

## The analysis of fluctuating asymmetry

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Fluctuating asymmetries result from the inability of individuals to undergo identical development of a bilateral trait on both sides of the body (Van Valen 1962). It has long been realized that a negative correlation exists between asymmetry and fitness (e.g. Beardmore 1960). Recently, in behavioural ecology, particularly in studies of sexual selection, there has been a growth of interest in the study of fluctuating asymmetries, both as measures of individual quality (e.g. Møller 1990, 1992a; Swaddle & Witter 1994; Witter & Swaddle 1994) and as indicators of the strength and direction of selection (e.g. Møller & Höglund 1991; Balmford et al. 1993; Møller & Pomiankowski 1993). However, the most appropriate method of quantifying and analysing fluctuating asymmetry has been controversial (Cuthill et al. 1993; Evans & Hatchwell 1993; Harvey et al. 1993; Møller 1993a; Sullivan et al. 1993; Watson & Thornhill 1994); in this paper, we highlight limitations in previous approaches and consider more appropriate methods of analyses.

There can be gross differences in values of fluctuating asymmetry between different populations of the same species (Valentine & Soulé 1973; Picton et al. 1990; Markowski 1993; Møller 1993b, in press), between years within populations (Zhakarov 1981; Møller 1993b) and at the extremities of a population range (Downhower et al. 1990; Parsons 1993). Comparisons between populations may be of intrinsic interest (references above), but behavioural ecologists are typically interested in within-population variation as an outcome of differences in condition or as an object of mate choice, in which case, heterogeneity of source invalidates museum and field studies based on pooled samples. For example, Møller (1992b) reported data on fluctuating asymmetry from 517 male barn swallows, *Hirundo rustica*, from colony sites in Denmark. These data are an accumulation of measurements from 18 different colonies spanning several years, so between-year, between-site and between-individual variation are confounded.

Møller, having collected all the samples himself, can in principle separate these effects statistically or analyse more homogeneous samples (e.g. Møller 1990). However, this will rarely be possible with museum collections (e.g. Wayne et al. 1986; Møller & Höglund 1991; Møller 1992a; Balmford et al. 1993; Manning & Chamberlain 1993, 1994) or uncontrolled field sampling (e.g. Solberg & Sæther 1994). These have additional biases including the following. (1) There may be differential mortality by level of fluctuating asymmetry, ornament size, or some interaction thereof. Hence measured relationships between asymmetry and size may reflect the action of natural selection rather than developmental constraints or condition-dependent expression. (2) Humans find symmetrical and elaborate objects more aesthetically pleasing (Eisenman & Rappaport 1967; Szilagyi & Baird 1977) and collectors, hunters and museum curators seeking 'typical' specimens are not immune to such biases. (3) Wear and damage asymmetry may not be discriminable from fluctuating asymmetry (see Cuthill et al. 1993; Møller 1993a).

Measurement error, like (signed) fluctuating asymmetry, is normally distributed with a mean of zero. So, since fluctuating asymmetries are generally very small relative to the size of the traits being measured (typically ca 1%; Møller & Pomiankowski 1993), measurements must be replicated to distinguish true asymmetry from measurement error. Measurement error has been shown to account for up to 25% of the variation in dental asymmetry data in wild mice (Bader 1965) and humans (Greene 1984) and 76% of the variation in wing length asymmetry in nymphalid butterflies (Mason et al. 1976). This point has been made previously by Palmer & Strobeck (1986), but has gone largely unheeded in the recent behavioural literature. Several recent papers provide no repeatability analyses (e.g. Thornhill 1992; Thornhill & Sauer 1992; Radesäter & Halldórsdóttir 1993). Even where