SIZE-DEPENDENT ASYMMETRY: FLUCTUATING ASYMMETRY VERSUS ANTISYMMETRY AND ITS RELEVANCE TO CONDITION-DEPENDENT SIGNALING

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Abstract.—Fluctuating asymmetry (FA) has received much recent attention in studies of the evolution of sexual signaling systems. Tests apparently showing that symmetry decreases as individual condition decreases have bolstered the view that FA plays a significant role in the evolution of sexual signals. However, a closer inspection of several examples of bilateral variation as a function of trait size (a correlate of condition) suggests a different pattern of variation. Rather than FA, these traits suggest a pattern of size-dependent asymmetry (a bimodal frequency distribution of R−E). We introduce some quantitative methods to test for condition- or size-dependent FA. Our analyses reject pure FA for four of the five published datasets involving signals (the fifth is equivocal), but confirm the presence of size-dependent FA in one non-signaling trait. In the studies not conforming to FA, the data appear to fit more closely a pattern of antisymmetry in individuals with smaller signaling traits. Our results thus suggest that current discussions and conclusions about the role of FA in the evolution of signaling systems should be reconsidered. More specifically, we note that condition-dependent asymmetry offers a more reliable indicator than condition-dependent FA. We caution, however, that additional work will be needed to determine whether the pattern is general and not an artifact. Our method of analysis could usefully be applied to studies of other continuous factors expected to be correlated with asymmetries, including heterozygosity, inbreeding, and environmental stress. Finally, we suggest that antisymmetry may have commonly been mistaken for FA in a variety of cases dealing with a variety of problems.

Key words.—Quality, sexual selection, signaling, size-dependence

Received July 23, 1996. Accepted June 4, 1997.

Subtle deviations from bilateral symmetry continue to attract a great deal of attention as possible measures of individual condition, or quality, in studies of natural and sexual selection (reviews in Möller and Pomiankowski 1993; Watson and Thornhill 1994; Markow 1995; Palmer 1996). In most studies, patterns of asymmetry variation are believed to represent fluctuating asymmetry (FA). If deviations from perfect bilateral symmetry are caused by small, random disturbances of development (VanValen 1962), then the distribution of such deviations should exhibit a normal distribution of differences between sides, with a mean of zero (Palmer and Strobeck 1992). Where subtle bilateral variation meets these statistical criteria for FA, deviations from symmetry in individuals or classes of individuals have been used as an index of developmental precision (reviewed in Palmer, in press). Although a great many studies of subtle bilateral variation have revealed FA, some have also revealed subtle directional asymmetry or antisymmetry. The value of these alternative patterns of bilateral variation as measures of developmental precision, however, remains open to debate (Graham et al. 1993).

A key assumption of those studies employing deviations from symmetry as an index for developmental precision is to what extent do these deviations meet the criteria for FA? Moreover, these criteria must be met in each class of individuals that is meant to be contrasted in developmental precision, as indicated by the degree of FA in each class. Groups of individuals are typically classified by factors that are thought to affect developmental precision. For example, degree of heterozygosity, inbreeding, or environmental stress have all been hypothesized to affect developmental stability (reviewed in Palmer 1996). Here, one must test for FA in each class to be contrasted. If the division between classes is clear, such as in contrasts among populations, then one need only to apply simple tests to each class. However, in many studies one wishes to test within-sample hypotheses about the correlation between a continuous factor thought to affect developmental precision and deviations from symmetry. Here, samples represent a mix of presumed developmental precision classes, leading to a compound distribution, and there is no simple method for testing for patterns of FA within samples. A good illustration of this problem is provided in recent literature on the symmetry of sexually selected traits (Möller and Pomiankowski 1993; Watson and Thornhill 1994), and it is this literature that initially drew our attention to the problem of testing for FA when within-sample variance in developmental precision is the target of the study.

Sexually Selected Trait Size and Symmetry

Several correlative studies in different taxa suggest that mating success is biased toward more symmetrical males (Möller and Pomiankowski 1993; Watson and Thornhill 1994; but see, e.g., Markow and Ricklefs 1992; McLachlan and Cant 1995; Tomkins and Simmons 1995). These include studies of traits thought to be under sexual selection for exaggeration, independent of their symmetry. Because both exaggeration and symmetry of the trait are expected to correlate with condition, which trait is under direct sexual selection by female choice and which is merely correlated, remains unclear. However, experimental studies have shown that females are clearly capable of directly discriminating among males based on the symmetry of signaling traits (Möller 1992a, 1993a; Swaddle and Cuthill 1994a, b). Thus, strong evidence exists for female choice based on male symmetry. Analogous, but more sparse, evidence also suggests intra-

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sexual selection on male symmetry (e.g., Thornhill 1992; Radesäter and Halldorsson 1993).

Møller and Pomiankowski (1993) argued that asymmetry of costly, sexually selected traits should be negatively related to the degree of trait expression. Condition or quality, the underlying variable, is expected to positively affect trait expression and negatively affect asymmetry. Thus, through shared correlations of opposite sign, degree of exaggeration and asymmetry are expected to be negatively correlated. The positive correlation between condition (or quality) and degree of trait exaggeration is a general prediction from sexual selection theory and is well supported empirically (Price et al. 1993; Andersson 1994; Johnstone 1995). The negative relationship between trait size and asymmetry has recently been observed in traits that are subject to female choice (Møller 1990, 1992b; Manning and Hartley 1991; Møller and Hoglund 1991; Swaddle and Witter 1994). The pattern also appears in male traits thought to be under intrasexual selection (Radesater and Halldorsson 1993) and in floral signals (Møller and Eriksson 1994; Møller 1995). Thus, empirical support for Møller and Pomiankowski’s (1993) argument appears to be growing.

Scatter plots of \( S = \frac{R - T}{R + T} \) versus trait or body size can be most informative. A close inspection of such associations between asymmetry and trait size in sexually selected traits reveals that female choice is the most common in all size classes, though they would be proportionally less common among individuals with smaller traits (see Fig. 1 and discussion below). However, in all five datasets, asymmetry or nearly symmetrical individuals were conspicuously absent among individuals with smaller traits. Therefore, although the original studies concluded that the variation they reported was FA, their scatter plots suggest antisymmetry rather than FA.

The distinction between FA and antisymmetry has significant implications for both developmental process and sexual selection. Antisymmetry is characterized by a platykurtic or bimodal distribution of the signed differences of left and right, with a mean of zero (Van Valen 1962). Unfortunately, even with appropriate attention to statistical descriptors, weak antisymmetry can be extremely difficult to distinguish from FA without rather large sample sizes (Palmer and Strobeck, unpubl., manuscript, and see below). Furthermore, the developmental origins of antisymmetry may not be the same as those of FA (Van Valen 1962, Palmer and Strobeck 1992, Palmer 1996). Thus, antisymmetry may or may not be related to developmental precision. Each of the original studies reporting a correlation between trait size and asymmetry conducted a single test for FA in their sample. Yet, as discussed above, this is clearly inappropriate because samples are made up of a mix of developmental precision classes (assumed to be correlated with trait size) and it is these classes that are the focus of their studies.

Here we develop testable predictions about the dependence of asymmetry on trait size where patterns of asymmetry resemble either FA or antisymmetry. We introduce methods to distinguish these patterns, and apply them to several published datasets. Our analyses suggest that size-dependent asymmetries often do not vary in FA, as has been consistently asserted, but rather vary in the degree of antisymmetry. Finally, we comment upon the utility of symmetry as an indicator of male quality when variance in symmetry results from antisymmetry versus FA. Our approach will be useful for any within-sample tests of the effects of continuous factors on deviations from symmetry. These include most of those factors thought to affect or correlate with developmental precision (e.g., heterozygosity, inbreeding, environmental stress, and genetic quality).

**Expected Relations between FA, Antisymmetry, and Trait Size**

Theoretically, asymmetry is expected to be linked only indirectly to trait size. Instead, asymmetry is expected to be directly linked to condition, which is also directly linked to trait size (Møller and Pomiankowski 1993). However, independent measures of condition are rarely made and trait exaggeration and condition are typically correlated (see above). Therefore, trait size is used as a surrogate measure of condition in most studies. We will follow this practice in our analyses.

To determine whether asymmetry varies with trait size, measures of asymmetry are usually plotted against trait size or some other measure of body size. The most frequently used measure of asymmetry is the unsigned difference between left and right members of a bilateral trait (Palmer and Strobeck 1986). The scatter of points on these plots can be used to determine whether increases in asymmetry as trait size declines reflect increased FA or increased antisymmetry. If FA increases as trait size declines, the lower bound of a plot of asymmetry against trait size is flat (Fig. 1c). As FA increases, the distribution of differences between left and right traits broadens (Fig. 1a), as does the distribution of unsigned differences (Fig. 1c). Differences near zero are always most frequent (Fig. 1c), and hence the lower bound of a plot of asymmetry against trait size remains near zero at all values of trait size (Fig. 1e).

Alternatively, if antisymmetry increases as trait size declines, the lower bound of a plot of asymmetry against trait size increases as trait size declines (Fig. 1f). As trait size declines, the distribution of signed differences changes from a distribution indistinguishable from unimodal to a bimodal distribution and then becomes increasingly bimodal (Fig. 1b). The mode of the distribution of unsigned differences shifts away from zero (Fig. 1d). As it does so, differences near zero become rare, and eventually the lower bound of distribution also departs from zero (Fig. 1d). Hence, the lower bound in a scatter plot of asymmetry against trait size moves away from zero as trait size declines (Fig. 1f).

Hypotheses concerning pattern in lower bounds of scatter plots can be tested. One method is to divide a scatter plot
Fluctuating asymmetry  

Antisymmetry  

**Fig. 1.** Hypothetical examples depicting effects of increasing fluctuating asymmetry and antisymmetry on trait distributions. (a) Frequency distributions of signed differences between left and right expressions of traits resulting from increased fluctuating asymmetry. Solid curve (i) least fluctuating asymmetry; long-dashed curve (ii) greatest fluctuating asymmetry. (b) Frequency distributions of signed differences between left and right sides resulting from increased antisymmetry. Solid curve (i) least antisymmetry; long-dashed curve (ii) greatest antisymmetry. Frequency distributions of unsigned differences between left and right expressions of traits under increasing fluctuating asymmetry (c) and increasing antisymmetry (d). Curves come from the same distributions as the corresponding curves in (a) and (b). (c,e,f) Unsigned differences between left and right as functions of trait size (condition). Levels of asymmetry that correspond to levels depicted in upper panels are indicated by arrows. Solid curves reflect mean levels of asymmetry; dashed curves fifth percentiles of asymmetry. Data points were drawn at random from distributions of asymmetries appropriate for the levels of trait expression.

into right and left halves and then compare the lower bound of the distribution of the left side with that of the right side (Schluter and Reppasy 1991). Briefly, the difference between left and right lower bounds is calculated from the data. Variance of the difference between bounds can be estimated using bootstrap methods and then used to calculate the probability of observing a more extreme difference by chance under the null hypothesis that the difference between lower bounds of the sides is zero.

**Methods**

We tested for relationships in the lower bounds of published scatter plots of asymmetry and trait size in data from
six studies, including barn swallows (Møller 1990, 1992b),
earwigs (Radesäter and Haldorsdóttir 1993), peacocks (Man
ning and Harteley 1991), and flower petals (Møller and Eri
ksson 1994; Møller 1995). Scatter plots were scanned into
digital images, and data were digitized from images using 
DataThief (Huyser and van der Laan 1992). This method of 
collecting data was very reliable. We compared results of 
regression analyses from digitized data with those published 
in the original papers. For example, our calculations of slope, 
intercept, and $F$-statistic of data digitized from figure 1 in 
Møller (1990) agreed with published results to the third deci
mal place. In the case of Møller and Eriksson (1994, their 
fig., 1a), we could not distinguish every individual point. We 
distinguished every point that we could and then we filled in 
the black areas of the plot with data points until our sample 
size matched that of Møller and Eriksson. The standardized 
regression coefficient calculated from digitized data ($-0.64$) 
closely matched the published value of $-0.65$.

We used a bootstrap method to test whether the lower 
bound of scatter plots increase as trait size declined (Schluter 
and Repasky 1993). We divided each dataset into two using 
as a boundary the midpoint of the range of trait size, and we 
calculated the fifth percentile as a measure of the lower bound 
of the distribution of each subset. The fifth percentile of the 
right side of the graph was subtracted from that of the left 
side of the graph to estimate the difference in lower bounds. 
Variance in the difference between samples was estimated 
using a parametric bootstrap method. One thousand pairs of 
samples were drawn from smoothed frequency distributions 
of the left and right datasets. We resampled from estimated 
distributions rather than from the original data because re-
sampling from original data produces poor estimates of vari-
ation in extreme values of distributions (Efron and Tibashirani 
1993). We used smoothed frequency distributions rather than 
normal distributions of estimated mean and variance because 
frequency distributions of unsigned differences differ mark-
edly from normal (Fig. 1c,d). Frequency distributions were 
smoothed by fitting nonparametric probability density func-
tions (Silverman 1986) to them using function density in the 
S language (Becker et al. 1988), at the default value of the 
smoothing parameter. We calculated the fifth percentile of 
each sample and calculated the difference between the lower 
bounds of each pair of samples. The relative frequency of 
resampled differences less than zero approximates the prob-
ability of observing the actual difference between lower 
bounds under the null hypothesis (Schluter and Repasky 

This test is conservative. To be detected, antisymmetry 
must be so pronounced that the lower bound of the distri-
bution of unsigned differences departs from zero as asym-
metry increases. Also, the lower bound of the distribution 
must depart from zero near the midpoint of the range of values 
of trait expression so that the lower bound of the left-hand 
subset of data will be greater than that of the right-hand 
subset. Hence, this test will fail to detect increases in anti-
symmetry in datasets in which changes in antisymmetry are 
subtle, or in cases where bimodality appears only in the small-
est trait classes. However, we found this method to be more 
powerful than tests of other possible predictions. For ex-
ample, one testable prediction about FA is that the mean value 
of unsigned residuals from a linear regression of unsigned 
assymmetry against trait expression (e.g., data in Fig. 1c) 
increases as expression declines, whereas changes in un-
signed residuals under antisymmetry (e.g., data in Fig. 1f) 
should be subtle or absent. This test has been used in anal-
ogous analyses of the shape of scatter plots (e.g., Aronvist 
et al. 1996). Unfortunately, with this test the probability of 
detecting changes in mean unsigned residuals of the magni-
itude of the data depicted in Figure 1c (FA) is only 0.06.

**Results**

Only one of the datasets examined clearly supported the 
hypothesis that increases in asymmetry that occur as trait 
size declines reflect increases in FA. The lower bound of the 
distribution of forces in earwigs (Radesäter and Haldorsdóttir 
1993) remained near zero over all values of trait size (Fig. 2a). 
The difference between the lower bounds of the left and right 
sides of the graph was zero, and the probability of observing a 
more extreme result by chance under the hypothesis that the 
lower bound remains constant was 0.999.

Two datasets yielded more equivocal test results. Too few 
observations were available to estimate the fifth percentile 
of asymmetry in Epilobium angustifolium petals (Møller 
1995; our Fig. 2b). If the minimum value of each subset is 
used as the lower bound, results of the test depend on 
the presence of an extreme value in the dataset. The test is 
significant if the point at 12.5-mm petal length is present ($P < 
0.001$) and nonsignificant if that point is omitted ($P = 0.650$). 
Visually, there are only three observations of petals less than 
4.5 mm in length, and although all of these are well above 
zero, there are too few observations of small petals to draw 
a reasonable conclusion. The difference between lower 
bounds was not significant for a second dataset of flower 
lengths petals, Erica vasculosa (Møller and Eriksson 1994; 
our Fig. 2c, $P = 0.362$). The lower bound of the distribution 
of unsigned differences appears to depart from zero but well 
left of the midpoint of the range of trait expression. Visually, 
this dataset is much more consistent with the hypothesis of 
antisymmetry than it is with FA. Once the lower bound de-
parts from zero at 7.4, none of the smaller 12 observations 
is anywhere near zero.

Variation in asymmetry in the three remaining datasets was 
clearly more consistent with patterns expected if antisym-
mmetry varies with trait size. Lower bounds of the distributions 
of asymmetry clearly increase as trait size declines (Fig. 2a-f). 
Differences in the lower bounds of the two barn swallow 
datasets were significantly different from zero (barn swallows, 
$1; P = 0.039$; barn swallows, $2; P = 0.016$). Too few 
observations of peacock train symmetry were available to use 
the fifth percentile as a measure of the lower bound of 
antisymmetry in train length, but if one were to use the 
minimum value on each side of the graph as the lower bounds, 
the probability of a more extreme result under the null hypothesis 
is less than 0.001. The peacock data are remarkable in that 
very few values of symmetry are near zero anywhere on the 
graph, suggesting that symmetrical trains appear to be rare 
even among males with the largest trait sizes.

These results highlight difficulties in testing for asymmetry
in samples. For example, a common procedure to test for FA is to use a goodness-of-fit test to evaluate the null hypothesis that a sample of signed differences comes from a normal distribution. FA is expected to be normally distributed with a mean of zero. Normal distributions are not expected in traits exhibiting antisymmetry, size-dependent (or condition-dependent) FA, or size-dependent antisymmetry. Samples from populations in which FA is size-dependent are expected to be leptokurtic, whereas samples from populations in which antisymmetry is size-dependent are expected to be platykurtic (Houle 1997; see also Wright 1968). Notably, simple predictions about kurtosis in more complex compound distributions, such as those including both normal and platykurtic components, are unlikely. The original investigators performed single-sample tests for normality on signed values before pursuing their analyses in five of the six studies that we examined. None detected significant departures from normality, and yet our results indicate that at least five of the cases should have detected departures from normality.

When considering kurtosis statistics for the entire dataset
from each study (Table 1), only two differed significantly from zero (Radesäter and Halldorsson 1993; Moller and Eriksson 1994), and both of these deviated in the direction of leptokurtosis, even though antisymmetry was suggested at smaller trait size in Moller and Eriksson (1994). Interestingly, Radesäter and Halldorsson (1993) reported that the distribution of earwig forceps asymmetry was leptokurtic, but the test that they employed failed to detect a departure from normality. In addition, although our analyses revealed that platykurtosis (antisymmetry) was significant at smaller trait size in (Moller 1990, 1992; Manning and Hartley 1991), the kurtosis estimates for the pooled samples did not differ significantly from zero (Table 1). Therefore, kurtosis statistics computed on pooled samples (compound distributions) whose underlying variation is heterogenous may yield misleading conclusions about presence or absence of departures from normality.

In conclusion, we suggest that visual inspection of datasets may be more powerful than statistical tests for initial detection of departures from FA. Moreover, we also provide a rigorous statistical test for such departures.

**Discussion**

Our analyses reveal a deficit of symmetrical or nearly symmetrical individuals in small size classes in five of the six studies we reanalyzed, where the degree of asymmetry was reported to be a decreasing function of trait size. Contrary to claims of the original authors of these studies, such a deficit is not consistent with the pattern expected of size-dependent FA. It is, however, consistent with the pattern expected of size-dependent antisymmetry. In the following sections, we suggest that antisymmetry may be much more common than previously believed. We then discuss the implications of our results for current ideas about symmetry as an indicator of condition. Some of our discussion assumes that the degree of exaggeration (size) of a sexually selected trait is correlated with individual condition. This is a well supported assumption in general (Price et al. 1993; Andersson 1994; Johnstone 1995), and specifically in the traits that we studied here (tails, Moller 1994; forceps, Radesäter and Halldorsson 1993). We note that condition-dependent antisymmetry offers significant advantages over condition-dependent FA as a signal, because it reveals condition more reliably to the receiver. Finally, we discuss the general problem of assessing within-sample hypotheses about asymmetry.

**Presence of Antisymmetry**

Two alternative hypotheses might account for the absence of symmetrical individuals with reduced trait expression. First, as suggested by Houle (1997), symmetry might directly affect condition, which could in turn affect trait expression. This seems unlikely in the cases we examined since, for example, tail length is determined at the same time as tail symmetry during molting, and therefore seems unlikely to affect condition in a way that could in turn affect symmetry. Second, symmetric individuals with reduced trait expression may have been lost from the population. Inspection of the data suggests that selection against these individuals would have to be complete in these samples to yield the patterns reported. Furthermore, although antisymmetry appears costly for some traits (e.g., Moller 1991; Balmford and Thomas 1992; Balmford et al. 1993; Evans and Hatchwell 1993; Thomas 1993), individuals expressing reduced but symmetrical traits seem the least likely to pay such costs.

Our reanalysis suggests antisymmetry may be more widespread than currently appreciated. Four decades ago, Mather (1953) showed that selection on a FA-like distribution resulted in an antisymmetry-like distribution, and the increased asymmetry associated with a pesticide resistance allele in blowflies (Clarke and McKenzie 1987) is clearly antisymmetry (McKenzie and Clarke 1988). Graham et al. (1993), arguing from a model of reaction-diffusion dynamics, suggest that any deviation from symmetry (FA, directional asymmetry, or antisymmetry) could arise from a lack of buffering capacity during development. Finally, because weak antisymmetry is exceedingly difficult to distinguish from FA (Palmer and Strobeck, unpublished manuscript; see above), many of the previous studies showing a relationship between genetic or environmental disturbance and symmetry, may have mistaken antisymmetry for FA.

**Condition-Dependent Antisymmetry in Signaling Traits**

If antisymmetry correlates with quality, as suggested above, then it is a reasonable target for sexual selection. Indeed, condition-dependent antisymmetry may offer a more reliable alternative to condition-dependent FA for signaling traits. Trait size was correlated with individual asymmetry in all six studies reviewed above. These correlations support the common view that asymmetry increases as individual condition decreases (reviews in, Hill 1995; Markow 1995; Polak, in press). However, since five of the six studies show a pattern consistent with antisymmetry, perhaps it is the level of antisymmetry rather than FA that reveals individual condition. This is not a commonly held view.

Antisymmetry is usually viewed as functionally significant (Van Valen 1962; Palmer and Strobeck 1992) or the outcome of a developmental process involving factors other than simple stochastic developmental noise. For example, in male fiddler crabs, where chelipeds typically exhibit striking antisymmetry (Jones and George 1982) and where claw signaling has a major impact on mating success (Crane 1975), sexual selection appears to have amplified symmetry rather
than symmetry. Significantly, in the five studies reviewed above where patterns were more consistent with condition-dependent asymmetry than condition-dependent FA, the traits examined all act as signals. In the only case where size-dependent FA was confirmed, it was in a trait (forces of earwigs) apparently under sexual selection by male-male competition rather than in a signal (Radesäter and Halldorsdóttir 1993; but see Tomkins and Simmons 1995).

We note that traits exhibiting condition-dependent anti-symmetry should actually be more reliable indicators of male condition than those exhibiting condition-dependent FA. In condition-dependent asymmetry, symmetrical individuals are rare in classes of individuals in poor condition (Fig. 1d), whereas for condition-dependent FA symmetrical individuals should be most common in all condition classes (Fig. 1c). Hence, females that choose symmetric mates on the basis of traits that are subject to condition-dependent asymmetry are more likely to obtain high quality mates than females that choose on the basis of traits that are subject to condition-dependent FA. The advantage remains whether females favor symmetric individuals, or discriminate against asymmetric individuals.

There is only one alternative to our conclusion of condition-dependent asymmetry, and that is that much of these data are somehow biased. Challenges facing those wishing to study patterns of subtle bilateral variation are numerous (Palmer 1994; see also Swaddle et al. 1994). Given the small magnitude of FA variation (often less than 1% of trait size; Palmer, in press), bilateral differences may easily be confounded by other factors including (1) imprecise measurement; (2) unconscious or conscious bias; and (3) subtle wear or breakage. However, since imprecise measurement, even if size dependent, introduces only random errors, it should merely amplify apparent FA (Palmer and Strobeck 1986), not create antisymmetry. Unfortunately, none of the authors report blind, repeat measurements of both small and large individuals, so this error cannot be judged. Conscious or random measurement bias could potentially yield antisymmetry. Since scatter plots are presented for only one of 10 sites in Møller (1995), and for only one of 19 species in Møller and Eriksson (1994), we cannot judge how representative the patterns of size-dependent flower asymmetry actually are. Finally, although birds with conspicuously damaged feathers were presumably excluded (unfortunately, neither Møller 1990, 1992 nor Manning and Hartley 1991 state this explicitly) as were "withered or damaged flowers" (Møller 1995; Møller and Eriksson 1994), it is unclear to us how the authors could have avoided individuals exhibiting subtle wear not apparent at the time of measurement.

Within-Sample Heterogeneity

Most natural populations of organisms represent a mixture of individuals of different genotypes or individuals from different growth environments. Statistical conclusions about properties of the entire heterogeneous population may differ from those about identifiable subsamples within the combined population. Consider, for example, a mixture of two groups of individuals where one group experienced high stress during development and thus exhibits high FA and the other group developed under "optimal" conditions and thus exhibits low FA. Each group considered by itself would exhibit bilateral variation indistinguishable from FA. However, the two groups pooled together, if of equal sample size and sufficiently different level of FA, would yield a pooled sample that departed from ideal FA in the direction of leptokurtosis (a narrow-peaked, long-tailed distribution; Wright 1968, Palmer and Strobeck 1992). Similarly, consider a mixture of two groups where, for some reason, one group exhibited weak antisymmetry and the other exhibited pure FA. The two groups pooled together, if of equal size and comparable variance of right-left differences, may yield a pooled sample that might not be distinguishable statistically from ideal FA (Palmer and Strobeck 1992). To avoid inappropriate statistical conclusions about the form of bilateral variation, tests for departures from ideal FA should be conducted on groups that are as homogeneous as possible. We have suggested one way in which to test for size-dependent FA or antisymmetry.

In conclusion, our analyses suggest that condition-dependent asymmetry occurs in signaling traits. We argue that females should prefer traits exhibiting condition-dependent asymmetry, over those exhibiting condition-dependent FA, because the former offers a more reliable signal of underlying condition. Clearly, cases of condition-dependent asymmetry must be analyzed carefully before concluding that the variation represents either FA or antisymmetry. Experimental demonstrations of preference for symmetry, and correlations between degree of asymmetry and trait size, offer no help in distinguishing antisymmetry from FA because they do not identify the underlying distributions of asymmetry. Even when tests on distributions are undertaken, antisymmetry may easily be mistaken for FA. Scatter plots of (R - L) or |R - L| versus trait size or other presumed correlates of asymmetry are perhaps the most informative.

Acknowledgments

We thank B. Montgomery for Data Thief; M. Adamson for logistical support; and J. Graham, D. Houle, J. Justus, L. Leamy, and A. Moore for comments on the manuscript. This research was supported by operating grants to LR and to ARP from the Natural Sciences and Engineering Research Council of Canada.

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HOYER, K., and J. VAN DER LAAN. 1992. DataTheft: Vers. 1.0.8. Electronically published by the authors and available via E-mail from kees1@paramount.nikhefs.nl, kim@paramount.nikhefs.nl, or by anonymous ftp from sun4.nl.


Corresponding Editor: L. Leamy