# Fluctuating asymmetry

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SIR — Fluctuating asymmetry describes the symmetrical distribution of random deviations from the population mean of a bilaterally symmetrical trait, presumed to arise from failure of homeostatic mechanisms in the face of developmental stress[7-10]. As individuals vary in their ability to resist disruption of symmetrical growth, the relationship between trait asymmetry and trait length can give valuable insights into how selection acts on trait length[10]. Traits under stabilizing selection often show U-shaped relationships between asymmetry and mean trait length[10], with extreme individuals poorly adapted to prevailing conditions. It is thus significant that recent studies indicate that many secondary sexual characters show negative relationships between asymmetry and size[2,4,5,10-12], indicating that sexual selection is directional and that individuals with large display traits are of 'high quality' (better adapted to prevailing conditions)[10]. Sullivan *et al.*[1] cast doubt on this evidence by suggesting two reasons for such negative corretions being artefacts. Their first critism, of the use of relative asymmetry, is well-founded, but we believe their subsequent suggestions to be misleading.

Relative asymmetry is the ratio of the absolute difference between the left and right side to the mean trait length. The problem arises here because relative asymmetry is necessarily negatively correlated with its denominator, mean trait length[1]. Use of relative asymmetry will only 'control' for differences in mean trait length when absolute asymmetry is isometrically related to mean trait length. Under such circumstances, relative asymmetry may be a useful index, but isometry must be empirically verified, not assumed. However, belief in the negative correlation between asymmetry and mean trait length does not rest on the dubious use of a ratio variable[13]; Møller and his coworkers[2,4,5,10,11] find the same relationship with absolute asymmetry, as do Sullivan *et al.* in their analysis of pheasant spurs[1].

The second criticism hints at a deeper problem in the analysis of asymmetry data, but the suggested solution is inappropriate and the true problem is not dressed. Sullivan *et al.* note that a hortening of one of a pair of bilaterally symmetrical characters "because of differences in growth rate, injury or damage" both increases absolute asymmetry and reduces mean length, thereby biasing the analysis toward a negative correlation between the two. Their solution is to examine the relationship between absolute asymmetry and the longest of the pair of traits, rather than the mean length. However, this reasoning is flawed on two counts. First, unlike asymmetry through damage or wear, true fluctuating asymmetry (imbalances in symmetrical growth) can result from overgrowth on one side as well as stunting on the other. Thus higher asymmetries through a failure of developmental homeostasis do not inevitably lead to a reduction in the mean trait length, merely an imbalance between the two sides. Second, analysis of the relationship between absolute asymmetry and the longest of the two traits in fact biases one towards finding a positive correlation, as we show below.

The relationship between absolute asymmetry and trait length can be examined in a number of ways. Sullivan *et al.* consider two: "asymmetry versus mean" and "asymmetry versus longest". However, not all such comparisons are equivalent, or appropriate. In the language of principal component analysis, the mean trait length represents the dimension in which the left and right sides are correlated and absolute asymmetry is the orthogonal dimension in which they are not. However, the dimensions "longest side" and "absolute asymmetry" are not orthogonal, but positively correlated, thus biasing the analysis. Intuitively, this is most easily understood in the situation where left and right sides are uncorrelated. When the longest side is much greater than the population mean, the short side can assume almost any value (hence asymmetry can be large); but when the longest side approaches the lower limit of the trait size distribution, the shorter side is more constrained (hence asymmetry is low). The problem is greatest when the correlation of left and right sides is relatively loose; precisely the situation that appears typical of display traits[4,5,10].

In recognizing that damage and wear (but not developmental stress) lead to both an increase in asymmetry and decrease in mean length, Sullivan *et al.* raise an important point that deserves amplification. As only fluctuating asymmetries, resulting from developmental stress, are of relevance to investigations of the direction and strength of selection, it is vital to exclude any measurements influenced by wear or damage. Sullivan *et al.* may not be able to distinguish true fluctuating asymmetries from damage or wear in their pheasant spurs, but with sexual plumage, breakages and wear are probably easier to identify *a priori*. With mean asymmetry more sensitive to such outliers than mean trait length, and ornaments perhaps particularly prone to damage, it is all the more important to exclude non-developmental asymmetries from analyses of fluctuating asymmetry. If one can exclude damage and wear effects, an analysis of the relationship between absolute asymmetry and mean trait size is both entirely appropriate and of great theoretical importance[10].

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