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CHARACTER-SPECIFIC HOMEOSTASIS DOMINATES FLUCTUATING ASYMMETRIES IN THE MEDFLY (DIPTERA: TEPHRITIDAE)

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ABSTRACT

Fluctuating asymmetry (FA) indicate random variation in size of bilaterally-produced traits, which occurs during development, and hence measures the degree of developmental instability. Whole-individual homeostasis has been assumed responsible for the negative correlation that has often been found between FA of many sexually selected traits and their size. We show that, theoretically, character-specific homeostasis can provide an equally convincing explanation for this correlation. Furthermore, we tested these two hypotheses for (1) a sexually dimorphic character and (2) sexually monomorphic characters of the male Mediterranean fruit fly, *Ceratitis capitata*, by manipulating density during larval development. Our results clearly support character-specific homeostasis.

Key Words: Fluctuating asymmetry, developmental homeostasis, sexual selection medfly, *Ceratitis capitata*

RESUMEN

La fluctuación asimétrica (FA) indica variación aleatoria en el tamaño de los rasgos producidos bilateralmente, los cuales ocurren durante el desarrollo, y por lo tanto mide el grado de inestabilidad del desarrollo. La homeóstasis de individuos completos ha sido asumida como la responsable de la correlación negativa que frecuentemente ha sido encontrada entre FA de muchos rasgos sexualmente seleccionados y de su tamaño. Se demuestra teóricamente, que la homeóstasis carácter-especifica puede proporcionar una explicación igualmente convincente para esta correlación. Además, se probaron estas dos hipótesis con respecto a 1) un carácter sexualmente dimórfico y 2) caracteres sexualmente mono-mórficos de los machos de la mosca del Mediterráneo, *Ceratitis capitata*, por medio de la manipulación de la densidad durante el desarrollo larval. Nuestros resultados claramente apoyan la homeóstasis carácter-específica.

Minute variations in growth rate that occur randomly during development accumulate and result in small variations in the final size of organs. These variations (or developmental 'noise') can be quantified by comparing the final sizes of a character that is produced more than once under the influence of the same genome, at the same developmental stage, while being exposed to the same environmental conditions. Because development repeats itself twice during growth of bilaterally produced organs, bilateral asymmetry can be used to give an estimate of developmental instability (Soule 1982, Soule & Cuzin-Roudy 1982, Leary & Allendorf 1989, Parsons 1990). This type of asymmetry is known as 'fluctuating asymmetry' (FA), and is usually measured as the absolute difference between the size values of left and right, divided by their mean (to control for the effect of size). A number of studies have shown that FA increases following environmental and genetic stress. The most common environmental factors that are known to increase FA are extreme temperatures, starvation and chemical stresses (Soule 1982, Parsons 1990). New mutations, increased homozygosity, recombination and directional selection are documented genetic factors that increase FA (Parsons 1990, Moller & Pomiankowski 1993b).

Recently, the study of FA has gained much interest because of its role in sexual selection. Females of different species, including the scorpionfly, *Panorpa japonica* (Thornhill 1992), barn swallow, *Hirundo rustica* (Moller 1992) and human (Thornhill & Gangestad 1992, Thornhill et al. 1995) have been shown to mate more readily with symmetric males. This, and other potential uses and implications of FA (e.g., Leary & Allendorf 1989, Moller & Pomiankowski 1993b), requires a good understanding of the mechanisms that affect FA.

There is a general agreement that symmetry is enhanced by genetic modifiers that increase the harmony of development (Leary & Allendorf 1989). Other parallel terms that have been used are 'developmental homeostasis', 'developmental stability' (Soule & Cuzin-Roudy 1982), and 'intrinsic genetic coadaptation' (Leary & Allendorf 1989), all of which imply a state of evolutionary

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equilibrium. More explicitly, these terms reflect the general view that evolutionary transitions away from symmetry are followed by an evolution of modifiers that restore symmetry (McKenzie & Klarke 1988, Leary & Allendorf 1989). The assumed nature of this stability, however, is debatable. Some studies argue that developmental homeostasis evolves separately for each of the individuals' characters, and hence that FA measures the degree of character-specific developmental stability. Others contend that homeostasis is holistic, affecting the development of whole organisms. Attempts to discriminate between these two hypotheses by examining within-individual correlations between FA of several characteristics have provided conflicting evidence (Soule & Cuzin-Roudy 1982, Watson & Thornhill 1994).

An important reason for the conflicting evidence shown by these correlations is well explained by Whitlock (1996). He points out that for each character in a bilaterally symmetric individual there exist only two samples of the variance of developmental instability. Because each of the measurements of FA is an unreliable statistical measure of variations within the individual (assuming common cause for different characters), then even if developmental instabilities of different characters are correlated, the within-individuals correlations of FA are often too coarse to show them. Therefore, to decrease the role of statistical errors due to random sampling, other types of correlations are required, ones that can use repetitions across individuals, or that involve only one bilaterally symmetric character. A decision about these other measures requires a better understanding of the possible mechanisms that induce fluctuating asymmetry.

The known list of causes of asymmetry suggests that there might be more than one mechanism involved. The distinction between character-specific and whole-individual homeostasis is often suggestive about these mechanisms. Whole-organism homeostasis is known to be a result of certain external factors, such as extreme temperatures, which results in instability in the whole organism. Whole-organism homeostasis is often assumed to be, however, also a function of overall individual 'quality' that may vary between individuals due to heritable or non-heritable differences in the ability and/or opportunity to capitalize and use resources. Heritable differences that may exist between individuals are expected to be diminished by natural selection, until a state of equilibrium between natural selection and the source of the heritable variations is reached (Falconer 1981). This point of equilibrium, characterized by an improved overall adaptedness, should be reflected by reduced FA.

In contrast, character-specific homeostasis is frequently assumed to be a result of heritable or non-heritable variations in size of each character. Extreme character sizes reduce harmony of development (and, as a result, increase FA) because they are usually not accompanied by corresponding changes in developmental organization, or in supportive tissues such as muscle, blood vessels or nerve cells, required for the enhancement of developmental stability. For an evolving character, under a regime of directional selection, this might be just a temporary stage followed by the evolution of these other modifications that will, eventually, increase developmental homeostasis of the character in its final state.

Investigations of FA, in relation to studies of sexual selection, have consistently interpreted results assuming that developmental homeostasis is a whole-organism characteristic, rather than character-specific. This assumption nicely links sexual selection theory with the empirical data that frequently (but not always) show a negative correlation between FA of sexually dimorphic traits and their size, a pattern that is not found in other traits (Moller & Höglund 1991, Moller & Pomiankowski 1993a). This pattern is readily explained by assuming that (i) FA is determined by a whole-organism developmental homeostasis, (ii) this homeostasis is correlated with the individual's overall quality or some of its components, and (iii) the sexual trait is a handicap. The term 'handicap' refers to a signal, such as a sexual ornament, which is costly to produce or maintain such that a male's optimal trait size (i.e., his investment in advertising) is correlated with his physical condition. As a result, better males produce more expensive sexual ornaments (Zahavi 1975, 1987, Nur & Hasson 1984, Pomiankowski 1988, Grafen 1990). Theoretical studies show that at evolutionary equilibrium, the male residual quality (after developing its sexual ornament) is expected to remain higher for high quality males, despite the fact that absolute investment in sexual ornaments by these males is greater (Nur & Hasson 1984, Grafen 1990, Iwasa et al. 1991). Hence, if developmental stability is caused by whole-organism mechanisms that depend on the male quality during development, larger sexual ornaments should be also more symmetric.

Despite the consistency of the negative correlation between the size of a sexual trait and FA with the whole-organism stability hypothesis, it can only provide support for this hypothesis if character-specific mechanisms cannot explain this pattern. Here we show that this is not the case. In the next section we show that size-dependent character-specific homeostasis provides an equally reasonable explanation for the negative correlation between FA of many sexual traits and their size. In the rest of the paper we present a simple experiment that tests these two hypotheses. Its results strongly support the character-specific mechanism.

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Size-dependent Homeostasis

The single character size-dependent homeostasis hypothesis suggests that individuals in a population evolve modifiers that improve homeostasis for a certain character size. Characters that develop to match this size will be the least asymmetric. Hence, we can call this size the least asymmetrical size (LAS). Sizes that deviate from LAS (either bigger or smaller) develop to be asymmetric. They are expected to be more asymmetric the more they deviate from LAS (Soule 1982, Soule & Cuzin-Roudy 1982). Therefore, traits that undergo stabilizing selection should normally produce a more or less symmetric V- or U-shaped distribution of FA around the mean size of the trait (the form of the distribution depending on whether the effect of deviation from LAS on FA is linear or exponential, respectively).

If there are no other size-dependent effects, such as directional natural or sexual selection, modifiers are most strongly favored if they improve developmental stability (hence, symmetry) of the size that they most frequently encounter (the term 'modifiers' has been used vaguely in the literature of FA; here, we use this term to simply refer to a set of heritable traits that affect a character's developmental stability, as a function of its size, although other size-dependent responses are also possible). Consequently, the most common size is also expected to be the LAS. However, the actual shape of the relationship between FA and size, its strength (i.e., its variance around the least squared regression line), and the value of LAS itself should heavily depend on the distribution of trait sizes in the population. For a normal distribution of sizes of a trait undergoing stabilizing selection, LAS is expected to correspond with the population's mean, mode and median, all of which fall onto a single point. A high standard deviation creates a weak selection on modifiers that improve homeostasis of any particular size, including the mean, because they are less likely to encounter that size. In contrast, selection pressure on modifiers that improve developmental stability of the LAS when standard deviation of sizes is small, must be stronger, hence also more canalizing (Fig. 1). Furthermore, a small standard deviation

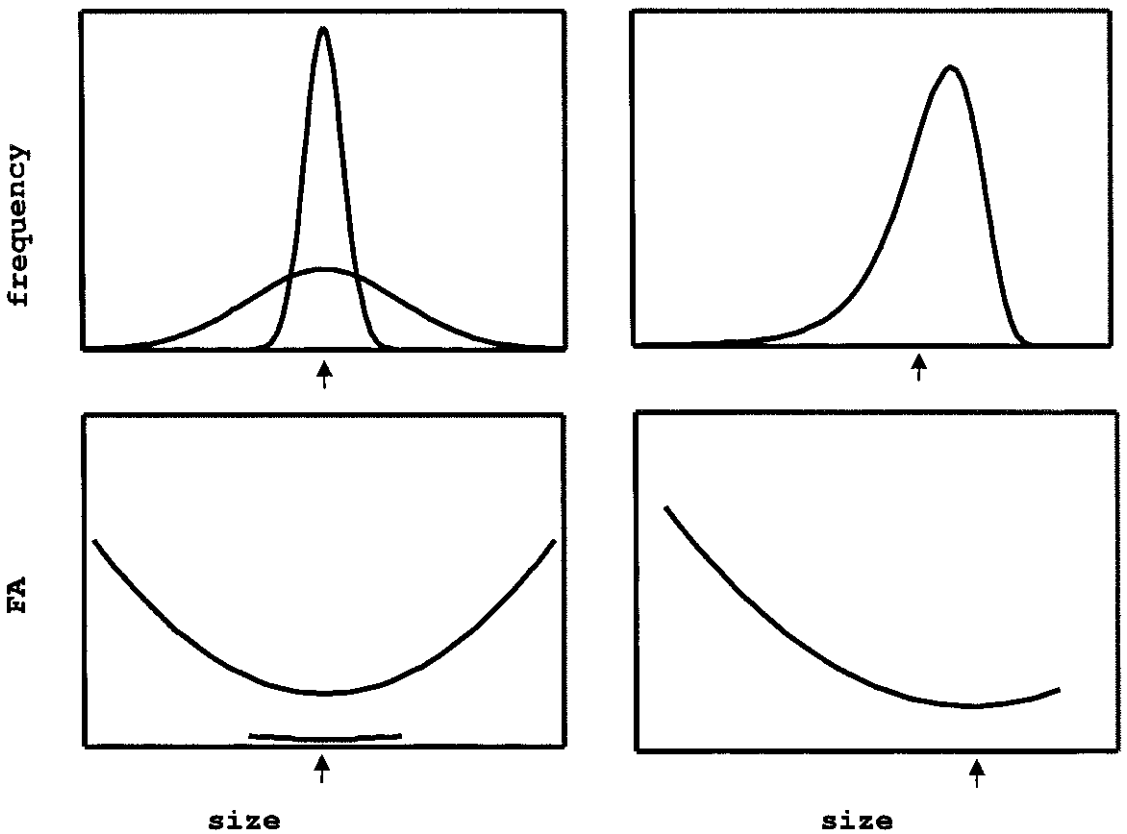


Fig. 1. The expected relationships between FA (bottom) and size frequency distribution (top), assuming character-specific developmental homeostasis. The pointers show average size (top), and the least symmetric size (bottom) for two normal curves that differ in their standard deviation (left) and a skewed curve to the left (right).

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of sizes should also lead to a small average FA, because the population is distributed tighter around the LAS. Empirical data show that non-sexual traits have either a U-shape distribution of FA with relation to size, or no pattern at all (Moller & Pomiankowski 1993a), which may reflect different standard deviations of sizes around the mean.

What if distribution of sizes is not normal, but skewed to one side? This question is of particular interest here, because many sexual ornaments may be at equilibrium between a strong directional sexual selection toward larger sizes, and a weak opposing force induced by biased mutations (Iwasa et al. 1991, Pomiankowski et al. 1991, Pomiankowski & Moller 1995). These opposing tendencies are likely to result in a skewed distribution of sizes to the left. In such cases, LAS is expected to be on the right side of the range of the sizes frequency distribution rather than in its center (Fig. 1). As a result, the relationship between FA and size should not be U shaped with symmetrical arms, but a short arm on the right, and a long arm on the left. As before, strong deviations from LAS in either direction should produce, on average, poor symmetry. Because this distribution results in a relatively weak selection on modifiers for developmental stability at any particular size, the tightness of the correlation between FA and size described by Figure 1 (bottom right) should be relatively weak. Consequently, a distribution of sizes that is strongly skewed to the left is likely to produce an apparent negative linear regression line between FA and size.

Furthermore, if reproduction is higher for individuals whose trait size is larger, which is the case for many sexually selected traits, then LAS is expected to shift even further to the right, because modifiers for large sizes are frequently associated with a higher than average reproduction rate. This will reduce further the right arm of the already asymmetric U shaped correlation between the trait's FA and size, and improve their apparent negative linear correlation.

PREDICTIONS

The findings of negative correlations between FA and size in sexual traits may, therefore, be consistent with both the whole-organism and the character-specific homeostasis hypotheses. Both hypotheses suggest that greater deviations from LAS should produce, on average, greater degrees of asymmetry at the individual level, and greater average values of FA, at the population level. However, there are still some different predictions that can be made to distinguish between the effects of these two hypotheses:

A. The primary factor that affects FA under the regime of a character-specific homeostasis, is the shape of the frequency distribution of trait sizes (weighted by the expected fitness benefits to the genetic modifiers of each particular size). Also, LAS is always expected to be intermediate between minimum and maximum sizes. If the distribution of sizes is highly skewed to the left, LAS is expected to be near the maximum, hence may be difficult to be empirically distinguished from it.

In contrast, the primary factor that affects developmental stability and FA at equilibrium within a whole-organism homeostasis regime, is the individual's adaptedness and the capacity to gain, store and use resources. For a sexually selected handicap at equilibrium, LAS is expected to correspond with the maximum trait size.

B. For character-specific homeostasis, stabilizing selection is expected to maintain LAS in the neighborhood of the mean. In response to directional selection, where mean size is driven away from equilibrium, the evolution of modifiers should lag behind, leaving LAS on one side of the mean, opposite to the direction of selection (e.g., for a trait that increases its size, LAS is expected to be smaller than the mean). The correlation between FA and size is therefore expected to be positive if the character is in a process of increasing in size (Moller & Pomiankowski 1993b, making, here, an implicit assumption of character-specific developmental stability).

Whole-organism homeostasis is expected to respond similarly in the case of stabilizing selection, but to result in an opposite correlation in the case of directional selection (negative for increasing size, positive in the case of decreasing size), because individuals who carry the novel extreme size have higher overall adaptedness.

METHODS

Following the predictions in section (A) above, this study is based on the specific prediction that if the ability to gain and use resources (reflecting developmental stress) can be better estimated by a parameter other than the particular trait's size, asymmetry of the trait should nevertheless be best correlated with its size if homeostasis is character-specific, but better correlated with that other parameter of quality if homeostasis is a whole-organism trait.

We used for our experiment a laboratory stock of the Mediterranean fruit fly (medfly) *Ceratitis capitata*, which has been raised by one of us (YR) under constant conditions since 1964. The adult population has been kept constant at about 3000 individuals, which is normally large enough to avoid frequent incidences of genetic drift (Roughgarden 1979). Temperature has been kept approximately constant at 25°C. Hence, relative to wild flies, this population has been probably kept under relatively narrow temporal fluctuations in selective pressure with regard to developmental conditions.

To manipulate developmental stress we raised larvae by collecting eggs of the same age, and put-

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ting them, at the same day, on 3 gm food at densities of 10 (8 repetitions), 20 (4), 40 (3) and 80 (3). We estimate typical densities of larvae in the culture stock to vary between 50 to a 100 per 3 gm food. The average egg hatch was 0.87 (SD = 0.08), and the proportion of larvae that pupated (from the hatched eggs) was 0.92 (SD = 0.05). Although the output numbers were a little smaller than the input numbers, for clarity we continue to refer to the original densities. Within this range of densities, the effect of density on survivorship was insignificant (we avoided a higher density, of 160 eggs per 3 gm, which, according to a preliminary test, reduced survivorship considerably). We collected the flies on the day of emergence, kept them alive and unfed overnight to let them fully expand their organs, and then put them individually in plastic tubes and stored them in a freezer, until we measured them. To avoid temporal biases in measurements, we sampled male flies taken from different densities at random until we got about 20 males of densities 10 and 20 (for which there were fewer males). We then continued to sample males of these two densities alone until we measured 22 males of each. Our final sample sizes were 22 (for density 10), 22 (20), 40 (40) and 29 (80). Some measurements were not recorded in all individuals because of physical damage to the adult flies. To minimize unconscious bias, measurements were made by a research assistant who had no knowledge of the motivation of this research or the significance of our marks on the plastic tubes in which the frozen flies were stored.

To determine the relationship between phenotypic quality and fluctuating asymmetry of traits that are not sexually dimorphic we measured head width, thorax width and length, and both wings width and length. For a sexually dimorphic trait we measured maximum width and length of the bilateral supra fronto orbital (SFO) bristle in males, which is the most modified sexually dimorphic organ in the medfly. On females this bristle is similar in shape and size to other bristles found on the head. On males, this bristle has an elongated stem and a modified wide spatula at the distal end, oriented forward (Fig. 2). Two recent studies suggest that the medfly SFO bristles are sexually selected character: Mendez et al. (unpublished) find indications that female medflies prefer intact males as opposed to males whose SFO bristles were removed, and Hunt et al. (1998) show that females prefer more symmetric SFO bristles (although not longer ones).

To measure the flies, we transferred their magnified video images from a dissecting microscope to a Power Macintosh, and used NIH Image for scaling and measurement. We measured both left and right of bilateral organs (bristles and wings), where the individual's means were computed as the average value of left and right. We removed the wings and bristles from the flies and put them on a glass microscope slide, using a cover glass to flatten them before taking measurements. Because the bristles' stems usually broke during removal, we used measurements of the bristle's lengths that were made on the head. Although the bristle is slightly curved, our technique of keeping in focus its two distal ends proved, by comparing these measurements with those made for stems of bristles that remained intact (21), to be highly consistent. Size differences between wings and bristles had no effect on the relative degree of the measurement error because both were enlarged to about the same size before their image was digitized.

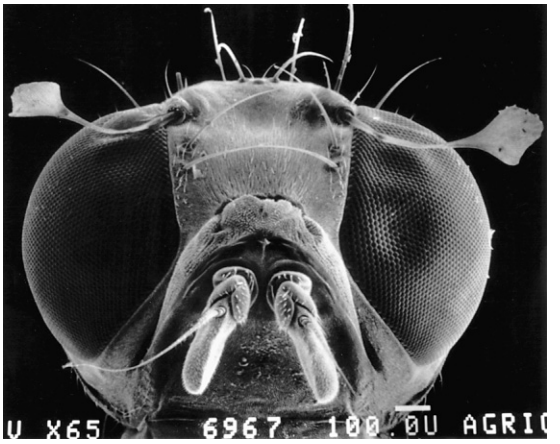


Fig. 2. The modified supra fronto orbital bristles on the head of a male Mediterranean fruit fly.

We calculated standardized values of FA of bilateral organs as the absolute value of left minus right, divided by their mean size. We standardized sizes by dividing each of them by the trait's mean size. This shifted the population mean of each trait to unity, enabling comparisons of distributions and standard deviations of traits of different sizes. For statistical analyses we used JMP, Version 3.1.5 for the PC (by SAS Institute, Inc.).

Results

Larval density had a significant effect on all measured sizes (Fig. 3) but one (bristle width). The strongest effect was on thorax length, which we therefore use as our best indicator of overall ability to gain and use resources. Head and thorax widths gave lower Chi-square values (Kruskal-Wallis tests) than that of thorax length, and we omit them from the analyses. For most purposes we were interested in looking, in individuals taken from the same gene pool, at the effect of variations in trait size on FA, regardless of the source for these variations. This roughly represents a state where individuals of different, usually unknown developmental history, are collected

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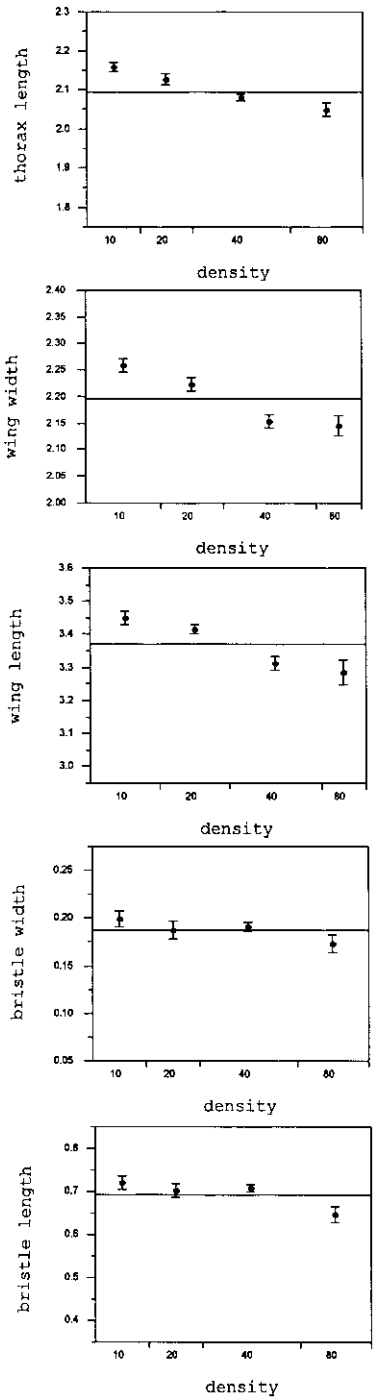


Fig. 3. The effect of larval density on adult size. Each figure shows all densities' mean (vertical line across), and the mean and standard error of each density. Distances between the horizontal ticks represent the relative sample size of each density. Statistical results (Kruskal-Wallis tests) from top down—thorax length: $O^2_{[3]} = 26.88$, $P < 0.001$; wing width: $O^2_{[3]} = 26.74$, $P < 0.001$; wing length: $O^2 = 25.85$, $P < 0.001$; bristle width: $O^2_{[3]} = 3.30$, $P = 0.35$; bristle length: $O^2_{[3]} = 13.63$, $P = 0.0035$.

at random in nature. Unless stated otherwise, we therefore used pooled data.

We found tight relationships between traits' FA and size distributions (Fig. 4). FA of bristle width and length both showed significant negative correlations with their corresponding size (Table 1). They also showed a highly skewed distribution to the left, and high standard deviation. In contrast, FA of wing length showed no correlation with size, and FA of wing width showed a parabolic, U-shape correlation with size ($y = 2.021 - 3.966x + 1.955x^2$; $F_{[2,72]} = 7.83$, $P < 0.001$). Wing length was also the only measure with a distribution that was not statistically different from normality. In accordance with their much larger standard deviations, the average FA of the bristle's width and length was about an order of magnitude larger than that of the wing's width and length.

In contrast with the tight association between FA and size of characters, the relationships between FA and the best quality indicator, thorax length, were weak, and fluctuating asymmetries of the bristle's parameters, both width and length, were much less affected by thorax length than by the corresponding trait size (Table 1). Similarly, FA of the wing width, which produced a significant quadratic (U-shape) relation to wing width (previous paragraph), showed no such pattern when correlated against thorax length ($y = 0.653 - 1.303x + 0.662x^2$; $F_{[2,72]} = 0.702$, $P = 0.5$). We also estimated least asymmetric size (LAS) of bristle's width and length by using moving averages: we sorted the data by size of the corresponding trait (Fig. 5, top) and grouped data points in tenths according to their ranked size. This resulted in groups of ten individuals, from small to large, ranked as 1-10, 2-11, 3-12 and so on till the end of the list. For each group we computed average FA and estimated LAS as the average size of the least asymmetric group. The average FA of the estimated LAS was significantly lower than the average FA of the ten points of maximum bristle width, but not in bristle length. The moving averages technique also exposed, once again, the tight relationships between FA and trait size. When we repeated the same procedure by grouping sizes by thorax length rather than by bristles' width and length (Fig. 5, bottom), the continuous trend found in the first two figures (Fig. 5, top), was lost.

Furthermore, if symmetry develops in response to whole-organism homeostasis, and the latter is affected by the individual's (residual) quality, then symmetry should be a good indicator of quality. Because larval density affected phenotypic quality (as indicated by its effect on adult fly size), this enabled another test of the relationships between FA and quality. We found no effect of larval density on FA (bristle length: $O^2_{[3]} = 2.769$, $P = 0.42$; bristle width: $O^2_{[3]} = 1.607$, $P = 0.66$; wing width: $O^2_{[3]} = 3.1247$, $P = 0.373$; wing length: $O^2_{[3]} = 1.359$, $P = 0.72$; Kruskal-Wallis tests).

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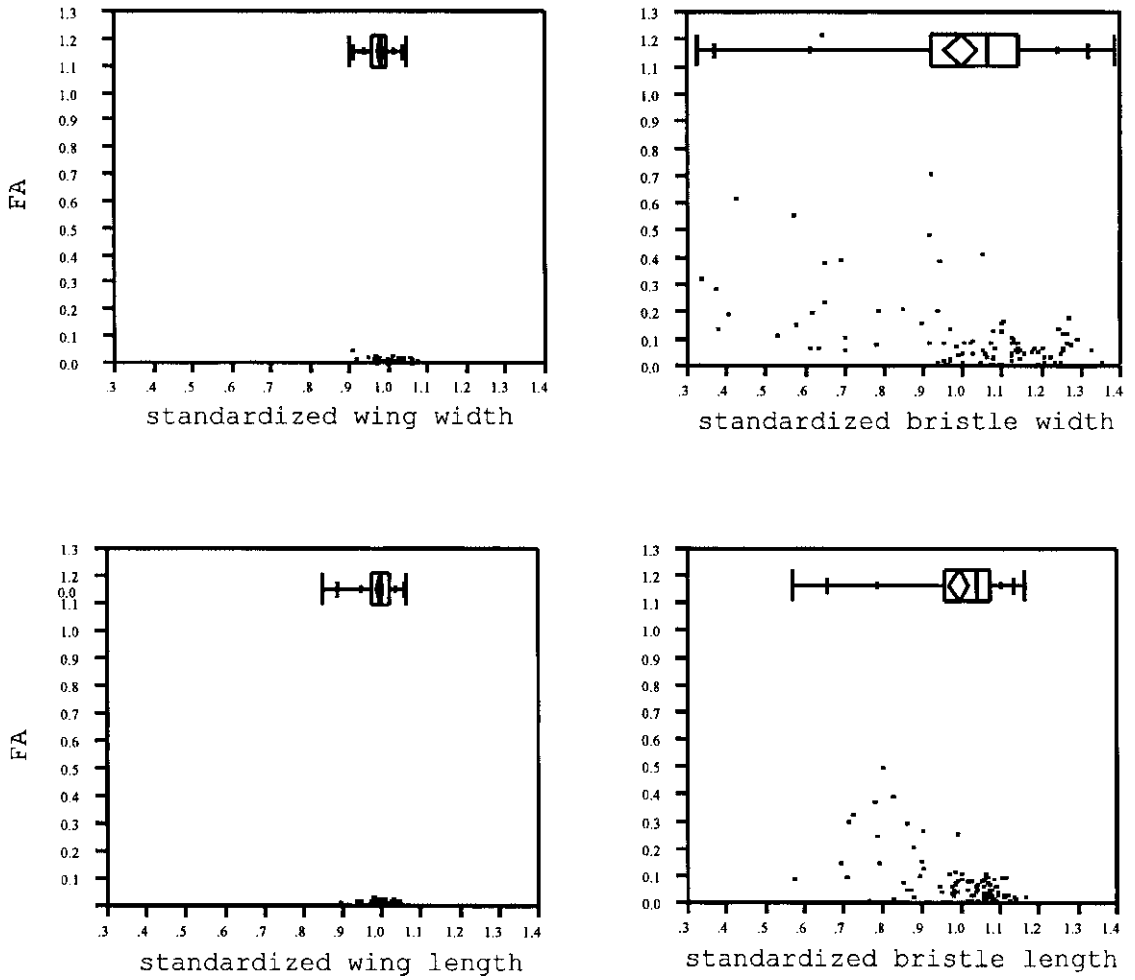


Fig. 4. The relationships between size frequency distributions and FA. Distributions are represented by quantile plots: each box shows the median as a vertical line across the middle, and the quartiles (25th and 75th percentiles) as its ends. The means diamond identifies the mean of the sample and the 95% confidence interval about the mean. Ticks represent 90%, 97.5%, 99.5% and maximum size from the box to the right, and 10%, 2.5%, 0.5% and minimum size, to the left.

Finally, only bristle's width and length measurements showed a positive correlation between their FA's (N = 104, r_s = 0.2918, P = 0.0027; Spearman rank correlation). All other pairs of measurements showed no correlation between their FA values (giving $-0.124 < r_s > 0.089$, and $0.31 < P > 0.77$).

Discussion

Our study indicates that character-specific homeostasis plays a major role in determining the degree of FA in the medfly. This, however, should not undermine the role of whole-organism homeostasis, supported by studies that show within individual correlations in FA of different characters (Soule & Cuzin-Roudy 1992, Watson & Thornhill 1994). The current study, and the fact that some of these previous studies support the whole-organism homeostasis, may suggests that both may be important, perhaps under different conditions, or for different organisms. Some sources of instability, for example, such as the effect of certain chemicals, or of extreme temperatures (Soule 1982, Parsons 1989) may directly affect instability of development of all traits, irrespective of their sizes, resulting in a true whole-organism effect on developmental homeostasis. However, then the source of instability affects some characteristics more than others, a greater tendency toward character-specific homeostasis should be detected. Alatalo et al. (1988) showed that sexually dimorphic characters have larger size variations than other characters. They did not look at the shapes of the size frequency distributions, but the

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TABLE 1. ASSOCIATION OF BRISTLE WIDTH AND LENGTH'S FA WITH BRISTLE CORRESPONDING SIZE AND WITH THORAX LENGTH (USING SPEARMAN'S RANK CORRELATIONS).

	N	r_s	Probability
Bristle width's FA × bristle width	104	-0.4060	<0.0001
Bristle length's FA × bristle length	104	-0.5023	<0.0001
Bristle width's FA × thorax length	103	-0.2447	0.0127
Bristle length's FA × thorax length	103	-0.1120	0.2599

large size variations of sexually dimorphic characters may make their FA more vulnerable to character-specific effects (size variations) than to whole-organism homeostasis.

In the study that we present here, larval densities affected bristles' length, but did not produce corresponding changes in their FA. This result corresponds with other studies that show low heritability for FA, relative to that of quantitative morphological traits' sizes (Parsons 1990). This suggests that in our study other sources of variation in FA were stronger than the stress created by

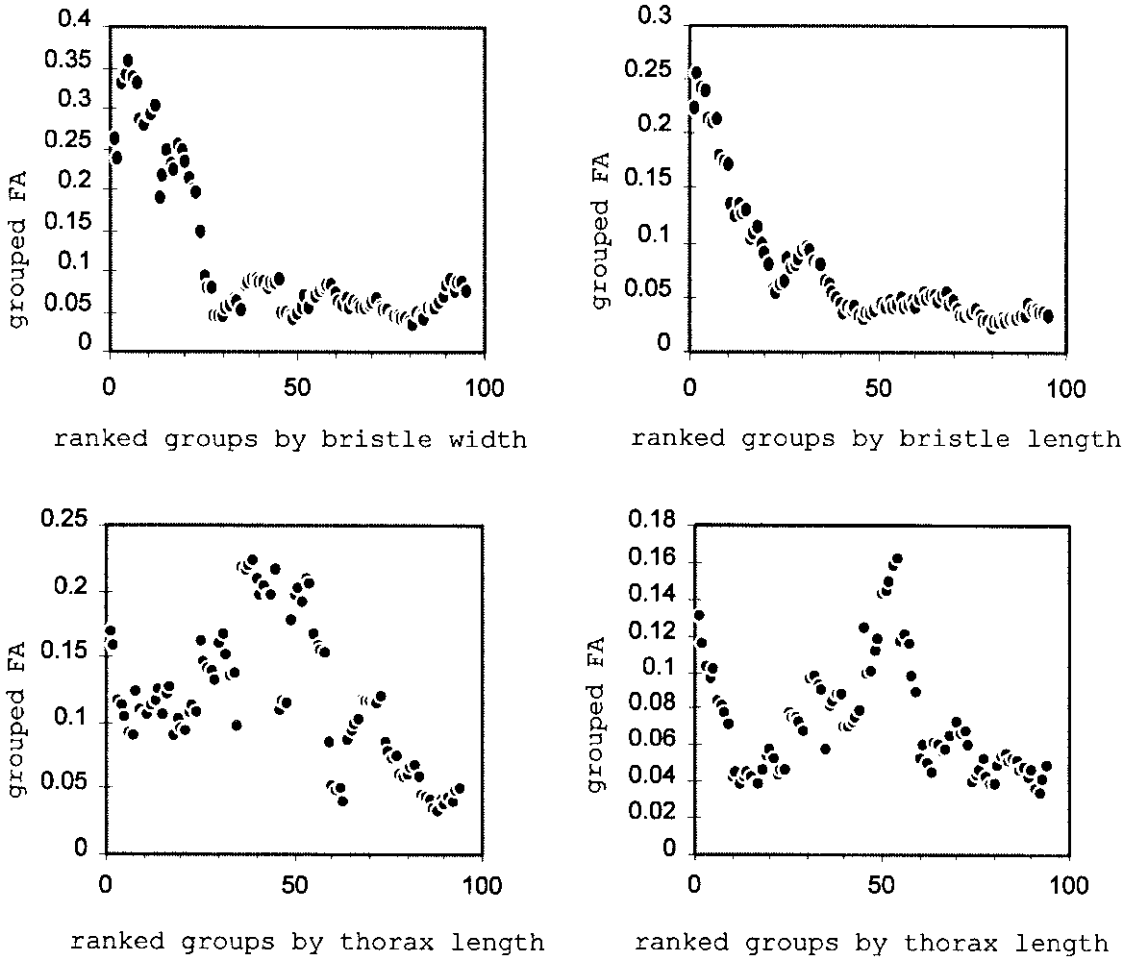


Fig. 5. The relationships between moving averages of FA and groups ranked by sizes. Each closed circle represents its minimal rank point (horizontal axis) and the group's average FA. For bristle width, minimum average FA is 0.0355, representing the rank order 81-90. Its corresponding average standard size is 0.224 mm. The minimum average FA is significantly lower than that of the top ten sizes (ranked 95-104), 0.0760 (one-tail t-test for unequal variances, $t_{[18]} = -2.35$; $P = 0.018$). For bristle length, minimum average FA is 0.0242, rank order, 80-89 ($N = 104$), and corresponding average standardized size, 0.755 mm. This minimum average is not statistically different from the average FA of the top ten sizes (ranked 95-104), 0.0349 (one-tail t-test for equal variances, $t_{[18]} = -0.80$; $P = 0.216$).

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density alone. Here, variations in FA appear to be the consequence of the sensitivity of character-specific developmental homeostasis to size frequency distributions. The high variance of sizes of a trait (e.g., the highly skewed bristle length) should weaken selection on modifiers that form stability of each particular size. This increases the frequency of modifiers for sizes that are at some distance from LAS. Consequently, phenotypic changes in average size in response to density should have a relatively weak effect on average FA. Size-dependent character-specific homeostasis should, therefore, weaken the response of FA to environmental variables, especially when these variables induce changes in size that are well within the natural range of variations of the trait size (also considering fluctuations in time). Hence, FA of a trait should generally be less sensitive to stress than the trait size itself. This only strengthens Whitlock's (1996) argument for the low heritability of FA.

FA has been assumed to be a measure of overall quality in a variety of studies of sexual selection (Watson & Thornhill 1994). However, if it is instead strongly influenced by character-specific modifications and size frequency distributions, then FA should not be regarded as a direct measure of overall quality but, at best, as its approximation. When size frequency distribution of a sexual handicap is skewed then, despite the general correlation between symmetry and quality, the very best individuals (whose sexual characters are largest) should develop, on average, a greater asymmetry than males with somewhat smaller handicap (Figs. 1 and 5). In other words, LAS should not correspond with trait size of best individuals. Thus, although symmetry is generally informative and correlated with quality, within a certain range of sizes it becomes non-informative, maybe even misleading criterion for quality (depending on the degree of female selectivity, and on the nature of the trait's size frequency distribution).

Our results show that we need to re-evaluate the current use of FA. For example, the assumption that FA is determined by whole-organism homeostasis, underlies the suggestion that a negative correlation between FA and male ornament size indicate handicaps, and a lack of it points at Fisherian ornaments, which are not informative about any of the male "qualities" except for attractiveness to females (Moller & Pomiankowski 1993c). If, however, symmetry of sexually dimorphic characters is dominated by character-specific homeostasis, differences in correlations between traits' FA and size may only reflect different size frequency distributions. The correlation between characters' FA and size would nevertheless differentiate between handicaps and Fisherian sexual traits only if handicaps consistently show highly skewed distributions and Fisherian sexual traits do not. Hence, in order to make this argument, it is essential to study also the frequency distribution of trait sizes.

The possibility that FA is less sensitive to environmental stress than traits' size poses another important question: why do female swallows, for example, use both tail symmetry and tail length as criteria of the male quality (Moller 1992)? This should only make sense in an adaptive manner if each provides a certain different additive component of information regarding the male quality (Hasson 2000). The character-specific homeostasis can provide an intriguing answer: while a well developed handicap advertises a male's superior phenotypic quality, the bilateral symmetry of a handicap may indicate, by presenting modifiers for its particular size, that the male is a descendant of a long line of similarly good phenotypes. Hence, while a handicap improves information about the male phenotypic quality, the handicap's symmetry indicates the probability that this phenotype is a product of "good genes".

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