

Experimental design and the signalling properties of fluctuating asymmetry

JOHN P. SWADDLE

*Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences,
University of Glasgow*

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Rohde et al. (1997) indicate a number of difficulties associated with the experimental study of the signalling properties of developmental instability (as measured by fluctuating asymmetry, Ludwig 1932). In particular they criticize a series of experimental studies of symmetry preferences in zebra finches, *Taeniopygia guttata* (Swaddle & Cuthill 1994a, b; Bennett et al. 1996; Swaddle 1996). Rohde et al.'s primary thrust is that the experimental treatments used in the above studies do not mimic fluctuating asymmetry, as the asymmetries are too large and not natural. Rohde et al. are quite correct; however, I would point out that these limitations are acknowledged in the papers cited and Rohde et al. do not report comprehensively the conclusions drawn by the authors. Additionally, Rohde et al. (1997) suggest alternative experimental designs which they claim are more appropriate for investigating the signalling properties of fluctuating asymmetry. However, the experimental designs they present are confounded and equivocal and therefore will not disentangle the signalling properties of symmetry from other extraneous factors.

Swaddle & Cuthill (1994a) applied two orange (O) and two green (G) bands to the legs of male zebra finches, so that each male wore two bands on each leg. There were six possible combinations of these four bands, which gave rise to two asymmetric (left leg: GG/right leg: OO; left leg: OO/right leg: GG), two cross-asymmetric (GO/OG; OG/GO) and two symmetric treatments (GO/GO; OG/OG). Males were then placed into a choice chamber apparatus and female zebra finches were allowed to display preferences for the differently banded males. Females preferred the symmetrically banded males over both

asymmetric and cross-asymmetric males. Swaddle & Cuthill (1994a) suggested three ways in which the reader could interpret their results. (1) As in the case of the leg-band colour preferences (e.g. Burley et al. 1982), the leg bands could 'mimic a specific morphological feature'. (2) 'Females have a general preference for symmetry that extends to arbitrary characters'. (3) 'Symmetry preferences have evolved specifically because symmetry reflects individual condition'. Swaddle & Cuthill (1994a) went on to state that it is not known whether this preference for symmetry is widespread or specific to signalling traits, and explicitly stated that their findings 'indicate that symmetry preference can be generalized, as manipulations were not altering an existing secondary sexual trait'. Swaddle & Cuthill (1994b) discussed the data reported in Swaddle & Cuthill (1994a) (as well as that reported by Møller 1992a, 1993) as a 'preference for symmetric arbitrary traits (i.e. traits that do not occur naturally on the individual) as manipulations have resulted in extremely abnormal plumage patterns; so far there has been no convincing manipulation of asymmetry levels in an existing secondary sexual character'. Clearly, none of the experimental treatments employed by Swaddle & Cuthill (1994a) represented a naturalistic condition and at no point did Swaddle & Cuthill claim that their leg-band manipulations represented a 'true' pattern of fluctuating asymmetry.

Swaddle & Cuthill (1994b) manipulated the chest plumage of male zebra finches by removing small portions of feathers in symmetric and asymmetric patterns and assessed female preference for these males in a choice chamber. Here, the manipulations resulted in asymmetries within the natural range of asymmetry values. Despite this, Swaddle & Cuthill (1994b) still made the conservative statement that 'females may prefer males because they have a predisposed bias toward

Correspondence to: J. P. Swaddle, Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, U.K. (email: gbza86@udcf.gla.ac.uk).

symmetric signalling structures', and discussed a possible perceptual mechanism by which a general preference for symmetry could arise (i.e. by mental prototyping). Swaddle (1996) employed the same leg-band treatments as Swaddle & Cuthill (1994a) and assessed their influence on zebra finch reproductive success; Swaddle made the explicit statement that 'the manipulation employed in this experiment altered the symmetry of an arbitrary (artificial) trait and so conclusions concerning symmetry of existing sexually-selected characters are limited'.

Rohde et al. (1997) imply that the leg-band experiments were designed to test for preferences for different levels of fluctuating asymmetry. This is not the case; the experiments were specifically designed to test for the influence of symmetry *per se* on signalling, which has implications for the study of fluctuating asymmetry. Cautious interpretation of these results are needed, especially in a research field that appears to generate so much debate.

Rohde et al. (1997) suggest that the results reported in the above papers do not demonstrate a preference for a symmetric phenotype, and merely reflect 'no more than the non-acceptance of extremely deviant or physically defective males'. This is an important point worthy of consideration; however, I find this argument inconsistent with the results reported in the papers. As the leg bands are clearly an artificial trait and every male wore the same number of the same coloured leg bands, all individuals showed a deviant phenotype. As none of the treatments was naturalistic, the preference for the symmetric treatment is even more intriguing and implies a general preference for symmetric patterns. In addition, Swaddle (1996) showed that the leg-band treatments had no influence on male social dominance hierarchies. Surely, if asymmetric and cross-asymmetric males were perceived as 'deviant' and symmetric males as 'non-deviant', symmetric individuals would do better in social encounters? In the experiment in which chest plumage was manipulated, Swaddle & Cuthill (1994b) indicated that birds that had more plumage removed were not any more unattractive than those with less plumage removed. If females were merely avoiding damaged individuals, birds with less plumage removed should be preferred. Also, when feather removal was controlled for between treatment groups, the symmetric treatment was still pre-

ferred over the asymmetric treatment. Additionally, as damage increases levels of asymmetry (e.g. Swaddle et al. 1996), a highly asymmetric damaged individual would be more naturalistic than a symmetric damaged individual, yet the symmetric individual is preferred. Hence, if these three papers (Swaddle & Cuthill 1994a, b; Swaddle 1996) are interpreted in concert, the empirical evidence does support the original conclusion: female preference for the symmetric males. The mechanism by which this preference arises is not known and is worthy of further investigation.

I agree with Rohde et al. (1997) that researchers interested in investigating the signalling role of fluctuating asymmetry should adopt careful experimental designs. Their statements lead to the question: how can fluctuating asymmetry be manipulated in a naturalistic way? For experimental manipulations to be performed the phenotype has to be altered, but this is Rohde et al.'s criticism of Swaddle & Cuthill (1994b). Rohde et al. do not suggest an alternative; they do, however, suggest two deviations upon the leg-band experiments, which they say are 'better' as their manipulations more accurately reflect 'true' fluctuating asymmetry. The first is to alter the amount of colour on the left and right legs, but retain the same pattern, to give an asymmetric leg-band arrangement of OOOG/OGGG and a symmetric arrangement of OOGG/OOGG. This arrangement, however, is inappropriate for studies of symmetry/asymmetry as a preference for symmetry could also be explained by a preference for OOGG, whether it appears on one leg or both (i.e. independent of symmetry). Hence this experimental design confounds a particular leg-band arrangement with symmetry and so any preference displayed for the symmetric arrangement is equivocal. The second experiment design they propose has different amounts of colours in symmetric and asymmetric treatments (e.g. asymmetric treatment: OOGG/OOOG; symmetric treatment: OOGG/OOGG) and so, as recognized by Rohde et al. themselves, confounds the symmetry manipulation with amount of colour and also cannot lead to unequivocal conclusions. This latter experimental design has already been criticized in the literature (e.g. Brookes & Pomiankowski 1994).

Given the shortcomings of experimental design in both proposals put forward by Rohde et al.

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