Fluctuating asymmetry and sexual selection

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Abstract

Fluctuating asymmetry occurs when an individual is unable to undergo identical development on both sides of a bilaterally symmetrical trait. Fluctuating asymmetry measures the sensitivity of development to a wide array of genetic and environmental stresses. We propose that fluctuating asymmetry is used in many signalling contexts for assessment of an individual's ability to cope with its environment. We hypothesize that fluctuating asymmetry is used in sexual selection, both in fighting and mate choice, and in competition for access to resources. Evidence is reviewed showing that the patterns of fluctuating asymmetry in secondary sexual characters differ from those seen in other morphological traits. Secondary sexual characters show much higher levels of fluctuating asymmetry. Also, there is often a negative relationship between fluctuating asymmetry and the absolute size of ornaments, whereas the relationship is typically U-shaped in other morphological traits. The common negative relationship between fluctuating asymmetry and ornament size suggests that many ornaments reliably reflect individual quality.

Introduction

Sexual selection was originally introduced by Darwin (1871) to explain the evolution of extravagant secondary sexual characters. Two mechanisms were suggested to result in sexual selection: competition between members of the same sex and choice of mates of the opposite sex. While the former has been relatively uncontroversial, mate choice continues to attract much attention from evolutionary biologists because of the existence of several models describing the evolution of mate preferences. First, Fisher's model of sexual selection suggests that secondary sexual characters evolve as a result of the coevolution between mating preference and the sexual character (Fisher, 1930; Lande, 1981; Pomiankowski, Iwasa & Nee, 1991). The individuals of the choosy sex, usually the females, get an advantage because their sons are more likely to inherit an attractive ornament and so have higher than average mating success. There is thus no func-

tion of the secondary sexual character other than its attractiveness. Second, handicap models suggest that secondary sexual characters are reliable signals of male genetic quality (Zahavi, 1975, 1987; Andersson, 1982a, 1986; Kodric-Brown & Brown, 1984; Nur & Hasson, 1984; Pomiankowski, 1988). If the costs of producing a larger ornament are greater for males in worse condition, then the optimal ornament expression is an increasing function of quality (Grafen, 1990a; Iwasa, Pomiankowski & Nee, 1991). Another version of the handicap idea suggests that ornaments reliably reflect parasite resistance, since only healthy individuals are able to produce the most extravagant sexual traits (Hamilton & Zuk, 1982). Third, secondary sexual characters may signal characteristics of potential mates that directly benefit the chooser. For example, the condition of the sexual trait may reflect infection by ectoparasites that can be transmitted to the female or her offspring (Freeland, 1976) or the parenting ability of a male (Heywood, 1989; Hoelzer 1989).

The direct benefits hypothesis works best when it is not easy for a female to assess those qualities of a potential mate that directly affect her fitness, but when they can be assessed indirectly through the development of extravagant ornamentation.

There is no consensus about the relative importance of these forces in the evolution of mate preferences. The main problem is that no easily measurable criteria have been set out to distinguish these processes. Here it is suggested that fluctuating asymmetry in secondary sexual characters may provide an answer to this problem. In this paper we provide a general discussion about (i) the patterns of fluctuating asymmetry in ordinary morphological traits and in secondary sexual characters, (ii) the factors that cause fluctuating asymmetry, and (iii) the potential use of fluctuating asymmetry in assessment of quality among conspecifics. We primarily consider signalling in sexual selection but also discuss the role of assessment in other signalling contexts.

Fluctuating asymmetry in morphological traits

Fluctuating asymmetry (FA) is one of three kinds of asymmetry demonstrated by bilateral morphological traits, the others being antisymmetry and directional asymmetry. FA occurs when the usual state of a bilateral trait is symmetrical and there is no tendency for one side to have larger character values than the other (Ludwig, 1932; Van Valen, 1962; Palmer & Strobeck, 1986; Leary & Allendorf, 1989; Parsons, 1990). For example, wing length and tail length in the barn swallow (*Hirundo rustica*) demonstrate FA; most individuals are symmetrical, some are slightly asymmetrical and only a few are highly asymmetrical (Fig. 1). The criteria used for determining whether wing length and other morphological characters mentioned in this paper demonstrate FA are that the frequency distribution of left-minus-right character values does not differ from a normal distribution with a mean of zero (Palmer & Strobeck, 1986). This is the case for wing length in barn swallows (test for normality: Kolmogorov-Smirnov one-sample test: D = 0.06, N = 181, N. S.; one-sample t-test of whether the mean value deviates from zero: t = 0.23, d. f. = 180, N. S.). Absolute FA is given by the difference between the numerical values of left and right measures
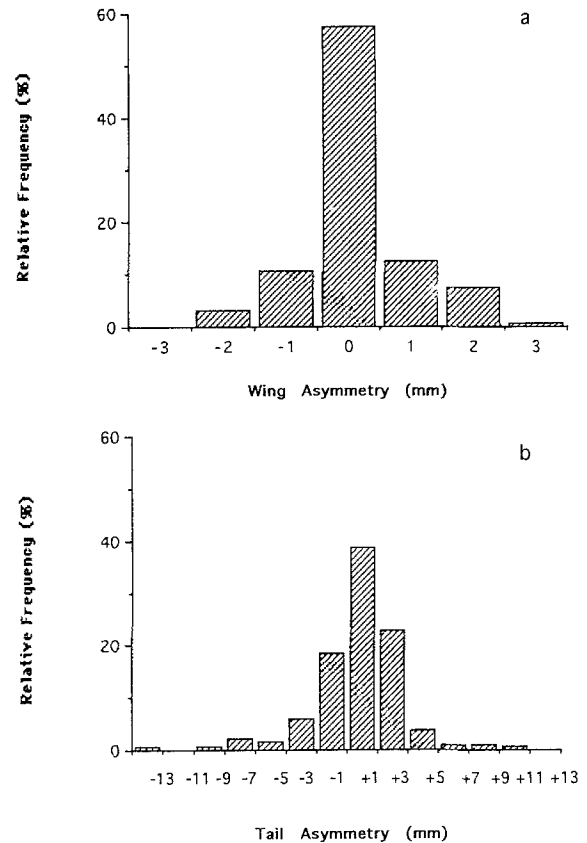

Fig. 1. Frequency distribution of fluctuating asymmetry (right-minus-left value) in wing length (a) and tail length (b) of 181 male barn swallows from Denmark 1991. Four males with more extreme tail asymmetries are not shown.

(Palmer & Strobeck, 1986). Asymmetries in the rest of the paper always refer to absolute asymmetries. FA can be measured in paired characters such as wing length, colour patterns (e.g., a breast stripe) or more complex structures (e.g., a peacock's train fan). The inability of an individual to undergo identical development of a trait on both sides of its body is a measure of developmental homeostasis. Individual FA thus measures the ability of individuals to cope with genetic or environmental stress (Jones, 1987; Leary & Allendorf, 1989; Parsons, 1990).

Most morphological traits studied demonstrate small degrees of FA, and the absolute magnitude of asymmetry is often negligible (Palmer & Strobeck, 1986; Leary & Allendorf, 1989; Parsons, 1990). A recent study of FA in the wing length of 32 different bird species revealed relative values that were most often less than 1% of the absolute size of the trait (Møller & Höglund, 1991). FA in most ordinary morphological traits is thus negligible and of

a magnitude that makes detection difficult without direct measurement.

The magnitude of individual FA is often larger for individuals at the tails of the frequency distribution of a character, with relatively smaller values in between (Soulé, 1982; Soulé & Cuzin-Roudy, 1982). The typical pattern of FA when plotted against the absolute size of the trait is U-shaped, as demonstrated by wing length of the barn swallow (Fig. 2). Sometimes a flat relationship of FA and size is reported. This is most likely to be due to small sample sizes that miss individuals with the largest and smallest trait values because of their rarity.

When population FA in a particular morphological character is compared across species the relationship between asymmetry and character size is allometric (Møller & Höglund, 1991; Møller, 1992a). Species with larger traits tend to have higher average levels of FA for both secondary
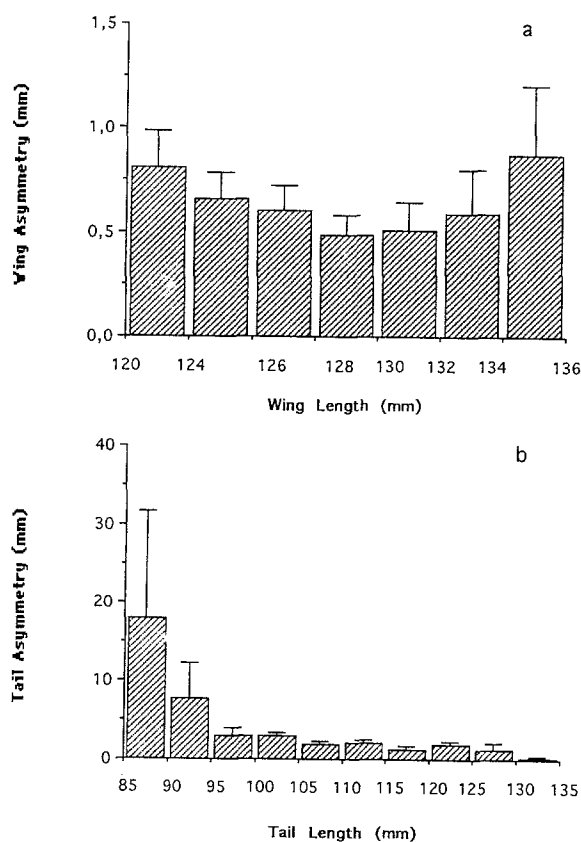
sexual characters and ordinary morphological traits (Møller & Höglund, 1991; Møller, 1992a; Møller & Eriksson, 1993a).

Secondary sexual characters differ from other morphological traits. They are often extravagant traits, bearing highly intricate patterns and striking coloration. Many sexual ornaments are known to be subject to strong directional selection arising from female choice (e.g., Andersson, 1982b; Møller, 1988; review in Møller, 1993a) or male-male competition (e.g., Conner, 1988; Otronen, 1988). In cases where exaggeration has gone to an extreme, sexual traits are likely to be very costly to produce and maintain and may be close to the limits of production. For example, experimental manipulation of the tail feathers of scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*), which are used to attract females, has shown that long tails severely disrupt flying and decrease the efficiency of catching aerial insects (Evans & Thomas, 1992). A similar effect has been reported from the barn swallow (Møller, 1989). Measures of the energetics of courtship, both in frogs (Ryan, 1988) and sage grouse (*Centrocercus urophasianus*) (Vehrencamp, Bradbury & Gibson, 1989), show that display is the most energetically costly act a male performs.

The pattern of FA in ornaments differs from that of ordinary morphological traits. First, the absolute magnitude of FA in secondary sexual characters is considerably larger than in other morphological traits (for example tail length in *Hirundo rustica*: Fig. 1; Møller, 1990a; Møller & Höglund, 1991). Average FA in male feather ornaments of sexually dimorphic birds was five to ten times larger than homologous traits in conspecific females and in both sexes of closely related monomorphic species without ornaments (Møller & Höglund, 1991). Wing asymmetry was of a similar magnitude as tail asymmetry in the species without ornamental feathers (Møller & Höglund, 1991). Absolute FA in ornaments is often so large that it can easily be determined by the naked eye, and it was on average nearly 5 cm in the extravagantly ornamented quetzal (*Pharomachrus mocinno*) (Møller & Höglund, 1991).

Second, individual FA is frequently negatively related to the absolute size of the paired ornament. In a number of bird species, individuals with the largest ornaments tend to have the smallest degree of asymmetry (*Hirundo rustica*: Fig. 2; Møller,

Fig. 2. Numerical value of fluctuating asymmetry in wing length (a) and tail length (b) of 181 male barn swallows from Denmark 1991 in relation to the size of the morphological trait. Values are means + one S.E.

1990a; Møller & Höglund, 1991; Manning & Hartley, 1991). Similarly, individual floral asymmetry is negatively related to the size of floral traits in several plant species (Møller, 1993b; Møller & Eriksson, 1993a). This pattern differs dramatically from that found in ordinary morphological traits. It also fits uncomfortably with the positive allometric relationship found in cross species studies that demonstrates that species with larger traits tend to have higher absolute levels of FA.

Absolute FA in ornaments is not ubiquitously negatively related to the absolute size of the paired ornament. A study of bird taxa with either single or multiple feather ornaments revealed that the average FA was similar in species with single and multiple ornaments. However, the negative relationship between individual FA and ornament size was much more common among single ornament than multiple ornament taxa (Møller & Pomiankowski, 1993). The reason for a flat or U-shaped relationship between individual asymmetry and size of an ornament in many bird species with multiple ornaments is probably that the development of these traits is not costly. These sex traits do not appear to have condition-dependent expression and therefore are interpreted best as representing arbitrary Fisherian traits (Møller & Pomiankowski, 1993).

Another comparative study showed that strong female mate preferences are associated with the pattern of ornament asymmetry (Møller, 1993a). Bird species with a directional female mate preference demonstrated a negative relationship between individual ornament asymmetry and size, while the relationship did not differ significantly from zero among ornamented species without such a preference (Møller, 1993a). This suggests that strong female preferences for the most extravagantly ornamented males are present only if the expression of the secondary sexual character reliably reveals male condition.

Flowers can be considered secondary sexual characters of plants. The patterns of fluctuating asymmetry in flowers are related to the flower preferences of pollinators (Møller, 1993b; Møller & Eriksson, 1993a, 1993b). Flowers visited by pollinators are generally more symmetric than the nearest neighbouring flower not visited by a pollinator (Møller & Eriksson, 1993b). Pollinator preference for symmetric flowers is also apparent in manipulation experiments of individual floral asymmetry

(Møller, 1993b). The relationship between floral asymmetry and the size of floral traits is generally negative which indicates that the largest flowers are developmentally most stable (Møller & Eriksson, 1993a). Large, symmetric flowers produce more nectar than small, asymmetric flowers and this relationship may account for the pollinator preference for the most symmetric flowers (Møller, 1993b).

A similar negative relationship between size and degree of FA regularly occurs in weapons used in fighting between males (Møller, 1992a). Weapons are often exaggerated structures and for that reason costly to produce or maintain, and they are therefore likely to show a considerable degree of condition-dependence with the largest characters produced by individuals in prime condition (e.g., Brown, 1984; Andersson, 1986; Bubenik & Bubenik, 1990). Below we consider the causes of FA and how these differences between morphological and sexual traits might be explained.

Causes of fluctuating asymmetry

There exists a vast literature on the causes of FA based on both observation and experimentation. There are two major causes of FA in morphological traits: (i) environmental stress, and (ii) genetic stress. We briefly review each of these causes of FA with particular reference to their importance for sexual selection and assessment.

Environmental stress
FA has been used as a measure of the ability of individuals to cope with different kinds of environmental stress (Jones, 1987; Leary & Allendorf, 1989; Parsons, 1990). A large number of different stressors have been demonstrated to cause FA in morphological traits during development, including extreme temperatures (Parsons, 1962; Siegel & Doyle, 1975; Sciulli et al., 1979), various chemicals including pesticides (Valentine & Soulé, 1973; Hoffmann & Parsons, 1989a, b), audiogenic stress (Sciulli et al., 1979), and food deficiency either in terms of quality or quantity (Parsons, 1990). Severe restriction of nutrients to mothers during pregnancy causes asymmetry in skeletal traits of offspring (Sciulli et al., 1979) and in external features such as bristle number in Drosophila (Parsons, 1990). It is not known whether nutrient deficiency, or any of

the other factors listed above, cause any differential effect on FA in secondary sexual characters compared to ordinary morphological traits.

Pathogens and parasites have also been demonstrated to have debilitating effects on the development of otherwise symmetrical morphological traits. Many human diseases are known to cause distortion of an otherwise symmetrical appearance (e.g. Bailit *et al.*, 1970; Livshits & Kobyliansky, 1991). A recent study of the effects of parasites on development of feathers in birds revealed that not all morphological characters were equally susceptible to parasite loads (Møller, 1992b). The loads of ectoparasites were experimentally manipulated in one year, and the effect of this manipulation on development of individual FA in feather traits was assessed following the subsequent moult. The large tail ornaments in male barn swallows became more asymmetrical than the homologous trait in females as a result of experimentally altered levels of mite infestations prior to the annual moult. Other feather traits, such as wing length and the length of the short, sexually monomorphic, central tail feathers, showed weak, non-significant effects of mites on FA and no difference between the sexes (Møller, 1992b). Different traits are therefore not equally susceptible to the stress caused by ectoparasitism. In barn swallows, mite infections affect asymmetry in secondary sexual characters much more than in comparable non-sexual traits.

Genetic stress

Increased FA has been related to inbreeding and this could either be due to increased levels of homozygosity or to exposure of deleterious alleles among inbred stocks, or both (Lerner, 1954). Subsequent studies demonstrated that homozygous individuals often were developmentally less stable than their heterozygous counterparts (Leary, Allendorf & Knudsen, 1983, 1984, 1985a; Clarke & McKenzie, 1987) and a number of studies have shown similar phenomena at the population level (Lerner, 1954; Soulé, 1979; Kat, 1982; Vrijenhoek & Lerman, 1982; Biémont, 1983; Leary, Allendorf & Knudsen, 1985b; Livshits & Kobyliansky, 1991; review in Mitton & Grant, 1984). This conclusion is based on observations in *Drosophila*, *Mus*, and other animal and plant laboratory and natural populations. Individuals heterozygous for one or more proteins generally develop less FA and have higher

fitness as measured by growth, fecundity and various measures of physiological performance (reviews in Mitton & Grant, 1984; Palmer & Strobeck, 1986).

In contrast, crosses between inbred stocks usually yield hybrids with lower FA (Mather, 1953; Thoday, 1956; Reeve, 1960). Hybrids between species or populations that are normally reproductively isolated generally have higher levels of FA than either of the parental species or populations (Tebb & Thoday, 1958; Zakharov, 1981; Graham & Felley, 1985; Leary, Allendorf & Knudsen, 1985). A natural experiment has also been reported in sunfish, where habitat disturbance brought two populations together that were previously isolated. Again, FA increased in the hybrids (Graham & Felley, 1985).

In all the cases mentioned above, it can be inferred that the degree of FA is negatively correlated with fitness. Inbreeding increases the fraction of loci homozygous for deleterious recessives. Outbreeding protects against rare deleterious recessive alleles and may also raise fitness if there is a heterozygote advantage. In contrast, crosses between species disrupt genomic adaptations that have developed since the populations became reproductively isolated and hence reduce fitness. Explicit demonstrations of negative correlations between individual fitness components and individual FA were reported by Thornhill (1992a, 1992b) for mating success and longevity in *Panorpa* scorpionflies, Markow and Ricker (1992) for mating success in *Drosophila*, and Møller (1993d) for mating success, reproductive success and survival in *Hirundo rustica*. Individuals with higher fitness components consistently had less FA.

An apparent exception to this generality is the perturbation to developmental stability caused by the incorporation of a new, advantageous mutant in Australian blowflies (*Lucilia cuprina*) (Clarke & McKenzie, 1987). This mutant confers insecticide resistance. When resistance first evolved it caused greatly elevated FA. But after 20 years of adaptation to the new mutant, FA has returned to the same level found in susceptible, wildtype flies. So even though the fitness increase associated with resistance was initially coupled to increased FA, subsequent selection on resistant flies has ameliorated this developmental instability and probably restored a negative correlation of fitness and FA.

Fluctuating asymmetry and selection

What selective forces can explain the different patterns of FA in ordinary morphological and sexual traits? We suggest that the principal difference lies in the mode of selection. In general most morphological traits are subject to long-term stabilizing selection. The net effect of selection may be directional on the time scale of a few generations. A good example of this is the quick change in body and bill demensions recorded in Darwin's medium ground finch which occurred during a period of drought (Boag & Grant, 1981). But over many generations any net directionality is likely to be small and may even be zero. In sexual characters there may also be a balance of selective forces at equilibrium. In several cases it has been shown that sexual selection for greater ornament size is balanced by viability selection against further increase (e.g., Endler, 1983). But over a longer time-scale we can infer that sexual characters have been subject to strong directional selection and may still be subject to continuing directional selection. The modes of selection affecting ordinary morphological traits and secondary sexual characters differ in four principle ways.

First, while ordinary morphological traits are stabilized by other components of viability selection, sexual characters are stabilized by sexual selection for increased extravagancy opposed by viability selection. This in itself is not an important difference. Second, the two categories of characters differ in terms of the recent history of selection. While secondary sexual characters have been subject to recent dramatic evolutionary changes due to net directional selection, ordinary morphological characters are often of the same size in a genus or a family. In the highly sexually selected birds of paradise, species differ dramatically in male ornamentation but hardly at all in ordinary traits in either sex (Coates, 1990). Similar high variance in sexual characters across species are present in animal genitalia (Eberhard, 1989). Third, the two types of traits probably also differ in the strength of the components of selection. In ornaments, measurements of natural and sexual components indicate that they are very large; in general they are probably much larger than the corresponding natural selection components for ordinary morphological characters. The final difference between secondary

sexual characters and other morphological characters concerns the effect of mutation. Mutation pressure on sexual traits that are exaggerated or show great intricacy of design will more often disrupt than improve their attractiveness to females. Mutation bias on ordinary morphological traits is likely to be much weaker (Pomiankowski, Iwasa & Nee, 1991; Iwasa, Nee & Pomiankowski, 1991). This means that sexual ornaments will be subject to continual directional selection because mutation bias creates an excess of poorly ornamented males at equilibrium.

The two forms of selection regimes, directional and stabilizing selection, are predicted to result in marked differences in the nature of genetic and phenotypic variation and asymmetry. The effect of stabilizing selection is to favour individuals with trait values close to the mean. Selection not only acts against individuals that have high or low trait values but also favours modifiers that limit variation in the expression of the trait (Prout, 1962; Milkman, 1970). These modifiers will also reduce FA. A trait that is developmentally stable will suffer fewer and less significant errors in development and so have a lower mean level of FA (Pomiankowski & Møller, 1993).

This simple principle can be extended to explain the U-shaped relationship of size and FA. Three routes may lead to this. First, individuals who produce traits larger or smaller than the selective optimum may suffer greater stress in development because they produce traits that deviate from the optimum size. Hence individuals from the tails of the frequency distribution will show greater variance in development. On average they will have larger differences between left and right sides and higher FA. A second reason is that individuals at the tails of phenotypic distributions tend to be homozygotes while modal individuals tend to be heterozygotes (Soulé, 1982; Soulé & Cuzin-Roudy, 1982). If heterozygosity buffers against a variety of stressors, modal individuals may on average develop smaller degrees of asymmetry than individuals in the tails of frequency distributions. A third possibility is that individuals vary in their ability to control development. Individuals with tight developmental control will have low FA and be distributed closely about the optimum trait size, whereas those with weaker developmental control will have higher FA and greater variation in trait size. The net effect

again is low FA in the modal size classes, with higher values at the extremes (Pomiankowski & Møller, 1993).

Under a regime of strong and persistent directional selection for larger character values, as can be generated by sexual selection, the pattern of FA is strikingly different. Strong directional selection for larger size favours existing genes and new mutants that code for higher trait values. Directional selection can also favour relaxation in the developmental control of morphogenesis as this creates greater phenotypic variation and so can aid the response to selection. This is particularly likely when sexual selection disproportionately favours individuals with greater than average values. The effect of these selective forces is predicted to increase FA. First, a trait that is larger than the optimum under natural selection is likely to impose greater stress during development. For example, large secondary sexual characters are more costly to produce and they take longer to produce than small characters (e.g., Bubenik & Bubenik, 1990). Second, selection for weaker control of development will lead to greater variability during morphogenesis and higher FA. This is shown by the greater phenotypic variability of secondary sexual characters which are known to have considerably higher coefficients of variation than ordinary morphological characters (e.g., Alatalo, Höglund & Lundberg, 1988). So as the size and the variability of the trait becomes larger under directional selection, mean FA will increase.

In addition to these effects on the mean, we can predict the relationship between size and FA. Under the most simple assumption, FA in a trait will be directly related to the size of that trait with all other factors merely acting as uncorrelated noise. Hence individuals that grow larger traits will be subject to greater stress and hence on average have higher FA. This predicts that the regression of FA on size will be positive. Such a pattern is likely if the ornament has evolved through Fisher's runaway process and its development is unrelated to condition.

Handicap models of reliable signalling predict a strong correlation between the condition of an individual and ornament size, as only males of high phenotypic or genetic quality can afford to construct large ornaments (Grafen, 1990b; Iwasa, Pomiankowski & Nee, 1991). This prediction is consistent with the finding that the expression of many sexual traits is sensitive to changes in condition (Andersson, 1986; Hill, 1991; Møller, 1991a). The superior condition of individuals with large ornaments may thus mask the increase in stress caused by greater ornamentation. The net effect, if ornament size is mainly determined by male condition, is that the regression of FA on size is negative (Pomiankowski & Møller, 1993). Individuals that produce the largest sexual traits are like to have the lowest FA when the trait reliably reflects condition, because a given level of ornamentation is more costly to low than to high quality individuals.

An old objection to this line or reasoning is that strong directional selection will deplete genetic variation, particularly in traits closely associated with fitness, making female choice for 'good genes' redundant (Maynard Smith, 1978; Taylor & Williams, 1982). However, there are several ways in which genetic variation can be maintained even under regimes of strong selection, for instance frequency-dependent selection, mutational input, and temporal variation in fitness. The heritability of FA has been estimated in a number of selection experiments as well as in laboratory breeding experiments (reviews in Palmer & Strobeck, 1986; Parsons, 1990; Livshits & Kobyliansky, 1991; Thornhill & Sauer 1992). The general conclusion is that there is a small, significant heritability of FA in ordinary morphological traits, while there are no estimates available for secondary sexual characters.

In conclusion, strong directional selection will lead to the evolution of costly secondary sexual characters. These will evolve condition-dependent expression that is reflected in a negative relationship between character size and individual FA. All signals have a morphological basis, and costly signals subject to strong directional selection are likely to demonstrate similar patterns of FA.

On the use of fluctuating asymmetry in assessment

Individual FA in secondary characters and other morphological traits may reflect abilities to cope with stress that may be of importance during assessment to individuals of the same or other species (competitors, predators, parasites, pollinators). We suggest that there are important consequences for

the two modes of sexual selection (male-male competition and female choice) and other cases of competition for resources.

Animals are able to discriminate between symmetric and asymmetric features and use asymmetry as a category in classification of objects. Discrimimation experiments on pigeons in operant conditioning chambers reveal that individuals are able to accurately classify novel test stimuli according to degree of asymmetry (Delius & Habers, 1978; Delius & Nowak, 1982; see also Rensch, 1958). This was the case even when the size of the stimuli was held constant. Some animals therefore have the perceptive abilities to discriminate between traits only differing in their degree of individual asymmetry.

In this and the following sections we consider two cases of assessment of FA. First, asymmetries in morphological traits may be of a magnitude that cannot be assessed directly by vision or other sensory modalities. These asymmetries may include those present in ordinary morphological traits such as wing length in the barn swallow (Fig. 1). While such asymmetries cannot be used directly in assessment of conspecifics, they may still represent a useful measure of the ability of individuals to cope with the environment and thus be a useful way to measure quality for the investigator.

Second, asymmetries may be large and quite obvious to human observers and may be used directly in assessment. Many paired secondary sexual characters are positioned next to each other, and this makes direct assessment of asymmetry particularly easy. For example, when a blue peacock (*Pavo cristatus*) spreads its train it is immediately obvious if an eye-spot is missing. It is possible that high quality individuals gain a signalling advantage by placing their paired traits next to each other to make assessment easy. Males of inferior quality will be unable to cheat by making assessment of asymmetries impossible or difficult if females pay attention to asymmetry.

Male-male competition

Fighting ability of males is known to be affected by the ability to acquire sufficient nutrients and to cope with debilitating pathogens and parasites (Freeland, 1976, 1981; Burley, Tidemann & Halupka, 1991; Johnson & Boyce, 1991; Spurrier, Boyce & Manly, 1991; Thornhill & Sauer, 1992).

These factors may be reflected by FA in the secondary sexual characters. Conspecifics should be able to assess fighting ability using the size and asymmetry of these traits. In addition, asymmetry in weapons such as claws, spurs, antlers and horns is also informative if asymmetry lessens the effectiveness of these traits in battle. An asymmetrical weapon may be less strong or reveal a weakness that can be exploited (Møller, 1992a).

There might also be direct effects of previous fighting success on the development of FA in secondary sexual characters. Stags are know to develop severe asymmetries in their antlers in response to body wounds acquired during fights in previous years because wounds cause distortion of the ability to symmetrically channel resouces to the right and the left antler during growth (Brown, 1984). Male and female conspecifics will therefore be able to directly assess the previous fighting success of stags from large antler asymmetry.

Female choice

The three major models of female choice make different predictions about the magnitude and the patterns of FA in secondary sexual characters. Handicaps are very costly sex traits, particularly to low quality individuals, and are likely to evolve condition-dependent expression. Only individuals of the highest quality are able to produce the largest ornaments. Handicaps will be subjected to strong directional selection due to mate choice and for that reason demonstrate high levels of population FA. The effect of condition on the expression of secondary sexual characters should be revealed in the relationship between individual FA and the size of secondary sex traits; individuals with the largest secondary sexual characters are predicted to demonstrate the smallest degree of asymmetry.

Fisherian sex traits are sexually attractive characters subject to directional selection due to mate choice and they should also demonstrate high levels of population FA. However, Fisherian traits, contrary to handicaps, are not particularly costly to produce or maintain. Their expression should not be condition-dependent and the relationship between the degree of individual FA and the size of the sex trait is predicted to be flat or U-shaped.

Secondary sexual characters may also signal direct fitness benefits like nuptial gifts, nest sites, territory, absence of contagious parasites, or parent-

ing ability. Direct assessment of these benefits provided by potential partners should be more important than indirect assessment through signals, because direct assessment will be more reliable. Parenting ability is perhaps the only exception to this rule of direct assessment because it cannot be assessed directly until reproduction is in progress. Signals of parenting ability are unlikely to be very expensive, because if they were they might impair the ability to provide parental care. If sex traits signal parenting ability, they are expected to be subject to weak directional selection and demonstrate low to intermediate levels of population FA. The relationship between individual FA and the size of a secondary sexual character will be flat or U-shaped because of the relatively low costs of the sex trait.

Whether mate choice is sensitive to asymmetry in sexual traits is not yet clear. Many studies have demonstrated that females pay attention to the expression of secondary sexual characters and that males with the most extreme ornaments are preferred over less ornamented males (Andersson, 1982b; Møller, 1988, 1990b; Petrie, Halliday & Sanders, 1990; Hill, 1991). These results have usually been interpreted to mean that the size of the ornament is the character assessed by females. However, females might in addition be assessing ornament asymmetry.

There is empirical evidence that females pay attention to FA of ordinary morphological characters. For example, Markow and Ricker (1992) showed that mated male Drosophila exhibited less FA than unmated males, although the causal relationship between individual FA and mating status was not verified. Asymmetric male fruitflies may be at a selective disadvantage if morphological asymmetries affected their ability to deliver courtship signals. Similarly, Thornhill (1992a) showed that asymmetric male Japanese scorpionflies Panorpa japonica were less successful during fights for nuptial gifts, and asymmetric males had lower mating succes than symmetric males. Asymmetric males also produced pheromones that were more attractive that those of symmetric males (Thornhill 1992b). Again, the causal relationship between asymmetry and mating status could not be verified experimentally.

Individual FA and size of secondary sexual characters are strongly negatively correlated in at least three of the bird species in which an effect of ornament size on mate preference has been inferred: barn swallow (Møller, 1990a), long-tailed widowbird (Euplectes progne) (Møller & Höglund, 1991) and blue peacock (Manning & Hartley, 1991). It is thus not possible to determine whether ornament size or ornament asymmetry is the cue used during female choice. Experimental manipulation of the size of the ornament does not resolve this problem because elongation of a tail ornament simultaneously leads to a reduction in the relative FA, while shortening leads to an increase in the relative FA.

A recent experiment on barn swallows involving independent manipulation of both ornament size and FA in ornaments suggested that both characters influenced female choice (Møller, 1992c). Most importantly, there was a significant interaction between ornament size and asymmetry. Males with symmetric tails had higher mating success than males with asymmetric tails. But long asymmetric tails were better than short symmetric tails. This supports a good genes interpretation. It suggests that males are unable to cheat by developing short tails in which the degree of asymmetry is easier to control. The alternative hypothesis that greater success in male-male competition may explain why male barn swallows with symmetrical tails acquired mates sooner during the mating season was ruled out by the fact that male fighting rates or fighting success did not differ between experimental treatments (Møller, 1992d).

Small degrees of asymmetry may also be costly if they impair manoeuvrability in flight either because of effects on the acquisition of resources or on the ability to compete with conspecifics. For example, asymmetry in the outermost elongated tail feathers of barn swallows cause loss of manoeuvrability in a flight maze (Møller, 1991b).

An alternative interpretation of the barn swallow data suggests that females prefer males with the most symmetric ornaments because such males provide better parental care (Balmford & Thomas, 1992; Borgia & Wilkinson, 1992). This was not the case. Males with the most preferred secondary sexual characters contributed relatively less to parental duties than males with less preferred sex traits (Møller, 1993c). Another explanation for the negative relationship between ornament asymmetry and ornament size is that asymmetric sex traits are less costly for males with small ornaments for aerody-

namic reasons (Balmford & Thomas, 1992). If this was the case, one should expect tail asymmetry to be positively, not negatively, related to tail length in all aerially insectivorous birds, even those species without tail ornaments. The relationship between tail asymmetry and tail length is neither positive nor negative among sexually monomorphic bird species representing independent evolutionary events of high aerial activity (Møller & Höglund, 1993). This does not support the view by Balmford and Thomas.

Discussion

In the preceding sections we have outlined how fluctuating asymmetry may prove to be an important concept in sexual selection theory. Different models of sexual selection have been suggested to account for the evolution of elaborate secondary sexual characters not directly used in male-male competition, but there is no general consensus concerning the relative importance of these models. The Fisherian and handicap models of female choice predict different correlations between the expression of sexual ornaments and the quality of individuals. We suggest that individual FA may represent a reliable, independent measure of individual quality, because FA is directly caused by the ability of individuals of given genotypes to cope with the environment (including conspecifics, parasites and pathogens). The magnitude and the patterns of individual FA in relation to the size of secondary sexual characters may therefore allow us to determine the relative importance of these two models of sexual selection.

Preliminary comparative analyses of the patterns of FA in secondary sex traits and other morphological traits clearly reveal that population FA in secondary sexual characters is much larger than in other morphological traits. This strongly suggests that ornaments are much more susceptible to disruption of developmental homeostasis than ordinary morphological traits. The strong directional selection that acts on ornaments is the most likely explanation for the high population levels of FA. This interpretation is consistent with earlier experimental data on *Drosophila* and *Rattus* demonstrating that directional selection causes a deterioration of developmental homeostasis as measured in terms

of FA (Thoday, 1958; Reeve, 1960; Leamy & Atchley, 1985). Similarly the incorporation of new mutants into the genome is generally associated with increased variability and FA (Fisher & Holt, 1944; McKenzie & Clarke, 1987). In addition, the exaggerated nature of many sexual ornaments and displays means that they are costly traits to produce and maintain. Exaggeration will itself cause stress and lead to an increase in population FA.

Individual FA in ornaments is often negatively related to the mean absolute size of the paired trait, while the common pattern is a U-shaped relationship between individual FA and the size of an ordinary morphological trait (Soulé, 1982; Soulé & Cuzin-Roudy, 1982; Møller & Höglund, 1991; Møller, 1992a). A negative relationship between ornament size and FA may be due to three different factors. First, individuals with the largest ornaments may generally have higher heterozygosity and therefore be less susceptible to the effects of parasites and pathogens and a number of other factors associated with heterozygosity (see section on genetic stress and FA). Second, ornament size may reflect overall quality independently of heterozygosity, and individuals in good condition may be less susceptible to the effects of environmental stress than other individuals. For example, it is well-known that the expression of ornaments is related to condition (Andersson, 1982a, 1986; Nur & Hasson, 1984). Good condition also generally leads to less FA in morphological traits (Parsons, 1990). Third, individuals that frequent more favourable and thus less stressful environments may become more extravagantly ornamented than conspecifics in less favourable environments. It is possible that the negative relationship between FA and size has a non-genetic basis. However individuals with the best genotypes will be selected to occupy the best environments, so it seems likely that environmental and genetic associations are highly correlated.

The absolute size of ornaments may reflect that it is a reliable indicator of individual quality, because the largest ornaments also demonstrate the least FA. The maintenance of reliable signalling reflecting the quality of individuals has been a subject of some controversy. Recent game theory models suggest that costly signals reliably reveal quality because high quality individuals pay a lower cost for a given level of signalling than low quality individuals (Grafen, 1990b). Dawkins and Guilford

(1991) recently stated that current models of reliable signalling assume no cost to the receiver of eliciting and evaluating honest signals, and they use the famous roaring contests in red deer (*Cervus elaphus*) stags as an example of large receiver costs. A receiver will only be able to determine the true quality of an opponent by going through a series of escalating stages of roaring and finally fight, and the cost of evaluating the quality of an opponent may therefore be considerable. Individuals in many signalling systems should therefore, according to Dawkins and Guilford (1991) settle contests by using conventional signals rather than paying the full cost of receiving the costly signal. Such systems would be open to cheating because receivers do not intend to pay the full cost of communication, and Dawkins and Guilford (1991) suggest that many signalling systems will be open to unreliable or dishonest signalling.

We suggest that individual FA may provide a reliable signal of quality that can be perceived without much cost, if directly assessable by vision or other sensory modalities. Cheating will generally not be possible because individual FA directly reflects the ability to cope with genetic and environmental stress including parasites and pathogens, the heterozygosity of the individual and the level of adaptation to local conditions. This will apply to secondary sexual characters that demonstrate large degrees of FA and a negative relationship with character size. Small amounts of FA in non-sexual, morphological traits may not be directly assessed by conspecifics, but FA may still correlate positively with various measures of fighting ability, if asymmetry is a general quality indicator.

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