
Fluctuating Asymmetry, Animal Behavior, and Evolution

JOHN P. SWADDLE

BIOLOGY DEPARTMENT
COLLEGE OF WILLIAM & MARY
WILLIAMSBURG, VIRGINIA 23187

I. WHAT IS FLUCTUATING ASYMMETRY AND WHY IS IT INTERESTING?

Fluctuating asymmetry refers to small deviations from a prior expectation of symmetric development in morphological traits (Ludwig, 1932). Across a population, signed asymmetries (i.e., signed difference between left and right sides) tend to show a normal (or leptokurtic) distribution where the mean is zero (i.e., symmetry) and individuals with relatively large asymmetries are rare. These morphological asymmetries are hypothesized to result from imperfect development, and are thought to reflect the inability of the genome to buffer developmental processes against intrinsic, random noise (Ludwig, 1932; Waddington, 1957; Zakharov, 1992). There are many genetic and environmental factors that can disrupt developmental stability and increase noise and asymmetry (review in Møller and Swaddle, 1997). However, the response of asymmetry to stressors appears to be taxon and trait specific (Leung and Forbes, 1996) because, in the traits of some species, fluctuating asymmetry does not appear to be affected even by severe, mortality-inducing stresses (Bjorksten *et al.*, 2001). It is therefore clear that the relationship between asymmetry and genetic and environmental stresses is not straightforward: asymmetry in one trait may result from different stressors than asymmetry in another trait.

Despite the lack of generality of such responses to stress, fluctuating asymmetry has often been used as an indicator of developmental instability (reviews in Clarke *et al.*, 1986; Parsons, 1992; Møller and Swaddle, 1997). Developmental stability is most commonly defined as the production of a predicted phenotype from a specified genotype in a particular environmental setting (Zakharov, 1992). Developmental instability reflects the

inability of the genome and developmental pathways to suppress random noise during development (Palmer and Strobeck, 1986; Zakharov, 1992). Therefore, to assess developmental instability a way of recording the degree of noise associated with development needs to be devised. As fluctuating asymmetry indicates the population variance around expected symmetric development, many researchers have proposed that fluctuating asymmetry is a strong candidate for assessing developmental instability (Mather, 1953; Clarke *et al.*, 1986; Zakharov, 1992). The strongest empirical evidence for developmental instability as a cause of fluctuating asymmetry comes from studies of the ability of single genotypes to resist perturbations at different magnitudes of environmental stress (Rettig *et al.*, 1997; Swaddle and Witter, 1998; Shykoff and Møller, 1999). However, such experiments do not always reveal genetically related responses to stress (e.g., Perfectti and Camacho, 1999; Andalo *et al.*, 2000). This topic is treated in more detail in Section IV.A.

If fluctuating asymmetry does reflect developmental instability, it is possible that phenotypic asymmetry can reveal information about the fitness of populations (Jones, 1987) and individual quality (Møller, 1990). To this end, many behavioral ecologists have tried to describe and understand the possible relationships between fluctuating asymmetry and fitness indicators (as briefly reviewed in Section II). The increased interest in fluctuating asymmetry–fitness relations has inspired a wide range of evolutionary biologists to focus attention on fluctuating asymmetry. Studies have begun to elucidate the genetic and developmental origins of these small asymmetries. By marrying the interest in fitness associations and the origins of fluctuating asymmetry, we have started to understand the evolutionary potential and importance of these small developmental asymmetries in both a behavioral and evolutionary context.

Although interest in fluctuating asymmetry has become intense (more than 200 studies of fluctuating asymmetry are indexed in *Web of Science* (<http://www.isinet.com/isi/products/citation/wos>) for the period January 1 to September 1, 2001), there is a general feeling that our level of understanding has not progressed at the same pace (Palmer, 1996b; Markow and Clarke, 1997; Møller and Swaddle, 1997; Houle, 1998; Van Dongen *et al.*, 2001). This review is intended as a critical, yet constructive, analysis of the importance of fluctuating asymmetry to studies of animal behavior and evolution. For those new to this area of research, this chapter indicates the growing complexity of fluctuating asymmetry analysis and highlights common pitfalls (Section III). In addition to remarking on past flaws, this review also aims to indicate the major empirical and theoretical gaps in our knowledge about fluctuating asymmetry (Section IV). In many cases, fundamental information concerning the genetic and developmental

origins, and possible behavioral consequences, of fluctuating asymmetry is simply lacking. For example, despite intense interest in asymmetry as a cue during mate choice, we do not know whether animals can actually perceive small morphological asymmetries (discussed in Section V.B).

As a particular focus for this review, one area of behavioral research in which fluctuating asymmetry has been frequently studied—sexual selection—is revisited, in light of our current knowledge, to indicate how work could progress in the near future (Section V).

II. FLUCTUATING ASYMMETRY AND FITNESS

For asymmetry to be important to studies of the evolution of animal behavior, a crucial question to address is whether asymmetry has any adaptive significance. The most popular way to answer this question, thus far, has been to look for associations between asymmetry and fitness and to study how these relationships are determined.

There have been numerous reviews of the relationship between fluctuating asymmetry and fitness indicators (Markow, 1995; Leung and Forbes, 1996; Palmer, 1996b, 2000; Møller, 1997; Møller and Swaddle, 1997; Clarke, 1998b; Thornhill and Møller, 1998; Simmons *et al.*, 1999a; Swaddle, 1999b; Van Dongen, 2001; Zakharov, 2001). There have also been a series of metaanalyses of fluctuating asymmetry in relation to various parameters, including fitness (Leung and Forbes, 1996; Møller and Thornhill, 1997; Thornhill and Møller, 1998; Vøllestad *et al.*, 1999), but these have generated much controversy (Markow and Clarke, 1997; Whitlock and Fowler, 1997; Palmer, 1999, 2000; Simmons *et al.*, 1999a). A major cause of controversy is the considerable inconsistency and flaws in methods used in different studies. In many cases it is not clear that authors have quantified and analyzed actual fluctuating asymmetry (rather than their own measurement error). Additional problems have been the inaccurate representation of published data, and the underreporting of nonsignificant or “opposite” results (Whitlock and Fowler, 1997; Palmer, 1999, 2000; Simmons *et al.*, 1999a). One particular complexity in employing metaanalyses is that researchers must go to great lengths to track down unpublished data (commonly referred to as the “file drawer problem”). As much fluctuating asymmetry research appears to have been performed on an *ad hoc* basis (Section VI), this presents a substantial challenge to any metaanalytic technique investigating an asymmetry relationship. For these reasons, this chapter does not attempt a metaanalysis as there appears little possibility that such a review could be satisfactorily comprehensive.

One element of the reviews on which there is wide agreement is the inconsistency in the relation between asymmetry and fitness. Fluctuating asymmetry of some traits is correlated with fitness indicators in some organisms, but not others (Leung and Forbes, 1996; Swaddle, 1999b). This pattern of inconsistency has not changed with the addition of more data. For example, feather and tarsal asymmetry are not related to levels of parasitism in the pigeon *Columbia livia* (Quek *et al.*, 1999). However, floral asymmetry in *Linum usitatissimum* and *Brassica rapa* (Salonen and Lammi, 2001) and fin asymmetry in the male gobie *Pomatoschistus microps* (Sasal and Pampoulie, 2000) are positively related to levels of parasitism.

There is a negative relation between horn asymmetry, female condition, and some (but not all) life history traits in the mountain goat *Oreamnos americanus* (Cote and Festa-Bianchet, 2001). However, feather and skeletal asymmetry are not related to body condition in the red-collared widowbird *Euplectes ardens* (Goddard and Lawes, 2000).

Probability of survival is negatively related to tarsal asymmetry in the water boatman *Callicorixa vulnerata* (Nosil and Reimchen, 2001) and the striped dolphin *Stenella coeruleoalba* (Pertoldi *et al.*, 2000). However, many life history traits are not related to morphological asymmetry in the winter moth *Operophtera brumata* (Van Dongen *et al.*, 1999b) and the brook stickleback *Culaea inconstans* (Hechter *et al.*, 2000).

The size of spermatophore passed from male to female in the field cricket *Gryllodes sigillatus* is negatively related to female appendage asymmetry (Farner and Barnard, 2000), which may indicate that males make mating decisions in relation to female asymmetry (although probably indirectly). In addition, there is some evidence to indicate that asymmetric male bushcrickets (*Requena vaticalis*) invest more highly in the nutritional content of their spermatophore, which was interpreted as asymmetric males investing more in parental effort (Simmons *et al.*, 1999b). However, neither male nor female limb asymmetry is related to ejaculate size in the moth *Plodia interpunctella* (Gage, 1998).

The preceding descriptions skim the surface of more recent studies, but they illustrate the diversity of interest in fluctuating asymmetry, the range of techniques used, and the variability in traits and taxa studied. It appears that some of the relationships between fitness and asymmetry found arise from direct influences of asymmetry. For example, asymmetry in mechanical traits can directly decrease competitive ability (Sneddon and Swaddle, 1999), auditory abilities (Bosch and Marquez, 2000), mating ability (Blackenhorn *et al.*, 1998), or predation (Swaddle, 1997b). Alternatively, asymmetry could be used as a direct visual cue in mate selection (Swaddle and Cuthill, 1994a; Morris and Casey, 1998). By

contrast, other relationships are mediated by indirect associations between asymmetry and fitness. For example, symmetric males may produce more attractive pheromones (Thornhill, 1992; Martin and Lopez, 2000). In many cases, authors have looked for broad correlations between asymmetry and fitness parameters, and so cannot distinguish between direct and indirect relationships (review in Swaddle, 1999b). As asymmetry can be related to trait size, many of the observational studies have also not accounted for how size–fitness relationships can give rise to relationships between trait asymmetry and fitness (Nachman and Heller, 1999). When there does appear to be a relationship between asymmetry and fitness, we rarely understand how this relationship is mediated.

One report has highlighted a powerful experimental technique to study relationships between developmental instability and fitness (Shykoff and Møller, 1999). By comparing the within-individual change (between successive feather molts) in outer tail length asymmetry in the barn swallow *Hirundo rustica* with changes in reproductive success, they found that individuals that increased in asymmetry (i.e., those that experienced an increase in developmental stress between molts) had reduced success. By exploring within-individual changes in asymmetry, we may draw closer to measures of developmental instability (as there is more than one measure of asymmetry for a given genotype; see Section IV.A) and, hence, be able to relate this parameter to evolutionarily important characters (such as reproductive success). This type of experiment has also been adopted in studies of clonal plants, but unlike the case of barn swallows, these data indicate that there are no relations between genotype-associated asymmetry and fitness indicators (e.g., Andalo *et al.*, 2000). Repeated lines of *Drosophila* are also an excellent model for studying fluctuating asymmetry–fitness relations. By producing known mutations in flies against the same genetic background, Bourquet (2000) produced lines of flies with various degrees of fluctuating asymmetry in sternopleural bristle number. However, there were no associations between bristle fluctuating asymmetry and either of two fitness indicators: reproductive success or competitive male mating success (Bourquet, 2000). It will be important to expand these experimental paradigms to other biological systems. At present, it appears that the relations between fitness and fluctuating asymmetry cannot be generalized and are trait specific.

III. METHODOLOGY ISSUES

As alluded to in the previous section, there are many methodological flaws among studies of fluctuating asymmetry. This is a major problem that

has been discussed many times, but still goes unheeded in many instances. Some of the mandatory first steps that every study needs to follow are summarized below. For more detailed discussion readers should refer to the many helpful articles on this topic (e.g., Palmer and Strobeck, 1986; Cuthill *et al.*, 1993; Palmer, 1994; Swaddle *et al.*, 1994; Van Dongen, 1998a,b; Van Dongen *et al.*, 1999a).

A. IDENTIFYING FLUCTUATING ASYMMETRY

Although identifying fluctuating asymmetry appears simple, it is important to distinguish it from directional asymmetry (where asymmetries are large and one side of the paired trait is predictably larger than the other, e.g., the left side is larger than the right in mammalian hearts) or antisymmetry (where asymmetries are also large but it is not possible to predict which side of the trait will be larger, e.g., either the left or right front claw can develop into the exaggerated signaling claw of the male fiddler crab *Uca*), as these other forms could lead to different predictions concerning the relationships between asymmetry and evolutionarily important parameters. For example, antlers of the roe deer *Capreolus capreolus* appear to display fluctuating asymmetry and this asymmetry is negatively correlated with survival (Pélabon and van Breukelen, 1998). But, curiously, antlers of the fallow deer *Dama dama* display directional asymmetry, and this asymmetry is not related to quality indicators (Pélabon and Joly, 2000). Fluctuating asymmetry and directional asymmetry are fundamentally different forms of asymmetry with different developmental origins. Directional asymmetries are preprogrammed lateral differences, whereas fluctuating asymmetries are deviations from what is normally perfect symmetry. Some researchers have reported fluctuating asymmetry “turning” into directional asymmetry or antisymmetry under increasing stress (Mather, 1953; McKenzie and Clarke, 1988; Graham *et al.*, 1993; Lens and Van Dongen, 2000). However, it is difficult to understand how such a massive restructuring of developmental programs would occur in such a short period of time.

Antisymmetry also appears to result from developmental processes distinct from fluctuating asymmetry (Van Valen, 1962; Palmer, 1996a). Interestingly, Rowe and colleagues have shown that several of the early studies of fluctuating asymmetry, including many of Møller’s studies (Møller, 1990, 1992a; Møller and Eriksson, 1994), were apparently measuring antisymmetry–fitness relations (Rowe *et al.*, 1997). Therefore, in some cases it appears that antisymmetry could be condition dependent. However, it is not clear whether these are isolated cases. It is also possible that fluctuating asymmetry could appear like antisymmetry at small sample sizes.

It has also been suggested that variation from a population mean directional asymmetry may be equivalent to fluctuating asymmetry, and there are ways to “adjust” measured directional asymmetry to become fluctuating asymmetry (Graham *et al.*, 1998). However, it is not clear, in an asymmetry that is (or was recently) under directional selection, whether a positive-signed deviation from the predicted form (e.g., left bigger than right) is equivalent to a negative-signed deviation (e.g., right bigger than left). We can make this assumption with fluctuating asymmetry but it is far more difficult with directional asymmetry, as directional selection on asymmetry suggests there is a difference in reproductive success for left-biased versus right-biased traits. Therefore, deviation from a mean directional asymmetry can often not be interpreted in the same way as variation in fluctuating asymmetry (e.g., Leamy *et al.*, 2000).

B. TRAIT SELECTION

Most research has focused on traits that are straightforward to measure—which is understandable as this will tend to reduce measurement error and make asymmetry measures more accurate. However, we should ask whether the asymmetries that people measure are behaviorally meaningful and whether there are others forms of asymmetry that should be measured. There are ways of measuring more complex shape asymmetry, that are especially important in studying the development of integrated units (e.g., Klingenberg and McIntyre, 1998; Mardia *et al.*, 2000; Klingenberg *et al.*, 2001). In these particular examples, researchers analyzed overall wing shape asymmetry, which is likely to be relevant to flight behaviors. The techniques employed quantified discrepancies in two-dimensional landmarks using established morphometric tools, such as Procrustes. The principles of these techniques could also be extended to three-dimensional morphometric assessments of asymmetry.

It has been suggested that assessing asymmetry of integrated units (or developmentally correlated traits) will render a more accurate estimate of true developmental instability than single-trait measures (Polak and Starmer, 2001). This makes sense, as this technique samples the same developmental instability with more than two data points. Combining size-standardized asymmetry measures from multiple traits into a single index (Windig and Nylin, 2000) could give an overall indicator of bodily asymmetry (Woods *et al.*, 1999). However, as fluctuating asymmetry appears somewhat trait specific, it is not clear what such a measure would indicate if traits that are not developmentally linked were combined. Even if all asymmetry measures are related to developmental instability, different traits may have differing buffering capacities, varying

susceptibility to environmental stressors (due to heterogeneity in biochemical pathways in development), and differing ontogenetic patterns and timing of asymmetry development. Therefore, interpreting multitrait indices of asymmetry (where traits are not developmentally linked) could be more problematic than interpreting single traits. When researchers have used multitrait indices, it is likely that they are sampling from a large part of the genome and that their data reveal responses to a combination of developmental conditions (Leung *et al.*, 2000; Hewa-Kapuge and Hoffmann, 2001).

Not all of development can be summarized by size and shape. Therefore, due consideration should be given to other forms of asymmetry. For example, position of traits on the left or right side, or coloration, could yield meaningful estimates of asymmetry in the appropriate systems (e.g., Polak, 1997; Martin and Lopez, 2000). Studies of these kinds have started to appear, but are still rare.

C. MEASUREMENT ERROR

As fluctuating asymmetry is relatively small, measurement error can swamp accurate estimates of asymmetry. Therefore, performing repeated measurements on the same individuals is essential to measuring fluctuating asymmetry. Some authors experienced at measuring fluctuating asymmetry are still performing repeat measures on only a subset of samples in their study (Cuervo and Møller, 1999; Woods *et al.*, 1999; Andalo *et al.*, 2000; Klingenberg *et al.*, 2001; Polak and Starmer, 2001). In most cases, it is not good enough to perform repeatability tests on a subset of the study sample. It is imperative to perform the repeats on all the samples to minimize measurement error. Several articles have discussed this (e.g., Palmer, 1994; Swaddle *et al.*, 1994; Merilä and Björklund, 1995; Van Dongen *et al.*, 1999a).

D. SAMPLING

Fluctuating asymmetry measurements are error prone and may have weak associations with the parameter of real interest (i.e., developmental instability; see Section IV.A). Therefore, obtaining a large and unbiased sample is important. As people have suggested that fluctuating asymmetry is related to survival, sampling from natural populations at particular age intervals may unwittingly bias samples in terms of fluctuating asymmetry (Møller and Swaddle, 1997). Because of the inherent random nature of asymmetries, it will often require a large sample size (>100 individuals) to

accurately estimate the variance associated with fluctuating asymmetry (Mogie and Cousins, 2001).

Analysis of statistical power is often overlooked but is important to studies of fluctuating asymmetry, as many conclusions tend to be drawn from a lack of statistical significance (Palmer, 1996b). The power of many tests in the literature appears to be less than 50% (J. P. Swaddle, unpublished data), yet many positive conclusions are drawn from this form of weak evidence. Other than considering the power of individual statistical analyses, Van Dongen and colleagues have applied a number of simulation tests to explore how large effects could arise from more limited sample sizes (Van Dongen, 1999; Van Dongen *et al.*, 2001). Most notably, increasing the number of repeat measurements on the same individuals (from two to nine repeats) can substantially increase the ability to discriminate asymmetry differences between two populations, even at relatively small sample sizes of between 20 and 40 individuals (Van Dongen, 1999). Future studies of fluctuating asymmetry should discuss the power of tests, especially when interpreting the lack of associations between fluctuating asymmetry and other parameters.

E. ABSOLUTE VERSUS RELATIVE ASYMMETRY

Often, size may be related to dependent variables in addition to asymmetry. Hence, size could mask or alter potential relationships between asymmetry and the dependent variables. Therefore, taking account of size could be necessary (depending on the data at hand). It is only relevant to use a relative measure of asymmetry when the relationship between size and asymmetry is isometric and intercepts the origin (Cuthill *et al.*, 1993). In addition, the relationship between size and the dependent variable would have to be isometric (Nachman and Heller, 1999). This will rarely be the case, and therefore it is necessary to account for size variation with other statistical models, such as analysis of covariance or residual analysis (Palmer, 1994; Swaddle *et al.*, 1994; Leung, 1998).

F. STATISTICAL MODELS

As many of the processes associated with determination of fluctuating asymmetry are stochastic, Van Dongen has suggested the use of statistical and modeling methods that treat variables with uncertainty distributions—such as Bayesian hierarchical modeling—as opposed to methods that treat variables as fixed effects (e.g., Van Dongen, 2000). These techniques are being investigated further, but without empirical data to support the assumptions it is not clear what forms of probability distribution should be

used in such modeling. A number of useful analytic tools and suggestions for forms of statistical models have been collated by A. R. Palmer (www.biology.ualberta.ca/palmer.hp/asym/asymmetry.htm). A review of this site before starting a new study would assist many authors.

IV. IMPORTANT GAPS IN OUR KNOWLEDGE ABOUT FLUCTUATING ASYMMETRY

There is great interest in fluctuating asymmetry as an indicator of developmental instability and fitness, but there are also significant gaps in our knowledge. If the gaps described below can be filled, it will help tremendously in interpreting the data already collected and galvanize future research.

A. DOES FLUCTUATING ASYMMETRY REFLECT DEVELOPMENTAL INSTABILITY?

The amount of asymmetry quantified in populations and individuals is an estimate of their developmental instability. The term “estimate” is important, as it is not known how accurately a single fluctuating asymmetry measure actually represents underlying instability (Whitlock, 1996). If an individual could develop a trait over and over again under identical environmental conditions there would be a certain degree of variability in the resulting phenotypic asymmetry. However, it is unclear how variable this repeated development in identical genetic and environmental conditions would be. At present, it is assumed that two data points (i.e., the left and right sides of a trait) sufficiently sample this theoretical distribution. Several authors have raised this as a substantial problem with interpreting fluctuating asymmetry data (Whitlock, 1996; Houle, 1997; Van Dongen, 1998a).

One way of addressing this issue has been developed by Whitlock and Van Dongen, in which (with certain assumptions) it is possible to estimate how much of the variance observed in fluctuating asymmetry is attributable to developmental instability (Whitlock, 1996, 1998; Van Dongen, 1998a). Their techniques concentrate on calculating the repeatability (R) of fluctuating asymmetry production (given an underlying level of developmental instability). This has most recently been summarized by Whitlock (1998) as

$$R \cong \frac{2}{\pi} - \frac{\pi - 2}{2} \cdot \left(\frac{1}{C_v^2} \right)$$

in which C_v is the coefficient of variation in signed absolute asymmetry, and $\pi \approx 3.142$. Essentially, R is greater (i.e., the measured asymmetry more closely resembles developmental instability) when fluctuating asymmetry is less variable, and when measurement error has been minimized by numerous repeated measures on both left and right sides. As C_v can be calculated from many published studies, R has been used to “correct” several estimates of developmental instability—especially in studies of heritability and individual asymmetry parameters (Van Dongen, 1998a; Whitlock, 1998; Gangestad and Thornhill, 1999). Although estimates of R have varied substantially from small values (0.072; Gangestad and Thornhill, 1999) to considerably larger values (0.36; Van Dongen and Lens, 2000), all these studies indicate that the evolutionary significance of developmental stability can be masked by the poor correlation between measured fluctuating asymmetry and true developmental stability. Analyses by Whitlock indicate that R is maximally 0.64, implying that fluctuating asymmetry (based on measurement of left and right sides of a bilateral trait) will never perfectly estimate developmental instability, even if measurement error is zero (Whitlock, 1998).

As is true for any model, Whitlock makes a number of assumptions about fluctuating asymmetry and developmental instability. These include the following: (1) values from left and right sides are drawn from the same normal distributions; (2) production of the left and right sides is independent (i.e., the value drawn from the distribution for the left side does not influence the value for the right); and (3) developmental instability follows a normal distribution. These assumptions imply that the model will not hold when either directional asymmetry or antisymmetry is present, or when traits are developmentally integrated (Whitlock, 1996).

A further application of the basic Whitlock model illustrates that some of these assumptions may have to be altered. Houle (2000) showed that the model predicts that the coefficient of variation in developmental instability would have to be “enormous” and far greater than for any other trait yet reported. However, a quantitative genetic analysis of bristle counts in *Drosophila falleni* indicates that genetically related fluctuating asymmetry may be extremely variable, yielding phenotypic coefficients of variation of approximately 85–100% (Polak and Starmer, 2001). Similar estimates of variation in asymmetry have been obtained for clonal cherimoya trees (*Annona cherimola*) (Perfectti and Camacho, 1999), in which the coefficient of variation for asymmetry was approximately 5 to 10 times greater than that for size of the same traits. Although this particular criticism may not hold, there may have to be other refinements of the model, as Houle also suggests that left and right sides may not be drawn from normal distributions (cf. Klingenberg and Nijhout, 1999) and that

developmental instability may not follow a normal distribution (Houle applies a γ distribution).

Although these modeling techniques are undoubtedly valuable, it will be crucial to explore empirically the repeatability of developmental stability estimates. Although many authors have categorically stated that it is not possible to generate repeated fluctuating asymmetry values for the same genotype under constant environmental conditions (Whitlock, 1996; Van Dongen, 1998a), I think there are productive ways of investigating the repeatability of fluctuating asymmetry. If genotypes and environmental conditions are held constant, it is possible to assess repeatedly bilateral symmetry across a broad taxonomic range by using clones, within- and among-population comparisons of asexual organisms, homogeneous strains of laboratory animals, and perhaps even organisms that show repeated growth of the same trait throughout life (e.g., feather traits regrown after molt in birds: Swaddle, 1997a; Swaddle and Witter, 1998). Interestingly, we already know that isolated lines of *Drosophila falleni* (originating from single pairs of virgin males and females) maintain consistent differences in asymmetry from each other over several generations (Polak and Starmer, 2001). This implies that each line has a somewhat consistent, genetically related expression of asymmetry. In contrast, the majority of variance in leaf and petal asymmetry in cherimoya trees can be accounted for by within-tree and within-clone variation. Little appears to be genetic in origin (Perfectti and Camacho, 1999). However, there were also significant environmental influences on asymmetry in that study, which may mask any genetic contributions to asymmetry. It would be interesting to repeat such a study under more controlled environmental conditions. In a similar study, there was just as much variation among genotypes as within genotypes for leaf and petal asymmetry in birdsfoot trefoil, *Lotus corniculatus* (Andalo *et al.*, 2000). There may also be problems with studying asymmetry in plants, as sessile organisms are more likely to experience consistently directed environmental pressures than most animals. Hence, studying the production and genetic origins of asymmetry in clonal animals is particularly appealing.

It will be interesting to explore the utility of radial and translational asymmetry in assessing developmental stability, as these forms of asymmetry will render substantially more than two data points per individual and, hence, give a better estimate of the distribution of developmental instability. Plants are well known for their translational symmetry (e.g., repeated development of leaves along an axis) and many invertebrate taxa show translational asymmetry (e.g., Fusco and Minelli, 2000) or pentaradial symmetry (e.g., echinoderms). Studies of this sort will allow researchers to inspect the predictions made by the Whitlock model

and give more insight into how reliably fluctuating asymmetry estimates developmental instability.

B. IS FLUCTUATING ASYMMETRY A TRAIT?

Many authors posit that developmental instability is a genome-wide phenomenon and so, if fluctuating asymmetry reflects developmental instability, there should be an organism-wide indication of asymmetry and among-trait correlations in asymmetry within the same individual (i.e., an “individual asymmetry parameter”; Soulé and Baker, 1968). In general, there is little evidence of an individual asymmetry parameter (review in Clarke, 1998a). Several (nonmutually exclusive) explanations for this have been developed. First, as described in the previous section, there could be a weak association between a single expression of fluctuating asymmetry and developmental instability (Whitlock, 1996). Second, the lack of among-trait correlations could indicate that developmental instability of one trait is not related to that of another. Another suggested explanation is that independent traits have sensitive phases of development at different times so that, if the environment is not constant throughout development, this would result in different levels of asymmetry (Swaddle and Witter, 1997; Hardersen, 2000). In addition, genetic effects could vary with stages of development (Clarke, 1998a). All of these hypotheses suggest that describing asymmetry in one trait may not reveal the same information as asymmetry in another, independent trait.

The lack of an individual asymmetry parameter could suggest that independent units of the genome influence asymmetry of different traits separately. The Clarke and McKenzie investigations of asymmetry production in the blowfly *Lucilia cuprina* in response to specific insecticide resistance are consistent with this hypothesis (McKenzie and Batterham, 1994; Clarke, 1997; Clarke *et al.*, 2000). There probably are not organism-wide developmental stability genes. However, it could be that developmental stability is a pleiotropic effect and so is likely to show inter trait variance in properties and heritability.

In summary, even if developmental stability is an organism-wide phenomenon, it seems highly unlikely (from both theoretical and empirical evidence) that fluctuating asymmetry can be viewed as a “trait” in itself. It appears to reflect different properties when expressed in different paired traits. This may be due to the inexact nature of fluctuating asymmetry, but it could also reflect the predominance of environmental factors in determining fluctuating asymmetry expression. As the environment will affect the development of independent traits to differing degrees, we should expect to see large variation in fluctuating asymmetry among traits.

However, asymmetry of individual characters can reveal information about developmental conditions and the ability of individuals to buffer development during a specific period of growth. This argument is a relevant expansion of points made in Section III.B, and indicates that trait selection is an extremely important step in any study of fluctuating asymmetry.

C. WHAT ARE THE ORIGINS OF FLUCTUATING ASYMMETRY?

Not surprisingly, there have been repeated calls to understand the genetic underpinnings of fluctuating asymmetry (Palmer and Strobeck, 1986, 1992; Markow, 1995; Møller and Swaddle, 1997). There are selection experiments that demonstrate that fluctuating asymmetry can be selected both for and against (e.g., Mather, 1953), and limited demonstrations of the heritability of fluctuating asymmetry (see below). There are also continuing searches for genetic correlates of fluctuating asymmetry through quantitative trait locus (QTL) mapping (Leamy *et al.*, 1997, 1998, 2000). However, a common suggestion is that fluctuating asymmetry has little (or perhaps no) genetic origin. For example, a simple point-source morphogen diffusion-threshold model, which included fluctuating asymmetry as purely random noise associated with independent (heritable) development of left and right sides, indicated that many of the reported “apparent” genetic correlations of fluctuating asymmetry are consistent with nongenetic origins (Klingenberg and Nijhout, 1999). In particular, when relations between developmental variables and the expression of the phenotype were nonlinear, and the developmental variables and the expression of the phenotype were nonlinear, and the developmental variables (controlling the overall growth of left and right sides independently) possessed genetic variation, apparent genetic properties for random developmental noise (i.e., fluctuating asymmetry) could emerge as general properties of the model (Klingenberg and Nijhout, 1999). Trait size and trait asymmetry became correlated under several conditions. This model implies that (given certain assumptions) it is not necessary to invoke any special genetic mechanisms to explain fluctuating asymmetry other than the mechanisms controlling the general growth and development of the left and right sides of traits. That is, there need not be developmental stability genes. In a similar manner, there are suggestions that canalization may be largely “controlled” by nongenetic factors although they appear heritable in experimental situations (Amzallag, 2000). It could be that fluctuating asymmetry is an epigenetic phenomenon.

The Klingenberg and Nijhout (1999) model is valuable in showing that certain data sets are consistent with a simple developmental explanation, yet there may still be observations that cannot be explained in this way. The authors themselves point out that there are specific genes in the Australian sheep blowfly *Lucilia cuprina* that disrupt and also restore developmental stability, yet have no associated effect on overall trait size/value (unpublished data from J. A. McKenzie referred to in Klingenberg and Nijhout, 1999). Repeated lines of *Drosophila melanogaster*, with known combinations of mutations against the same genetic background, have consistent among-mutation heterogeneity in sternopleural bristle asymmetry, implying that these mutations affect fluctuating asymmetry in a predictable and quantifiable manner (Bourquet, 2000). In addition, a quantitative genetic study of wild-caught *Drosophila falleni* lines demonstrated that additive and dominant genetic effects (perhaps with some localization to the X chromosome) influence positional asymmetry of bristles, and that trait size and asymmetry are largely genetically independent (Polak and Starmer, 2001). In addition, studies of identical twins indicate a strong concordance in asymmetry of dermal ridge patterns on the fingertips within genotypes compared with variation among genotypes (Kilgariff *et al.*, 2000). However, common maternal and environmental effects were not accounted for in this study.

Although the Klingenberg and Nijhout (1999) model is appealing in its simplicity and ability to explain much of the apparent variation in asymmetry, it appears possible that there are specific genes (or gene complexes) that affect fluctuating asymmetry. The Klingenberg and Nijhout (1999) model is also valuable in that it shows that selection against fluctuating asymmetry is a slow process and that asymmetry can commonly be maintained in populations even in the face of strong truncation selection. This is a topic that causes a number of researchers to doubt whether genetic variance for fluctuating asymmetry could be maintained in populations (Møller and Swaddle, 1997).

If there are genes that affect developmental instability, which genes are they and how do they act? To relate this question to the current working models of developmental stability, it is necessary to consider both the production of stochastic "noise" and the regulation (or suppression) of that noise. The generation of developmental noise is not well understood at the genetic level (Roux-Rouquie, 2000), although there are suggestions that some gene expression could occur stochastically (McAdams and Arkin, 1999). In addition, there may be a whole suite of cell-signaling and activation factors that do not occur perfectly, and so introduce random noise at many levels (e.g., binding sites not working to the same degree of efficiency). In terms of regulation of noise, it could be that there are many

gene products that affect the same developmental pathway (i.e., there is redundancy), and so there might be inherent back-up plans to maintain stability that only go awry in rare cases. In addition, genes could affect developmental instability through pleiotropic effects (i.e., a single gene having multiple phenotypic effects). Suitable candidates could be transcriptional factors or the large family of cytokines. At present, all of these hypotheses are purely speculative.

In general, there is a growing need for the theoretical advances on the origins of fluctuating asymmetry to be tested by empirical investigations. Leamy and colleagues have encouraged researchers to think of general genetic correlates of asymmetry, and have searched for elements of the genome associated with variance in asymmetry through QTL mapping (Leamy *et al.*, 1997, 1998, 2000). These data illustrate that there may be a small number of loci associated with fluctuating asymmetry and that these behave in a dominant manner (Leamy *et al.*, 1998). However, this pattern could also be consistent with nongenetic origins of fluctuating asymmetry (Klingenberg and Nijhout, 1999). In future studies, it will be important to search for loci associated with fluctuating asymmetry (and developmental instability) under varying environmental stressors. It could be that gene expression varies with environmental conditions and it is only in circumstances of increased stress that genes are activated that increase developmental buffering (cf. Rutherford and Lindquist, 1998). These investigations will provide considerable insight into the direct effects of the environment on the origins of fluctuating asymmetry. It is also necessary to consider how any observable genetic variation in fluctuating asymmetry and developmental instability is related to fitness parameters, preferably within the same experimental situation.

Understanding the genetic architecture of fluctuating asymmetry will also reveal levels of genetic and phenotypic redundancy and, hence, could help explain why asymmetry may persist in the face of strong selection against it (as in the barn swallow). My hypothesis is that there is a large amount of genetic redundancy. If so, then many genotypes could give rise to the same level of asymmetry, and this redundancy is a major factor maintaining asymmetry in populations (see Section IV.E).

D. IS FLUCTUATING ASYMMETRY HERITABLE?

The validity of assessing the heritability of fluctuating asymmetry is contentious. Møller and Thornhill (1997) reviewed the literature and stated that asymmetry shows a small, but significant, heritability across many taxa and traits. However, many researchers have criticized the Møller and Thornhill review and have pointed out flaws in their data,

analysis, and interpretations (Leamy, 1997; Markow and Clarke, 1997; Whitlock and Fowler, 1997; Palmer, 2000). In many cases, it would appear that there is little additive genetic variance for fluctuating asymmetry and it is, as yet, unclear how heterogeneous the heritability of fluctuating asymmetry is among taxa and traits (Van Dongen, 2000). If fluctuating asymmetry is not a trait per se, it may be meaningless to try to quantify whether it is generally heritable for particular characters (Section IV.B). Estimates of heritability in multitrait indices of fluctuating asymmetry suggest a greater additive genetic component to developmental instability in some cases (Swaddle, 1997c; Pechenkina *et al.*, 2000) but not all (Bryden and Heath, 2000).

By applying corrections for the loose correlation between fluctuating asymmetry and developmental instability, Gangestad and Thornhill have suggested that developmental instability is much more heritable than previously reported (Gangestad and Thornhill, 1999). However, subsequent estimates (Section IV.A) have indicated that the Gangestad and Thornhill estimate of R may not be representative (too low) and that the heritability of developmental instability is itself still low (Van Dongen *et al.*, 2001). Using R as a "correction" factor to make it seem that fluctuating asymmetry is more heritable is inappropriate. R is an indication of how imprecisely fluctuating asymmetry reflects developmental instability and so it seems counterintuitive to use it to support the exactness of fluctuating asymmetry. Surely it adds variance to estimates rather than shifting the mean in any particular direction. It is true that more accurate estimates of developmental stability are needed. If researchers study traits that are believed to reflect developmental instability more closely, it appears that heritability can be substantial (Polak and Starmer, 2001). Researchers should concentrate on more careful experimental design rather than post-hoc statistical manipulation of data that were not collected appropriately.

Studies that incorporate replicate estimates of the heritability of fluctuating asymmetry in a developmentally linked morphological unit, in which heritability is assessed across a range of environments, will be particularly illuminating. Such experiments are underway (e.g., Polak and Starmer, 2001) but are presently too few for general conclusions. There have also been attempts to analyze reaction norms of asymmetry (Loeschcke *et al.*, 1999; Shykoff and Møller, 1999; Andalo *et al.*, 2000), which indicate that asymmetry changes across environmental gradients. As most reports assess fluctuating asymmetry in terms of absolute asymmetry (i.e., unsigned difference between left and right sides), a change in mean asymmetry will also be associated with a change in asymmetry variance. Altering variance implies that measures of heritability will be different across the environmental gradient. It would be interesting in subsequent

investigations of reaction norms to include data on individual organisms and to show the variation in slopes of individual reaction norms and how much variance is associated with the “grouped” means reported thus far.

As it seems that fluctuating asymmetry has (at best) low additive genetic variance, the variation reported in populations must be largely environmentally determined. This has important implications for studies of heritability—as asymmetry could have “apparent” heritability through any mechanism that links the genome with the propensity for individuals to develop and grow under favorable conditions. These could be maternal conditions, or consistent environmental conditions throughout various life cycle stages. If asymmetry is selected against through some proximate mechanism (e.g., mate preference, or predation), genes linked with developing under favorable environmental conditions would be favored. If so, we could observe apparent heritability of asymmetry in natural populations even though the asymmetry has no genetic component. However, this also suggests another area for heritability studies in relation to fluctuating asymmetry. If asymmetry is determined largely by the environment, it would be relevant to assess whether there is heritability of developmental conditions—which extend beyond studies of maternal effects (e.g., inheritance of territory quality, feeding locations, or breeding locations).

E. IS LOW FLUCTUATING ASYMMETRY ADAPTIVE?

As can be seen from the preceding treatment of fluctuating asymmetry–fitness relations (Section II), it is difficult to claim that low asymmetry is always adaptive. An even more challenging question to ask is whether fluctuating asymmetry of some traits could be a neutral phenotypic character (and so not related to adaptive behavior or morphology)? Perhaps fluctuating asymmetry is selected against through natural selection only when the asymmetries reach a threshold value (which would vary among traits, and perhaps reach these higher values only in a minority of traits). If this hypothesis is true, it would be predicted that fluctuating asymmetry in some traits, but not others, is related to fitness parameters. This is the pattern we see in nature. Interestingly, a study of fitness correlates in the wasp *Trichogramma brassicae* indicates that asymmetry must rise beyond a threshold value before it has a negative association with fitness (Hewa-Kapuge and Hoffmann, 2001). As in the case of developmental canalization, variation in fluctuating asymmetry may be exposed only under extreme developmental (genetic and/or environmental) stress. Therefore, only under extreme conditions could asymmetry be selected on—acting to restore developmental stability to

prestress levels in that particular environment. Thus, fluctuating asymmetry may have adaptive significance only under these conditions.

Fluctuating asymmetry is, in part, determined by the random noise associated with development (e.g., inequalities of cell division, signal receptors not working at equal efficiency). Developmental noise is likely to have multiple causes. Similarly, a range of genotypes can produce the same degree of asymmetry in their phenotype, and the evidence published to date indicates that many genetic and environmental factors affect developmental stability. These observations raise the possibility that there is a large amount of genetic redundancy in determination of both noise and stability. If so, selection or drift could often act without there being any effect on resultant asymmetry, and fluctuating asymmetry has the capacity to be a neutral character.

Alternatively, developmental stability may have a genetic component but low asymmetry appears adaptive only when that genetic component is located close to genes that affect fitness. Therefore, asymmetry–fitness relationships may be due to genetic linkage. Identifying QTLs that influence fluctuating asymmetry could be an approach used to test this hypothesis.

Although this seems patently obvious, it is important to stress that if fluctuating asymmetry does have adaptive significance, it is highly likely that this adaptive value was not the original cause of the evolution of the asymmetry. Fluctuating asymmetry did not evolve to reveal fitness, but rather as a by-product of symmetric development. It arose without function, but may now affect fitness in some cases.

These scenarios, speculative as they are, indicate that the patterns of documented asymmetry may be consistent with fluctuating asymmetry being a neutral character or one subject to infrequent natural selection. Discovering the genetic origins of fluctuating asymmetry and knowing how stressors affect developmental stability are necessary to test whether fluctuating asymmetry is adaptive. Searching for additional inconsistencies in asymmetry–fitness correlations without learning more about asymmetry production will not be the most productive use of research time and funding.

V. A REVISED LOOK AT FLUCTUATING ASYMMETRY AND SEXUAL SELECTION

In some cases, but by no means all, symmetric individuals are preferred over asymmetric competitors during mate choice or intrasexual competition (Thornhill and Møller, 1998; Swaddle, 1999b). As most of these studies have reported correlations between mate selection parameters and asymmetry, it is not possible to ascertain the role that asymmetry may

actually play in sexual selection (review in Swaddle, 1999b; see Schlaepfer and McNeil, 2000 for a more recent example). Six studies have investigated a direct effect of fluctuating asymmetry in sexual selection processes by manipulating degrees of phenotypic asymmetry within a natural range. Of these cases, three indicate that individuals with low asymmetry in secondary sexual traits have an advantage over their more asymmetric counterparts (Swaddle and Cuthill, 1994a; Møller and Sorci, 1998; Morris and Casey, 1998). The remaining three studies indicate that fluctuating asymmetry in other sexually selected characters had no detectable influence on mate selection or social dominance (Swaddle and Witter, 1995; Jablonski and Matyjasiak, 1997; Tomkins and Simmons, 1998). Even in the much-cited study of the barn swallow, manipulations of phenotypic asymmetry were unnaturally large (Møller, 1992b) or created novel phenotypic conditions (e.g., high ultraviolet-reflective paint applied to tail feathers; see Swaddle and Cuthill, 1994a) that are difficult to interpret with respect to fluctuating asymmetry (Møller, 1993b). The jury is still out on whether fluctuating asymmetry plays a role in sexual selection. There have been too few tests of the role asymmetry may play. Given the substantial research effort devoted to fluctuating asymmetry, this may be surprising to those peripheral to this area of research. To me, it is indicative of how an idea became accepted too quickly without fundamental tests of the predictions initially proposed by Møller (1990). A “back-to-basics” approach is much needed and overdue.

As described in Section IV, our present state of knowledge suggests that fluctuating asymmetry is largely nongenetic in origin. This has important consequences for the role asymmetry may play in sexual selection. How fluctuating asymmetry may be associated with nongenetic benefits in sexual selection, and how symmetry preferences may arise in the absence of any detectable benefits, are considered below. These observations have implications for how sexual selection should be studied in future. This is discussed in Section V.C.

A. NONGENETIC BENEFITS OF LOW FLUCTUATING ASYMMETRY

It is commonly claimed that, if fluctuating asymmetry plays a role in sexual selection, preferences for symmetric individuals would provide strong support for “good genes” models of sexual selection (e.g., Møller and Pomiankowski, 1993; Gangestad *et al.*, 1994; Scheib *et al.*, 1999; Van Dongen *et al.*, 2001). This is contrary to the evidence that fluctuating asymmetry is largely determined by environmental conditions during development. A preference for symmetry may be more related to direct environmental factors than to indirect inherited benefits through the

genes. It is an oversimplification to consider fluctuating asymmetry to be a tool to distinguish between the relative roles of direct and indirect benefits in models of sexual selection (Møller and Pomiankowski, 1993).

One of the most cited cases in which asymmetry influences mate selection and reproduction is that of the barn swallow. In this species, female mate choice is affected by gross levels of tail feather asymmetry, resulting in symmetric males gaining higher reproductive success than asymmetric males (Møller, 1992b, 1993b), and females contributing relatively more parental care when mated to a symmetric male (Møller, 1994a). In addition, the symmetry of barn swallow tail feathers is a sensitive indicator of a range of suboptimal environmental conditions, ranging from parasitic infestation to radioactive contamination (Møller, 1992a, 1993a). Møller has used such relationships to support the hypothesis that fluctuating asymmetry of elongated tail feathers reveals "good genes" in male barn swallows. However, more recent studies have indicated that this model system may not be as straightforward as once reported. In a 3-year test of whether parental asymmetry is related to offspring quality, there appeared to be no relationship between the asymmetry of either parent with offspring size, immunocompetence, or condition (Cadée, 2000a). In addition, fluctuating asymmetry of many traits, including length of the outer tail feathers, does not appear heritable (Cadée, 2000b). Only in years when environmental variance is low do asymmetry measures approach significant heritability, which indicates that asymmetry values are dominated by environmental effects in most years. Hence, there appears to be little heritable benefit of low asymmetry to swallow offspring and thus little support for good genes models of sexual selection.

If fluctuating asymmetry carries little heritable benefit, direct benefits of selecting against asymmetry should be considered. There are accounts of mate selection being mediated through environmental effects on asymmetry. For example, horn length asymmetry may be related to some aspects of phenotypic fitness in female mountain goats. This relationship appears to arise because more advantageous environmental conditions lead to increased female condition and, hence, a better chance of successful reproduction; more advantageous environmental conditions reduce horn asymmetry (Cote and Festa-Bianchet, 2001). Therefore, asymmetry can be a marker of phenotypic fitness because of the common effect of the environment on condition and asymmetry. Interestingly, in a laboratory study of *Drosophila melanogaster*, the only asymmetry measure (orbital bristles) that was consistently increased by environmental stressors was also the one with the smallest additive genetic component (Woods *et al.*, 1999). It may be this type of trait that is important in determining mating preferences, as asymmetry in such traits could give conspecifics a

window into the nutritional and energetic, developmental environment encountered by potential mates. This may be especially relevant in species whose breeding/nesting habitat shows some level of heritability, or in species that show repeated growth associated with the timing of breeding (e.g., winter/spring feather molt in birds may reveal the condition of individuals as they enter the breeding season).

Another relevant study has shown that humans display a preference for symmetry when judging attractiveness of monozygotic twins. This not only emphasizes the significant influence of environmental effects on asymmetry production, but also explicitly shows that preferences based on asymmetry differences can exist when the asymmetries are wholly environmentally determined (Mealey *et al.*, 1999).

Understanding the relative roles of the genome and the environment in asymmetry production appears crucial to interpreting whether asymmetry could play a role in sexual selection. This is not a surprising statement; phenotypic traits must have a genetic basis in order for selection to result in change. However, researchers often plough ahead and record fluctuating asymmetry in relation to sexually selected behaviors or morphology without any knowledge of genetic causes. That approach adds more data points to review articles, but it would be more helpful if researchers married genetic, developmental, and behavioral approaches and studied the causes and consequences of asymmetry simultaneously. There are limited cases in which this has occurred. Perhaps the best two examples are barn swallows (see references) and the European earwig *Forficula auricularia*. In the latter, male forceps size is heritable and plays a role in mating preferences, but forceps asymmetry is not heritable, appears to result from developmental buffering, and does not influence female choice (Tomkins and Simmons, 1998, 1999; Tomkins, 1999). Preliminary investigations of zebra finch chest bar asymmetry indicate that this characteristic is not heritable (J. P. Swaddle, unpublished data), but females prefer males with symmetric bars (Swaddle and Cuthill, 1994a).

In addition to making sure they are measuring a repeatable characteristic (Section IV.A) and understanding how the asymmetry is produced (Section IV.C), researchers need to expand their consideration of the benefits of low asymmetry to include immediate environmental factors in addition to heritable consequences.

B. PERCEPTUAL PROCESSES AND ASYMMETRY

There are two general issues I want to raise in terms of how perceptual processes affect studies of asymmetry and sexual selection: perceptual bias and asymmetry detection.

1. Perceptual Bias for Symmetry

The notion that a preference for low asymmetry can arise as a by-product of species or object recognition is discussed at length elsewhere (Swaddle and Cuthill, 1994a; Swaddle, 1999a). Below is a brief summary of the most salient points.

Fluctuating asymmetry is characterized by a normal (or leptokurtic) distribution of signed asymmetry scores (i.e., left minus right) that is centered around a mean of zero (Palmer and Strobeck, 1986). Individuals in a population should always be exposed to this form of distribution of asymmetries in visual cues (or signals) they assess to judge potential mates and competitors. There are both theoretical and empirical data to show that animals (including humans) form a mental template that is the average of their previous experience against which they compare a new form (Kalish and Guttman, 1957; Blough, 1969; Dill and Heisenberg, 1995; Enquist and Johnstone, 1997). As the average expression of fluctuating asymmetry will always be close to symmetry (i.e., zero asymmetry), animals could possess symmetry preferences because a symmetric form is closer to their mental template than is an asymmetric form (Johnstone, 1994; Swaddle and Cuthill, 1994a). Hence, a symmetry preference can arise as a by-product of other, more general cognitive processes, such as species recognition. This particular process has yet to be tested explicitly, but is worthy of much greater consideration than it is currently given in the sexual selection literature.

As fluctuating asymmetry is a byproduct of symmetric development (Section IV.E), this discussion of symmetry preferences suggests that the role of asymmetry in sexual selection results from the interaction of two by-products: a by-product of development, and a by-product of perception. As the relationship between the selection pressure and the target trait (i.e., low fluctuating asymmetry) is mediated by at least two indirect links, perhaps it should not be surprising to see little evolutionary effect on fluctuating asymmetry. There is likely to be stronger selection on other genes/traits that affect fluctuating asymmetry as a by-product (i.e., selection on trait size, and/or selection on perceptual mechanisms for object recognition).

2. Ability to Detect Asymmetry

If fluctuating asymmetry is used as a direct cue in sexual selection, it is important to demonstrate that animals can perceive small differences in the magnitude of phenotypic asymmetry. As most fluctuating asymmetry in nature tends to be small (commonly less than 1% relative asymmetry in most individuals in a population) it is questionable whether animals can reliably detect and respond to such minor variation (Swaddle, 1999c).

Experiments that have demonstrated a direct, visual role for asymmetry in sexual selection have manipulated the asymmetry of traits that are unusually asymmetric in their natural state: 21% relative asymmetry in male swordtail fish (*Xiphophorus cortezi*) bar patterns (Morris and Casey, 1998); 10% asymmetry in the chest plumage of male zebra finches (*Taeniopygia guttata*) (Swaddle and Cuthill, 1994a). Even in exaggerated secondary sexual characters, mean fluctuating asymmetry is often much lower than these values (Balmford *et al.*, 1993). When the population frequency distribution of signed asymmetry scores is more platykurtic, for example, in the barn swallow, it is possible that some individuals could have greater asymmetry even though the population mean is rather low. From Møller's reports of fluctuating asymmetry in the outer tail feathers of male swallows (Møller, 1990, 1992a, 1994b), it seems that approximately half the population possesses tail feather asymmetry above the population mean of 2.3%. Some have asymmetries of more than 6%. In more leptokurtic distributions, however, most individuals will have asymmetry values below the population mean.

Experiments have started to explore the capacity of European starlings, *Sturnus vulgaris*, to discriminate symmetry from asymmetry. Although these experiments have used unnaturalistic cues, they indicate that starlings cannot accurately detect length asymmetries of the size they would most commonly experience in the wild (Swaddle, 1999c). However, if the asymmetries are sufficiently conspicuous, the birds can categorize images as being symmetric or asymmetric (Swaddle and Pruett-Jones, 2001), but there appears a threshold effect in terms of asymmetry detection (Swaddle, 1999c). Therefore, if asymmetry is large enough it could play a direct role in sexual selection. There are some experiments that have manipulated asymmetry within the natural range, and the experimental asymmetry seems large enough to be detected. These studies show that sometimes asymmetry is an important cue (Swaddle and Cuthill, 1994a; Morris and Casey, 1998), whereas in other cases asymmetry does not affect sexual selection processes (Swaddle and Witter, 1995; Tomkins and Simmons, 1998). Experiments that have manipulated asymmetry to unrealistic levels have shown that if an asymmetry is large enough it will be avoided during mate selection: for example, Møller altered the relative asymmetry of male swallow tails from 2.3% to approximately 22% (Møller, 1992b). Once more naturalistic experimentation has been performed, it would be interesting to review the studies to see whether reported effect sizes are positively related to the magnitude of the asymmetry (both manipulated and unmanipulated). It may be that asymmetry can be used as a cue only in species where the asymmetries are large and variable.

One report indicates that, among humans, there are facial features correlated with overall facial symmetry that can be detected when only one side of the face is visible (Scheib *et al.*, 1999). This form of correlation could, potentially, lead to an apparent preference for symmetry even when asymmetry differences are not detectable. Therefore, studying correlates of symmetry (even when the symmetry is artificially produced) is an important feature of experimental design as, at present, we do not know how most organisms will perceive the symmetry of any given trait.

C. RECOMMENDATIONS FOR STUDYING FLUCTUATING ASYMMETRY AND SEXUAL SELECTION

In addition to the specific suggestions made in the previous section, there are several important issues relevant to studying the role of fluctuating asymmetry in sexual selection.

First, researchers should develop *a priori* arguments as to why asymmetry of a particular trait may play a role in sexual selection. In general, the asymmetry of the trait will have to be conspicuous (large variance and mean absolute asymmetry) and related to other fitness indicators. Second, it is necessary to consider more fully how animals may perceive their environment (and each other) and how development progresses. Although it is convenient to assess fluctuating asymmetry in terms of two-dimensional lengths of traits, this may not be the way that an animal assesses asymmetry in that trait or accurately represents the variation in developmental trajectories. The potential role of fluctuating asymmetry in sexual selection lies at the intersection of perception and development. We need to consider variation in size, shape, and coloration—and demonstrate how these are related to perceptual abilities and developmental programs (e.g., measuring shape and size variation in integrated units).

It is highly unlikely that asymmetry is judged independently of other cues. It is possible to design studies to investigate the relative effect of asymmetry in realistic ways, yet few have been reported thus far (Swaddle, 1999b,c; Swaddle and Pruett-Jones, 2001). Within such experiments it is important to realize that to alter asymmetry the size of the two sides is altered, which could influence mate selection processes independent of the asymmetry. Therefore, it is crucial to balance any manipulation of size (whether that is average of left and right, or independent assessment of left or right) across the experimental design (Swaddle, 1997d). An example of such a design is to present animals with a population of asymmetry values, and to balance presentation of asymmetry cues in terms of size characteristics (cf. Swaddle, 1999c). In this particular example, the intent

was for birds to discriminate between symmetric and asymmetric patterns. By randomizing average trait size among paired (symmetric and asymmetric) presentations, a schedule was produced in which birds could not succeed by simply favoring average size, left size, or right size (Swaddle, 1999c).

In terms of size–asymmetry relations, authors commonly report the relationship between size and asymmetry of a trait to interpret the mode of selection acting on trait size (Møller and Pomiankowski, 1993; Møller and Swaddle, 1997). Supposedly, a U-shaped relationship is indicative of stabilizing selection, whereas a negative relation between size and asymmetry indicates directional selection—which could imply active sexual selection for increased size. However, there is no clear prediction as to the relationship between developmental stability, phenotypic variance, and trait size under directional selection regimens (review in Swaddle *et al.*, 2002), and possession of relatively larger traits in cases of sexual dimorphism is not a clear predictor of directional selection (Swaddle *et al.*, 2000; Karubian and Swaddle, 2001). Therefore, interpreting size–asymmetry relations is problematic, and a negative relationship may not reliably indicate directional sexual selection.

Future investigations of the role of fluctuating asymmetry in sexual selection could further address the relative direct and indirect effects of asymmetry on mate selection processes through matched observational studies and naturalistic phenotypic manipulations. Does fluctuating asymmetry directly affect performance, or is it indirectly related through its relationship with other parameters important to mate selection?

VI. FLUCTUATING ASYMMETRY, ANIMAL BEHAVIOR, AND EVOLUTION

Many researchers have stated that fluctuating asymmetry must be both heritable and related to fitness for it to be evolutionarily relevant (Markow, 1995; Van Dongen and Lens, 2000). Although this is obviously true for adaptive evolution, it need not be true if fluctuating asymmetry is a neutral character (Section IV.E).

Fluctuating asymmetry data may be particularly challenging to evolutionary biologists, as experiments indicate that asymmetry can have direct fitness effects (indicating a selection pressure) and yet have little or no additive genetic variance. This scenario would indicate that fluctuating asymmetry would have a minimal effect on long-term evolution but would still appear relevant to behavioral ecologists and functional morphologists investigating the proximate mechanisms of behaviors and biomechanics. For example, analysis of the effects of within-individual variation of flight

feather asymmetry between subsequent molts has shown that the noise associated with the production of asymmetry has significant effects on flight performance (Swaddle, 1997a). Presumably, reduced flight performance will have physiological and behavioral costs, and hence will likely directly affect fitness (cf. Witter *et al.*, 1994). This study indicates that small variation in asymmetry can have large direct consequences. Similarly, small variation in limb asymmetry negatively influences antipredatory performance in the house fly *Musca domestica* (Swaddle, 1997b) and the lizard *Psammotromus algirus* (Martin and Lopez, 2001), predation ability in the male yellow dungfly *Scathophaga stercoraria* (Swaddle, 1997b), and fighting ability in the male shore crab *Carcinus maenas* (Sneddon and Swaddle, 1999). In any of these cases, if asymmetry shows heritability, then there is the potential for natural selection against asymmetry. Early experiments clearly indicated that some birds are influenced by the symmetric appearance of artificial characters (Møller, 1993b; Swaddle and Cuthill, 1994b; Swaddle, 1996), which indicated active mate preference selection mechanisms against asymmetry, yet, these interpretations may have little relevance to the evolutionary design of sexually selected characters if there is no heritability for asymmetry.

There are two well-studied systems in which there are heritability estimates, fitness correlations, and analyses investigating whether asymmetry influences behavior: the barn swallow and *Drosophila* (review in Møller and Swaddle, 1997). The barn swallow is a much lauded example of behavioral processes in sexual selection, and it also quickly became a model species for studying fluctuating asymmetry (Møller, 1994c). Møller has reported that outer tail feather asymmetry is both heritable and negatively related to a variety of fitness parameters (Møller, 1997; Møller and Thornhill, 1997). In addition, Møller has suggested that female swallows judge their mates on the basis of this asymmetry (Møller, 1992b), in association with a number of other characteristics (Møller, 1994c). Studies have indicated that parental asymmetry is not related to offspring asymmetry or offspring quality (Cadée, 2000a). Also, it is not clear how much asymmetry would actually influence natural mate choice mechanisms given the strength of the relations between other visual and social cues with mate preferences in barn swallows (Møller, 1994c).

The heritability of asymmetry in chaetae and sternopleural bristles appears low in *Drosophila* (Reeve, 1960; Scheiner *et al.*, 1991), although it does appear possible to select for bristle fluctuating asymmetry (Mather, 1953). In addition, heritability of asymmetry between correlated developmental units of bristle morphology is greater than heritability of simple bristle count asymmetry, implying that developmental instability of bristles may have a significant additive genetic component but that previous

measures of fluctuating asymmetry do not represent this (Polak and Starmer, 2001). However, there is little evidence that bristle asymmetry is related to fitness parameters in species of *Drosophila* (Markow, 1987; Markow and Ricker, 1992; Markow *et al.*, 1996; Polak, 1997; Hoffmann *et al.*, 1998; Hoikkala *et al.*, 1998)

Hence, even in these two well-studied systems, it is not clear how much fluctuating asymmetry would actually affect adaptive evolutionary processes. Perhaps, in many systems, fluctuating asymmetry is a neutral trait or a trait with minimal additive genetic variance.

This does not mean that fluctuating asymmetry is not relevant to studies of animal behavior. One of the goals of this review is to illustrate how, if behavioral ecologists want to answer meaningful evolutionary questions about fluctuating asymmetry, they need to integrate approaches and tools from other disciplines and learn from their successes. In a complementary fashion, behaviorists have a great deal to contribute in terms of the direct effects of asymmetry on fitness, which behavioral ecologists are accustomed to studying through phenotypic manipulation experiments. At the moment, studies often appear sporadically as reports from researchers who decide to measure asymmetry in their favorite study organism and correlate it with any fitness measure at hand. While reporting such data has its merits in terms of raising awareness of the asymmetry debate, it fuels the fires of people with extreme views (both pro and con) and does little to bring resolution to any broader questions about fluctuating asymmetry and evolution. Researchers (and funding agencies) should consider longer-term studies of the impact and origins of fluctuating asymmetry, and they should follow through on correlations to understand what is really mediating those relationships. The study of fluctuating asymmetry suddenly became fashionable, and then was rapidly pilloried, but it is indeed a genuine and intriguing area of study for evolutionary biologists—including those interested in animal behavior.

VII. SUMMARY

The intention of this chapter has been to show why fluctuating asymmetry is relevant to behavioral ecologists, to illustrate where our knowledge about fluctuating asymmetry is lacking in important areas, and to offer suggestions that will help behavioral ecologists fill those gaps. In particular, relationships between asymmetry and fitness are reviewed. These relationships appear to be taxon and trait specific. The specificity of such relationships probably arises from the weak correlation of fluctuating asymmetry with developmental instability. This is one of the areas in which

more knowledge is needed, and several suggestions are made concerning how better to assay developmental instability. Common methodological problems of studying fluctuating asymmetry are discussed briefly.

In addition, it is important to understand how asymmetries arise, whether fluctuating asymmetry can be described as a generalized trait, whether asymmetries have a significant additive genetic component, and whether fluctuating asymmetry can be viewed as having adaptive significance. A hypothesis is presented that fluctuating asymmetry may have significant genetic redundancy and, in many cases, could be viewed as a neutral character. Fluctuating asymmetry may have nonlinear associations with fitness and only when asymmetry exceeds a threshold value will an apparent relationship with fitness parameters be observed. Also, environmental influences may dominate the development of fluctuating asymmetry—although there are limited indications of specific genes influencing asymmetry production.

Many behavioral ecologists have quantified fluctuating asymmetry in secondary sexual characters and investigated whether such asymmetry plays a role in sexual selection processes. Evidence of selection for symmetric individuals is commonly used to support “good genes” models of sexual selection. This position is refuted, as fluctuating asymmetry is largely affected by environmental influences, and a number of ways to expand our studies of sexual selection to incorporate direct, environmental benefits are suggested. In addition, some fundamental areas of sexual selection that require more attention before any conclusions can be drawn about the role of fluctuating asymmetry are highlighted. Notably, it is important to understand whether symmetry preferences exist and, if so, how they can arise independently of asymmetry–fitness associations. A better understanding of whether animals can detect and if so, how they respond to, natural asymmetry cues is also needed.

In the final section, a link between behavioral studies of fluctuating asymmetry and broader evolutionary questions is made, and it is suggested that researchers adopt a more integrated approach that brings together a proximate understanding of the impact of asymmetry with more long-term studies of the origins of asymmetry and evolutionary consequences of selection against fluctuating asymmetry.

Acknowledgments

I thank Rowan Lockwood, Dan Cristol, Paul Heideman, Charles T. Snowdon, Peter Slater, Tim Roper, and an anonymous reviewer for extensive, constructive comments on earlier drafts that dramatically improved the final version. I was financially supported by NSF Grant IBN-0133449.

References

- Amzallag, G. N. (2000). Canalization as a non-genetic source of adaptiveness during morphogenesis: Experimental evidence from analysis of reproductive development in *Sorghum bicolor*. *BioSystems* **57**, 95–107.
- Andalo, C., Bazin, A., and Shykoff, J. A. (2000). Is there a genetic basis for fluctuating asymmetry and does it predict fitness in the plant *Lotus corniculatus* grown in different environmental conditions? *Int. J. Plant Sci.* **161**, 213–220.
- Balmford, A., Jones, I. L., and Thomas, A. L. R. (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.
- Bjorksten, T. A., Pomiankowski, A., and Fowler, K. (2001). Temperature shock during development fails to increase the fluctuating asymmetry of a sexual trait in stalk-eyed flies. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 1503–1510.
- Blackenhorn, W. U., Reusch, T., and Muhlhauser, C. (1998). Fluctuating asymmetry, body size and sexual selection in the dung fly *Sepsis cynipsea*: Testing the good genes—assumptions and predictions. *J. Evol. Biol.* **11**, 735–753.
- Blough, D. S. (1969). Generalization gradient shape and summation in steady-state tests. *J. Exp. Anal. Behav.* **12**, 91–104.
- Bosch, J., and Marquez, R. (2000). Typanum fluctuating asymmetry, body size and mate choice in female mid-wife toads (*Alytes obstetricans*). *Behaviour* **137**, 1211–1222.
- Bourquet, D. (2000). Fluctuating asymmetry and fitness in *Drosophila melanogaster*. *J. Evol. Biol.* **13**, 515–521.
- Bryden, C. A., and Heath, D. D. (2000). The heritability of fluctuating asymmetry for multiple traits in chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **57**, 2186–2192.
- Cadée, N. (2000a). Parent barn swallow fluctuating asymmetry and offspring quality. *J. Avian Biol.* **31**, 495–503.
- Cadée, N. (2000b). Genetic and environmental effects on morphology and fluctuating asymmetry in nestling barn swallows. *J. Evol. Biol.* **13**, 359–370.
- Clarke, G. M. (1997). The genetic and molecular basis of developmental stability: The *Lucilia* story. *Trends Ecol. Evol.* **12**, 89–90.
- Clarke, G. M. (1998a). The genetic basis of developmental stability. IV. Individual and population asymmetry parameters. *Heredity* **80**, 553–561.
- Clarke, G. M. (1998b). Developmental stability and fitness: The evidence is not quite so clear. *Am. Nat.* **152**, 762–766.
- Clarke, G. M., Brand, G. W., and Whitten, M. J. (1986). Fluctuating asymmetry: A technique for measuring developmental stress caused by inbreeding. *Aust. J. Biol. Sci.* **39**, 145–153.
- Clarke, G. M., Yen, J. L., and McKenzie, J. A. (2000). Wings and bristles: Character specificity of the asymmetry phenotype in insecticide-resistant strains of *Lucilia cuprina*. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 1815–1818.
- Cote, S. D., and Festa-Bianchet, M. (2001). Life-history correlates of horn asymmetry in mountain goats. *J. Mammal.* **82**, 389–400.
- Cuervo, J. J., and Møller, A. P. (1999). Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relation to sex and mating system. *Biol. J. Linn. Soc.* **68**, 505–529.
- Cuthill, I. C., Swaddle, J. P., and Witter, M. S. (1993). Fluctuating asymmetry. *Nature* **363**, 217–218.
- Dill, M., and Heisenberg, M. (1995). Visual pattern memory without shape recognition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **349**, 143–152.

- Enquist, M., and Johnstone, R. A. (1997). Generalization and the evolution of symmetry preferences. *Proc. R. Soc. Lond. B Biol. Sci.* **264**, 1345–1348.
- Farner, D. C., and Barnard, C. J. (2000). Fluctuating asymmetry and sperm transfer in male decorated field crickets (*Gryllobates sigillatus*). *Behav. Ecol.* **47**, 287–292.
- Fusco, G., and Minelli, A. (2000). Developmental stability in geophilomorph centipedes. In "Progress in Studies on Myriapoda and Onychophora" (J. Wytwer and S. Golovatch, Eds.), pp. 73–82. *Fragmenta Faunistica* **43** (Suppl.), Polish Academy of Sciences, Warsaw, Poland.
- Gage, M. J. G. (1998). Influences of sex, size, and symmetry on ejaculate expenditure in a moth. *Behav. Ecol.* **9**, 592–597.
- Gangestad, S. W., and Thornhill, R. (1999). Individual differences in developmental precision and fluctuating asymmetry: A model and its implications. *J. Evol. Biol.* **12**, 402–416.
- Gangestad, S. W., Thornhill, R., and Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethol. Sociobiol.* **15**, 73–85.
- Goddard, K. W., and Lawes, M. J. (2000). Ornament size and asymmetry: Is the tail a reliable signal of male quality in the red-collared widowbird? *Auk* **117**, 366–372.
- Graham, J. H., Emlen, J. M., and Freeman, D. C. (1993). Developmental stability and its applications in ecotoxicology. *Ecotoxicology* **2**, 175–184.
- Graham, J. H., Emlen, J. M., Freeman, D. C., Leamy, L. J., and Kieser, J. A. (1998). Directional asymmetry and measurement of developmental instability. *Biol. J. Linn. Soc.* **64**, 1–16.
- Hardersen, S. (2000). Effects of carbaryl exposure on the last larval instar of *Xanthocnemis zealandica*: Fluctuating asymmetry and adult emergence. *Entomol. Exp. Appl.* **96**, 221–230.
- Hechter, R. P., Moodie, P. F., and Moodie, G.E.E. (2000). Pectoral fin asymmetry, dimorphism and fecundity in the brook stickleback, *Culaea inconstans*. *Behaviour* **137**, 999–1009.
- Hewa-Kapuge, S., and Hoffmann, A. A. (2001). Composite asymmetry as an indicator of quality in the beneficial wasp *Trichogramma* nr. *brassicae* (Hymenoptera: Trichogrammatidae). *J. Econ. Entomol.* **94**, 826–830.
- Hoffman, A. A., Hercus, M., and Dagher, H. (1998). Population dynamics of the *Wolbachia* infection causing cytoplasmic incompatibility in *Drosophila melanogaster*. *Genetics* **148**, 221–231.
- Hoikkala, A., Aspi, J., and Suvanto, L. (1998). Male courtship song frequency as an indicator of male genetic quality in an insect species, *Drosophila montana*. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 503–508.
- Houle, D. (1997). Comment on "A meta-analysis of the heritability of developmental stability" by Møller and Thornhill. *J. Evol. Biol.* **10**, 17–20.
- Houle, D. (1998). High enthusiasm and low *R*-squared. *Evolution* **52**, 1872–1876.
- Houle, D. (2000). A simple model of the relationship between asymmetry and developmental stability. *J. Evol. Biol.* **13**, 720–730.
- Jablonski, P. G., and Matyjasik, P. (1997). Chaffinch (*Fringilla coelebs*) epaulette display depends on the degree of exposure but not symmetry of intruder's epaulettes. *Behaviour* **134**, 1115–1121.
- Johnstone, R. A. (1994). Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature* **372**, 172–175.
- Jones, J. S. (1987). An asymmetrical view of fitness. *Nature* **325**, 298–299.
- Kalish, H. I., and Guttman, N. (1957). Stimulus generalization after equal training on two stimuli. *J. Exp. Psychol.* **53**, 139–144.

- Karubian, J., and Swaddle, J. P. (2001). Selection on females can create "larger males." *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 1–4.
- Kilgariff, J. L., Lambert, K. M., Henneberg, M., and Townsend, G. (2000). Fluctuating asymmetry of dermatoglyphic patterns in female monozygotic twins. *J. Dent. Res.* **79**, 1053.
- Klingenberg, C. P., and McIntyre, G. S. (1998). Geometric morphometrics of developmental instability: Analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution* **52**, 1363–1375.
- Klingenberg, C. P., and Nijhout, H. F. (1999). Genetics of fluctuating asymmetry: A developmental model of developmental instability. *Evolution* **53**, 358–375.
- Klingenberg, C. P., Badyaev, A. V., Sowry, S. M., and Beckwith, N. J. (2001). Inferring developmental modularity from morphological integration: Analysis of individual variation and asymmetry in bumblebee wings. *Am. Nat.* **157**, 11–23.
- Leamy, L. (1997). Is developmental stability heritable? *J. Evol. Biol.* **10**, 21–29.
- Leamy, L., Pomp, D., Eisen, E. J., and Cheverud, J. M. (2000). Quantitative trait loci for directional but not fluctuating asymmetry of mandible characters in mice. *Genet. Res.* **76**, 27–40.
- Leamy, L. J., Routman, E. J., and Cheverud, J. M. (1997). A search for quantitative trait loci affecting asymmetry of mandibular characters in mice. *Evolution* **51**, 957–969.
- Leamy, L. J., Routman, E. J., and Cheverud, J. M. (1998). Quantitative trait loci for fluctuating asymmetry of discrete skeletal characters in mice. *Heredity* **80**, 509–518.
- Lens, L., and Van Dongen, S. (2000). Fluctuating and directional asymmetry in natural bird populations exposed to different levels of habitat disturbance, as revealed by mixture analysis. *Ecol. Lett.* **3**, 516–522.
- Leung, B. (1998). Correcting for allometry in studies of fluctuating asymmetry and quality within samples. *Proc. R. Soc. Lond. Biol. Sci.* **265**, 1623–1629.
- Leung, B., and Forbes, M. R. (1996). Fluctuating asymmetry in relation to stress and fitness: Effects of trait type as revealed by meta-analysis. *Ecoscience* **3**, 400–413.
- Leung, B., Forbes, M. R., and Houle, D. (2000). Fluctuating asymmetry as a bioindicator of stress: Comparing efficacy of analyses involving multiple traits. *Am. Nat.* **155**, 101–115.
- Loeschke, V., Bundgaard, J., and Barker, J. S. F. (1999). Reaction norms across and genetic parameters at different temperatures for thorax and wing size traits in *Drosophila aldrichi* and *D. buzzatii*. *J. Evol. Biol.* **12**, 605–623.
- Ludwig, W. (1932). "Das Rechts-Links Problem in Tierreich und beim Menschen." Springer-Verlag, Berlin.
- Mardia, K. V., Bookstein, F. L., and Moreton, I. J. (2000). Statistical assessment of bilateral symmetry of shapes. *Biometrika* **87**, 285–300.
- Markow, T. A. (1987). Genetics and sensory basis of sexual selection in *Drosophila*. In "Evolutionary Genetics and Invertebrate Behavior" (M. D. Huettel, Ed.), pp. 89–95. Plenum, New York.
- Markow, T. A. (1995). Evolutionary ecology of developmental instability. *Annu. Rev. Entomol.* **40**, 105–120.
- Markow, T. A., and Clarke, G. M. (1997). Meta-analysis of the heritability of developmental stability: A giant step backward. *J. Evol. Biol.* **10**, 31–37.
- Markow, T. A., and Ricker, J. P. (1992). Male size, developmental stability, and mating success in natural populations of three *Drosophila* species. *Heredity* **69**, 122–127.
- Markow, T. A., Bustoz, D., and Pitnick, S. (1996). Sexual selection and a secondary sexual character in two *Drosophila* species. *Anim. B. Behav.* **52**, 759–766.
- Martin, J., and Lopez, P. (2000). Chemoreception, symmetry and mate choice in lizards. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 1265–1269.

- Martin, J., and Lopez, P. (2001). Hindlimb asymmetry reduces escape performance in the lizard *Psammodromus algirus*. *Physiol. Biochem. Zool.* **74**, 619–624.
- Mather, K. (1953). Genetical control of stability in development. *Heredity* **7**, 297–336.
- McAdams, H. H., and Arkin, A. (1999). It's a noisy business! Genetic regulation at the nanomolar scale. *Trends Genet.* **15**, 65–69.
- McKenzie, J. A., and Batterham, J. A. (1994). The genetic, molecular and phenotypic consequences of selection for insecticide resistance. *Trends Ecol. Evol.* **9**, 166–169.
- McKenzie, J. A., and Clarke, G. M. (1988). Diazinon resistance, fluctuating asymmetry and fitness in the Australian sheep blowfly, *Lucilia cuprina*. *Genetics* **120**, 213–220.
- Mealey, L., Bridgstock, R., and Townsend, G. C. (1999). Symmetry and perceived facial attractiveness: A monozygotic co-twin comparison. *J. Pers. Soc. Psychol.* **76**, 151–158.
- Merilä, J., and Björklund, M. (1995). Fluctuating asymmetry and measurement error. *Syst. Biol.* **44**, 97–101.
- Mogie, M., and Cousins, M. (2001). Are sample sizes usually at least an order of magnitude too low for reliable estimates of leaf asymmetry? *J. Theor. Biol.* **211**, 181–185.
- Møller, A. P. (1990). Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. B. Behav.* **40**, 1185–1187.
- Møller, A. P. (1992a). Parasites differentially increase fluctuating asymmetry in secondary sexual characters. *J. Evol. Biol.* **5**, 691–699.
- Møller, A. P. (1992b). Female preference for symmetrical male sexual ornaments. *Nature* **357**, 238–240.
- Møller, A. P. (1993a). Morphology and sexual selection in the barn swallow *Hirundo rustica* in Chernobyl, Ukraine. *Proc. R. Soc. Lond. B Biol. Sci.* **252**, 51–57.
- Møller, A. P. (1993b). Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.* **32**, 371–376.
- Møller, A. P. (1994a). Symmetrical male sexual ornaments, paternal care, and offspring quality. *Behav. Ecol.* **5**, 188–194.
- Møller, A. P. (1994b). Sexual selection in the barn swallow (*Hirundo rustica*). IV. Patterns of fluctuating asymmetry and selection against asymmetry. *Evolution.* **48**, 658–670.
- Møller, A. P. (1994c). "Sexual Selection and the Barn Swallow." Oxford University Press, Oxford.
- Møller, A. P. (1997). Developmental stability and fitness: A review. *Am. Nat.* **149**, 916–932.
- Møller, A. P., and Eriksson, M. (1994). Patterns of fluctuating asymmetry in flowers: Implications for honest signalling for pollinators. *J. Evol. Biol.* **7**, 97–113.
- Møller, A. P., and Pomiankowski, A. (1993). Fluctuating asymmetry and sexual selection. *Genetica* **89**, 267–279.
- Møller, A. P., and Sorci, G. (1998). Insect preference for symmetrical artificial flowers. *Oecologia* **114**, 37–42.
- Møller, A. P., and Swaddle, J. P. (1997). "Asymmetry, Developmental Stability and Evolution." Oxford University Press, Oxford.
- Møller, A. P., and Thornhill, R. (1997). A meta-analysis of the heritability of developmental stability. *J. Evol. Biol.* **10**, 1–16.
- Morris, M. R., and Casey, K. (1998). Female swordtail fish prefer symmetrical sexual signal. *Anim. Behav.* **55**, 33–39.
- Nachman, G., and Heller, K. E. (1999). Fluctuating asymmetry as an index of fitness: Causality or statistical artifact? *Oikos* **86**, 357–365.
- Nosil, P., and Reimchen, T. E. (2001). Tarsal asymmetry, nutritional condition, and survival in water boatmen (*Callicorixa vulnerata*). *Evolution* **55**, 712–720.

- Palmer, A. R. (1994). Fluctuating asymmetry analyses: A primer. In "Developmental Instability: Its Origins and Evolutionary Implications" (T. A. Markow, Ed.), pp. 335–364. Kluwer, Dordrecht.
- Palmer, A. R. (1996a). From symmetry to asymmetry: Phylogenetic patterns of asymmetry variation in animals and their evolutionary significance. *Proc. Natl. Acad. Sci. USA* **93**, 14279–14286.
- Palmer, A. R. (1996b). Waltzing with asymmetry. *Bioscience* **46**, 518–532.
- Palmer, A. R. (1999). Detecting publication bias in meta-analyses: A case study of fluctuating asymmetry and sexual selection. *Am. Nat.* **154**, 220–233.
- Palmer, A. R. (2000). Quasireplication and the contract of error: Lessons from sex ratios, heritabilities and fluctuating asymmetry. *Annu. Rev. Ecol. Syst.* **31**, 441–480.
- Palmer, A. R., and Strobeck, C. (1986). Fluctuating asymmetry: Measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* **17**, 391–421.
- Palmer, A. R., and Strobeck, C. (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.
- Parsons, P. A. (1992). Fluctuating asymmetry: A biological monitor of environmental and genomic stress. *Heredity* **68**, 361–364.
- Pechenkina, E. A., Benfer, R. A., Vershoubskaya, G. G., and Kozlov, A. I. (2000). Genetic and environmental influence on the asymmetry of dermatoglyphic traits. *Am. J. Phys. Anthropol.* **111**, 531–534.
- Pélabon, C., and Joly, P. (2000). What, if anything, does visual asymmetry in fallow deer antlers reveal? *Anim. Behav.* **59**, 193–199.
- Pélabon, C., and van Breukelen, L. (1998). Asymmetry in antler size in roe deer (*Capreolus capreolus*): An index of individual and population conditions. *Oecologia* **116**, 1–8.
- Perfectti, F., and Camacho, J. P. M. (1999). Analysis of genotypic differences in developmental stability in *Annona cherimola*. *Evolution* **53**, 1396–1405.
- Pertoldi, C., Podesta, M., Loeschcke, V., Schandorff, S., Marsili, L., Mancusi, C., Nicolosi, P., and Randi, E. (2000). Effect of the 1990 die-off in the northern Italian seas on the developmental stability of the striped dolphin *Stenella coeruleoalba* (Meyen, 1833). *Biol. J. Linn. Soc.* **71**, 61–70.
- Polak, M. (1997). Ectoparasitism in mothers causes higher FA in their sons: Implications for sexual selection. *Am. Nat.* **149**, 955–974.
- Polak, M., and Starmer, W. T. (2001). The quantitative genetics of fluctuating asymmetry. *Evolution* **55**, 498–511.
- Quek, K. C., Sodhi, N. S., and Kara, A. U. (1999). Absence of positive correlation between fluctuating asymmetry and parasitism in the rock pigeon. *J. Avian Biol.* **30**, 225–229.
- Reeve, E. C. R. (1960). Some genetic tests on asymmetry of sternopleural chaeta number in *Drosophila*. *Genet. Res.* **1**, 151–172.
- Rettig, J. E., Fuller, R. C., Corbett, A. L., and Getty, T. (1997). Fluctuating asymmetry indicates levels of competition in an even-aged popular clone. *Oikos* **80**, 123–127.
- Roux-Rouquie, M. (2000). Genetic and epigenetic regulation schemes: Need for an alternative paradigm. *Mol. Genet. Metab.* **71**, 1–9.
- Rowe, L., Repasky, R. R., and Palmer, A. R. (1997). Size-dependent asymmetry: Fluctuating asymmetry versus antisymmetry and its relevance to condition-dependent signaling. *Evolution* **51**, 1401–1408.
- Rutherford, S. L., and Lindquist, S. (1998). Hsp90 as a capacitor for morphological evolution. *Nature* **396**, 336–342.
- Salonen, V., and Lammi, A. (2001). Effects of root hemiparasitic infection on host performance: Reduced flower size and increased flower asymmetry. *Ecoscience* **8**, 185–190.

- Sasal, P., and Pampoulie, C. (2000). Asymmetry, reproductive success and parasitism of *Pomatoschistus microps* in a French lagoon. *J. Fish Biol.* **57**, 382–390.
- Scheib, J. E., Gangestad, S. W., and Thronhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 1913–1917.
- Scheiner, S. M., Caplan, R. L., and Lyman, R. F. (1991). The genetics of phenotypic plasticity. III. Genetic correlations and fluctuating asymmetries. *J. Evol. Biol.* **4**, 51–68.
- Schlaepfer, M. A., and McNeil, J. N. (2000). Are virgin male lepidopterans more successful in mate acquisition than previously mated individuals? A study of the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Can. J. Zool.* **78**, 2045–2050.
- Shykoff, J. A., and Møller, A. P. (1999). Fitness and asymmetry under different environmental conditions in the barn swallow. *Oikos* **86**, 152–158.
- Simmons, L. W., Tomkins, J. L., Kotiaho, J. S., and Hunt, J. (1999a). Fluctuating paradigm. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 593–595.
- Simmons, L. W., Beesley, L., Lindhjem, P., Newbound, D., Norris, J., and Wayne, A. (1999b). Nuptial feeding by male bushcrickets: An indicator of male quality? *Behav. Ecol.* **10**, 263–269.
- Sneddon, L. U., and Swaddle, J. P. (1999). Asymmetry and fighting performance in the shore crab, *Carcinus maenas*. *Anim. Behav.* **58**, 431–435.
- Soulé, M. E., and Baker, B. (1968). Phenetics of natural populations. IV. The population asymmetry parameter in the butterfly *Coenonympha tullia*. *Heredity* **23**, 611–614.
- Swaddle, J. P. (1996). Reproductive success and symmetry in zebra finches. *Anim. Behav.* **51**, 203–210.
- Swaddle, J. P. (1997a). Within-individual changes in developmental stability affect flight performance. *Behav. Ecol.* **8**, 601–604.
- Swaddle, J. P. (1997b). Developmental stability and predation success in an insect predator–prey system. *Behav. Ecol.* **8**, 433–436.
- Swaddle, J. P. (1997c). On the heritability of developmental stability. *J. Evol. Biol.* **10**, 57–61.
- Swaddle, J. P. (1997d). Experimental design and the signalling properties of fluctuating asymmetry. *Anim. Behav.* **54**, 1034–1037.
- Swaddle, J. P. (1999a). Visual signalling by asymmetry: A review of perceptual processes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **354**, 1383–1393.
- Swaddle, J. P. (1999b). Is fluctuating asymmetry a visual signal? In “Animal Signals” (Y. Espmark, T. Amundsen, and G. Rosenqvist, Eds.), pp. 155–175. Tapir Academic Press, Trondheim.
- Swaddle, J. P. (1999c). Limits to length asymmetry detection in starlings: Implications for biological signalling. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 1299–1303.
- Swaddle, J. P., and Cuthill, I. C. (1994a). Female zebra finches prefer males with symmetric chest plumage. *Proc. R. Soc. Lond. B Biol. Sci.* **258**, 267–271.
- Swaddle, J. P., and Cuthill, I. C. (1994b). Preference for symmetric males by female zebra finches. *Nature* **367**, 165–166.
- Swaddle, J. P., and Pruett-Jones, S. (2001). Experimental investigation of the acquisition of learned symmetry discrimination in starlings. *Am. Nat.* **158**, 300–307.
- Swaddle, J. P., and Witter, M. S. (1995). Chest plumage, dominance and fluctuating asymmetry in female starlings. *Proc. R. Soc. Lond. B Biol. Sci.* **260**, 219–223.
- Swaddle, J. P., and Witter, M. S. (1997). On the ontogeny of developmental stability in a stabilized trait. *Proc. R. Soc. Lond. B Biol. Sci.* **264**, 329–334.
- Swaddle, J. P., and Witter, M. S. (1998). Cluttered habitats reduce wing asymmetry and increase flight performance in European starlings. *Behav. Ecol. Sociobiol.* **42**, 281–287.
- Swaddle, J. P., Witter, M. S., and Cuthill, I. C. (1994). The analysis of fluctuating asymmetry. *Anim. Behav.* **48**, 986–989.

- Swaddle, J. P., Pruett-Jones, S., and Karubian, J. (2000). A novel evolutionary pattern of reversed sexual dimorphism in fairy-wrens: Implications for sexual selection. *Behav. Ecol.* **11**, 345–349.
- Swaddle, J. P., Arnold, S. J., and Pruett-Jones, S. (2003). Phenotypic variance and evolution of sexual dimorphism. (Submitted.)
- Thornhill, R. (1992). Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behav. Ecol.* **3**, 277–283.
- Thornhill, R., and Møller, A. P. (1998). The relative importance of size and asymmetry in sexual selection. *Behav. Ecol.* **9**, 546–551.
- Tomkins, J. L. (1999). The ontogeny of asymmetry in earwig forceps. *Evolution* **53**, 157–163.
- Tomkins, J. L., and Simmons, L. W. (1998). Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L. *Anim. Behav.* **56**, 347–356.
- Tomkins, J. L., and Simmons, L. W. (1999). Heritability of size but not symmetry in a sexually selected trait chosen by female earwigs. *Heredity* **82**, 151–157.
- Van Dongen, S. (1998a). How repeatable is the estimation of developmental stability by fluctuating asymmetry? *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 1423–1427.
- Van Dongen, S. (1998b). The distribution of individual fluctuating asymmetry: Why are the coefficients of variation of the unsigned FA so high? *Ann. Zool. Fenn.* **35**, 79–85.
- Van Dongen, S. (1999). Accuracy and power in the statistical analysis of fluctuating asymmetry: Effects of between individual heterogeneity in developmental instability. *Ann. Zool. Fenn.* **36**, 45–52.
- Van Dongen, S. (2000). The heritability of fluctuating asymmetry: A Bayesian hierarchical model. *Ann. Zool. Fenn.* **37**, 15–23.
- Van Dongen, S. (2001). Modelling developmental instability in relation to individual fitness: A fully Bayesian latent variable model approach. *J. Evol. Biol.* **14**, 552–563.
- Van Dongen, S., and Lens, S. (2000). The evolutionary potential of developmental instability. *J. Evol. Biol.* **13**, 326–335.
- Van Dongen, S., Molenberghs, G., and Matthysen, E. (1999a). The statistical analysis of fluctuating asymmetry: REML estimation of a mixed regression model. *J. Evol. Biol.* **12**, 94–102.
- Van Dongen, S., Sprengers, E., Löfstedt, C., and Matthysen, E. (1999b). Fitness components of male and female winter moths (*Operophtera brumata* L.) (Lepidoptera, Geometridae) relative to measures of body size and asymmetry. *Behav. Ecol.* **10**, 659–665.
- Van Dongen, S., Sprengers, E., and Löfstedt, C. (2001). Lack of evolutionary potential of developmental instability of front tibia length in the Indian meal moth (*Plodia interpunctella*). *Belgian J. Zool.* **131**, 75–82.
- Van Valen, L. (1962). A study of fluctuating asymmetry. *Evolution* **16**, 125–162.
- Vøllestad, L. A., Hindar, K., and Møller, A. P. (1999). A meta-analysis of fluctuating asymmetry in relation to heterozygosity. *Heredity* **83**, 206–218.
- Waddington, C. H. (1957). “The Strategy of the Genes.” Allen and Unwin, London.
- Whitlock, M. (1996). The heritability of fluctuating asymmetry and the genetic control of developmental stability. *Proc. R. Soc. Lond. B Biol. Sci.* **263**, 849–853.
- Whitlock, M. (1998). The repeatability of fluctuating asymmetry: A revision and extension. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 1429–1431.
- Whitlock, M. C., and Fowler, K. (1997). The instability of stability studies. *J. Evol. Biol.* **10**, 63–67.
- Windig, J. J., and Nylin, S. (2000). How to compare fluctuating asymmetry of different traits. *J. Evol. Biol.* **13**, 29–37.

- Witter, M. S., Cuthill, I. C., and Bonser, R. H. C. (1994). Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.* **48**, 201–222.
- Woods, R. E., Sgrò, C. M., Hercus, M. J., and Hoffmann, A. A. (1999). The association between fluctuating asymmetry, trait variability, trait heritability, and stress: A multiply replicated experiment on combined stress in *Drosophila melanogaster*. *Evolution* **53**, 493–505.
- Zakharov, V. M. (1992). Population phenogenetics: Analysis of developmental stability in natural populations. *Acta Zool. Fenn.* **191**, 7–30.
- Zakharov, V. M. (2001). Ontogeny and population: Developmental stability and population variation. *Russian J. Ecol.* **32**, 146–150.