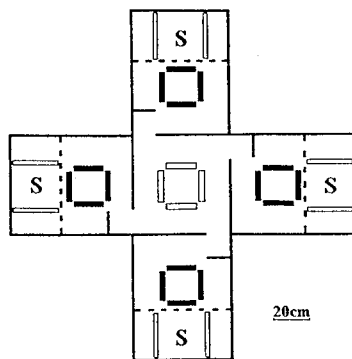


Preference for symmetric males by female zebra finches

John P. Swaddle & Innes C. Cuthill

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

FLUCTUATING asymmetries are the small random deviations from symmetry that occur in the development of bilaterally symmetrical traits¹. Such asymmetries are believed to be a direct indicator of phenotypic, perhaps genotypic, quality². Relative levels of asymmetry are much greater in secondary sexual characters than in normal morphological traits². It has been proposed that females use the amount of asymmetry in secondary sexual ornamentation as a cue in mate choice³, because the highest quality individuals have the most symmetrical, as well as elaborate, ornaments²⁻¹⁰. Using a choice chamber similar to that in ref. 11, we show here that female zebra finches choose symmetrically leg-banded males over asymmetrically banded ones. This demonstrates unequivocally that females use symmetry as a criterion in partner preference, although whether the symmetry preference is specific to secondary sexual characters is unknown.



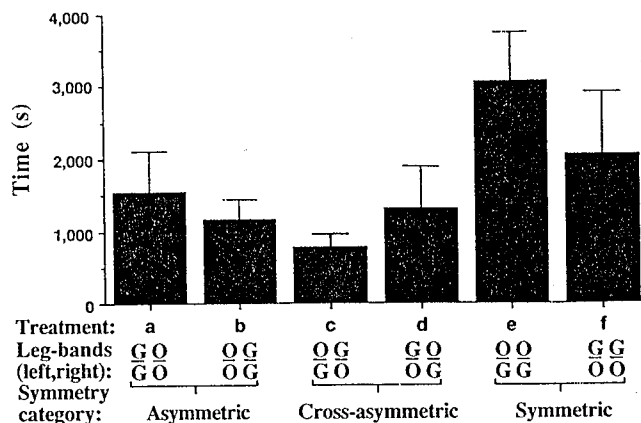
Fluctuating asymmetries (FAs) are thought to arise from the inability of individuals to buffer themselves against environmental or genetic stresses during development^{2,12}. There are intraspecific differences in the extent to which individuals resist these developmental accidents, and these individual differences are heritable^{10,12}. 'Good genes' models of sexual selection predict that mate choice should be based on traits that honestly reflect heritable fitness gains¹³; it has been suggested that FAs provide just such information^{2,5}. It is therefore significant that bilaterally symmetrical secondary sexual ornaments show greater FAs than ordinary morphological characters, and are sufficiently large to be detected by eye^{2,7}. Furthermore, asymmetry is negatively correlated with ornament size^{4,7}, implying that high quality individuals not only invest more in ornament growth but also resist the developmental stresses that cause asymmetry. But only one study has investigated whether females actually use symmetry as a cue in mate choice. By experimentally manipulating tail length of male swallows, the order of pairing was found to be consistent with mate choice based on both ornament size and symmetry³. But as tail asymmetry impairs flight performance¹⁴, choice may be based on this rather than tail symmetry itself. Here we directly test for an effect of ornament symmetry on partner preference, using an established experimental model in which the signal used in mate choice can be manipulated without confounding effects on flight performance.

Through experimental manipulations, zebra finches (*Taeniopygia guttata*) were found to show sexual preferences for members of the opposite sex that were wearing specific coloured leg bands¹¹. Preferences shown in the choice chamber are highly related to actual mate choice and pairing in free-flight aviaries¹⁵⁻²². Birds banded with 'attractive' colours tended to have higher reproductive success¹⁶, a higher proportion of same-sex offspring^{18,22}, lower parental investment per offspring and lower mortality rates¹⁵. All the leg-band combinations were symmetrical for left and right legs. By manipulating the symmetry of the leg-band combinations, while keeping the amount of each colour constant between treatments, we investigated whether female zebra finches prefer symmetrically banded males. Although males were shown to have specific colour preferences for banded females^{11,15-22}, for simplicity our experiment is limited to female choice.

Ten male and ten female wild-type zebra finches of roughly the same age were obtained from two different breeders, to ensure that stimulus and test birds were not familiar with each other. Every bird was ringed with a numbered orange leg band (colour bands were supplied by A. C. Hughes, Middlesex, UK, as in ref. 11). The test apparatus was similar, but not identical, to that used in ref. 11. Our apparatus included a sheet of one-way glass at the end of every stimulus compartment (Fig. 1). This

FIG. 1 The choice chamber, plan view. Hollow bars represent fixed perches; filled bars represent microswitch perches; dashed lines represent one-way glass; S, stimulus cage. Background room illumination was provided by two 80 W fluorescent tubes 1.5 m above the apparatus. In addition, an 8 W fluorescent tube was placed at the back of each stimulus cage to provide an increasing illumination gradient from test to stimulus cages and to ensure correct functioning of the one-way glass. Females were pre-exposed to the apparatus for a total of 6 h each before the experimental trials began. The 10 experimental females were those out of a pool of 14 birds that moved most actively within the apparatus during this pre-experimental phase. The birds, when not in the experimental apparatus, were housed in two same-sex cages with abundant food and water at a constant temperature of 18 °C on a 14:10 h light:dark photoperiod. The cages were visually, but not acoustically, isolated. Following the protocol in ref. 11, they also received passive exposure to the leg bands by placing a cage of non-experimental males (from the same suppliers as the experimental males) that were wearing the experimental bands facing the cage of females. This reduces any neophobic reaction to novel leg coloration, and perhaps allows initial acquisition of band preferences¹¹. Colours were rotated between these non-experimental males each day.

FIG. 2 The mean time (\pm s.e.) spent facing males of each colour band treatment. Note that, owing to presence of a central 'neutral' compartment (Fig. 1), these times need not sum to the trial length; on average, females spent 37% of the 5 h trial in front of males. Transformation of the data was not required. Analysis was by nested mixed-model (repeated measures) ANOVA, with 'female' as a random effect, 'symmetry category' as a three-level fixed effect (symmetric, asymmetric and cross-symmetric), and ring position (a versus b, c versus d, e versus f) as a fixed effect nested within symmetry category. The treatments are defined in the text and figure legend, with ring colours O, orange and G, green. Females spent a significantly greater amount of time in front of symmetrically banded males than asymmetrically or cross-asymmetrically banded males ($F_{2,18} = 6.09$; $P = 0.010$; group differences tested by orthogonal contrasts (ref. 29); symmetric versus asymmetric and cross-asymmetric, $t = 3.39$, $P = 0.003$; asymmetric versus cross-asymmetric, $t = 0.81$, $P = 0.501$). Within symmetry categories there was no preference for particular ring positions ($F_{3,27} = 0.81$, $P = 0.501$).



ensured that the stimulus males could not see the test female, and so negated any effects that female display characteristics might have on male behaviour.

At the beginning of each experimental trial, four male (stimulus) birds were placed in the peripheral cages of the apparatus, one in each cage (Fig. 1). A female (test) bird was placed in the centre of the apparatus and allowed to fly freely between these stimulus compartments. All stimulus birds wore two green and two orange leg bands so that treatments differed only in symmetry, not in total colour. Four bands of two colours, with two on each leg, can be arranged in six combinations: two asymmetric (left and right leg different colours); two cross-asymmetric (each leg has both colours, but relative positions differ); and two symmetric treatments (each leg has both colours in the same relative positions). Within each of these experimental categories were the two possible mirror-image alternatives (see legend to Fig. 2), allowing us to deconfound effects of ring position from symmetry.

The experiment consisted of thirty trials, during which all test females were used three times and all stimulus males were used twelve times. The experimental design was balanced so that all males appeared in each treatment group an equal number of times, all 15 of the possible 4-way permutations of the 6 treatments (a to f) were presented, and all treatment groups appeared in every stimulus cage position an equal number of times. Thus, although only 10 stimulus males wore the rings, any preference for ring combinations cannot be confounded with preference for a particular male, a particular stimulus cage, or a cage position. Females were randomly allocated to trials. Following a 2-hour acclimatization period during which all females visited all males at least once, each trial lasted for 5 hours. The time spent in front of each male was determined by means of microswitch

perches placed in every stimulus compartment, and linked to a computer.

Females spent a significantly greater amount of time in stimulus compartments where there was a symmetric, as opposed to asymmetric or cross-asymmetric, banded male (Fig. 2). The females displayed no ring-position preference within symmetry categories (Fig. 2). These results indicate that female zebra finches can detect and respond to colour pattern symmetry. As the symmetric manipulation was preferred over the asymmetric treatment, it is bilateral symmetry (left leg same as right) that is important rather than within-leg vertical symmetry (upper ring same as lower). Furthermore, as symmetric is preferred over cross-asymmetric, it is not just the average colour of the two legs that must be similar, but the specific pattern arrangement.

These findings also indicate that symmetry preference can be generalized, as manipulations were not altering the symmetry of an existing secondary sexual trait. This can be interpreted in similar ways to the demonstration of ring-colour preference itself^{11,15-22}. Either the rings mimic a specific morphological feature whose colour symmetry is assessed in natural mate choice, or females have a general preference for symmetry that extends to arbitrary characters. In the latter case, the bias may be a by-product of a perceptual system designed for symmetry detection in other contexts (compare with pitch preference in frogs²³, tail-length preference in platyfish²⁴, or emergent properties in general²⁵). Alternatively, symmetry preference may have evolved specifically because symmetry reflects individual condition and is detectable in bilateral secondary sexual traits^{2,3,5}. Whether symmetry preference is widespread, and/or specific to signalling traits is unknown, but it is clear that symmetry is correlated with various measures of fitness^{2,10,26,27}, so there must be co-evolutionary consequences for signal design²⁸. □

Received 7 June; accepted 18 October 1993.

- Ludwig, W. *Das Rechts-Links Problem im Tierreich und beim Menschen* (Springer, Berlin, 1932).
- Møller, A. P. & Pomiankowski, A. *Genetica* (in the press).
- Møller, A. P. *Nature* **357**, 238-240 (1992).
- Manning, J. T. & Hartley, M. A. *Anim. Behav.* **42**, 1020-1021 (1991).
- Møller, A. P. *Anim. Behav.* **40**, 1185-1187 (1990).
- Møller, A. P. *Proc. R. Soc. B* **248**, 199-206 (1992).
- Møller, A. P. & Höglund, J. *Proc. R. Soc. B* **245**, 1-5 (1991).
- Thornhill, R. *Behav. Ecol.* **3**, 277-283 (1992).
- Thornhill, R. *Behav. Ecol. Sociobiol.* **30**, 357-363 (1992).
- Thornhill, R. & Sauer, P. *Anim. Behav.* **43**, 255-264 (1992).
- Burley, N., Krantzberg, G. & Radman, P. *Anim. Behav.* **30**, 444-455 (1982).
- Van Valen, L. *Evolution* **16**, 125-142 (1962).
- Bradbury, J. W. & Andersson, M. B. *Sexual Selection: Testing the Alternatives* (Wiley, Chichester, 1987).
- Møller, A. P. *Proc. R. Soc. B* **243**, 59-62 (1991).
- Burley, N. *Auk* **102**, 647-651 (1985).

- Burley, N. *Am. Nat.* **127**, 415-455 (1985).
- Burley, N. *Anim. Behav.* **34**, 1732-1741 (1986).
- Burley, N. *Evolution* **40**, 1191-1206 (1986).
- Burley, N. *Ethology* **76**, 133-151 (1987).
- Burley, N. *Am. Nat.* **132**, 611-628 (1988).
- Burley, N. *Anim. Behav.* **36**, 1235-1237 (1988).
- Burley, N. *Science* **211**, 721-722 (1981).
- Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. *Nature* **343**, 66-67 (1990).
- Basolo, A. L. *Science* **250**, 808-810 (1990).
- Enquist, M. & Arak, A. *Nature* **361**, 446-448 (1993).
- Russell, E. S. A. *N. Y. Acad. Sci.* **57**, 597-605 (1954).
- Beardmore, J. A. *Heredity* **14**, 411-422 (1960).
- Endler, J. A. & McLellan, T. A. *Rev. Ecol. Syst.* **19**, 395-421 (1988).
- SPSS Inc. *SPSSX User's Guide* 3rd edn (SPSS Inc., Chicago, 1988).

ACKNOWLEDGEMENTS. We thank M. Witter, J. Hutchinson and N. Burley for discussion and comment, A. Pomiankowski and A. Møller for access to unpublished manuscripts, and the SERC for financial support of J.P.S.