

Small males are more symmetrical: mating success in the midge *Chironomus plumosus* L. (Diptera: Chironomidae)

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Abstract. Male *Chironomus plumosus* most successful at acquiring mates showed lower levels of fluctuating asymmetry in length of wing than their rivals. These males were not of the most common size, but were the smallest in the population. These results are consistent with the prediction that where there is directional selection for small individuals, fluctuating asymmetry will be positively correlated with size. However, for a species that mates on the wing, selection may act upon symmetry per se rather than body size. Uncoupling the effects of size from those of asymmetry suggested that fluctuating asymmetry might, on its own, account for the observed mating success of *C. plumosus*. It is suggested that the success of the more symmetrical males is due to their improved aerobic ability. *Chironomus plumosus* provides an example of the importance of fluctuating asymmetry in male characters that are not purely ornamental and these results are therefore more readily interpreted in terms of natural rather than sexual selection.

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The ability of a genome to buffer errors in embryogenesis is seen in differences between the right and left sides of traits that are ideally bilaterally symmetrical. The degree of this fluctuating asymmetry is increased by environmental stress during development and has repeatedly been shown to be negatively correlated with fitness characters such as longevity, growth rate, fecundity and heterozygosity (Mitton & Grant 1984; Palmer & Strobeck 1986; Parsons 1990). Fluctuating asymmetry is a heritable trait in many animals (Van Valen 1962; Thornhill & Sauer 1992; Watson & Thornhill 1994) and thus may be a measure of overall fitness.

Fluctuating asymmetry is also associated with variation in male mating success: individuals with relatively low levels of fluctuating asymmetry are often found to achieve a greater proportion of matings (e.g. Thornhill 1992a, b; Liggett et al. 1993; Radesäter & Halldórsdóttir 1993). This might be expected since males with low levels of fluctuating asymmetry are likely to be of superior overall fitness. Møller (1990) suggested that

female barn swallows, *Hirundo rustica*, use the size and symmetry of sexually selected male tail feathers as an estimate of genetic health. Alternatively, low fluctuating asymmetry in functional characters may afford an advantage in intra-sexual competition among males in the absence of epigamic selection, as the result of natural selection for aerodynamic performance, for example (Møller 1991; Balmford et al. 1993a; Thomas 1993).

On purely Newtonian grounds, size per se is expected also to affect aerodynamics. Small flying devices, whether animal or machine, have a smaller turning moment than larger ones. This effect is also subject to natural selection and can have independent consequences for mating success (reviewed by Alexander et al. 1978 and specifically for chironomids by A. J. McLachlan & R. M. Neems, unpublished data). There are thus at least two characters that may be important in the mating success of midges such as *C. plumosus*: fluctuating asymmetry and size.

In *C. plumosus* the relationship between size and mating success is an unusual one. There is a tendency to think of large size as the universal determinant of mating success in the male (see Greenwood & Adams 1987 for a review). In *C. plumosus*, however, small males gain a disproportionately high number of matings in aerial

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swarms which are visited by females for copulation (see McLachlan & Neems, in press, for a review). Patterns of fluctuating asymmetry in traits under stabilizing selection often vary with trait magnitude in a U-shaped manner. This is because extreme phenotypes show less developmental stability than those close to the mean of the population (Soulé & Cuzin-Roudy 1982). Here we measure the relationship between trait size and fluctuating asymmetry in a species where it is known that there are advantages to small size. We have two aims. First, we test the hypothesis that there is detectable fluctuating asymmetry in male *C. plumosus* and that there is variability in the degree of fluctuating asymmetry between males. Second, we set out to separate the effects of size and of fluctuating asymmetry on the mating success of *C. plumosus* and examine the implications for the evolution of the mating system in this species.

METHODS

We measured fluctuating asymmetry as the difference between the two wings and body size as mean wing length. The latter is an appropriate measure of body size (1) because wing length is strongly correlated with other measures of size such as dry weight in chironomids (McLachlan 1986) and (2) because mean wing length and the difference between wings are statistically independent variables. Wing lengths were measured in 224 males collected by net from mating swarms. We also measured 135 male-female pairs, captured while they were mating. Samples were taken in the evenings between April and June 1992 at Washington Wildfowl Park, Northumberland. Swarms of males form over landmarks each evening in order to attract dispersed mates. Searching females enter the swarm and leave it again after a short period paired with a male. The pair are poor fliers and settle briefly near the swarm (McLachlan & Neems, in press). Net sweeps through such swarms yield mostly unpaired males while paired males and their mates can be captured on the ground near the swarm.

To avoid statistical difficulties associated with the measurement of relative fluctuating asymmetry (Cuthill et al. 1993; Møller 1993; Sullivan et al. 1993), when examining slopes relating two

variables such as wing length and asymmetry, fluctuating asymmetry was calculated as the absolute difference between right and left wing lengths to the nearest 0.05 mm. Where slopes are not involved, as in comparing means, we adopt relative fluctuating asymmetry as the measure of symmetry. Relative fluctuating asymmetry was calculated as absolute fluctuating asymmetry/wing length. This measure is suitable for application to our data where many individuals show no measurable difference between wings. Wings were measured from the distal edge of the anal lobe to the wing-tip at $40\times$ under a dissecting microscope fitted with a calibrated eye-piece. We determined the repeatability of measurements by measuring a single wing 100 times. The variance of this within-wing sample was compared to the variance of the difference between left and right wings in our sample of male flies from the swarm. For the purposes of this test, data from the first 100 flies measured were used. A variance ratio test on $\log_{10}X$ transformed measurements shows that within-wing variance is significantly smaller than between-wing variance ($F_{1,98} = 55.8$, $N_1 = N_2 = 100$, $P < 0.001$). This means that measurement error is unlikely to affect our ability to detect asymmetry between wings. To avoid individual bias, all wings were measured by one of us (M.C.). The single exception was a subset of 25 male flies which we both measured as a second check against bias. In this test the number of asymmetrical individuals found was identical in both cases.

The majority of individuals had no measurable asymmetry and detectable differences were always either one or two of the smallest scale divisions, so we followed the advice of Sullivan et al. (1993) in grouping individuals into size classes. An interval of 0.2 mm by mean wing length was chosen and mean absolute fluctuating asymmetry was calculated for each class. The difficulty of using mean wing length is that a damaged wing is necessarily shorter than the other and a false average is the consequence. However, we were able to detect damage readily and so the use of mean wing length is acceptable (see Cuthill et al. 1993).

We used least-square regression analysis to determine whether a relationship exists between absolute fluctuating asymmetry and wing length. To test the slope of the regression against a null hypothesis of allometry we followed Alatalo et al. (1988), Fairbairn (1992), Green (1992) and Petrie

(1992), in using reduced major axis regression (RMA). We tested the significance of departure of the observed slope (b_{RMA}) from allometry with a Student's t -test (Sokal & Rohlf 1981). RMA data were first transformed $\log_{10}X$ on both axes.

We separated the effects of fluctuating asymmetry and of wing length on mating success by using relative fluctuating asymmetry as a measure of symmetry. We also compared males and females over the same size range to test hypotheses about the relationship between wing length and absolute fluctuating asymmetry in males. All statistical tests were two tailed and considered significant at alpha of 5%.

RESULTS

Measurements of absolute fluctuating asymmetry in males from mating swarms showed no tendency for one wing to be longer than the other (142 males showed no difference between right and left measurements, 47 had a longer right wing, 35 had a longer left wing; sign test binomial: $P>0.05$). Nor was there any difference between right and left wings in the magnitude of symmetry deviations (Wilcoxon signed-rank test: $z=1.015$, $P>0.05$). There was a highly significant increase in mean absolute fluctuating asymmetry with wing length for these unmated males ($Y=0.011X-0.027$, $r=0.895$, $F_{1,7}=27.9$, $P<0.001$; Fig. 1).

It is tempting to conclude that small males are more symmetrical than their larger rivals. However, there are some precautions to be taken before reaching a conclusion. This is because the same proportional differences between two wings must necessarily yield smaller absolute differences in smaller animals. To test whether the apparent positive correlation between size and absolute fluctuating asymmetry is real or an artefact of this kind we adopted two tests. First, we tested whether the correlation is proportional to size (i.e. isometric). Second, if an artefact, the females should yield the same result as the males. For the latter test we measured 135 females over the same size range as the males.

When the regression was tested against a null hypothesis $b_{RMA}=1$ (i.e. isometry) between mean absolute fluctuating asymmetry and wing length, we found that the increase was greater than expected from these purely allometric considerations; that is, the slope of the line was greater

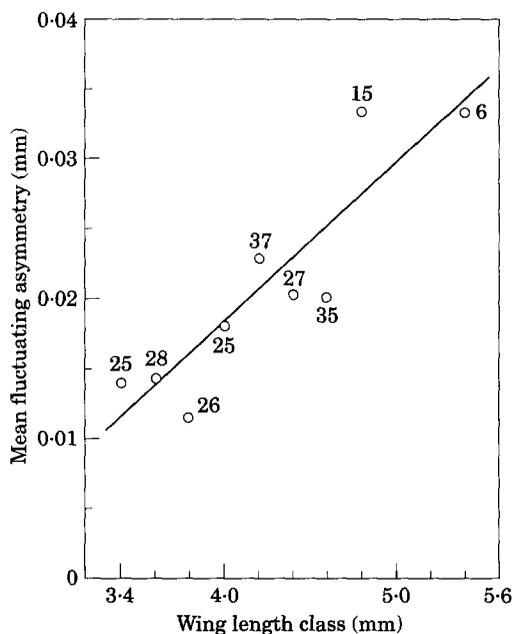


Figure 1. Mean fluctuating asymmetry versus wing length class in unmated male *C. plumosus* collected from swarms. Numbers accompanying points denote sample size in each class.

than unity ($b_{RMA}=2.5$, Student's $t=3.4$, $df=7$, $P<0.02$). This means that absolute fluctuating asymmetry was disproportionately large in individuals with long wings. The reciprocal conclusion is that small males had smaller levels of absolute fluctuating asymmetry than can be accounted for purely by allometric effects. In other words, small males were relatively, as well as absolutely, more symmetrical than larger rivals. It is reasonable to conclude that the relationship between fluctuating asymmetry and size in the male is the result of selective pressures.

Female wing asymmetry was fluctuating (50 individuals with no difference, 20 with right wing longer, 27 with left wing longer; sign test binomial, observed $P>0.05$; Wilcoxon signed-rank test: $z=0.492$, $P>0.05$). (Note that some of the female wing pairs were not included in this test because they had already been detached and could not, therefore, be readily assigned to the left or right side.) Females selected from this set that covered the same range of sizes as the males gave six female wing classes ranging from 3.9 to 5.0 mm in wing length. The six male classes were from 3.8 to 4.8 mm. There was no association

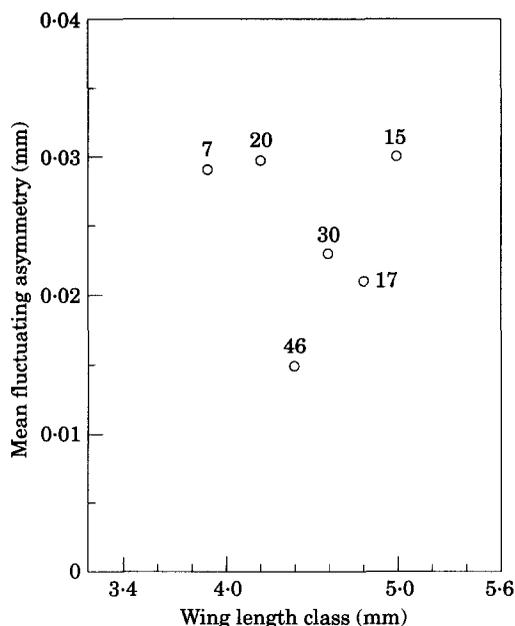


Figure 2. Mean fluctuating asymmetry versus wing length class in mated female *C. plumosus*. Numbers accompanying points denote sample size in each class.

between mean absolute fluctuating asymmetry and wing length in females ($Y=0.0367 - 0.0025X$, $r = -0.150$, $F_{1,4}=0.19$, $P>0.05$; Fig 2), whereas in males of this range there was a significant increase in mean absolute fluctuating asymmetry with wing length ($Y=0.016X - 0.048$, $F_{1,4}=9.56$, $P<0.05$), and, as with the full sample of males, this increase was positively allometric (Students $t=3.02$, $df=4$, $P<0.05$). In other words, females did not show the same relationship between size and absolute fluctuating asymmetry as did males.

Thus both the presence of positive allometry between size and absolute fluctuating asymmetry in males and the absence of an association between size and this variable in females reflect real differences in the magnitude of symmetry deviations relative to wing length in swarming male midges.

Next, we asked whether there was a relationship between fluctuating asymmetry and mating success. We did this by comparing fluctuating asymmetry in the males caught in mating pairs with the unmated males in the swarm. Using relative fluctuating asymmetry as a measure to eliminate differences in wing length between samples, the outcome of the comparison between mated and

swarm males was that mated males exhibited a lower mean relative fluctuating asymmetry than swarm males (mated males $N=135$, mean relative fluctuating asymmetry \pm SD = 0.00243 ± 0.00664 ; for swarm males in the same range $N=224$, mean relative fluctuating asymmetry \pm SD = 0.00476 ± 0.00649 ; Mann-Whitney U -test with tied ranks: $U=390$, $N_1=135$, $N_2=224$, $P<0.02$). Hence we conclude that success at mating might be accounted for by fluctuating asymmetry, independent of size.

DISCUSSION

The midge *C. plumosus* mates on the wing, so wings are central to its mating effort. We have shown that among males, it is the smallest that are the most symmetrical. Success at mating is similarly associated with wing size, the smallest males being the most successful at acquiring mates (reviewed by McLachlan & Neems, in press). Theory, based on Soulé (1982) and Soulé & Cuzin-Roudy (1982), makes specific predictions about the relationship between size and fluctuating asymmetry. These predictions, later explained and developed by Møller & Höglund (1991) and Møller & Pomiankowski (1993a, b) show that under stabilizing selection the individuals of average size should have lower fluctuating asymmetry than those of extreme size. The outcome is a U-shaped or positive distribution. Under conditions of directional selection, by contrast, characters should show covariance. In other words, if there is directional selection for size, then size should correlate with fluctuating asymmetry. Given the unexpected selection for small size in *C. plumosus*, this is precisely what we have found; small individuals are more symmetrical and larger ones less so. These findings are in agreement with those of Møller and his co-workers.

We separated the effects of fluctuating asymmetry and wing size on mating success by comparing mating success in males of the same size. Results lead to the conclusion that symmetry might account for variations in mating success of male *C. plumosus*. If a way were found to manipulate fluctuating asymmetry in a swarm of males, the question of causality between mating success and fluctuating asymmetry could be properly established. Until then the matter remains unresolved. These results are most easily understood

in terms of natural selection rather than sexual selection. In other words, it seems likely that the aerodynamics of mate capture rather than sexual attraction has been the main subject of selection. This is the conclusion reached by Balmford et al. (1993b) working with tail length in birds with forked tails, and by Evans & Hatchwell (1993) from work with sunbirds.

Small size in male midges is associated with fitness beyond mating success on a single occasion. Small *C. plumosus* have a higher lifetime reproductive success than competitors (R. M. Neems, J. Lazarus & A. J. McLachlan, unpublished data). By implication, small males may also be fitter and hence genetically superior to the average male.

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