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Museum studies measure FA

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The analysis of individual variation in the level of fluctuating asymmetry within a population has become of great interest to behavioural ecologists. This is because the level of fluctuating asymmetry displayed in morphological traits is often associated with components of individual fitness (Møller & Pomiankowski 1993; Swaddle & Witter 1994; Watson & Thornhill 1994). As a consequence of this, symmetry may be an important component of signal design in ornamental traits (Møller 1990; Møller & Pomiankowski 1993; Swaddle & Cuthill 1994a, b; Watson & Thornhill 1994). However, a problem in analysing fluctuating asymmetry is that between-individual differences in fluctuating asymmetry are readily confounded with other effects, notably measurement error, physical damage, and spatiotemporal variation within the species. We highlighted these and other difficulties in Swaddle et al. (1994), which Simmons et al. (1995) have misinterpreted as a refutation of the utility of museum collections. This was not our intention, and we agree wholeheartedly with Simmons et al. (1995) that scientific collections can provide valuable information for comparative analyses, but only if the sources of bias outlined by Swaddle et al. (1994) can be ruled out. Our worry was that most published studies either cannot rule out such biases, or fail to present the necessary analyses (e.g. since acceptance of our original paper, Alibert et al. 1994; Eggert & Sakaluk 1994; Malyon & Healy 1994; Manning & Ockenden 1994; plus references in Swaddle et al. 1994). Our aim was to establish specific criteria that morphometric studies need to satisfy before they can provide useful information (see also Palmer & Strobeck 1986). These criteria can indeed be met in museum studies (e.g. Tomkins & Simmons 1995).

Simmons et al. (1995) agree that heterogeneity of sources may invalidate museum studies and that controlled sampling within populations is required for the appropriate interpretation of fluctuating asymmetry data. However, at several points, Simmons et al. (1995) misinterpret our paper as being applicable only to studies involving museum collections. We explicitly stated that, 'heterogeneity of source invalidates museum and field studies based on pooled samples' (Swaddle et al. 1994), then illustrated this with an example based on a field study (Møller 1992). We suggest that if the appropriate information is available, population, site and year differences can be teased out statistically, but this is rarely performed in uncontrolled field studies and museum collections. Deliberate, or unconscious, pooling of data from several statistical populations creates many problems beyond those specific to morphometric studies (Hurlbert 1984).

There are two other points raised by Simmons et al. (1995) with which we disagree. First, they consider that whilst a negative relationship between fluctuating asymmetry and trait size can arise from sample heterogeneity (Swaddle et al. 1994), failure to find a relationship may not be confounded in the same way. We dispute the accuracy of this statement. Any apparent correlation of asymmetry with trait size (including zero) can be generated by a combination of between-population differences in optimal trait size, level of developmental homeostasis, or post-developmental viability selection (on size and/or asymmetry). Second, Simmons et al. (1995) claim that whether a (true) negative relationship between trait asymmetry and size results from condition-dependent expression or post-developmental viability selection, females still have a reliable indicator of male quality. This may be true if the population is carefully sampled at the appropriate time of year. However, discriminating between the many reputed cost(s) that maintain honest signalling is a prime research goal for sexual selection theorists, and an area of considerable controversy for fluctuating asymmetry researchers in particular (e.g. Evans & Thomas 1992; Balmford et al. 1993; Evans & Hatchwell 1993; Evans et al. 1994).

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Thus, it is vital to know how any relationship between asymmetry and size is generated. In this respect, perhaps only laboratory studies (e.g. Swaddle & Witter 1994) and cohort analyses in the field (e.g. Zakharov 1981) can actually tell us how asymmetry/size relationships are generated.

Finally, even once the researcher is satisfied that data are homogeneous, or sources of heterogeneity are included as factors in the analysis, there are still several steps that should be taken before meaningful conclusions can be drawn. As stated in Swaddle et al. (1994), fluctuating asymmetry must be distinguished from the two forms of adaptive asymmetry (directional asymmetry and antisymmetry). The asymmetry recorded must also be shown to be larger than that due to measurement error (Palmer & Strobeck 1986; Swaddle et al. 1994). As fluctuating asymmetries result from developmental accidents, they must also be separated from trait damage that is not a reflection of intrinsic developmental processes (Cuthill et al. 1993). Studies of fluctuating asymmetry should explicitly state that all of these considerations have been taken into account; most fail in at least one case (e.g. Alibert et al. 1994; Eggert & Sakaluk 1994; Malyon & Healy 1994; Manning & Ockenden 1994; references in Swaddle et al. 1994).

In summary, we advise that the precautions and data analysis techniques that we recommended in our original paper (Swaddle et al. 1994) are employed in all studies of fluctuating asymmetry. As Simmons et al. (1995) recognize, only carefully constructed studies will satisfy these criteria and provide data from which meaningful conclusions can be drawn.

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