

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

LOCKE ROWE,^{1,2} RICHARD R. REPASKY,¹ AND A. RICHARD PALMER³

¹Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada

²E-mail: lrowe@zoo.toronto.edu

³Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

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 antisymmetry (a bimodal frequency distribution of $R - L$). 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 nonsignaling 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 antisymmetry 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 Møller 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 (Møller 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 (Møller and Pomiankowski 1993; Watson and Thornhill 1994; but see, e.g., Markow and Ricker 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 (Møller 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-

sexual selection on male symmetry (e.g., Thornhill 1992; Radesäter and Halldórsdóttir 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,c; Manning and Hartley 1991; Møller and Höglund 1991; Swaddle and Witter 1994). The pattern also appears in male traits thought to be under intrasexual selection (Radesäter and Halldórsdóttir 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 $(R - L)$ or $|R - L|$ versus trait or body size can be most informative. A close inspection of such associations between asymmetry and trait size in sexually selected tail feathers (Møller 1990, 1992b; Manning and Hartley 1991) and flower petals (Møller and Eriksson 1994; Møller 1995) suggests a pattern not consistent with that expected if bilateral variation were FA. Houle (1997) and Palmer and Strobeck (1997) note that the reported decline in asymmetry with increasing trait size in some cases appears to reflect declines in antisymmetry rather than FA. In particular, if variation among individuals in their degree of symmetry reflects FA, then symmetrical or nearly symmetrical individuals should be 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, symmetrical 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 (VanValen 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 (VanValen 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 symmetry 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 resembles 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. 1e). 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

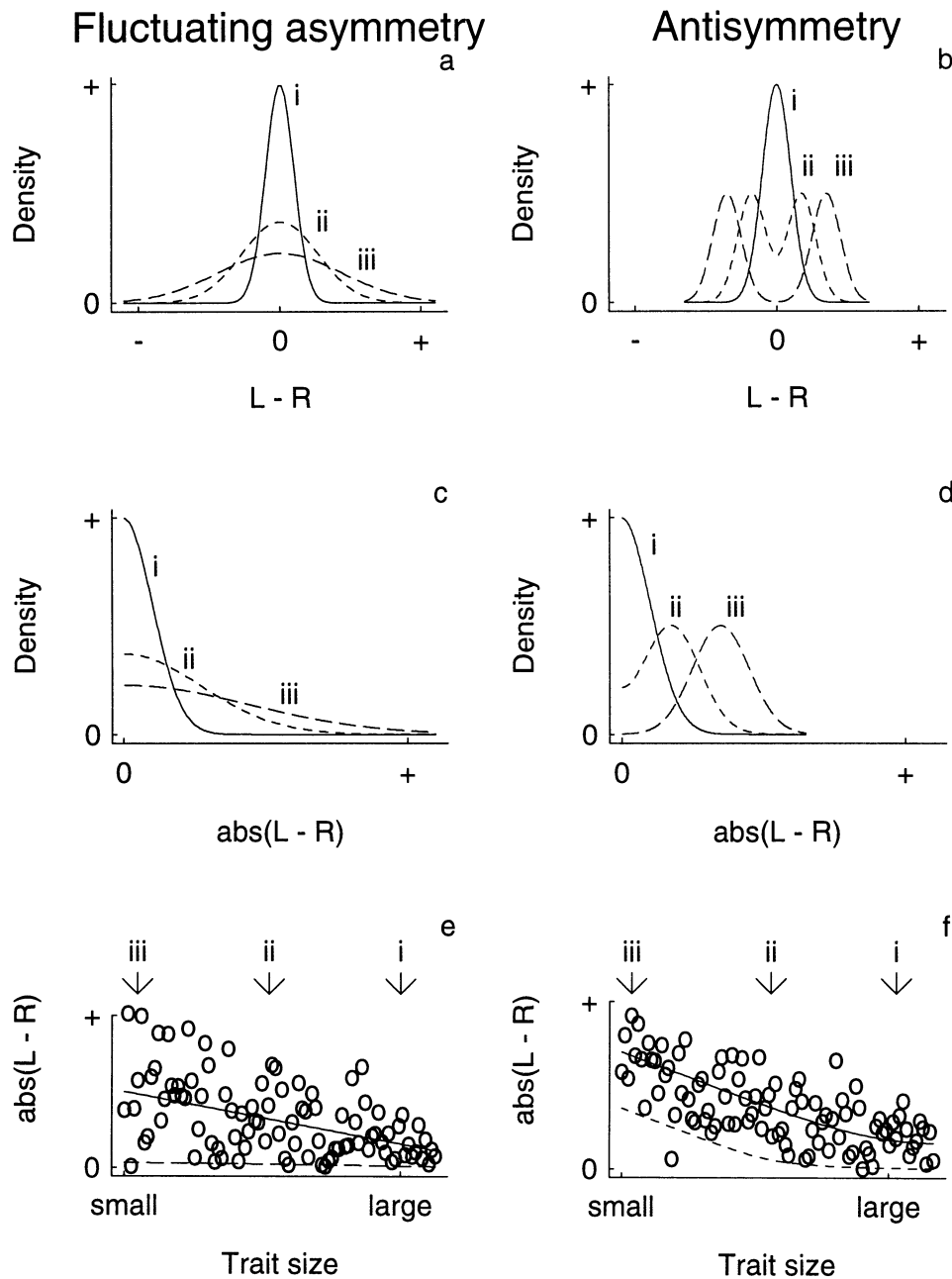


FIG. 1. Hypothetical examples depicting effects of increasing fluctuating asymmetry and antisymmetry on trait distributions. (a) Frequency distributions of signed differences between left and right expressions of traits resulting from increased fluctuating asymmetry. Solid curve (i) least fluctuating asymmetry; long-dashed curve greatest (iii) 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 (iii) 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). (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 Repasky 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 Halldórsdóttir 1993), peacocks (Manning and Hartley 1991), and flower petals (Møller and Eriksson 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 decimal 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 bounds of scatter plots increase as trait size declined (Schluter and Repasky 1991). 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 resampling from original data produces poor estimates of variation in extreme values of distributions (Efron and Tibshirani 1993). We used smoothed frequency distributions rather than normal distributions of estimated mean and variance because frequency distributions of unsigned differences differ markedly from normal (Fig. 1c,d). Frequency distributions were smoothed by fitting nonparametric probability density functions (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 probability of observing the actual difference between lower bounds under the null hypothesis (Schluter and Repasky 1991).

This test is conservative. To be detected, antisymmetry must be so pronounced that the lower bound of the distribution of unsigned differences departs from zero as asymmetry 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 antisymmetry in datasets in which changes in antisymmetry are subtle, or in cases where bimodality appears only in the smallest trait classes. However, we found this method to be more powerful than tests of other possible predictions. For example, one testable prediction about FA is that the mean value

of unsigned residuals from a linear regression of unsigned asymmetry against trait expression (e.g., data in Fig. 1e) increases as expression declines, whereas changes in unsigned residuals under antisymmetry (e.g., data in Fig. 1f) should be subtle or absent. This test has been used in analogous analyses of the shape of scatter plots (e.g., Arnqvist et al. 1996). Unfortunately, with this test the probability of detecting changes in mean unsigned residuals of the magnitude of the data depicted in Figure 1e (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 forceps asymmetry in earwigs (Radesäter and Halldórsdóttir 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 14.5 mm in length, and although all of those 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, *Eruca vesicaria* (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 departs 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 antisymmetry varies with trait size. Lower bounds of the distributions of asymmetry clearly increase as trait size declines (Fig. 2d–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 asymmetry were available to use the fifth percentile as a measure of the lower bound of asymmetry 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

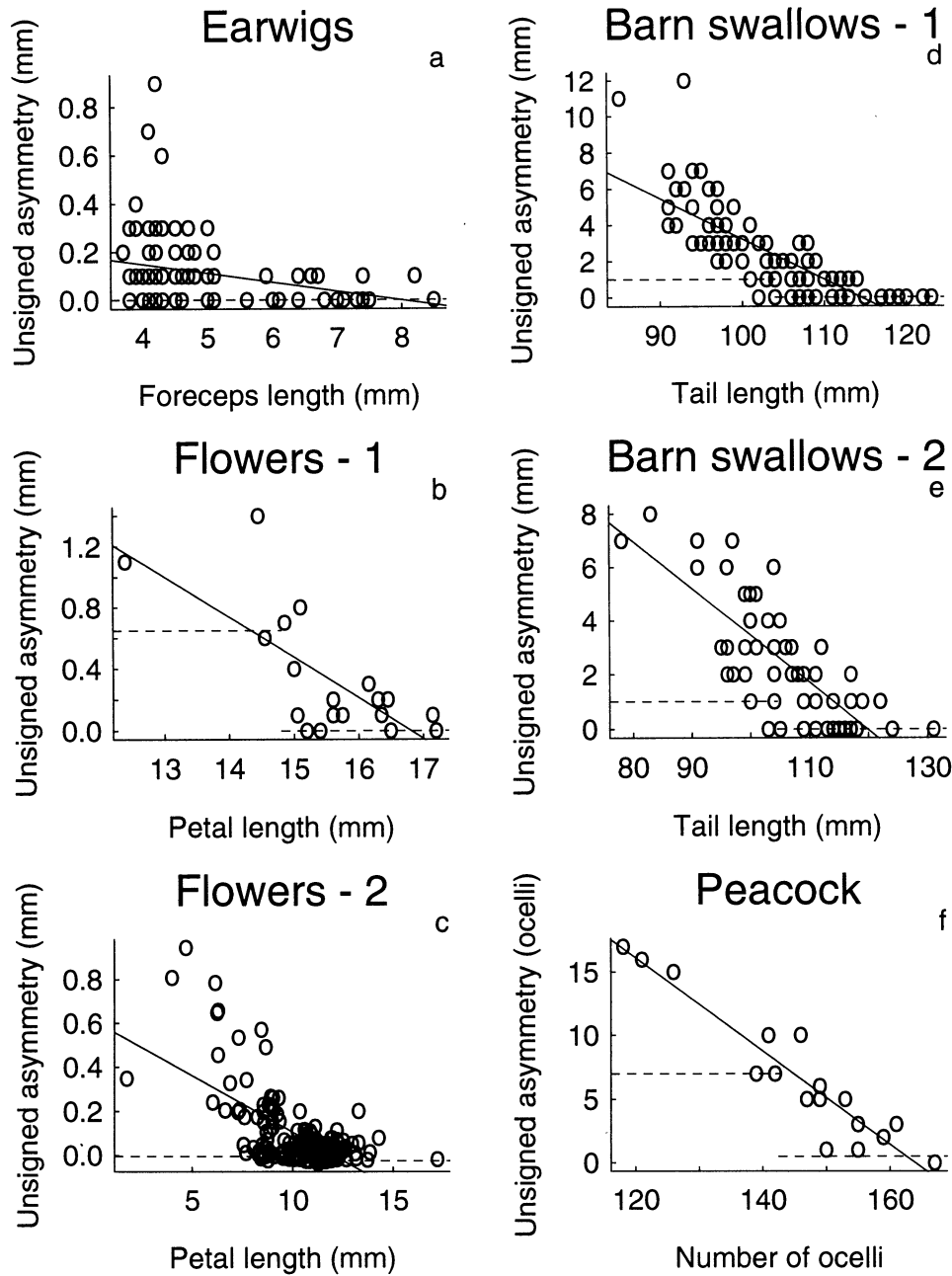


FIG. 2. Scatter plots of unsigned measures of asymmetry and mean trait expression. Solid lines were fit by least squares linear regression. Dashed lines represent fifth percentiles of the observations encompassed by their lengths. Percentiles were interpolated using function quantile in the S language (see Becker et al. 1988). Sources: (a) figure 1 in Radesäter and Halldórsdóttir (1993); (b) figure 2 in Møller (1995); (c) figure 1a in Møller and Eriksson (1994); (d) figure 1 in Møller (1990); (e) figure 2a in Møller (1992); (f) figure 1 in Manning and Hartley (1991).

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

TABLE 1. Summary statistics of symmetry data presented in Figure 2. Standard errors of kurtosis were calculated from 200 bootstrap samples, which yield unbiased estimates, whereas traditional estimates (e.g., Sokal and Rohlf 1981) are extremely conservative. Negative values of kurtosis indicate platykurtosis (e.g., antisymmetry) whereas positive values indicate leptokurtosis.

Data set	n	Mean (SE)	Kurtosis (SE)
		L - R	L - R
Radesäter and Halldórsdóttir 1993	127	0.12 (0.01)	6.0 (2.5)
Møller 1995	19	0.34 (0.09)	1.5 (1.3)
Møller and Eriksson 1994	156	0.09 (0.01)	8.3 (2.2)
Møller 1990	96	2.31 (0.24)	1.9 (1.0)
Møller 1992	60	2.57 (0.30)	-0.1 (0.4)
Manning and Hartley 1991	17	6.65 (1.29)	-0.3 (0.5)

from each study (Table 1), only two differed significantly from zero (Radesäter and Halldórsdóttir 1993; Møller and Eriksson 1994), and both of these deviated in the direction of leptokurtosis, even though antisymmetry was suggested at smaller trait size in Møller and Eriksson (1994). Interestingly, Radesäter and Halldórsdóttir (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 (Møller 1990, 1992b; 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 heterogeneous 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, Møller 1994; petals, Møller 1995; forceps, Radesäter and Halldórsdóttir 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 prob-

lem of assessing within-sample hypotheses about asymmetries.

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 asymmetry appears costly for some traits (e.g., Møller 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, unpubl. manuscript; and 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 (VanValen 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 asymmetry rather

than symmetry. Significantly, in the five studies reviewed above where patterns were more consistent with condition-dependent antisymmetry 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 (forceps of earwigs) apparently under sexual selection by male-male competition rather than in a signal (Radesäter and Halldórsdóttir 1993; but see Tomkins and Simmons 1995).

We note that traits exhibiting condition-dependent antisymmetry should actually be more reliable indicators of male condition than those exhibiting condition-dependent FA. In condition-dependent antisymmetry, 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 antisymmetry 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 antisymmetry, 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 non-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 antisymmetry 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 antisymmetry occurs in signaling traits. We argue that females should prefer traits exhibiting condition-dependent antisymmetry, 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. Montgomerie 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.

LITERATURE CITED

- ANDERSSON, M. 1994. *Sexual selection*. Princeton Univ. Press, Princeton, NJ.
- ARNQVIST, G., L. ROWE, J. J. KRUPA, AND A. SIH. 1996. Assortative mating by size: a meta-analysis of mating patterns in water striders. *Evol. Ecol.* 10:265–284
- BALMFORD, A., AND A. L. R. THOMAS. 1992. Swallowing ornament asymmetry. *Nature* 359:487
- BALMFORD, A., I. L. JONES, AND A. L. R. THOMAS. 1993. On avian asymmetry: Evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. B Biol. Sci.* 252:245–251.
- BECKER, R. A., J. M. CHAMBERS, AND A. R. WILKS. 1988. *The new S languages*. Wadsworth and Brooks/Cole Advanced Books and Software, Pacific Grove, CA.
- CLARKE, G. M., AND J. A. MCKENZIE. 1987. Developmental stability of insecticide resistant phenotypes in blowfly: a result of canalizing natural selection. *Nature* 325:345–346.

- CRANE, J. 1975. Fiddler crabs of the world. Ocypodidae: genus *Uca*. Princeton Univ. Press, Princeton, NJ
- EFRON, B., AND R. J. TIBSHIRANI. 1993. An introduction to the bootstrap. Chapman and Hall, New York.
- EVANS, M. R., AND B. J. HATCHWELL. 1993. New slants on ornamental asymmetry. *Proc. R. Soc. Lond. B Biol. Sci.* 251:171–177.
- GRAHAM, J. H., D. C. FREEMAN, AND J. M. EMLÉN. 1993. Antisymmetry, directional asymmetry, and dynamic morphogenesis. *Genetica* 89:121–137.
- HILL, G. E. 1995. Ornamental traits as indicators of environmental health. *BioScience* 45:25–31.
- HOULE, D. 1997. Comment on "A meta-analysis of the heritability of developmental stability." *J. Evol. Biol.* 10:17–20.
- HUYSER, K., AND J. VAN DER LAAN. 1992. DataThief. Vers. 1.0.8. Electronically published by the authors and available via E-mail from keeshu@paramount.nikhef.nikhef.nl, jan@paramount.nikhef.nikhef.nl, or by anonymous ftp from sun4nl.nl.
- JOHNSTONE, R. A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol. Rev.* 70:1–65.
- JONES, D. S., AND R. W. GEORGE. 1982. Handedness in fiddler crabs as an aid in taxonomic grouping of the genus *Uca* (Decapoda: Ocypodidae). *Crustaceana* 43:100–102.
- MANNING, J. T., AND M. A. HARTLEY. 1991. Symmetry and ornamentation are correlated in the peacock's train. *Anim. Behav.* 42:1020–1021.
- MARKOW, T. A. 1995. Evolutionary ecology and developmental stability. *Annu. Rev. Entomol.* 40:105–120.
- MARKOW, T. A., AND J. P. RICKER. 1992. Male size, developmental stability, and mating success in natural populations of three *Drosophila* species. *Heredity* 69:122–127.
- MATHER, K. 1953. Genetical control of stability in development. *Heredity* 7:297–336.
- McKENZIE, J. A., AND G. M. CLARKE. 1988. Diazinon resistance, fluctuating asymmetry and fitness in the Australian sheep blowfly, *Lucilia cuprina*. *Genetics* 120:213–220.
- McLACHLAN, A., AND M. CANT. 1995. Small males are more symmetrical: Mating success in the midge *Chironomus plumosus* L. (Diptera: Chironomidae). *Anim. Behav.* 50:841–846.
- MØLLER, A. P. 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* 40:1185–1187.
- . 1991. Sexual ornament size and the cost of fluctuating asymmetry. *Proc. R. Soc. Lond. B Biol. Sci.* 243:59–62.
- . 1992a. Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238–240.
- . 1992b. Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characters. *J. Evol. Biol.* 5:691–699.
- . 1992c. Patterns of fluctuating asymmetry in weapons: evidence for reliable signalling of quality in beetle horns and bird spurs. *Proc. R. Soc. Lond. B Biol. Sci.* 248:199–206.
- . 1993a. Female preference for apparently symmetrical male sexual in plants. *J. Evol. Biol.* 7:97–113.
- . 1994. Sexual selection and the barn swallow. Oxford Univ. Press, Oxford.
- . 1995. Bumblebee preference for symmetrical flowers. *Proc. Nat. Acad. Sci.* 92:2288–2292.
- . 1996. Sexual selection, viability selection, and developmental stability in the domestic fly *Musca domestica*. *Evolution* 50:746–752.
- MØLLER, A. P., AND M. ERIKSSON. 1994. Patterns of fluctuating asymmetry in flowers: implications for sexual selection in plants. *J. Evol. Biol.* 7:97–113.
- MØLLER, A. P., AND J. HÖGLUND. 1991. Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond. B Biol. Sci.* 245:1–5.
- MØLLER, A. P., AND A. POMIANKOWSKI. 1993. Fluctuating asymmetry and sexual selection. *Genetica* 89:267–279.
- PALMER, A. R. 1994. Fluctuating asymmetry analyses: a primer. Pp. 335–364 in T. A. Markow, ed. *Developmental instability: its origins and evolutionary implications*. Kluwer, Dordrecht, Netherlands.
- PALMER, A. R. 1996. Waltzing with asymmetry. *BioScience* 46:518–532.
- PALMER, A. R., AND C. STROBECK. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* 17:391–421.
- . 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zool. Fenn.* 191:57–72.
- . 1997. Fluctuating asymmetry and developmental stability: heritability of observable variation vs. heritability of inferred cause. *J. Evol. Biol.* 10:39–43.
- POLAK, M. In press. Parasites, fluctuating asymmetry and sexual selection. In N. Beckage, ed. *Parasites: effects on host hormones and behavior*. Chapman and Hall, New York.
- PRICE, T., D. SCHLUTER, AND N. E. HECKMAN. 1993. Sexual selection when the female directly benefits. *Biol. J. Linn. Soc.* 48:187–211.
- RADESÁTER, T., AND H. HALLDÓRSDÓTTIR. 1993. Fluctuating asymmetry and forceps size in earwigs, *Forficula auricularia*. *Anim. Behav.* 45:626–628.
- SCHLUTER, D., AND R. R. REPASKY. 1991. Worldwide limitation of finch densities by food and other factors. *Ecology* 72:1763–1774.
- SILVERMAN, D. B. 1986. Density estimation for statistics and data analysis. Chapman and Hall, New York.
- SWADDLE, J. P., AND I. C. CUTHILL. 1994a. Preference for symmetric males by female zebra finches. *Nature* 367:165–166.
- . 1994b. Female zebra finches prefer males with symmetrical chest plumage. *Proc. R. Soc. Lond. B Biol. Sci.* 258:267–271.
- SWADDLE, J. P., AND M. S. WITTER. 1994. Food, feathers and fluctuating asymmetries. *Proc. R. Soc. Lond. B Biol. Sci.* 255:147–152.
- SWADDLE, J. P., M. S. WITTER, AND I. C. CUTHILL. 1994. The analysis of fluctuating asymmetry. *Anim. Behav.* 48:986–989.
- THOMAS, A. L. R. 1993. The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond. B Biol. Sci.* 254:181–189.
- THORNHILL, R. 1992. Fluctuating asymmetry and the mating system of the Japanese scorpionfly, *Panorpa japonica*. *Anim. Behav.* 44:867–879.
- TOMKINS, J. L., AND L. W. SIMMONS. 1995. Patterns of fluctuating asymmetry in earwig forceps: no evidence for reliable signalling. *Proc. R. Soc. Lond. B Biol. Sci.* 259:89–96.
- VAN VALEN, L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125–142.
- WATSON, P. J., AND R. THORNHILL. 1994. Fluctuating asymmetry and sexual selection. *Trends Ecol. Evol.* 9:21–25.
- WRIGHT, S. 1968. *Evolution and the genetics of populations*. Vol. 1. Genetics and biometrical foundations. Univ. of Chicago Press, Chicago.

Corresponding Editor: L. Leamy