-band arrangement (in the present case two blue over two orange bands) regardless of whether it appears on one leg or both (i.e. regardless of symmetry). This possibility cannot be completely ruled out with the present design. However, three studies on zebra finches did not detect a difference in female responses to 'asymmetric' and 'cross-asymmetric' treatments (Swaddle & Cuthill 1994a; Bennett *et al.* 1996; Swaddle 1996), indicating that there is no effect of the kind suggested by Swaddle (1997). Hence, the more parsimonious interpretation of our results is that the preference revealed is a true preference for symmetry over asymmetry. Another important reason for employing the specific leg-band design of the present experiment was that the same design had been used in a previous study on female symmetry preferences in the same blue-throat population (Fiske & Amundsen 1997). Thereby, we could compare the strength of the symmetry preferences of the two sexes. To our knowledge, such a comparison of responses by the two sexes has never before been made in experiments on non-human species.

A host of studies in various taxa have tested whether females prefer symmetrical partners (e.g. Møller 1992; Thornhill 1992; Gangestad *et al.* 1994). In contrast, very few studies have tested whether males prefer symmetry in female ornaments. In a study where male college students rated rough sketches resembling women according to attractiveness, Singh (1995) found that sketches with symmetrical breasts were judged as more attractive than sketches with asymmetrical breasts. Møller & Zamora-Muñoz (1997) reported that males of a polygynous cerambycid beetle (*Stenurella melanura*) preferred to mate with females having symmetrical antennae when released on to a flower with one naturally symmetrical and one naturally asymmetrical female. The present experiment is, to our knowledge, the first to let males choose between

live females whose symmetry has been manipulated (in this case by employing an artificial ornament).

When addressed, male mate choice and female ornamentation have frequently been explained as functionless by-products resulting from a genetic correlation between the sexes (Lande & Arnold 1985; Lande 1987; Muma & Weatherhead 1989; Hill 1993; Cuervo *et al.* 1996). The genetic correlation hypothesis can hardly be tested empirically, and is not rejected by the present study. If the male preference is non-adaptive and exists purely due to a genetic correlation, choosiness can only be maintained if it carries no cost to the male. But rejecting certain potential mates may be extremely costly, especially if there are few females available. Indeed, the worst-case scenario for choosy males is failing entirely to reproduce because all mating opportunities have been foregone. On the other hand, being indiscriminate may also be costly for the mainly socially monogamous bluethroat, since accepting the first mating opportunity may prevent the male from mating with females of higher quality. In this study, we have established that males prefer symmetrical females, which would be adaptive if symmetry in natural traits conveys information about female quality (see the review in Møller & Swaddle (1997)). This assumes that males encounter enough available females in the wild. The assumption may not be unlikely in the case of bluethroats, since territory-holding males are often visited by several females during the mate acquisition period (T. Amundsen, personal observation). In particular, early-arriving males of high quality would probably benefit from being choosy (Amundsen *et al.* 1997). However, this experiment does not document that male mate choice is adaptive. Studies on other species with conventional sex roles have looked for, but failed to find, evidence that female ornaments are maintained by adaptive male choice (Hill 1993; Cuervo *et al.* 1996). Clearly, more studies are needed before any conclusions on the adaptiveness of male mate choice can be drawn.

The use of leg bands to investigate symmetry preferences (e.g. Swaddle & Cuthill 1994a; this study) inevitably creates asymmetries far more pronounced than those normally occurring in natural traits. The documented symmetry preference may either be general, extending to artificial traits, or it may be specifically linked to some morphological trait which the leg bands mimic. Whether male aversion to exaggerated band colour asymmetries is also evident in response to more modest degrees of asymmetry in natural ornaments, remains to be demonstrated. In female zebra finches, the preference for symmetry in experiments with artificial ornaments was very similar to the preference for symmetry in plumage manipulated within the range of natural ornamentation (Swaddle & Cuthill 1994b).

As first suggested by Møller (1990), a preference for symmetry may have evolved because symmetry somehow signals quality. An alternative explanation suggests that the preference has evolved as a by-product of biological recognition systems (Enquist & Arak 1994; Johnstone 1994; Swaddle & Cuthill 1994b). A receiver is likely to encounter a given trait in many different variants, due to fluctuating asymmetries or presentations in spatially different positions and orientations. The resulting average phenotype will be symmetrical. Computer simulations have shown

that generalization over the range of stimuli associated with an ornament may give rise to a preference for symmetry (Enquist & Arak 1994; Johnstone 1994; Enquist & Johnstone 1997). This mechanism may be relevant for males as well as females, since both sexes will be exposed to the numerous variants and representations of a trait. If symmetry preferences have evolved as a by-product of recognition, they may thus be prevalent in both sexes.

Interestingly, Fiske & Amundsen (1997), using essentially the same experimental design as the one employed here, found that bluethroat females on average spent 60% of the responsive time with the symmetrical male. Hence, the average magnitude of the symmetry preference is very similar for male and female bluethroats. In our view, the most important finding of the present experiment is that males show a similar symmetry preference to that previously reported for females (Fiske & Amundsen 1997). The evolution of the documented male and female symmetry preference might be explained both in terms of biological recognition (Enquist & Arak 1994; Johnstone 1994; Swaddle & Cuthill 1994b) and adaptive mate choice (Møller 1990).

Using an artificial ornament, this is the first study to experimentally demonstrate a male preference for symmetry in live females. The result indicates that, in some species, males may be equally responsive to symmetry as females are. Hence, symmetry preferences may be even more widespread than previously thought. It remains to be demonstrated if male symmetry preferences serve an adaptive function, allowing males to select superior female mates.

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