The effect of leg band symmetry on female–male association in zebra finches

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Abstract. Studies have shown that female zebra finches, *Taeniopygia guttata*, prefer to associate with males wearing symmetric leg band combinations. In this study, I used a four-choice chamber apparatus to investigate this preference, and to determine whether it is influenced by band coloration. I created band combinations by banding males with four leg bands. The symmetrical combinations consisted of two bands on each leg; the asymmetrical combinations consisted of three bands on one leg and one band on the other leg. For each of the symmetry treatments, all four bands were either light green or red. Females did not spend significantly more time associating with males wearing symmetrical bands or with males wearing red bands. The duration of male–female associations was not influenced by an interaction between symmetry category and band colour treatment. None of 10 females spent the most time with males with red symmetrical bands.   © 1998 The Association for the Study of Animal Behaviour

The study of fluctuating asymmetry has captured the attention of behavioural ecologists (Watson & Thornhill 1994). Fluctuating asymmetries are small, random deviations from perfect symmetry found in traits that are usually bilaterally symmetrical (Ludwig 1932). These asymmetries seem to arise when the developmental process is disrupted by genetic and environmental stresses (Palmer & Strobeck 1986), and resistance to these stresses is sometimes heritable (e.g. Thornhill & Sauer 1992). An individual's level of asymmetry therefore may reflect phenotypic or genotypic quality, if high-quality individuals are more resistant to stress and thereby develop more symmetrical traits (Møller & Pomiankowski 1993; but see Jennions 1996). Møller (1992) suggested that asymmetry in secondary sexual characters may provide a particularly reliable measure of quality. These characters are often large or elaborate and appear to be costly to produce. They may thus be more susceptible to developmental disruption than are ordinary morphological traits (Watson & Thornhill 1994). Consequently, the symmetry of sexual signals may provide a direct visual cue that females can use to select high-quality mates (Møller 1992). Studies of mate choice that inves-

tigate fluctuating asymmetry may help to resolve the continued debate as to whether female preferences are for male 'viability' or 'attractiveness' genes (Jennions 1993).

Some studies have documented a positive correlation between male trait symmetry and some measure of potential reproductive success (for a review see Watson & Thornhill 1994); others have not (e.g. Markow et al. 1996; Moodie & Moodie 1996). A relationship between trait symmetry and reproductive success does not prove that symmetry is a visual cue directly used during mate choice. First, symmetry is often correlated with other characters that directly effect mating success. For example, female scorpionflies, *Panorpa japonica*, prefer pheromones from males with symmetrical forewings, even though they are not in visual contact with males (Thornhill 1992). Second, symmetry between different traits is often uncorrelated (Dufour & Weatherhead 1996), and the documented relationship will vary depending on which trait is the focus of study. Third, there may be natural selection against asymmetry because of increased locomotive costs (Balmford et al. 1993; Thomas 1993), which could lower mating success by reducing male competitiveness during agonistic interactions (Balmford & Thomas 1992). To test the hypothesis that female choice is based on visual assessment of the

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symmetry of male signals, it is necessary to manipulate symmetry in sexual signals where natural selection against asymmetry is absent or can be controlled.

In zebra finches, *Taeniopygia guttata*, the colour of leg bands influences female choice (Burley 1986). This system therefore provides a rare opportunity to manipulate the symmetry of a preferred trait. Swaddle & Cuthill (1994a) carried out a choice-chamber experiment and documented a female preference for males with symmetrical leg band combinations. Females spent more time with males with bilaterally symmetrical band combinations compared to cross-asymmetrical combinations in which the relative position of each colour (top/bottom) differed between legs, or asymmetrical combinations where the bands on each leg differed in colour. Swaddle (1996) placed males, each with one of six band-combinations, and an equal number of females into free-flight aviaries. Males with symmetrical band combinations did not mate sooner, and there was no significant difference in average clutch size or inter-clutch interval between symmetry treatments. Males with symmetrical band combinations, however, fledged more offspring that survived past parental care ($P=0.03$, but uncorrected for multiple statistical tests of other reproductive differences between symmetry categories). Additional choice experiments have shown that females prefer males with symmetrical versus cross-asymmetrical band combinations when the two band types used either did, or did not, reflect the ultraviolet waveband (Bennett et al. 1996). Swaddle & Cuthill (1994b) also manipulated male chest plumage symmetry and demonstrated a female preference for symmetry.

Results from other species have been more ambiguous. In choice experiments with paradise whydahs, *Vidua paradisaea*, Oakes & Barnard (1994) reported a significant female preference for males with asymmetrical tails. This result is controversial though, because males with asymmetrical tails may have had the longest apparent tail length (Brookes & Pomiankowski 1994; Jennions & Oakes 1994). Manipulation of outer tail feather symmetry in barn swallows, *Hirundo rustica*, led to higher reproductive success for males with symmetrical tails (Møller 1992). This outcome may, however, have been due to the detrimental effect of tail asymmetry on flight performance (Balmford & Thomas 1992). Møller (1993) therefore used

white correction fluid on the feather tips of outer tail feathers to create tails that appeared either symmetrical or asymmetrical to a human when viewed against an appropriate background. Males in the symmetrical treatment again had greater reproductive success. It is unclear whether this result is due to a preference for apparently symmetrical tails or for symmetrical artificial traits, because correction fluid reflects ultraviolet and was probably highly visible to the females (Swaddle & Cuthill 1994b; Bennett et al. 1996).

Here I present the results of a choice-chamber experiment using a similar design to that of Swaddle & Cuthill (1994a). I tested whether female zebra finches (1) preferentially associated with males with symmetrical leg band combinations, (2) preferentially associated with males wearing red rather than light green bands, and (3) whether band colour influenced symmetry preferences (Møller 1992). In previous studies, females have preferred males with red bands to those with light green bands (e.g. Burley 1988). The band combinations that I used differed from those of Swaddle & Cuthill (1994a) in that each band combination consisted of a single colour. Variation in symmetry was due to differences in the amount of coloration on each leg. This design created asymmetries more similar to those seen in nature than to those of previous studies, where males have either had different colours on each leg, or differences in the relative position of distinct colours on each leg. The latter asymmetries are rarely encountered in nature.

METHODS

The experimental apparatus consisted of a central section with an elevated perch from which four stimulus cages were visible (Fig. 1). Zebra finches show a strong preference for higher perch sites (Swaddle 1996) and, unless interacting with males, the female remained on this central perch. Food and water was available ad libitum in this central area. I provided background lighting by two 80 W fluorescent tube ceiling lights, and an 8 W fluorescent tube, placed above each stimulus cage. The front of each cage consisted of mesh chicken wire so that females and males were clearly visible to one another. A wooden perch was in front of each cage and fitted with a microswitch linked to a BBC microcomputer that recorded the time
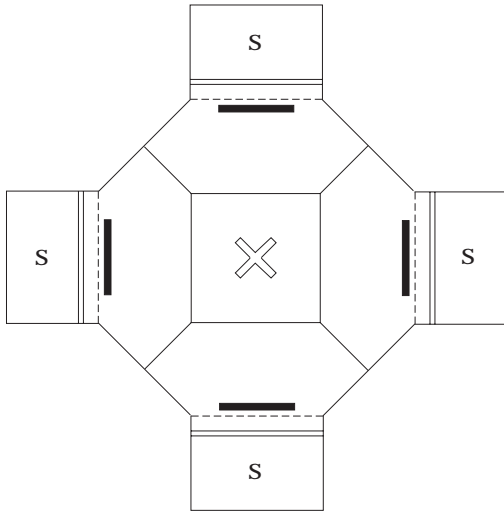
Figure 1. The choice chamber viewed from above. S=stimulus cage. Solid bars represent perches with microswitches, open bars represent ordinary perches. Dotted lines represent the wire front to the stimulus cages. The central perch was higher than the square of wall immediately surrounding it, and all four cages were visible from this perch. All other perches were lower in height than the wall. Hence, once a female was on a microswitch perch, she could only see the male in the corresponding stimulus cage.

females spent on the perch. Internal barriers around the central area were positioned so that a female perched in front of a stimulus cage could see only the male in that cage. There was no visual contact between males. The main difference between my apparatus design and that of Burley and co-workers (e.g. Burley et al. 1982; Burley 1986, 1988) and of Swaddle & Cuthill (1994a) is that I did not provide a central area in which the female was visually isolated from the males. Given that solitary females may leave such a central area simply to be in visual contact with a conspecific, my design should increase the likelihood of documenting only female–male associations that arise from the active intention of the female to associate with a particular male. This is particularly so because the most preferred (highest) perch was in the central section.

I used 10 males and 10 females. All three previous choice-chamber studies of symmetry preferences reported highly significant results using equivalent or smaller numbers of females (10, six and eight, respectively: Swaddle & Cuthill

1994a, b; Bennett et al. 1996; see Discussion). Males were obtained from Wytham Field Station breeding stock, and the 10 healthiest looking were selected. Females were obtained either from a local breeder ($N=6$) or from the Wytham stock ($N=4$). Males and females were kept in single-sex aviaries with food (commercial grain and millet) and water freely available. The sexes were visually but not acoustically isolated. The 10 females were picked from an initial pool of 18 females. I selected those females that spent the greatest amount of time perched in front of males during 6–8 h of pre-experimental exposure to the choice-chamber apparatus, which increases the certainty that the females eventually tested were interested in males.

During pre-exposure, I placed a female in the central section of the choice chamber; each stimulus cage contained a single, unbanded, non-experimental male. This procedure was carried out to familiarize females with the test apparatus. Females were also pre-exposed to leg bands prior to the start of experimental trials. I placed a cage containing six non-experimental males in the main female aviary. Each male wore one of six band-combinations (see below), and combinations were rotated among males daily until each male had worn each band combination once.

The six band-combinations fell into three symmetry categories: symmetrical (two bands per leg), asymmetrical left (three bands on the left leg, one on the right leg) and asymmetrical right (three bands on the right leg and one band on the left leg). Each band was reduced to two-thirds of its original size, so that three bands on one leg was equivalent to two original bands, to ensure that the bands did not constrict leg movement. Within each symmetry category there were two colour treatments. Either all four bands were light green, or they were all red. Leg bands were obtained from the same source as that used by Swaddle & Cuthill (1994a) and Burley et al. (1982) (A. C. Hughes, Middlesex, U.K.). The bands are made of lightweight plastic, and band asymmetry is unlikely to make males 'lopsided'.

At the start of each trial, a male was placed in each of the four stimulus cages and the female was then released into the central area. Trials lasted 5 h following an initial 2-h habituation period. The time spent perched in front of each male was recorded. The experiment consisted of 30 trials, with each female randomly allocated to three

trials. Each of the 15 four-way permutation of the six band-combinations was presented twice, each male wore every band combination twice, and each of the six band-combinations appeared in each stimulus cage 20 times. This experimental design controls for preferences for particular males or stimulus cages (Swaddle & Cuthill 1994a). No female was tested more than once per day.

Statistical analysis of time spent with each band category was by a mixed-model (repeated measures) ANOVA with 'female' as a random effect, 'symmetry category' as a fixed effect with three levels (symmetrical, asymmetrical left, asymmetrical right) and 'colour' as a fixed effect with two levels (red or light green). Differences between symmetry categories were tested by orthogonal contrasts so that correction for multiple testing was not required. I calculated repeatability of the total time per trial that females spent perched in front of stimulus males using a one-way ANOVA. All tests were two-tailed. For descriptive purposes, I calculated the average time each female spent with each band combination and then ranked on a female-by-female basis. Data were analysed using SYSTAT for Windows on a PC, and SAS on the Vax mainframe computer in Oxford.

RESULTS

Females spent $31.4 \pm 4.0\%$ ($\bar{X} \pm$ SE) of each trial perched in front of males (range of means per female=15.4–75.8%). The total time per trial spent perched in front of stimulus males was significantly repeatable among females ($F_{9,20}=6.36$, $P<0.003$), indicating that females varied in their tendency to associate with males. The proportion of time females spent associated with males was similar to that reported by Swaddle & Cuthill (1994a) (37%). Of the time spent in association with males, the mean $\pm$ SE percentage spent with the most preferred male was $63 \pm 3.32\%$ (range=34.6–97.1%). In 22 of 30 trials, the female spent more than 50% of the total time in association with males with the most preferred male, and in 28 of 30 trials, she spent more than 40% of the time with the most preferred male. Although I did not record the number of display jumps ('hops') females made to each band-combination, I did observe females hopping on microswitch perches, consistent with courtship behaviour.
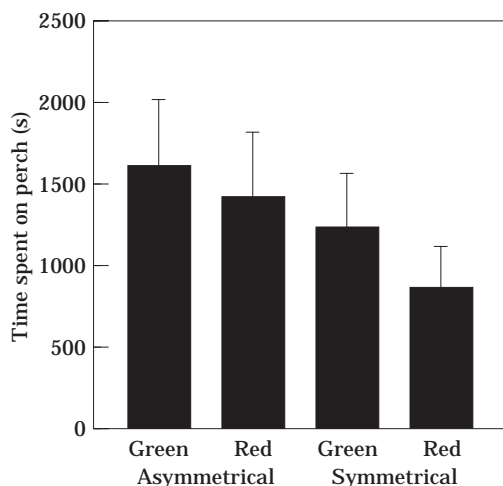

Figure 2. The mean $\pm$ SE amount of time that females spent perched in front of males with each of the colour treatments. For clarity, asymmetrical left and right have been combined. Hence, $N=20$ trials for each symmetrical treatment and 40 trials for each asymmetrical treatment.

Females did not spend a significantly different amount of time in front of males in the three symmetry categories ($F_{2,18}=1.87$, $P=0.148$; Fig. 2). Group differences were tested by orthogonal contrasts; there was no difference between the symmetrical combination versus the two types of asymmetrical combinations ($F_{1,18}=2.52$, $P=0.130$) or between the left and right asymmetrical combinations ($F_{1,18}=1.75$, $P=0.203$). The trend was opposite to that expected, because females spent more time with asymmetrically banded than symmetrically banded males. Females did not spend a significantly different amount of time in front of males with one of the two colours ($F_{1,9}=2.45$, $P=0.152$). The trend was opposite to that expected, because females spent more time with green-banded than red-banded males. The colour of the bands also had no effect on the female response to symmetry, because there was no significant interaction between symmetry category and colour treatment ($F_{2,18}=0.50$, $P=0.616$).

Based on the average time that each female spent with the six band-combinations, 0 of 10 females spent the most time with males with red symmetrical bands. This remained the case when I calculated a single mean time for asymmetry by combining the left and right asymmetry categories to reduce the analysis to four band-combinations

(red or green, asymmetrical or symmetrical). When I ranked the average time spent with each of the four combinations, red symmetrical was least preferred (mean rank=3.2), compared to green asymmetrical (1.7), green symmetrical (2.5) and red asymmetrical (2.6).

DISCUSSION

Female Preference for Red Bands

In zebra finches, a female preference for red over green leg bands has been reported in several choice-chamber experiments (e.g. Burley et al. 1982; Burley 1986, 1988). Female patterns of association with males in choice-chamber experiments reflect pairing patterns in free-flight aviaries despite male–male competition (Clayton 1990). In aviary studies, both an advantage (e.g. Price & Burley 1994) and no mating advantage (Ratcliffe & Boag 1987) for males with red bands over those with light green bands has been reported. In general, however, studies strongly support a female preference for red leg bands (Collins & ten Cate 1996).

A colour preference for leg bands in birds is thought to be a consequence of generalization of female preferences for bill coloration. For example, in double-bar finches, *Poephila bichenovii*, males have blue bills, and females prefer blue bands over red bands; in zebra finches, males have red bills, and females prefer red over blue bands (Burley 1986). If this explanation is correct, choice experiments for bill colour and leg band colour should yield similar results, and Burley & Coopersmith (1987) and De Kogel & Prijs (1996) both reported that female zebra finches prefer redder bills. Other studies, however, failed to confirm this finding when other variables were controlled (Immelman 1962; Houtman 1992; Collins et al. 1994; Sullivan 1994; Weissman et al. 1994; Vos 1995). In this context, my failure in this study to document a preference for red bands is unremarkable. Several possibilities have been suggested for these differing results for bill coloration preferences, including the role of display rate, learning during development (reviewed in Collins & ten Cate 1996) and inter-population variation. Similar reasons may account for differences in preferences for leg band colours. These explanations remain speculative until a sufficient number of studies are published to permit meta-analyses.

Female Preference for Symmetry

The present results do not agree with the conclusion reached by Swaddle & Cuthill (1994a), because I found no preference for symmetrical leg band combinations. This difference in outcome may have arisen because my asymmetrical band combinations had a more subtle form of asymmetry than their asymmetrical or cross-asymmetrical band combinations. I created asymmetrical combinations in which the relative amount of colour on each leg differed. This approximates the type of asymmetry seen in a trait with fluctuating asymmetry, defined as a difference in the relative expression of a paired trait on opposite sides of the body. In contrast, Swaddle & Cuthill (1994a) had asymmetrical band combinations in which each leg had a different colour, and their cross-asymmetrical combinations presented a reversal of the relative position of two colours on each side of the body (see also Bennett et al. 1996). These are not forms of asymmetry that arise from fluctuating asymmetry in natural traits, so it is difficult to extrapolate from the symmetry preference that they observed to a general preference for greater symmetry in natural traits. Females may have discriminated against cross-asymmetrical and asymmetrical band combinations because they were such unnatural forms of asymmetry.

Sample Size and Interpretation

The present results could be attributed to Type II statistical errors because of the small sample size involved (10 females, with each female seeing each band combination a mean of two times). Although incorrect failure to reject a null hypothesis is always a possibility, this conclusion is implausible if the zebra finches in the present study showed the same intensity of preference seen in other studies. My sample sizes were consistent with those used in previous studies. Swaddle & Cuthill (1994a) used 10 females that saw each combination twice, Swaddle & Cuthill (1994b) used six females that saw each combination once, and Bennett et al. (1996; experiment 3) used eight females that saw each combination once. All three studies reported highly significant differences for the comparison between symmetrical and asymmetrical treatments ($P=0.003$, $P=0.002$ and $P=0.014$, respectively). Together, these results suggest that, if my study animals

were behaving in the same way, I should have found at least a trend towards females spending more time with symmetrical males. The ANOVA showed the reverse trend. Looking at individual females, three of 10 females spent the most time, on average, with males with asymmetrical band combinations (or four females if means are calculated after combining asymmetrical left and right).

Similarly, Burley (1986) tested 15 females who saw each colour combination three times. Based on the average time spent with each colour combination over three trials, 14 of 15 females spent the most time with red-banded males. This directional preference is so strong that I should have found at least a trend towards a preference for red over green bands if my females had the same strength of preference. Again, the ANOVA showed the reverse trend. When I calculated the mean time each female spent with red- rather than green-banded males (regardless of symmetry), six of 10 females spent more time with green-banded males (Fisher's exact test, two-tailed $P < 0.01$), a result that significantly differs from that of Burley (1986). When I calculated mean times for each of the four combinations (red or green, symmetrical or asymmetrical), eight of 10 females spent the most time with males with green bands.

None of the 10 females tested spent the most time with males with red symmetrical bands. I do not claim that zebra finches do not prefer red and/or symmetrical bands; I make the local claim that there was no evidence for such preferences in this study. If such preferences did exist, then they were far weaker than those reported earlier. This finding highlights a fact known to every field biologist, that there is variation in female choice decisions both among and within populations, and patterns of choice vary depending on contingent circumstances (Jennions & Petrie 1997). It would be surprising if the same were not also true in laboratory tests, where subjects come from different sources and are raised under different conditions. How prevalent and how strong are particular female preferences? To answer this question requires numerous replicated studies that can be subjected to a meta-analysis. The present study contributes to this type of broader analysis.

ACKNOWLEDGMENTS

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