



## Environmental versus genetic influences on fluctuating asymmetry in the house fly, *Musca domestica*

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The causes of fluctuating asymmetry (FA) are poorly understood, yet it has been widely used as a measure of fitness. Many studies have demonstrated that individuals with low FA are preferred as mates, and it has been argued that this is because FA provides an indicator of genetic quality. However, the relative importance of genes versus environment in determining the level of FA shown by an organism is currently the subject of much controversy. As yet there is no clear consensus as to whether FA generally has a heritable component and if so how large this might be, or indeed if it is sensible to generalize at all. In *Musca domestica* flies with low wing length FA have been found to enjoy higher mating success. In order to interpret this finding we assess whether wing length FA in this species is heritable, and also how it is influenced by environmental stresses induced by temperature and crowding. We also examine whether offspring viability is related to parental FA. We found that wing length FA in *M. domestica* had no detectable heritable components, and parental FA did not influence offspring viability. FA was influenced by rearing temperature, with flies exhibiting highest FA at the lowest rearing temperature (15°C). Larval survival rate was greatest, and the resulting adults largest, at the intermediate rearing temperature (25°C) compared to higher or lower temperatures, suggesting that 25°C is close to the optimum for the development of *M. domestica*. Adult size appears to provide a better indicator of stress during development than does wing FA. These results are discussed in relation to the utility of FA as a tool for use in evolutionary studies.

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ADDITIONAL KEY WORDS:—Diptera – Muscidae – developmental stability – heritability – rearing conditions – environmental stress – temperature – density.

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## INTRODUCTION

Fluctuating asymmetry (FA) can be defined as small departures that are random in direction from anticipated bilateral symmetry (Ludwig, 1932; Van Valen, 1962). It has been proposed that these tiny departures from perfect symmetry can be used as a measure of the health, genetic quality and developmental stability of individuals or populations (reviews in Leary & Allendorf, 1989; Parsons, 1990, 1992; Watson & Thornhill, 1994; Møller, 1997; Møller & Thornhill, 1998). This simple and seemingly powerful tool has numerous applications, and a flurry of studies of FA in relation to evolutionary and conservation biology have appeared in the last decade. However, it seems that FA has on occasion been used rather uncritically and with inappropriate methodology (Palmer, 1996; Palmer & Strobeck, 1997). For example many studies assume that bilateral characters exhibit FA without checking for alternative forms of asymmetry such as directional asymmetry or antisymmetry. As a result, scepticism has grown as to the utility of FA. For FA to have evolutionary significance it must be related to fitness and have a heritable basis. The heritability of FA is currently the subject of some debate (for conflicting views see Møller & Thornhill, 1997; Leamy, 1997a; Markow & Clarke, 1997; Palmer & Strobeck, 1997; Swaddle, 1997; Whitlock & Fowler, 1997). Overall most workers agree that FA often has a heritable component, but that this is typically small (Whitlock & Fowler, 1997).

It is desirable that studies of fitness in relation to FA be backed up by studies of the causes of FA (genetic versus environmental) wherever possible. Møller (1996) examined relationships between FA and fitness in the housefly, *Musca domestica* (Diptera: Muscidae) L. He found that FA in wing length was negatively correlated with mating success in both sexes, and was also negatively correlated with resistance to disease and the likelihood of predation by swallows. However, more recently we found no relationship between symmetry and mating success in a different population of *M. domestica*; instead, large flies enjoyed greater mating success (Goulson *et al.*, 1999). Nothing is known as to whether FA of wing length in *M. domestica* is heritable, and whether it responds to environmental stress. The aim of this study was to quantify these two influences on wing FA in *M. domestica*. We assess the heritability of FA in wing length using parent–offspring regressions, and examine whether offspring viability is related to parental FA. We also assess the influence of temperature and crowding during larval development on wing FA and on two other potential indicators of stress, larval survival and adult size.

## METHODS

### *Effects of density and temperature on development and morphology*

Wild flies were collected from a poultry house in Braishfield, Hampshire, U.K. in February 1998 using a butterfly net. Approximately 500 flies were caught, and

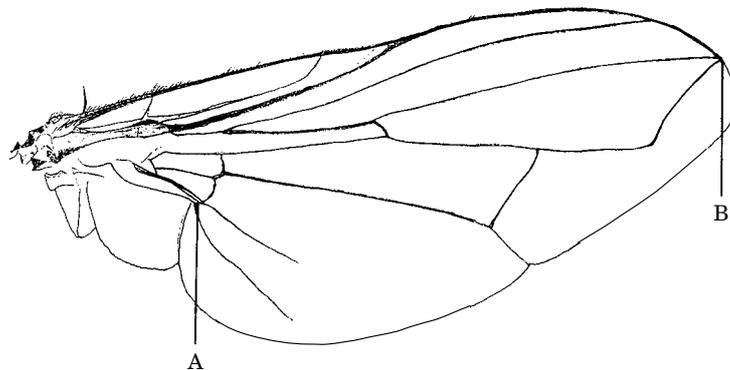


Figure 1. Wing of *M. domestica*, indicating the points between which wing measurements were taken (A and B).

were confined with an oviposition substrate (cotton wool soaked in milk), water and food (20 parts powdered milk: 10 parts sugar: 1 part yeast). Many of the females had probably mated at the time of capture, but further matings were observed in captivity. Using a paintbrush either 20, 50, 100 or 250 eggs were transferred to pint pots containing a rearing medium (0.51 portions of a mix of 2.5 l bran, 250 ml powdered milk, 450 ml water and 30 ml yeast). The pots were covered with nappy liners and placed in an incubator in darkness until emergence of the adults. During larval development the pots were stored at 15, 25 or 35°C. The four rearing densities and three temperatures thus gave 12 different treatments; each was replicated four times.

Pots were checked daily for emergence, the adults were removed, and killed by freezing for 15 min. Each fly was sexed by examining the external genital opening on the terminal visible abdominal segment, and its wet weight was recorded. Measurements of wing length were obtained for twenty flies from each pot, 10 males and 10 females. This sample was randomly taken from flies that emerged during the period of peak emergence. The experiment was terminated when 10 days had passed since the last flies had emerged.

#### *Wing measurements*

Wing length asymmetry was measured since Møller (1996) found this attribute to be most closely related to mating success in *M. domestica*. Wings were removed from the flies and mounted on a slide using D.P.X. and a coverslip. Wing measurements were made between the vein junctions marked in Figure 1 and as such are slightly less than the total length of the wing. Two methods of wing measurement were compared. A sample of wings were measured under the dissecting microscope using an eyepiece graticule and also using a video camera mounted to the dissecting microscope, with measurements taken from a video monitor using Vernier callipers. Repeated measurements using each system indicated a higher repeatability using the latter. The accuracy of this measurement system was then assessed in more detail; both wings from 103 wild-caught flies were measured twice

by the same person on two different days. Pearson product-moment correlation coefficients were calculated between successive measurements on each wing.

#### *Analysis of the effects of rearing density and temperature*

The number of adults emerging from each pot were analysed using Generalised Linear Interactive Modeling (GLIM) (McCullagh & Nelder, 1989) with binomial error structure, according to temperature and rearing density (equivalent to a factorial analysis of variance). The maximum possible emergence (the number of eggs placed in the pot) was used as the denominator for these binomial data. The proportion of males emerging from each pot was also analysed in GLIM using binomial errors to test whether the sexes exhibited differential survival under differing rearing conditions. For each morphological variable a single mean was calculated for males and females emerging from each replicate pot and used in analyses. Effects of temperature and rearing density on morphological variables were examined using analysis of variance with sex included as a factor. Mean wing length was calculated for each fly and then a grand mean calculated per replicate. Similarly FA was calculated for each fly and then a mean FA per replicate calculated for use in analyses. Although FA of individuals typically has a half-normal distribution, when using mean FA of many flies the distribution approaches normality. Following a log transformation these data approximated a normal distribution (Kolmogorov-Smirnov test for normality,  $P=0.20$ ). Directional asymmetry was tested for using a paired *t*-test (comparing left versus right wing lengths). A separate test was carried out on all males combined and all females combined. The presence of antisymmetry was examined by quantifying kurtosis of the distribution of left minus right wing lengths.

#### *Effects of parental phenotype on offspring viability and FA*

Offspring of wild-caught flies were reared as above at a density of 100 per pot at 25°C. Within 24 h of emergence F1 flies were cooled to render them inactive and then separated according to sex (they do not mate within this period (Murvosh, Fye & Labrecque, 1964)). Before use in experiments, flies were kept for 7–9 days in 30 × 30 × 30 cm cages with food and water, to allow time for maturation (Reiman, Moen & Thorsen, 1967). All flies used for mating were of equal age ( $\pm 1$  day). Randomly selected pairs of flies were confined in round transparent plastic pots (10 cm diameter × 5 cm depth) with an oviposition medium and left for up to three days. Flies that did not mate were discarded. The first batch of eggs to be laid was collected and 50 eggs placed on a pot with rearing medium as above. The parents were killed by freezing, and their wet weight and wing measurements were recorded. In total, 24 pairs of flies produced fertile offspring. The rearing pots were stored at 25°C until emergence of adult offspring. Emergence was checked daily and adults removed, killed by freezing, counted, sexed and stored in a freezer at  $-30^{\circ}\text{C}$  for later measurement of wings. For logistical reasons weight of offspring was not recorded in this experiment.

Variations in numbers of offspring emerging per brood and mean emergence date per brood were compared with parental phenotype using Spearman rank

correlation to examine whether parental phenotype was related to offspring viability. These two variables were each correlated with the weight, mean wing length and FA of the male parent, the female parent and the mean parental value. Heritability ( $h^2$ ) was estimated by linear regressions of the brood means for wing length and FA regressed against these measurements on the male parent, the female parent and the mean parental value. Often FA data violate the assumptions of linear regression analyses because the data depart from normality (Swaddle, Witter & Cuthill, 1994). However, Kolmogorov–Smirnov tests demonstrated that mean offspring FA per brood did not depart significantly from normality.

## RESULTS

### *Measurement of FA*

Correlation between successive measurements of the same wings were 0.991 ( $P < 0.001$ ) and 0.990 ( $P < 0.001$ ) for left and right wings, respectively ( $n = 100$ ). Asymmetry measures also exhibited a significant (but lower) correlation ( $R = 0.610$ ,  $P < 0.001$ ,  $n = 100$ ). This indicates that measurements were sufficiently precise to allow analysis of wing size and wing FA, but the small size of asymmetries compared to wing lengths clearly renders them subject to larger measurement errors. A mixed-model ANOVA was used to demonstrate that with this measurement system between-individual variation in estimated asymmetry was significantly greater than could be accounted for by measurement error ( $F_{102,204} = 2.66$ ,  $P < 0.001$ ) (Swaddle *et al.*, 1994). The coefficient of variation of FA was 0.98 and is fairly typical for studies of FA in insects (Whitlock, 1996) giving an hypothetical repeatability ( $R$ ) (*sensu* Whitlock, 1998) of 0.26.

Examination of skew and kurtosis of the distribution of left minus right wing lengths (L–R) for the offspring flies (all experiments combined) indicated that for males the L–R values were right skewed ( $g_1 \pm \text{SE}$ ;  $1.16 \pm 0.14$ ,  $P < 0.01$ ) and leptokurtic ( $g_2 \pm \text{SE}$ ;  $7.11 \pm 0.28$ ,  $P < 0.01$ ) (Sokal & Rohlf, 1995). Females L–R values were left skewed ( $g_1 \pm \text{SE}$ ;  $-0.94 \pm 0.14$ ,  $P < 0.01$ ) and leptokurtic ( $g_2 \pm \text{SE}$ ;  $3.99 \pm 0.28$ ,  $P < 0.01$ ). Thus there is no evidence of antisymmetry since bimodal distributions tend to be platykurtic (Sokal & Rohlf, 1995). Neither males nor females exhibited directional asymmetry ( $t = 0.13$ ,  $P > 0.05$  and  $t = -1.78$ ,  $P > 0.05$  for males and females, respectively).

There was no significant correlation between absolute FA and mean wing length in either sex, and exploration of these data revealed no higher order relationships such as a U-shaped curve (as is found, for example, when FA is plotted against wing length in swallows (Møller & Pomiankowski, 1993)). Thus absolute FA, rather than relative FA (absolute asymmetry divided by mean wing length (Ludwig, 1932; Palmer & Strobeck, 1986) was used in analyses.

### *Effects of density and temperature on development and morphology*

The proportion of eggs which survived to adulthood varied greatly with temperature but not with rearing density (Table 1). Survival was greatest at 25°C

TABLE 1. Test statistics from analysis of the effects of rearing density, rearing temperature and sex on survival of larvae and aspects of the morphology of the resulting adults. Statistics are  $F$  values unless otherwise stated. Degrees of freedom are given in brackets. There were no significant interactions between density and temperature. \* $P < 0.05$ , \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

	Density	Temperature	Sex
Survival	$_{(3,34)}0.61$	$_{(2,34)}30.2^{***}$	—
Sex ratio	$_{(2)}\chi^2 = 2.12$	$_{(2)}\chi^2 = 0.54$	—
Development time	$_{(3,65)}0.18$	$_{(2,65)}767^{***}$	$_{(1,65)}0.27$
Weight	$_{(3,65)}0.25$	$_{(2,65)}39.1^{***}$	$_{(1,65)}7.83^{**}$
Mean wing length	$_{(3,70)}2.83^*$	$_{(2,70)}90.7^{***}$	$_{(1,70)}32.8^{***}$
FA	$_{(3,70)}0.13$	$_{(2,70)}5.55^*$	$_{(1,70)}0.33$

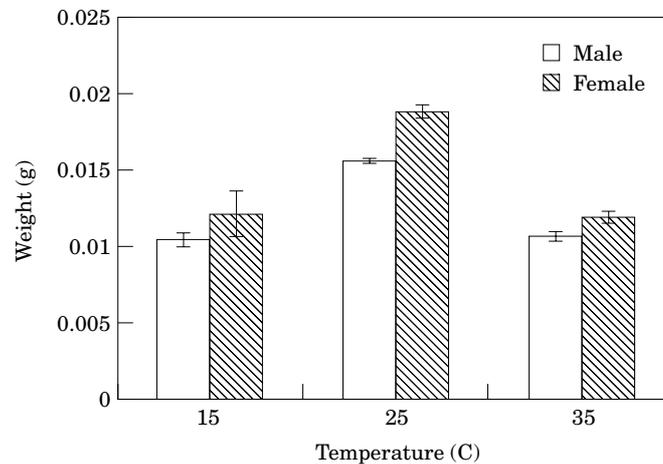


Figure 2. Wet weight of flies reared at three temperatures (means  $\pm$  SE). Means shown are the grand means of the mean weight of flies in each replicate rearing pot (16 per temperature).

(overall 50.2%), lowest at 15°C (9.0%) and intermediate at 35°C (37.7%). The sex-ratio did not vary with temperature or rearing density. Overall 46.4% of emerging flies were male.

The development time from egg to adult varied greatly with temperature (Table 1), being greatly extended at 15°C (means (days)  $\pm$  SE;  $57.5 \pm 1.77$ ,  $14.7 \pm 0.28$  and  $12.05 \pm 0.31$  at 15, 25 and 35°C, respectively). There was no effect of rearing density on development time, and the development times of males and females did not differ (Table 1).

The effect of rearing temperature on fly weight was highly significant (Table 1); flies were heaviest at 25°C but of similar weight at 15 and 35°C (Fig. 2). Weight did not differ with rearing density, but females were consistently heavier than males. Mean wing length showed a similar pattern, with highly significant variation with

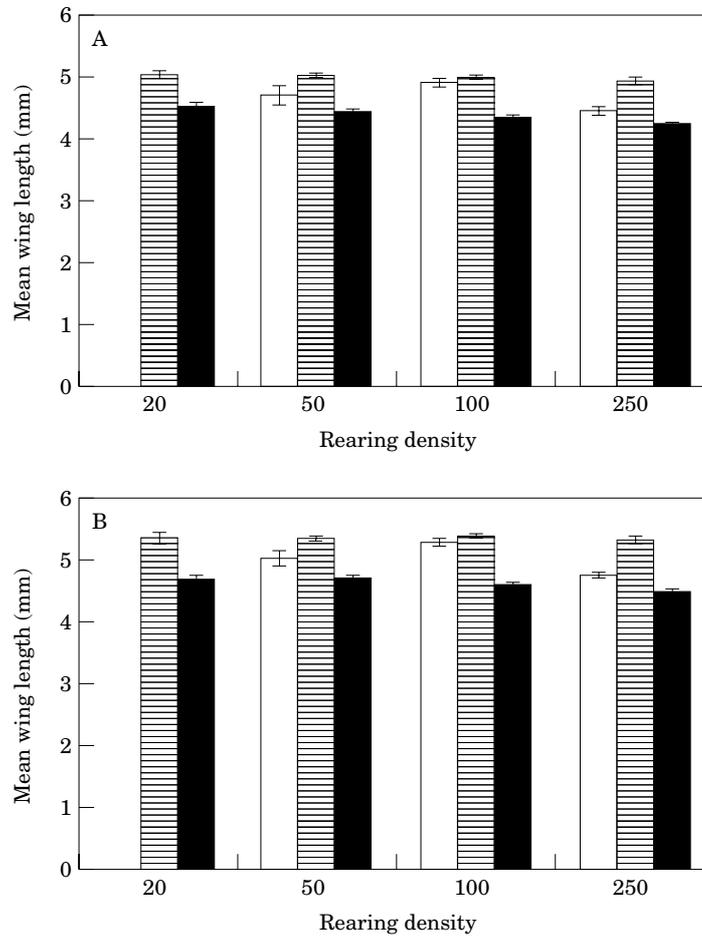


Figure 3. Wing lengths of flies according to rearing density and temperatures (means  $\pm$  SE). Means shown are the grand means of the mean wing length per fly averaged per replicate and then averaged per treatment (there were 4 replicates per treatment). SEs calculated using the means from each replicate. A, males; B, females. (□) 15°C; (▨) 25°C; (■) 35°C.

rearing temperature (Table 1); mean wing lengths being largest at 25°C (Fig. 3). Female wing lengths were on average greater than male's. Wing length also differed with rearing density, with wings tending to be slightly smaller at high densities (Fig. 3). FA was highest at 15°C, with little difference in FA between the 25°C and 35°C treatments (Fig. 4). FA did not vary according to rearing density or sex (Table 1).

There were no significant interactions between temperature and rearing density for any of the morphological variable measured.

#### *Heritability of wing length FA*

In total 474 offspring were obtained (mean per brood 20.6, SE 2.92). Regression of mean brood wing length and measures of asymmetry against parental values

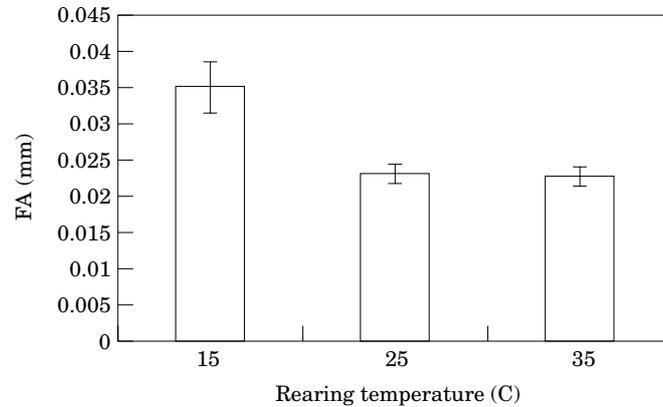


Figure 4. Absolute FA of flies reared at three temperatures (means  $\pm$  SE). Means shown are the grand means of the mean asymmetry of flies in each replicate rearing pot (16 per temperature).

TABLE 2. Values of  $h^2 \pm$  SE from regression of offspring brood means of wing length and measures of asymmetry against parental values. None of the values are significant ( $P > 0.05$ )

	Male parent	Female parent	Parental mean
Mean wing length	$0.003 \pm 0.161$	$-0.021 \pm 0.057$	$-0.026 \pm 0.092$
Absolute FA	$0.070 \pm 0.083$	$-4.4 \pm 10^{-4} \pm 0.002$	$-8.2 \times 10^{-4} \pm 0.004$

TABLE 3. Spearman rank correlation coefficients between parental wing size and symmetry and the number of offspring reaching adulthood (of 50 eggs) and the mean development time per brood. None of the values are statistically significant ( $P > 0.05$ )

	Parent attribute	No. adult offspring	Mean development time
Mean wing length	Male	-0.137	0.008
	Female	0.148	0.371
	Parental mean	-0.008	0.231
Absolute asymmetry	Male	-0.069	-0.068
	Female	0.076	-0.063
	Parental mean	0.085	-0.078

revealed no significant relationships, and very low values of  $h^2$  of FA (Table 2). To calculate estimates of the heritability of the underlying developmental stability, estimates of  $h^2$  for FA are divided by the repeatability ( $R^2 = 0.26$ ), which in this case give a  $h^2$  for developmental stability of  $3.2 \pm 10^{-3}$  based on parental means (Whitlock, 1996).

#### *Effects of parental FA on offspring fitness*

Spearman rank correlation coefficients revealed no relationships between parental wing length or symmetry and mean offspring development time or the number of offspring surviving to adulthood (Table 3).

## DISCUSSION

We found considerable variation in survival, development rate, adult size and FA according to temperature, with weaker effects resulting from crowding. Little is known of the natural temperatures and densities experienced by *M. domestica* in the wild, but they probably span those chosen. *M. domestica* lay large batches of eggs (>100), so larvae presumably sometimes encounter high densities. Larvae are found throughout the year, and since they inhabit decomposing material are probably sometimes exposed to high temperatures. We found no evidence of a heritable component of FA or adult size, and no effect of adult FA on offspring viability. Also, we did not find any evidence of directional asymmetry, although in an earlier study of *M. domestica* originating from the same site we did find significant directional asymmetry with left wings tending to be longer than right wings (Goulson *et al.*, 1999). This suggests that the type of asymmetry found in populations may vary according to environmental conditions.

One of the least controversial aspects of FA is that it can be induced by environmental stress, although the evidence is sometimes conflicting (Markov, 1995). Exposure to toxins may increase levels of FA in flies. For example, lead or benzene induced greater amounts of FA in sternopleural bristle number of *Drosophila melanogaster* (Graham *et al.*, 1993). At the highest concentrations benzene induced directional asymmetry. *Musca vetustissima* emerging from the dung of cattle treated with avermectin D exhibited greater FA in wing venation than flies emerging from uncontaminated dung (Clarke & Ridsdill-Smith, 1990). However, no such trend was found in *M. vetustissima* when the maggots fed upon dung from sheep treated with ivermectin (Wardhaugh, K. G. reported in Markov, 1995), and FA in bristle number of *D. melanogaster* was not affected by phenylthiourea (Parsons, 1961).

Effects of temperature are more consistent. Parsons (1962) found that elevated temperatures increased bristle asymmetry in *D. melanogaster*. Clarke and McKenzie (1992) found that FA in bristle counts of *Lucilia cuprina* was least at 27°C and increased at higher or lower temperatures. These results are very similar to our own, since we found FA to be highest at 15°C and lowest at 25°C, although there was little appreciable increase from 25 to 35°C. Clarke and McKenzie (1992) also found that FA in *L. cuprina* increased linearly with crowding. They argue that FA provides one of the most reliable indicators of environmental stress in *L. cuprina*, and so could be used as a quality control indicator for insect mass rearing. In both *L. cuprina* and *M. domestica*, intermediate temperatures gave the highest survival rate and the heaviest and largest flies. This strongly suggests that high or low temperatures are indeed stressful to developing flies. However, using wing length FA in *M. domestica* does not appear to be a particularly sensitive indicator of stress. Weight or wing length are both more simple to measure accurately and were more sensitive to rearing conditions. Wing length was the only variable to exhibit a significant response to crowding and temperature. Thus if one wished to monitor stress on laboratory or wild cultures of *M. domestica* we would recommend using a measure of size rather than of FA. Large flies of both sexes are also more successful in obtaining mates, suggesting that size may be directly related to fitness (Goulson *et al.*, 1999).

If FA does provide a measure of the genetic quality of individuals, then we might expect the offspring of symmetrical flies to derive fitness benefits from the acquisition of 'good' genes. Our studies found no evidence for increased viability of the offspring of flies with low FA. We also found no evidence for heritable component of FA or

of wing size, with all values of  $h^2$  being close to zero and far from significance. The heritability of FA remains controversial. Møller and Thornhill (1997) carried out a meta-analysis of studies of the heritability of FA and concluded that in general FA appears to have a small but significant heritable component with an overall mean  $h^2$  of 0.27. However, this analysis has received considerable criticism on a number of grounds. Several authors question whether calculating an overall value for  $h^2$  is meaningful (Leamy, 1997a; Markow & Clarke, 1997; Palmer & Strobeck, 1997; Pomiankowski, 1997). Not all of the data used appear to be correct, or were incorrectly cited (Leamy, 1997a; Markow & Clarke, 1997; Palmer & Strobeck, 1997; Whitlock & Fowler, 1997). Furthermore, many of the studies used were flawed in that the measurement error exceeded the asymmetry, other types of asymmetry such as antisymmetry or directional asymmetry were not tested for, or because trait size (which may be correlated with asymmetry) was not taken into account (Leamy, 1997a; Markow & Clarke, 1997; Palmer & Strobeck, 1997). Recently, a detailed study of FA of various traits in the butterfly *Inachis io* found, as did we, that there was little or no heritable component to FA (Windig, 1998). Similarly Leamy (1997b) found no detectable heritability in skeletal characters of mice. Clearly broad conclusions cannot be drawn from limited data. The present study examined heritability in only one trait (albeit one which has been found to be related to several aspects of fitness), and in only one population. If FA in wing length of *M. domestica* has no heritable basis, but simply indicates the environment in which the fly developed, then the enhanced mating success of symmetrical flies (Møller, 1996) cannot be due to sexual selection for partners of high genetic quality. Markow (1995) called for a re-evaluation of the importance of FA; we provide another small piece of evidence against the usefulness of FA as a heritable indicator of fitness.

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