Fluctuating asymmetry and sexual selection

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Interest in fluctuating asymmetry, FA (Box 1), has recently spread across diverse disciplines in the life sciences, including medicine, genetics, conservation and developmental biology, and behavioral ecology[51]. FA allows researchers to evaluate a basic aspect of viability fitness, namely, developmental stability – the capacity to develop properly in the face of genetic and environmental stresses that tend to upset development. Behavioral ecologists have recently begun asking whether random deviations from bilateral symmetry in individuals (i.e. in traits that show FA at the population level) are correlated with mating success and if mate-choice criteria related to symmetry yield more symmetrical or more viable offspring. The main impetus for such study is the quest to evaluate condition-dependent models of sexual selection (e.g. Ref. 5), which postulate that traits that evolved by sexual selection will be designed to convey information about individual viability. The focus of this review is on the potential usefulness of FA in determining the aspects of viability fitness that are assessed in sexual selection.

Sexual-selection studies typically identify traits of males that proximately relate to sexual success, such as body size, courtship performance or ornamentation. Such traits may be termed 'adaptive', but such an interpretation is fraught with ambiguity[6]. To analyse male sexual traits and female mate-selection mechanisms as 'adaptations', that is, as having been designed by selection as phenotypic solutions to specific fitness-related problems, we must understand their functional design[7,8]. One way to investigate functional design is to relate secondary sexual traits and sexually discriminatory behaviors to the efficacy of mechanisms in adults and offspring which causally mediate fitness, such as those underlying metabolic, immunological and developmental competence.

Determining the connections between aspects of male fitness and criteria used by females to discriminate between potential mates is central to understanding the nature of sexual selection. For example, the functional form of the relationship between the size and symmetry of a male ornament that is a target of sexual selection may aid in distinguishing the roles of 'good genes' versus 'fisherian' sexual selection in its evolution[9–14]. A predominantly negative relationship indicates condition-dependent development of the trait as expected under sexual selection for good, viability-enhancing genes. Flat or positive relationships are predicted for fisherian traits that enhance fertility via their 'aesthetic' quality.

Behavioral ecologists are being attracted to the study of within-individual morphological variability, manifested in random deviations from bilateral symmetry, as a means of ascertaining the stress susceptibility of developmental regulatory mechanisms. Several early successes indicate that incorporating measures of symmetry into sexual-selection studies may help link individual sexual success to a basic component of viability – developmental stability

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in species with reproductive ecologies permissive of a role for FA in sexual selection.

Single-trait FA and overall developmental competence

A preliminary question is whether sexual selection for developmental competence should tend to address whole-organism or trait-specific homeostatic mechanisms. Whole-organism mechanisms seemingly exist. In *Drosophila*, the development of musculature depends on a series of temporally separate patterning processes that integrate segment-specific regulatory signals and signals that are common to all segments[24]. Also, allometry may

Although the logic behind the burgeoning interest in FA's role in sexual selection seems tight, the matter evidently is complicated. Studying traits that are easy to measure in species that are close at hand leads to discrepant results among studies of different organisms (contrast Refs 15 and 16 with 17, Ref. 18 with 19, and Refs 20–22 with 23. References 22 and 23 illustrate species-dependent effects of symmetry in *Drosophila*; Box 2). We feel that the next step in evaluating the role of FA in sexual selection is to focus on traits that should reveal the most about developmental competence

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Box 1. Fluctuating asymmetry

Fluctuating asymmetry (FA) has long been of interest to population[1,2] and conservation biologists[3]. FA is a population phenomenon defined as random deviation from perfect bilateral symmetry in a morphological trait for which differences between the right and left sides have a mean of zero and are normally distributed. FA is thus distinguished from two other forms of asymmetry which normally do not reflect perturbations of development, i.e. directional and antisymmetry. The degree of random asymmetry expressed by individuals can vary greatly in a given population. While individual random asymmetry often is proximately caused by environmental stress, the ability to execute developmental programs correctly and uniformly in the face of such stress has a genetic basis. One important strength of asymmetry as a measure of individual viability is that it represents a deviation from a *known* morphogenetic ideal, that is, perfect symmetry. Since both sides of any bilateral trait are produced by the same genome, the degree of symmetry reveals an individual's ability to canalize development in the face of stress[1,4]. Unlike indices of phenotypic quality, such as body size or fecundity, for which it is difficult to specify an optimum (e.g. optimum size may vary year to year depending upon food availability or abiotic conditions), asymmetry seemingly provides an *unambiguous and consistently valid* measure of maladaptation. However, note that since a large proportion of individuals in a population will have asymmetries close to zero for any given trait due to chance alone, it may be necessary to study deviations from symmetry in multiple traits to obtain reliable measures of developmental competence for individuals[50].

require some whole-organism coordination. Negative correlations between heterozygosity and asymmetry suggest a whole-organism effect, as does the generation of multi-trait asymmetry by mutation and other genetic perturbations[3,4,25]. For example, if the strength of asymmetry correlations among traits varies with heterozygosity, then heterozygosity must at least partly underlie whole-organism regulation. If multiple traits respond to experimentally imposed directional selection on a single trait's FA, operation of a whole-organism mechanism is again suggested.

Mate evaluation of overall developmental competence based on traits whose developmental control is dominated by trait-specific mechanisms would require an integrated analysis of many separate phenotypic features (see Box 1). Focusing on a few traits that are mainly under the influence of whole-organism regulation would be more efficient; such traits might provide a comprehensive summary of asymmetry throughout the body. However, the often poor correlations between the asymmetry of different traits within individuals (see below) suggest that organism-wide regulatory mechanisms generally are weak compared to trait-specific ones. If the asymmetry of individual, secondary sexual traits is not more predictive of overall asymmetry than the asymmetry of individual, nonsexual traits, then there is no evidence that sexual traits have been designed by selection to reveal the quality of whole-organism homeostatic mechanisms *per se*. Since morphological features that we might try to correlate with sec-

ondary sexual traits may be under strong trait-specific regulation, it may be necessary to use composite indices integrating symmetry measures of many traits in order to detect any revealing capacity of secondary sexual traits with regard to organism-wide developmental competence.

Studies often fail to find inter-trait FA correlations within individuals[17,19,23,26–30]; but see Box 3. Inter-trait correlations may be degraded by differential timing of development. A stress imposed at a certain time will mainly affect traits that are then at a pivotal stage of development. At one point in a given trait's development, stress might test whole-organism homeostatic mechanisms and at other times trait-specific ones. Restricting correlations to traits that develop at about the same time might yield higher correlations. In evaluating the issue of inter-trait correlations, it may be important to distinguish between studies focusing on known targets of selection versus studies without such knowledge. Traits under directional sexual selection may be more likely to reveal overall developmental competence (see below), and so FA in such traits should be better correlated with multi-trait FA. One probably could argue that few studies have measured enough different traits to arrive at a realistic estimate of inter-trait FA correlations.

Directional selection, condition-dependent handicaps and FA

Møller and Pomiankowski[9,10] detail the argument that the FA of condition-dependent handicaps under directional selection for size should provide information concerning overall developmental competence. There are two theoretical reasons for thinking that such secondary sexual traits should honestly advertise the quality of mechanisms that regulate development: they are (1) thought to be expensive to produce, perhaps representing an absolute limit to production; and (2) under strong directional selection, which creates genetic stresses that reduce the effectiveness of developmental homeostatic mechanisms (Box 4). This effect of directional selection appears quite general – transient developmental destabilization also has been observed in the evolution of pesticide resistance[36].

Observed patterns of FA in secondary sexual traits often differ from those in nonsexual morphological traits in ways that support the above theory. Secondary sexual characteristics sometimes show greater FA than do non-sexual traits[15,37–39] and so may be especially vulnerable to stress-induced developmental perturbations. In one experiment in which parasitic stress was manipulated experimentally[40], a trait previously established as being under sexual selection for symmetry[18] responded more strongly than nonsexual traits. In accord with the notion that individuals with large secondary sexual characteristics are of overall higher quality, FA is often negatively related to trait size in secondary sexual traits, while FA is either positively related or unrelated to size in other traits[15,16,28,35,37–39,41].

Thus, from the standpoint of an individual trying to assess the overall quality of a potential mate's developmental mechanisms, the crucial result of directional selection on a given trait may be to disable trait-specific homeostatic mechanisms, thereby better revealing the capabilities of whole-organism mechanisms. However, recent work suggests that empirical findings in support of this general model may not always come easily[17], so it may be worth considering potential complications.

Production and maintenance expenses *per se* may have little to do with the difficulty of making a trait symmetrical.

Consider an analogy – the work of a cabinet-maker. Plenty of food, electrical power and excellent wood will not yield the best product if his tools are of poor quality, or his skill is wanting. Energy and material resources alone do not make the job easy. Moreover, it is reasonable to assume that expensive traits are under closer control of homeostatic mechanisms than less expensive traits; the strength of selection for stabilizing development of a trait (or re-stabilizing it after a period of directional selection) should be positively related to the proportion of the organism's total developmental energy budget used in its construction. And how much do we know about the expense of sexual traits like elaborate tail ornaments relative to basic equipment such as wings, skulls, beaks and femurs? Comparisons of the actual expense of traits and their patterns of FA expression are needed.

Directional selection weakens developmental regulation only during evolutionary response. Destabilization lasts only until evolution ceases and trait-specific regulatory mechanisms undergo compensatory adjustments. Directional evolution probably is no longer persistent in some secondary sexual traits and the genetic basis for their regulation may have had time to 'catch up' and compensate for the new expression of the trait. In traits where FA is actively discriminated against in sexual selection[18], compensation time may be short. Simultaneous sexual selection for size and symmetry leads to stabilizing selection on size when the trait is complex or costly enough to have condition-dependent development. Moreover, in most cases one would not be able to tell how long a time has elapsed since a trait has been directionally evolving. Thus, exaggerated expression may not be a consistently useful criterion for deciding what traits are likely to be under weak trait-specific regulation.

The symmetry of conformationally complex traits whose performance depends upon a precise two- or three-dimensional structure may reveal susceptibility to developmental stress with great sensitivity. Increasing the size of a trait via directional selection may not loosen the hold of the original regulatory mechanisms as much as redesigning the trait toward a higher level of complexity (e.g. male versus female pedipalps in spiders). There are many ways in which a complex structure can be measured. An understanding of the precise functional design of the structure of interest may lead to more relevant measurements[17]. Powerful new morphometric procedures[42] that fully represent geometric and conformational complexities should be favored over simple linear measures.

Non-directionally selected traits and FA

Directional selection is not the only circumstance under which FA of a single trait may reflect overall developmental competence. Symmetry of inexpensive traits which perform in narrow fitness domains should also reveal overall developmental competence, because selection to stabilize their development via trait-specific mechanisms will be weak. Lion-whisker-spot patterns serve as an example of a low-cost trait whose symmetry is related to survivorship[43].

Allometric growth implies a mechanism to coordinate size and shape relationships throughout an organism. However, some traits break the usual allometric relationship. Disruption of allometry can be due to directional selection for increased size of a trait or from selection that stabilizes the trait regardless of body size (e.g. in lock-and-key genitalia of spiders). Traits that are out of allometry are being shielded from whole-organism regulatory mech-

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Box 4. Directional selection and developmental homeostasis

Directional selection places trait-specific homeostatic mechanisms under genetic stress as control of the trait's development is relaxed to expedite the response to selection. Readaptation of regulatory mechanisms to stabilize the trait at a new level of expression lags behind the changing expression of the trait itself during directional evolution. Like testosterone-mediated expression of secondary sexual traits, these genetic effects constitute an honesty-enforcing mechanism associated with directionally evolving extravagant sexual characters. Testosterone reduces immunological competence[33,34] (see Box 5); individuals with weak immune systems risk illness if they develop traits that are too extravagant, because this necessitates higher testosterone titers than their already-disadvantaged immune functions can bear. Similarly, the directional sexual selection that leads to exaggerated expression of a trait handicaps the systems controlling development[35]. So, an individual expressing a high degree of symmetry in a trait that is directionally evolving in the population effectively proclaims that, in spite of the genetic stress to which his homeostatic mechanisms are being subjected, they remain strong enough to stabilize development. Since directional selection leading to exaggerated sexual traits probably disables trait-specific regulatory mechanisms, asymmetry expressed in these traits may reflect the integrity of organism-wide regulation, thereby revealing overall developmental competence. Alternatively, if trait-specific control mechanisms within an individual are designed similarly across traits, then the performance of one such mechanism while subject to genetic stress may provide a comprehensive test of developmental stability.

Box 5. Immunocompetence and FA

The symmetry of secondary sexual traits might reveal the quality of mechanisms that indirectly affect development by ameliorating stresses that homeostatic mechanisms must contend with. Immune system quality may underlie much variation in individual symmetry. Traits whose developmental mechanisms are under genetic stress due to directional selection may be especially vulnerable to disruptive effects of pathogens. Simultaneously, the raised testosterone levels that cause differentiation of sexual traits tend to weaken the immune system's opposition to pathogens. So, not only is the immune system down while a secondary sexual trait is growing, but any slip in its performance during this time may be registered with extraordinary sensitivity in the asymmetry of the trait. Another special feature of the relationship between immunocompetence and symmetry in secondary sexual traits of vertebrates is that their symmetry could more precisely reflect the potential of a mature immune system than traits that develop during subadult life – secondary sexual traits arise only after the immune system has completed development.

It would be interesting to examine the effects of artificially increased testosterone titers on the size and symmetry of secondary sexual versus nonsexual traits. This experiment would create cheaters for a trait that is normally expressed honestly, because the negative relationship between testosterone and immunocompetence prevents low-quality individuals from developing extravagant traits without risking sickness or pathogen-induced asymmetry. If sexual traits are designed to reveal immunocompetence via symmetry, then their symmetry should be more positively correlated with testosterone titers than the symmetry of nonsexual traits.

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anisms that a majority of the phenotype obey. Loss of such input may destabilize development.

An ability to correct early mistakes in development is expected to be part of any organism's set of developmental adaptations. All else being equal, correction mechanisms probably function better when given more time. The opportunity for correction is minimized in traits whose development is delayed until late in ontogeny, or traits that undergo rapid seasonal development in adults. The speed with which an individual invests in a developing trait may bear more on the difficulty of perfecting the trait than the amount invested *per se*. Asymmetry in many secondary sexual traits may be non-correctable because of their late or seasonal development.

In some sexual selection systems, females may evaluate a morphological trait which is under stabilizing selection and whose proper functioning is directly related to viability

(see Box 2). Sexual selection of this type might involve assessment of the trait's size, conformation and/or symmetry; but directional evolution and trait exaggeration would not be expected. The FA of these traits would provide information on trait-specific rather than whole-organism developmental homeostasis. The symmetry of traits under stabilizing selection may also affect sexual success by influencing performance in intrasexual competition[20,21,27,41].

Relating FA to sexual performance

Minor mistakes in morphological development may be compensated for behaviorally. Thus, sexual signals that can be modulated easily during display (e.g. aspects of bird or frog vocalizations that can be adjusted neuromuscularly) may be inappropriate candidates for assessment of FA's role in sexual selection. The suggestion has also been made that a certain amount of subtle FA (e.g. that which persists in direction and magnitude between molts in hemi-metabolus arthropods) may be unrelated to stress resistance, and would arise even in ideal developmental environments due to a specific genetic predisposition[44]. Like measurement error, such FA would represent a source of 'noise' in studies of the signal function of FA in sexual selection.

Correlations between composite measures of FA and sexual success or viability may be affected by variation among traits in the degree of difficulty involved in producing perfect symmetry. When relating composite FA to performance, it may be advisable to weight traits according to their structural complexity so as to control for this in the analysis. Embryologist colleagues might help rate the developmental challenge of perfecting specific traits. Another scheme might be to use a preliminary data set to determine the coefficient of variation in each trait's FA as an estimate of the challenge involved in 'getting it right', and using it to weight the contribution of each trait's FA measure to the composite measure.

More complex traits also may be more difficult to measure precisely. Thus, it is important to assess the magnitude of measurement error separately for each trait under study and make appropriate adjustments during analysis. Since measurement error itself creates the appearance of FA even in its absence, spurious correlations between trait complexity and FA may be taken as real without trait-specific assessment of measurement error. This mistake could even lead to conclusions that sexually selected traits show more FA than non-sexual traits in studies where sexual traits are harder to measure accurately than non-sexual traits.

Integrative potential of FA

The susceptibility of developmental homeostasis to diverse sources of stress could make FA an exceptionally comprehensive viability assay[45]. FA is generated by unusual temperature conditions, environmental pollutants, increased maternal age and radioactivity[30]. One can imagine how FA could inform individuals making mating decisions about the efficacy of many fitness-mediating systems of prospective partners. For example, in animals that routinely consume chemically defended food sources FA could reveal the efficiency of an individual's detoxification mechanisms. FA may also reveal disease susceptibility (Box 5)[26,28,40]. Traits that develop over long periods may provide an historical synopsis of stress resistance. On the other hand, FA could turn out to be a less-integrative fitness indicator than, for example, body size. Large size requires a consistent record of above-average resource accrual in diverse circumstances and verifies the long-term performance of a variety of systems that causally mediate fitness. In contrast, an individual's level of asymmetry may be determined early and in relatively stable environments: cocoon, womb, egg.

Experiments that impose evolutionarily relevant environmental stress across groups of adults and offspring germane to the species' mating system (e.g. winners versus losers of sexual competitions) are needed to determine the consequences of sexual selection for developmental competence. It is worth noting that lab studies providing too uniform, or too mild, a developmental environment may alter the expression of FA from that in nature by changing the kind of stress(es) that principally affects FA. Similar problems arise in studies of the heritability of FA susceptibility (Box 6).

We suggest including work on the effects of pathogen-related stress. Many of the environmental stresses so far reported to affect FA could be incidental consequences of parasite or pathogen effects. For example, parasites will typically have more negative effects on development in stressed or old individuals[4] or populations at high density[49]. Furthermore, since pathogens are less likely to be homogeneously distributed throughout the bilateral cell groupings of a developing organism than abiotic or nutritional stresses, pathogen-caused stress may be especially likely to cause FA.

To the extent that FA integrates an individual's susceptibility to many stresses it would not provide especially accurate information regarding specific vulnerabilities. Such an integrative function might give important viability information even when all the same environmental stresses do not persist across generations or across individuals of the same generation, because information would at least be available concerning how individuals handled the stress they did encounter. A more-complex scenario would be if different traits express FA in response to different kinds of stress. Do FA correlations between traits increase or decrease with the kind, intensity or combination of stresses imposed on a population? We need much more knowledge about how FA expression is organized in relation to the type(s) of stress encountered.

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Seabird colonies and the appeal of the Information Center Hypothesis

Twenty years ago, Ward and Zahavi[1] proposed in a widely cited paper that colonial roosting and breeding in birds evolved through the benefits arising from the information exchange about food location (the Information Center Hypothesis, ICH). Despite the considerable interest that the ICH has generated, there is little evidence supporting it[2]. The ICH can only be accepted after the importance of other hypotheses explaining colonial behaviour have been carefully evaluated[2]. Furthermore, it is crucial to evaluate the hypothesis' assumptions before attempting any test of its predictions[3].

In a recent *TREE* article, Clode[4] claimed that the greater tendency to breed in colonies shown by offshore-, compared with inshore-feeding seabirds clearly provides support for the ICH. However, the ICH is one among many hypotheses that have been proposed for the evolution of bird colonies[5–7]. Knowledge about the foraging strategies in offshore-feeding seabirds is still very scant[8,9] and evidence for the ICH has not yet been provided. Given the long distances that offshore feeders have to travel in order to find their resources[9,10], they might benefit by placing their nest site at the center of their foraging area[11]. The role of nest site availability on colony formation can only be dismissed if nesting sites are uniformly distributed and virtually unlimited[12]. Distribution of nesting sites in seabirds might differ in relation to their foraging range. In contrast to inshore-feeding seabirds, offshore-feeding seabirds often have only a single island within a local area on which to nest[5].

Colonies could also give the females a wider choice for finding a mate, or enable them to obtain the benefits arising from sperm competition. Males could benefit through the higher possibility of obtaining extra-pair copulations[13,14]. Colonial seabirds where the female usually lays only one egg show high copulation rates and extra-pair copulations are not uncommon[15,16]. These extra-pair copulations can also be a mechanism for the female to reduce hatching failures due to egg infertility[16]. Current evidence does not permit one to conclude that coloniality in seabirds evolved due to the colonies' function as information centers[2,5,6]. Other mechanisms are at least as likely, and further, the use of a colony as an information center may arise as an epiphenomenon after colonial breeding has been established for other reasons.

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