Fluctuating Asymmetry

Secondary article

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Article Contents

Fluctuating asymmetry refers to small random deviations from perfect symmetry in bilaterally paired structures; it is thought to reflect an organism's ability to cope with genetic and environmental stress during development and its utility as an indicator of such stresses is based on the assumption that perfect symmetry is an *a priori* expectation for the ideal state of bilateral structures. Fluctuating asymmetry has been used as an indicator of individual quality in studies of natural and sexual selection and as a bioindicator tool for environmental monitoring and conservation biology.

What Is Fluctuating Asymmetry?

Fluctuating asymmetry is a particular form of biological asymmetry, characterized by small random deviations from perfect symmetry. The fundamental basis for the study of fluctuating asymmetry is an *a priori* expectation that symmetry is the ideal state of bilaterally paired traits. Fluctuating asymmetry measures deviations from the ideal state of symmetry, and is therefore thought to reflect the level of genetic and environmental stress experienced by individuals or populations during development. It has attracted a great deal of attention because bilaterally symmetrical traits are extremely common in nature and because the measurement of fluctuating asymmetry appears to represent a relatively simple method of assessing biologically important stress at the individual and population levels.

Asymmetry of an individual is measured as the right minus the left value of the bilaterally paired trait. By studying the distribution of these asymmetries at the population level, we can distinguish between three types of biological asymmetry: fluctuating asymmetry, directional asymmetry, and antisymmetry. Fluctuating asymmetry is characterized by small random deviations from perfect bilateral symmetry. These small random deviations result in a normal or leptokurtic distribution of asymmetry around a mean of zero. Directional asymmetry is characterized by a symmetry distribution that is not centred around zero but is biased significantly, towards larger traits either on the left or the right side. Antisymmetry is characterized by being centred around a mean of zero; however, symmetric individuals are rarer than those seen in fluctuating asymmetry distributions, such that the distribution is platykurtic or, in the extreme, bimodal. Directional symmetry and antisymmetry are developmentally controlled and therefore likely to have adaptive significance. Fluctuating asymmetry, on the other hand, is not likely to be adaptive as symmetry is expected to be the ideal state (Van Valen, 1962; Palmer, 1994; Gangestad and Thornhill, 1999).

Measuring fluctuating asymmetry

Although subtracting the measurement of the right side of a trait from that of the left side forms the basis of the analysis, accurately quantifying fluctuating asymmetry is not simple. The measurement of fluctuating asymmetry is complicated by the fact that its magnitude and distribution are the same as the magnitude and distribution of measurement error. Therefore, in order to establish that real differences in symmetry rather than just measurement error are being reported, it is imperative to establish that the measures of fluctuating asymmetry explain a statistically significant proportion of the observed total variance between the sides. To achieve this it is necessary to make repeated measures of the left and right sides of the trait. The repeated measures need to be made on the same subjects in ignorance of the initial measure, with the same equipment and under the same laboratory or field circumstances as those of the main data. Furthermore, to eliminate observer bias, ideally all measurements should be made in ignorance of the measurement recorded for the side's pair. For analysis of a potential fluctuating asymmetry data set, certain criteria must be met: the measurements must represent actual deviations from symmetry and not measurement error, and the distribution of fluctuating asymmetry must conform to that expected for it, rather than for directional asymmetry or antisymmetry. Various procedures have been recommended for this stage of the analysis, the most widely used being a mixed model analysis of variance (ANOVA), which will determine whether fluctuating asymmetry is significantly different from measurement error, and whether the asymmetry distribution has a mean of zero (Palmer, 1994). The mixed model ANOVA does not reveal significant departures in the fluctuating asymmetry distribution towards platykurtosis, characteristic of antisymmetry, and therefore the asymmetry distribution should also be described statistically in terms of its kurtosis and assessed visually. Once fluctuating asymmetry has been established to exist in a trait, data analysis should proceed by testing first for the relation between trait size and fluctuating asymmetry. If there is a relationship, this needs to be accounted for, and methods exist for controlling for size dependence (Palmer, 1994). Data can be analysed between groups, treatments or populations by using methods for comparing trait variances. Relationships between individual fluctuating asymmetry and continuous variables such as fitness measures need to be conducted on absolute fluctuating asymmetry values, sometimes called 'unsigned fluctuating asymmetry'. Caution should be exercised when analysing unsigned fluctuating asymmetry, as it has a half-normal distribution, which violates the assumptions of most parametric statistics.

A more accurate assessment of developmental stability can be obtained by pooling the fluctuating asymmetry measures of several traits per individual. However, as different traits may have different selection pressures on their symmetry, the traits that are being pooled need to be chosen carefully. It is a common observation that there is at best a very weak relationship between fluctuating asymmetries measured from two different traits for the same individuals.

Fluctuating Asymmetry as a Measure of Individual Quality

Interest in fluctuating asymmetry originated because of its potential for measuring population-level stress. Recently, much interest has also been devoted to the examination of fluctuating asymmetry as an indicator of individual quality. This interest has been most vivid in the area of sexual selection and in particular mate choice.

Sexual selection

Sexual selection is broadly represented by aggressive competition between males for access to females or their ova (male–male competition/sperm competition) and by choice by females among potential mates. It is in the interests of a male to be able to assess accurately the competitive ability of a rival, and also to indicate reliably its own competitive ability, so as to avoid contests in which it has little chance of winning and a high chance of being hurt. For females, the high cost of investing in relatively few large ova means that females should be very choosy about the quality of the males they select as mates. In both of these contexts the assessment of fluctuating asymmetry of secondary sexual traits has been suggested as a mechanism through which individual assessment of quality might be achieved.

There are three hypotheses why fluctuating asymmetry in sexually selected traits might be a particularly sensitive indicator of a male's quality: (1) sexually selected traits are frequently ornamental, and may therefore be released from the functional costs of asymmetry found in other traits; (2) sexually selected traits have often been exposed to a recent history of directional selection, which is thought to disable the genetic modifiers that normally serve to maintain trait symmetry; (3) sexually selected traits are often condition-dependent in their expression, such that developmental stress is likely to be revealed in trait expression.

Mate choice

Since 1990 there has been a great deal of interest in the role of fluctuating asymmetry in mate choice: it may either be the signal that females are paying attention to, or be a correlate of male quality. A convincing demonstration that fluctuating asymmetry is the signal that females are paying attention to during mate choice requires that symmetry be manipulated or that the effects of other traits be partialled out. For sexual selection studies in relation to fluctuating asymmetry, this has only been done in very few cases. In invertebrates, experimental manipulations of leg-tuft asymmetries in male spiders resulted in symmetrical males being preferred by females, but forceps length manipulations in the European earwig did not. In vertebrates, female choice in a lizard was correlated to male femoral pore (scent gland) symmetry, independently of femoral pore number. Two studies have shown female preferences for symmetry of the tail streamers of the barn swallow, but a thorough investigation in the red-winged blackbird found no evidence for a role of fluctuating asymmetry in sexual selection. Leg-band symmetry in birds such as zebra finches and blue throats as well as body-bar number asymmetries in swordtail and molly fish have been demonstrated to be important cues for female choice. However, these preferences are for gross asymmetry rather than for the small deviations that are characteristic of fluctuating asymmetry. In humans there is clear preference for facial symmetry. However, facial asymmetry in humans tends to be directional asymmetry rather than fluctuating asymmetry and therefore the relationship between facial symmetry and developmental stability is unclear.

The generality of the preference of females for low asymmetry in males is equivocal. A meta-analysis of the role of fluctuating asymmetry in sexual selection did show a significant effect of male symmetry. However, this study has been criticized because the data set shows a significant publication bias in favour of the hypothesis, and further that there is a significant change in the degree of support for the hypothesis over time (Simmons *et al.*, 1999). A meta-analysis taking these two sources of bias into account has found significant advantage in sexual selection for males with symmetrical traits, although the fail safe number of the general effect size was below the critical value for confidence in the result (Tomkins and Simmons, in press).

Condition-dependence

For fluctuating asymmetry to be indicative of individual quality, it is necessary for it to be condition-dependent. In other words, individuals that experience poor environments or have low genetic quality should display high levels of trait fluctuating asymmetry. Indeed the fluctuating asymmetry in sexually selected traits is hypothesized to be more condition-dependent than that in other traits. Negative relationships between sexually selected trait size and fluctuating asymmetry in birds' tails and spurs, in primate teeth and in beetle horns have been cited as broad evidence for condition-dependence of fluctuating asymmetry in sexually selected traits. Nevertheless, the generality of the condition-dependence of fluctuating asymmetry is far from clear. A number of convincing experimental studies of jungle fowl, stalk-eyed flies, dung flies and dung beetles have found no relation between environmental stress and the level of fluctuating asymmetry in sexually selected traits. Inbreeding studies have found no evidence of increased levels of fluctuating asymmetry in a sexually selected trait in the guppy fish, or in the yellow dung fly or in the wings of *Drosophila* fruitflies. A meta-analysis of the relationship between stress and fluctuating asymmetry concluded that there was evidence for the condition-dependence of fluctuating asymmetry in sexually selected traits (Leung and Forbes 1996). However, this analysis includes negative relations between fluctuating asymmetry and sexually selected trait size as evidence for condition-dependence: a relationship that may arise for other reasons such as aerodynamic costs.

Heritability

The heritability of fluctuating asymmetry is critical for the arguments that it may be indicative of good genes in sexual selection. However, whether fluctuating asymmetry is heritable remains a subject of controversy. Møller and Thornhill, 1997 presented a meta-analysis of the heritability of fluctuating asymmetry that found that there was a low but significant heritability. This finding received much criticism, however (*Journal of Evolutionary Biology*, vol. 10, 1997). In particular, it was argued that because fluctuating asymmetry estimates the between-sides variance in a trait using only two data points, it represents a very weak estimate of a genome's developmental instability. Furthermore, it was maintained that any additive genetic variation for asymmetry will be low because the genetic correlation between left and right traits will be very high. Fuller and Houle (in press) provide the latest review of the heritability of fluctuating asymmetry, showing that only one out of 24 half-sib analyses found a significant heritability. Their conclusion is that the issue of the heritability of fluctuating asymmetry is unresolved, but although the heritability of fluctuating asymmetry is certainly low, the heritability of developmental instability may be somewhat higher. Fuller and Houle's model for estimating the heritability of fluctuating asymmetry suggests that a half-sib breeding design with enormous sample sizes is required before studies are likely to detect significant heritabilities.

Natural selection

Natural selection on fluctuating asymmetry has received less attention than sexual selection. However, both hypotheses assume that fluctuating asymmetry has costs and reflects the quality of an individual. Probably the best documented naturally selected cost of fluctuating asymmetry is that of impaired flight performance in birds with asymmetrical wings or tails. Models predict that aerodynamic performance of asymmetric individuals is decreased in comparison to that of symmetric individuals. These models have been supported by comparative studies, field and laboratory manipulations, and evidence of selection against asymmetry through predation and severe weather. Predation as a cost of wing asymmetry has also been demonstrated for houseflies that are predated by swallows and by dung flies. Meta-analysis of the relation between fluctuating asymmetry, growth, survival and fecundity have all revealed significant effect sizes. Nevertheless, these data were extremely heterogeneous and the data set relating fluctuating asymmetry to survival also showed signs of publication bias. Hence, although there are well-documented naturally selected costs of fluctuating asymmetry in some taxa, the generality of the relationship between the level of fluctuating asymmetry and magnitude of cost through natural selection is as yet unclear.

Fluctuating Asymmetry as an Indicator of Genetic Stress

Two major genomic features that have been thought to benefit developmental stability of individuals are heterozygosity and genomic coadaptation. Heterozygosity relates to genetic variance in individual or population, while genomic coadaptation relates to internal balance of genes within chromosomes. There are also other factors, more or less related to the above two, that have been suggested to have an effect on the developmental stability of individuals and thus levels of fluctuating asymmetry. These factors include changes in genetic variance, for example loss of variance due to inbreeding, episodes of directional selection and mutations. In the following we will discuss the first three in more detail.

Loss of genetic variance

Inbreeding reduces the genetic variance, and has repeatedly been shown to cause a reduction in the mean phenotypic value of fitness-related traits. The effect that inbreeding tends to reduce fitness has been called inbreeding depression. It should be noted that inbreeding has greater effect on fitness-related traits than it has on traits that are not closely connected with fitness.

There are two reasons why loss of genetic variation should cause increased fluctuating asymmetry. Loss of genetic variance causes individuals to be more homozygous. Because different alleles may have different optima for producing their enzymatic products, heterozygous individuals may be better able to maintain adequate levels of enzymatic activity over a wider range of environmental variation than will homozygous individuals. In other words, heterozygous individuals are less sensitive to environmental variables than are homozygous individuals (Falconer, 1989). Therefore, as long as the enzyme activity is related to the measured characters, it is expected that homozygous individuals may show increased levels of fluctuating asymmetry when compared to heterozygous individuals. Evidence from several different organisms including fruitflies, rainbow trout and laboratory rodents show that reduced genetic variance due to inbreeding does increase the levels of fluctuating asymmetry. However, there is also abundant evidence from equally diverse taxa for no association, or even negative associations, between inbreeding and fluctuating asymmetry. This suggests that the relationship between fluctuating asymmetry and loss of genetic variance due to inbreeding is not uniform and reduces the general applicability of fluctuating asymmetry as a measure of inbreeding.

Heterozygosity

Heterozygosity of protein polymorphisms is an indicator of genetic variability and has been suggested to be positively related to several fitness components such as viability, growth rate and developmental stability. In fact, the maintenance of genetic diversity in natural populations has been accounted to this fitness benefit of heterozygotes (Mitton and Grant, 1984; Charlesworth and Charlesworth, 1987). The underlying reason for an expectation of such positive association between heterozygosity and fitness is that heterozygotes have been suggested to be buffered against environmental variation and thus to be phenotypically plastic i.e. maintain the optimal phenotype in the face of environmental fluctuation. In other words, individuals with relatively high levels of heterozygosity may have higher fitness because they also show a relatively high level of individual homeostasis or stability. However, the literature on the association of heterozygosity and fitness is at best suggestive and cannot be said to apply as a general rule (Britten, 1996).

Heterozygotes are predicted to show lower levels of fluctuating asymmetry than homozygotes. If the level of fluctuating asymmetry is determined by more than only a few loci, then differences in fluctuating asymmetry should be more readily detected between individuals from different populations than between individuals from the same population (Palmer and Strobeck, 1986). It has also been shown in some studies that fluctuating asymmetry tends to increase with increased inbreeding, giving some support for the notion that reduced heterozygosity may indeed increase the levels of fluctuating asymmetry. However, the evidence is contradictory and more studies are needed before generalizations are possible (see also Loss of Genetic Variance above).

Hybridization

Hybridization between locally adapted populations or different taxa may disrupt coadapted gene complexes. Coadapted gene complexes may evolve in a population if natural selection favours alleles in several loci that interact to produce developmentally stable phenotypes. Estimating the extent and nature of coadapted gene complexes and determining the effects of their disruption may help us to understand the establishment of reproductive isolation in the process of speciation. It has been suggested that disruption of coadapted gene complexes resulting from hybridization may result in increased levels of developmental instability. However, there are two different predictions of the effects of hybridization depending on the populations that are hybridizing. If the two populations are inbred and suffer from inbreeding depression, it is assumed that hybridization should increase developmental stability and thus be reflected as reduced levels of fluctuating asymmetry. However, if two locally adapted populations are hybridizing, it is assumed that there may be coadapted gene complexes and their disruption will result in lower developmental stability and thus increased levels of fluctuating asymmetry (Graham, 1992).

Applied Uses of Fluctuating Asymmetry: Environmental Monitoring and Conservation

The idea that environmental and genetic stress may increase the levels of fluctuating asymmetry in individuals and populations makes fluctuating asymmetry a potential tool for biomonitoring programmes and conservation biology. A pertinent problem in conservation biology is to find suitable early indicators of stress caused by toxins or, for example, habitat fragmentation and habitat loss. It is important to find reliable early indicators of such stress to enable conservation programmes to be started before the first serious effects of stress are evident and it is too late to act. Fluctuating asymmetry has also been suggested to be useful in assessing the status of endangered species (Leary and Allendorf, 1989).

Fluctuating asymmetry has been used as a bioindicator in a broad array of applications. In water ecosystems, greater levels of fluctuating asymmetry have been found in fish from areas that have been heavily polluted with DDT and in invertebrates such as shrimp and chironomid larvae in the vicinity of an agricultural fertilizer factory. Over a decade has elapsed since the nuclear power plant accident in Chernobyl, Ukraine. Since the accident a few studies on its biological consequences have been conducted using fluctuating asymmetry as an indicator of stress. These studies found that in three species of plant the degree of fluctuating asymmetry significantly decreased along a 225 km transect from Chernobyl southeast towards a largely uncontaminated area. Similar results have been found with barn swallows: populations close to Chernobyl have three to four times higher levels of fluctuating asymmetry in their outer tail feathers compared to birds in control areas. Habitat fragmentation and habitat loss as well as other types of habitat destruction are major causes of extinctions at individual and population levels. There is some evidence that fluctuating asymmetry may be a useful indicator of stress due to habitat fragmentation. For example, in Brazilian tropical forests it has been found that several birds species have elevated levels of fluctuating asymmetry in forest fragments in comparison to those in continuous forests. Similar relationships between degree of fragmentation and the level of fluctuating asymmetry have been found in other birds, in lizards and in squirrels. These results and others show that fluctuating asymmetry may be used as an indicator of environmental stress due to pollutants or habitat fragmentation. However, again, there exist several studies that have not found relationships between environmental degradation and levels of fluctuating asymmetry, suggesting that it may not automatically be used as an indicator of stress. In particular, the lack of relationship between environmental degradation and fluctuating asymmetry should not be interpreted as proof that there is no significant stress in the system.

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