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Abstract

Most animal species exhibit sexual size dimorphism (SSD). SSD is a trait difficult to quantify for genetical purposes since it must be simultaneously measured on two kinds of individuals, and it is generally expressed either as a difference or as a ratio between sexes. Here we ask two related questions: What is the best way to describe SSD, and is it possible to conveniently demonstrate its genetic variability in a natural population? We show that a simple experimental design, the isofemale-line technique (full-sib families), may provide an estimate of genetic variability, using the coefficient of intraclass correlation. We consider two SSD indices, the female–male difference and the female/male ratio. For two size-related traits, wing and thorax length, we found that both SSD indices were normally distributed. Within each family, the variability of SSD was estimated by considering individual values in one sex (the female) with respect to the mean value in the other sex (the male). In a homogeneous sample of 30 lines of *Drosophila melanogaster*, both indices provided similar intraclass correlations, on average 0.21, significantly greater than zero but lower than those for the traits themselves: 0.50 and 0.36 for wing and thorax length respectively. Wing and thorax length were strongly positively correlated within each sex. SSD indices of wing and thorax length were also positively correlated, but to a lesser degree than for the traits themselves. For comparative evolutionary studies, the ratio between sexes seems a better index of SSD since it avoids scaling effects among populations or species, permits comparisons between different traits, and has an unambiguous biological significance. In the case of *D. melanogaster* grown at 25°C, the average female/male ratios are very similar for the wing (1.16) and the thorax (1.15), and indicate that, on average, these size traits are 15–16% longer in females.

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Introduction

Most animal species exhibit phenotypic differences between males and females, and after Darwin (1871) sexual size dimorphism (SSD) in particular has retained the attention of numerous evolutionary biologists (Maynard Smith 1978; Charnov 1982; Thornhill and Alcock 1983; Bradbury and Anderson 1987; Stearns 1987; Michod and Levin 1988; Reiss 1989; Andersson 1994; Fairbairn 1997; Simmons 2001). Several adaptive interpretations of SSD have been subject to experimental or theoretical analyses (Slatkin 1984; Arak 1988; Hedrick and Temeles 1989; Kirkpatrick and Ryan 1991).

A general requirement for SSD to evolve is that the trait of interest should be controlled by genes differently expressed in the two sexes. Since the genetic correlations between the sexes are usually high for morphometric

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traits, theoretical and empirical analyses have predicted a slow evolutionary rate of SSD (Lande 1980; Arnold 1985; Roff 1997; Merilä *et al*. 1998). In contrast with this expectation, however, field studies have found rapid divergence of phenotypic SSD in geographic populations of the house finch (Badyaev and Hill 2000; Badyaev *et al*. 2001). Recent investigations in *Drosophila* have also yielded evidence for different quantitative trait loci (QTL) in males and females for various traits such as bristle number (Mackay 2001), lifespan (Nuzhdin *et al*. 1997; Leips and Mackay 2000; Vieira *et al*. 2000) and olfactory behaviour (Mackay *et al*. 1996).

Although widespread in animals, SSD does not follow a general rule: females can be either larger or smaller than males. Usual adaptive interpretations involve either sexual selection (e.g. competition among males or female choice) or natural selection, assuming divergent ecological advantages. In *Drosophila melanogaster*, females are larger than males but there is no consensus interpretation for this difference. Larger females have a higher fecundity related to more ovarioles in the ovaries (Boulétreau-Merle *et al*. 1982) and should be favoured by natural selection. Things are not so clear for males. Laboratory experiments have shown that larger males generally have a mating advantage (Partridge *et al*. 1987; Santos *et al*. 1988), but not in all conditions (Zamudio *et al*. 1995). Moreover, such experiments were done with well-fed males, while in nature males must share their time between foraging and mate acquisition. As shown by Blanckenhorn *et al*. (1995) for a water strider, it is possible that, when resources are limiting, smaller males might be favoured by sexual selection since they require lower amounts of food.

Whatever the evolutionary interpretation of its SSD, *D. melanogaster* remains an ideal model for genetic investigations. Several studies have analysed SSD changes occurring as a correlated response in various selection regimes, and thus have shown that SSD is genetically variable (e.g. Frankham 1968; Palezona and Alicchio 1973; Cowley *et al*. 1986; Curtsinger 1986; Reeve and Fairbairn 1996, 1999). We are however aware of only one study (Bird and Schaffer 1972) that directly addressed the heritability of SSD itself in selection experiments. Reeve and Fairbairn (1999) investigated whether a monosexual selection on fecundity could produce a change in SSD as a correlated response, but the results were inconclusive, at least for thorax length.

In *Drosophila*, the isofemale-line analysis (full-sib families) is a widespread technique for investigating the genetic variability of natural populations (Hoffmann and Parsons 1988; Capy *et al*. 1994; David *et al*. 2004) and genotype–environment interactions (David *et al*. 1994; Karan *et al*. 1999, 2000). Such investigations have shown that size-related traits are highly heritable, that SSD is a plastic trait, and that female and male sizes are positively correlated. The fact that genetic correlations between males and females were on average close to 0.80 (Karan *et al*. 1999) suggests that two thirds ($R^2 = 0.64$) of the size genes are expressed equally in both sexes. In other words, 36% of the genes might be expressed specifically in one sex only, leaving significant opportunity for the evolution of SSD. In another study, Reeve and Fairbairn (1996), using a half-sib design, found a still higher value ($r = 0.93$).

SSD may be expressed either as a difference (e.g. female minus male) or as a ratio (e.g. female/male) (Bird and Schaffer 1972; Cowley *et al*. 1986; Cowley and Atchley 1988; David *et al*. 1994; Ranta *et al*. 1994; Reeve and Fairbairn 1996, 1999). The difficulty for calculating heritability is that we need an individual estimate of a trait which must be measured on different individuals.

Up to now, most investigations on SSD have estimated its heritability from selection experiments (e.g. Bird and Shaffer 1972; Reeve and Fairbairn 1996). We present here the results of another method which can be of general use when full-sib data are available (Singh *et al*. 1989). More precisely, the individual variability in one sex is estimated with respect to the mean value in the other sex. For each isofemale line, we have considered the individual values of the females but only the mean of their brothers. SSD can be expressed either as a difference or as a ratio, and in each case it is possible to calculate a within-family variance.

Using this technique we found that the intraclass correlations of SSD were significantly greater than zero but lower than the intraclass correlations of wing and thorax length. Female–male difference or female/male ratio gave similar intraclass correlations but very different evolvabilities. For comparative purposes, the ratio seems more appropriate than the difference, since it avoids scaling effects and provides an immediate biological interpretation.

Materials and methods

***Flies investigated*:** We investigated three samples of ten isofemale lines each, collected in the same place (Grande Ferrade estate near Bordeaux, southern France), at the same time of the year (end of autumn) but in different years (1992, 1997, 1999). For the 1992 sample, lines were kept in the lab for four months (four generations) before measurements. It is unlikely that variability among lines was increased owing to genetic drift since, in another study (Gibert *et al*. 1998a), mean values of wing length remained stable over nine generations. For the 1997 and 1999 samples, measurements were done on the second laboratory generation. Field-collected females were isolated in culture vials to produce laboratory, first-generation progeny (G1). Ten pairs of these G1 flies were used as parents for producing the next generation. A

short egg-laying duration (4 h at 20–21°C) was used to limit larval density, which was between 70 and 150 individuals per vial. Moreover, the use of a high-nutrient, killed-yeast medium prevented any visible crowding effect on body size (see Karan *et al*. 1999). After removal of the parents, vials with eggs were incubated at 25°C. After emergence from pupae, adults were transferred to fresh food and 10 females and 10 males from each line were measured a few days later. Here we consider only two size-related traits: thorax length measured from the neck to the tip of the scutellum and total wing length, measured, in a left side view, from the thoracic articulation to its extremity. Measurements were made with an ocular micrometer in a binocular microscope with magnification of 25× for the wing and 50× for the thorax. Micrometer units were transformed into mm × 100. We did not investigate the repeatability of length measurements on the same fly. In a previous paper (Imasheva *et al*. 2000) we found that measurement errors produced a significant increase of variability for small length traits, while they were negligible for longer traits, such as total wing length.

***Sexual size dimorphism (SSD)*:** SSD analysis implies separate measurements on both sexes, and two general possibilities exist: the female–male difference (F–M) or the female/male ratio (F/M) (Ranta *et al*. 1994). With the isofemale-line design, such dimorphism values can be calculated for each line, using the means of males and females (e.g. David *et al*. 1994). For genetic analysis, we need however a dimorphism value at an individual level. A convenient approach is to consider for one sex (e.g. females) the individual variations F_i, but for the other sex (males) only the average value M_m. For the ratio we calculate the F_i/M_m, and for the difference the $F_i–M_m$ values. Such values are individual data providing a mean and a variance. Calculations can be done either on a whole population or also, in our case, separately for each line. Notice that SSD could also be analysed by using male individual variability. In that case, the ratio becomes F_m/M_i. Relative variabilities (CVs) are identical in males and females (Karan *et al*. 1999) and both methods provided similar conclusions. For the sake of simplicity we present here only the F_i/M_m data.

Results

Mean values and sources of variation (ANOVA)

With the isofemale-line technique, significant variations among lines are regularly observed, reflecting a genetic variability in the wild population (Capy *et al*. 1994). However, repeated samples from the same population are generally not available. Here we had three such samples, collected in different years, and we first asked two questions: Are there significant differences between samples? Is there a significant interaction between lines and sex? Results for the two traits measured (wing and thorax length) were submitted to a two-way ANOVA (table 1). Sex had the major effect (males are smaller than females). Lines also exhibited, as expected, highly significant genetic variations. There was however no difference between samples collected in different years, and no interaction between year and sex. Finally, a highly significant line by sex interaction means that genetic variability among lines is not identical in males and females. In other words, we may expect that SSD will be genetically variable. The genetic variability among the 30 lines sample is illustrated in figure 1 as a correlation diagram between male and female wing length.

Frequency distributions of traits and SSD indices

For investigating SSD, we considered two indices: the female/male (F/M) ratio and the female minus male (F–M) difference. As stated in Materials and methods, we used in each line the individual female values but the mean value of their brothers.

A general statistical problem when using transformed variables is the shape of the frequency distributions of the new indices. For continuous variables such as wing or thorax length, it is generally assumed that the distribu-

Table 1. Results of a mixed-model ANOVA on wing and thorax length (sex as fixed effect; year as random; line nested in year).

		Wing			Thorax		
Source	d.f.	MS	*F*	*P*	MS	*F*	*P*
Year (1)	2	264.1	0.54	0.59 ns	84.02	1.88	0.17 ns
Line (year) (2)	27	489.76	20.33	< 0.001	44.67	11.16	< 0.001
Sex (3)	1	210413	2294	< 0.001	29962	3327	< 0.001
1*3	2	91.71	2.09	0.14 ns	9.01	0.97	0.39 ns
2*3	27	43.84	1.82	0.007	9.27	2.32	< 0.001
Error	540	24.09			4.00		

d.f., Degree of freedom; MS, mean square; *F*, variance ratio, *P*, probability.

tions are Gaussian. Such should not be the case for a ratio (e.g. Ranta *et al*. 1994). We used the whole sample of 300 flies of each sex for analysing the shapes of the distributions of all traits. For wing and thorax length, a preliminary analysis showed no significant difference between sexes in the shape of the distribution. Each distribution was standardized to the same mean (one) by dividing individual values by the overall mean, thus keeping constant the shape and the CV of each distribution. Then, male and female data of each trait were pooled, providing a total sample of 600 observations. The distributions of wing and thorax length were unimodal and symmetrical with no significant skewness or kurtosis. However, the hypothesis of strict normality was rejected in both cases, owing to some irregularities among classes (see figure 2). Such a result is quite surprising and we have no explanation for it. A possibility would be that the bias is due to the fact that the total sample was not drawn from a single panmictic population but made by the addition of 30 independent lines. However, the departure of the distributions from normality is not very big, and ANOVA is known to be a robust technique, so that the conclusions from table 1 are valid.

Result for the SSD indices (F–M and F/M) however failed to show any significant departure from normality. As illustrated in figure 2 for thorax length, the observed distributions were more regular than that of the trait itself. We conclude that either of these indices can be used for describing SSD.

Values of traits and SSD indices in different years

The mean values of wing and thorax length and of SSD indices of the different samples are given in table 2. Variations between years for wing and thorax length are small and nonsignificant, suggesting that the population sampled was stable for these traits over time. The same conclusion applies to SSD indices. They are not different between years but significantly variable among lines. Interestingly, we notice that the variance ratios (*F* parameters) are always superior for wing and thorax length than for SSD. This suggests that SSD indices are less variable among lines than the traits themselves.

For the French population investigated, the F–M difference is 37.45 ± 1.25 for the wing but only 14.13 ± 0.52

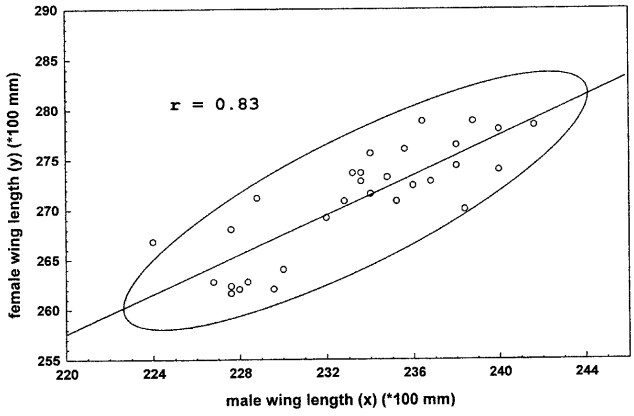

Figure 1. Correlation diagram between male and female wing length. Each value is the mean of an isofemale line. Ellipse of 90% probability is given to help visualize the overall distribution. The regression line is a type 1 regression, female as a function of male: F = 39.80 + 0.99 M + *e*. This kind of regression is implicit when calculating a female/male ratio.

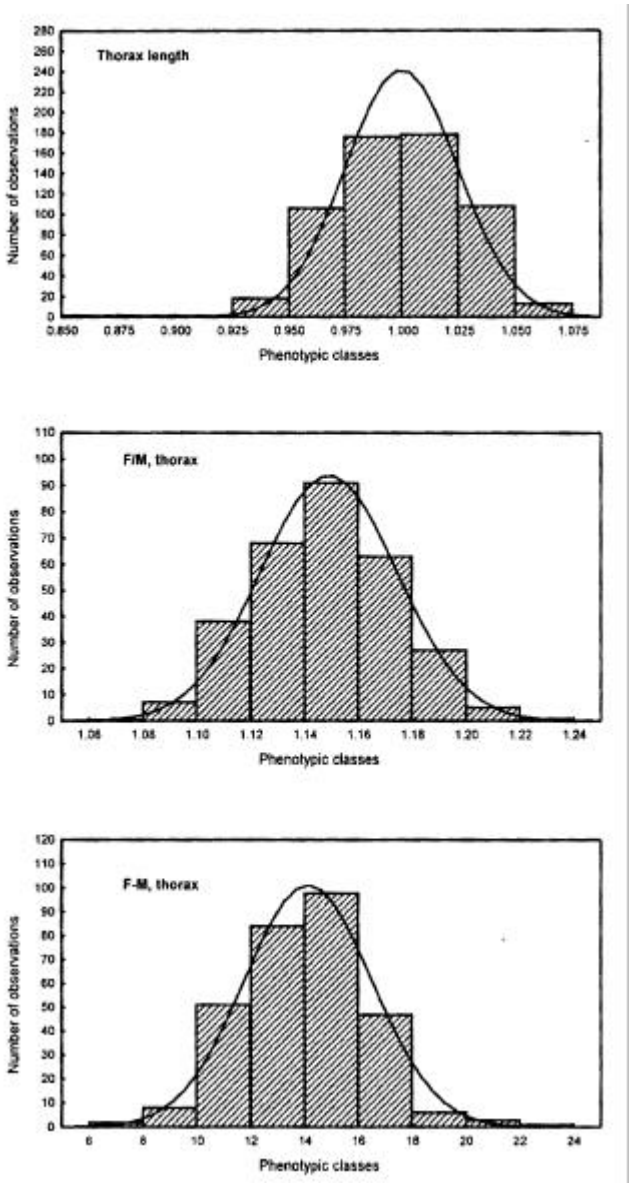

Figure 2. Frequency distributions of thorax length and SSD indices F/M ratio and F–M difference based on the total sample. Experimental histograms are compared with the corresponding normal distributions. Normality was rejected by statistical tests (Kolmogorov–Smirnov, Lilliefors and Shapiro–Wilk *W*) for thorax length, but accepted for F/M or F–M.

for the thorax. The dimorphism, expressed in that way, appears much greater for the wing. This is a mere consequence of the fact that in *Drosophila* the wing is much longer than the thorax. When dimorphism is expressed as a ratio, the difference between the two traits almost disappears, since the mean values are 1.161 ± 0.005 and 1.149 ± 0.006 for wing and thorax length respectively. This very small difference is however significant: Student's test $t = 3.06$; $P = 0.003$; paired data. For a given trait, the F–M and the F/M indices calculated for each line are highly correlated ($r > 0.95$), suggesting that they provide basically the same information. This relationship is illustrated in figure 3 for the wing. From a biological point of view, the SSD ratio might be preferred, since it tells that female traits are on average 15–16% longer than those of males.

Genetic analyses

Using standard methods, we calculated (table 3) for each sample the intraclass correlation *t*, sometimes called isofemale-line heritability (Capy *et al*. 1994) and the genetic CV, also called evolvability (Houle 1992).

For wing and thorax length, we found high intraclass correlation, greater for the wing (0.50 ± 0.03) than for the thorax (0.37 ± 0.03). The difference among paired data ($d = 0.130 \pm 0.028$, $n = 6$, $P < 0.01$) is highly significant.

SSD indices exhibited regularly lower values of *t*. Mean values were 0.188 ± 0.034 and 0.243 ± 0.049 for wing and thorax length respectively ($n = 6$ in each case). For the two index types, means were 0.225 ± 0.047 and 0.207 ± 0.041, for the ratio and the difference respectively ($n = 6$). ANOVA (not shown) applied to these data did not reveal any significant effect either due to trait or to index type. Moreover the *t* values for the ratio and the difference are highly and positively correlated ($r = 0.98$, $n = 6$), again suggesting that both indices provide the same genetic information. For a given sample and trait, the best estimate of *t* seems to be the average value found for the two indices, the mean of which is 0.216 ± 0.044 ($n = 6$). When intraclass correlations of SSD and of trait values are compared, they appear however to be independent. Indeed we found (figure 4) a negative, although nonsignificant, correlation between them.

Evolvability (CVg) was slightly superior for wing length ($m = 1.94 \pm 0.07$, $n = 6$) than for thorax length ($m = 1.48 \pm 0.03$, $n = 6$). The average difference of paired data is highly significant ($d = 0.455 \pm 0.088$, $n = 6$, $P < 0.001$). Evolvability was still less (average 1.02 ± 0.17, $n = 6$) for the F/M ratio, but, quite surprisingly, much greater for the F–M difference (average 7.12 ± 1.04, $n = 6$).

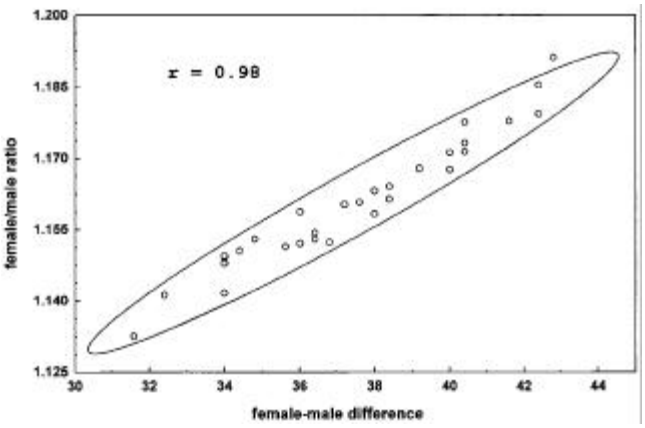

Figure 3. Correlation diagram between two sexual dimorphism indices of wing length among isofemale lines.

Table 2. Mean values of size traits and SSD indices and results of a one-way ANOVA (lines nested in samples).

		Wing length		Thorax length		SSD ratio		SSD difference	
		Female	Male	Female	Male	Wing	Thorax	Wing	Thorax
Mean values	1992 ($n = 10$)	270.5 ± 4.55	234.5 ± 3.97	108.6 ± 1.77	95.0 ± 1.76	1.154 ± 0.019	1.144 ± 0.019	36.00 ± 4.55	13.66 ± 1.77
	1997 ($n = 10$)	269.6 ± 4.86	232.0 ± 4.79	108.6 ± 1.95	94.2 ± 1.79	1.162 ± 0.021	1.154 ± 0.021	37.68 ± 4.86	14.48 ± 1.95
	1999 ($n = 10$)	272.3 ± 5.18	233.6 ± 5.03	109.8 ± 2.25	95.5 ± 2.07	1.166 ± 0.022	1.149 ± 0.024	38.68 ± 5.18	14.26 ± 2.25
Overall mean	($n = 30$)	270.8 ± 1.25	233.4 ± 1.40	109.0 ± 0.52	94.9 ± 0.54	1.161 ± 0.0054	1.149 ± 0.0055	37.45 ± 1.25	14.13 ± 0.519
Comparison (ANOVA)									
Samples	F (2,27)	0.59^{ns}	0.77^{ns}	1.49^{ns}	2.01^{ns}	2.34^{ns}	1.07^{ns}	2.09^{ns}	0.97^{ns}
Lines	F (27,270)	12.51***	9.51***	7.13***	6.30***	3.70***	5.05***	3.49***	4.41***

Mean values are the mean of *n* lines. Degrees of freedom are given for ANOVA: MS, mean square; *F*, variance ratio. SSD ratio, sexual dimorphism expressed as a female/male ratio; SSD difference; sexual dimorphism expressed as a female–male difference.
Significance level: ns, nonsignificant; ***$P < 0.001$.

Table 3. Values of genetic parameters for size traits and SSD in different samples.

	Wing length				Thorax length				SSD ratio				SSD difference			
	Female		Male		Female		Male		Wing		Thorax		Wing		Thorax	
Sample	CVg	*t*	CVg	*t*	CVg	*t*	CVg	*t*	CVg	*t*	CVg	*t*	CVg	*t*	CVg	*t*
1992	2.06	0.59	1.87	0.53	1.49	0.45	1.55	0.40	0.65	0.13	0.59	0.11	4.88	0.13	4.16	0.09
1997	1.99	0.53	1.66	0.38	1.55	0.40	1.54	0.38	0.73	0.13	1.49	0.38	5.64	0.15	10.32	0.35
1999	1.91	0.49	2.13	0.47	1.37	0.30	1.39	0.28	1.35	0.32	1.32	0.28	8.44	0.27	9.28	0.25
Mean	1.99	0.54	1.89	0.46	1.47	0.38	1.49	0.35	0.91	0.19	1.13	0.26	6.32	0.18	7.92	0.23
± S.E.	0.04	0.03	0.14	0.04	0.05	0.04	0.05	0.04	0.22	0.06	0.28	0.08	1.08	0.04	1.90	0.08

CVg, Genetic coefficient of variation (evolvability); *t*, intraclass correlation.

Genetic correlations between traits were estimated using the 30 family means (see Via 1984; Gibert *et al*. 1998b). Correlations between wing and thorax were high (figure 5A), identical in both sexes ($r = 0.78$), and slightly greater than the within-line average values, 0.680 ± 0.042 and 0.708 ± 0.034 ($n = 30$), for males and females respectively. For the SSD indices, we also found a positive correlation between the two traits, but slightly less than for the traits themselves: *r* of 0.66 and 0.68 for the ratio and the difference respectively. SSD values of wing were also positively correlated to those of thorax (figure 5B), *r* of 0.66 and 0.68 for the ratio and the difference respectively. This suggests that about 45% of the genes responsible for SSD are expressed in a similar way in wing and thorax.

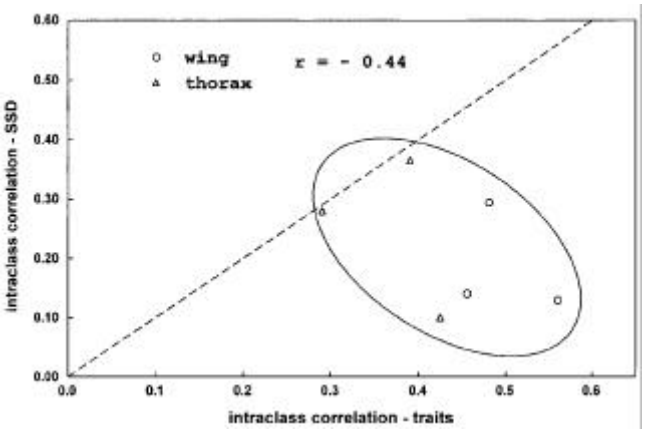

Figure 4. Relationship between intraclass correlation of trait length (wing or thorax) and intraclass correlation of SSD. Sexes were averaged for trait values; ratio and difference indices were averaged for SSD. Mean values: traits, 0.433 ± 0.037; SSD indices, 0.215 ± 0.043; average difference (paired data): 0.218 ± 0.68 ($n = 6$, $P < 0.01$).

Discussion and conclusions

Although SSD is an important phenomenon in evolutionary biology, few investigations have been devoted to the analysis of its genetic variability. Sophisticated statistical methods such as REML (restricted maximum likelihood) allow the treatment of male and female traits as different and thus permit calculation of individual values of dimorphism (Mignon-Grasteau *et al*. 1998). We show here that the simple and widespread method of isofemale lines may also be used to assess genetic variation of SSD.

The isofemale-line technique here implemented is a full-sib design which can be used to investigate the genetic architecture of a natural population of various species, provided they can be reared under identical conditions (David *et al.* 2004). It is convenient for estimating the mean of a quantitative trait in a natural population and it also provides some information about its genetic variability. This last point however raises some difficulties. According to classical quantitative-genetic analysis (Falconer 1989) intraclass correlation *t* among full sibs should be half the heritability of the trait. This relationship, however, assumes that the genetic variance is purely additive. Empirical observations have shown that *t* is generally closer to h^2 than to $0.5\ h^2$. For example, in *Drosophila*, a compilation of heritability values obtained with usual methods (parent–offspring regression, half-sib analysis or directional selection) was done by Roff and Mousseau (1987). They found average heritabilities of 0.325 ± 0.014 ($n = 66$) and 0.319 ± 0.021 ($n = 30$) for wing and thorax length respectively. Using the isofemale-line technique, Capy *et al*. (1994) found average intraclass correlations of 0.403 ± 0.021 ($n = 55$) and 0.232 ± 0.019 ($n = 55$) for the same traits respectively. Clearly *t* (intraclass correlation) is intermediate between h^2 and $0.5\ h^2$.

There are two possible explanations for this result: either the variance among lines is overestimated, because of common environment effects, or the genetic variance, among lines, is not purely additive, and includes significant nonadditive (dominance and epistasis) components, and also potential maternal effects.

We extensively investigated the common environment hypothesis and came to the conclusion that it is of minor importance. For example we used two different culture vials for rearing the same family and never found a significant vial effect (J. R. David, unpublished data). Acci-

dental effects among culture vials should also produce erratic variations when successive generations of the same line are measured. A detailed analysis (Gibert *et al*. 1998a) revealed this was not the case: mean wing length values of successive generations were strongly correlated, revealing a good genetic repeatability. We also investigated the possible influence of larval density upon size trait values, and failed to find any effect for densities ranging between 20 and 320 eggs per vial (Karan *et al*. 1999). It is worth emphasizing that such stable results are obtained when using a special rearing medium in which a large amount of dead yeast decreases the environmental variance (David 1962). For example, with that kind of food, the within-line CVs are usually less than 2% (Gibert *et al*. 1998a). Such is not the case in other investigations which used a more diluted food. For example, Imasheva *et al*. (1994) reported an average within-line CV of 2.95 ± 0.15. It is possible that an accidental increase of the within-line variance may reduce the intraclass correlation. Indeed, Hoffmann and Parsons (1988) reported a very low intraclass correlation ($t = 0.04 \pm 0.03$) for wing length, something we never found with our rearing method.

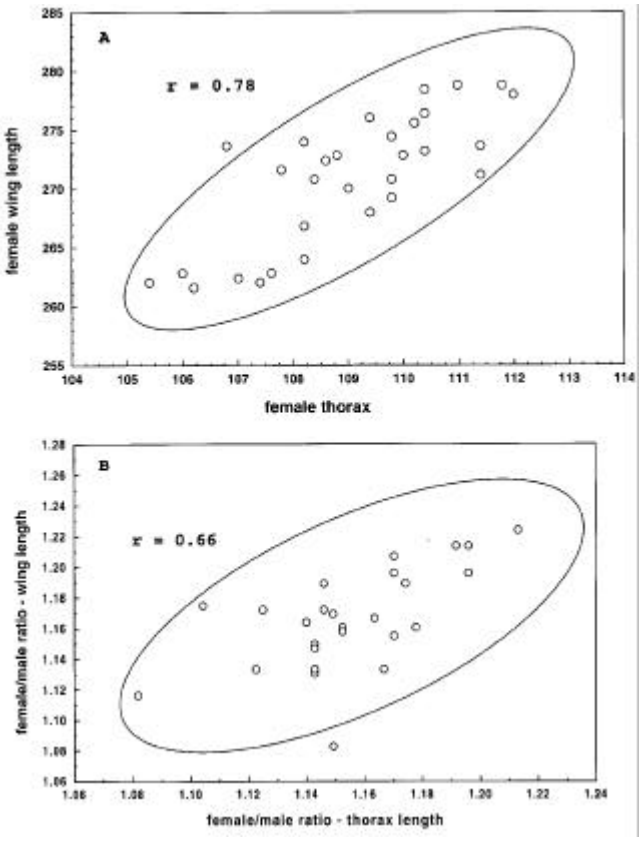

Figure 5. Correlation among family means: A, between wing and thorax lengths in female; B, between SSD ratios of wing and thorax. Ellipses of 90% probability are shown to better visualize the shapes of distributions.

For all these reasons we consider that intraclass correlation in an isofemale-line design provides a gross measure of genetic variation, including nonadditive components and also possible maternal effects. Other investigators (e.g. Ritchie and Kyriacou 1994) also drew attention to the fact that a behavioural trait, which did not respond to directional selection, indicating lack of additive genetic variation, did nevertheless show significant genetic variation among isofemale lines.

SSD is generally expressed either as a difference or as a ratio, and both have drawbacks. The difference between the sexes (F–M) is likely to be strongly influenced by absolute differences in body size, owing to allometric relationships (Reiss 1989; Fairbairn 1997), especially when different species are compared. Also, the difference will exhibit large heterogeneity among size traits, as shown here for wing and thorax length. To obviate this difficulty, relative differences standardized to mean size might be used (Ranta *et al*. 1994). An SSD ratio (F/M) is such a relative measure, the meaning of which is easily understood. Moreover, it allows direct comparison among different traits: in *Drosophila* SSD ratios are almost identical for wing and thorax length. Ratios often exhibit some inconveniences, one being an expected non-normal distribution (LaBarbera 1989; Ranta *et al*. 1994; Sokal and Rohlf 1995). Perhaps surprisingly, in our data set the shape of the wing and thorax length distributions departed slightly but significantly from normality, whereas that of the two SSD indices did not. Although we do not have any clear explanation for this result we may conclude that, in the present case, there is no statistical objection against the use of the ratio. A classical way to remedy the expected non-normal distribution of a ratio is a logarithmic transformation, since log F/M = log F – log M. We did this and found that the difference between logs was also normally distributed. We think, however, that the real ratio provides a more straightforward biological interpretation: female wing length is 16% longer than that of the male. Whether normality of SSD indices holds for other data sets needs to be evaluated further.

The two estimates of SSD (F/M ratio and F–M difference) provided significant intraclass correlations (on average 0.215 ± 0.018, $n = 4$). As one might expect, they were smaller than for each size trait. This value can be compared to the average realized heritabilities of SSD found by Bird and Schaffer (1972) and Reeve and Fairbairn (1996): respectively, 0.15 and 0.13. Log transformations produced similar estimates. A smaller value of heritability of SSD than for the traits themselves seems a general feature in animals (Mignon-Grasteau *et al*. 1998). Our results for *Drosophila* also confirm data obtained with an REML technique on chicken and duck (Mignon-Grasteau *et al*. 1998), showing that both SSD indices provide similar heritabilities. We therefore suggest that

our method could and should be more widely applied, for example in half-sib or diallel designs.

The much higher evolvability found for the F–M difference than for the ratio must be considered with caution, since it might be due to a scaling effect (see Roff 1997, p. 122). Such scaling effects were described for sex dimorphism in bristle number by Frankham (1968). In most genetic investigations so far performed on SSD, either in *Drosophila* (Bird and Schaffer 1972), mice (Korkman 1957; Eisen and Hanrahan 1972; Schmidt 1993) or birds (Buvanendran 1969; Pilla 1974; Singh *et al*. 1989; Badyaev *et al*. 2001), the F–M difference was preferentially considered. This might be related to the higher evolvability found for this SSD index: any change due to selection should be more visible on the F–M difference than on the ratio. In domestic birds, directional selection has been performed for increasing body weight. Owing to a scaling effect, such selection has often increased the F–M difference without really changing the allometric relationship between sexes (see Mignon-Grasteau *et al*. 1999). In this respect, the F/M ratio in adults is likely to be more informative concerning the evolution of SSD itself.

Using an SSD ratio (thorax width), Reeve and Fairbairn (1996) found several discrepancies between expected and realized heritabilities. One possible explanation was that various selection regimes resulted in different modifications of growth trajectories in males and females. Clearly, more precise investigations are needed for understanding the significance and genetic bases of SSD indices.

When comparing different species, major changes in SSD may be found. For example, in the drosophilid family, males and females may be about the same size (Kacmarczyk and Craddock 2000; Karan *et al*. 2000). It would be interesting to know if, in such cases, SSD is still genetically variable.

Sexually dimorphic characters imply a functional interaction between the genes responsible for the sexual phenotype and the genes determining the trait of interest. In this respect, sexual dimorphism of morphological traits may be analysed not only by investigating the mean values of male and female, plus the associated genetic correlation, but also by comparing the heritabilities in the two sexes (Cowley *et al*. 1986; Cowley and Atchley 1988; Reeve and Fairbairn 1996): a significant difference is likely to favour the evolution of SSD. Although females are on average larger than males in *D. melanogaster*, the F/M ratio may be quite variable depending on the trait measured, from 1.04 up to 1.28 (Cowley and Atchley 1988; Reeve and Fairbairn 1999). Other traits not related to size are also sexually dimorphic and convenient for analysing sex–trait interactions. Such interactions play a major role in the control of body pigmentation (Gibert *et al*. 1999; Hollocher *et al*. 2000). Indeed, the interacting genes producing the black pigmentation of the male abdomen of *D. melanogaster* have been identified recently (Kopp *et al*. 2000). Other quantitative investigations in *Drosophila*, using a QTL approach, have also demonstrated different QTLs in males and females (Mackay *et al*. 1996; Nuzhdin *et al*. 1997; Leips and Mackay 2000; Vieira *et al*. 2000; Mackay 2001). Also, a DNA microarray analysis has revealed different gene expressions in sexes and, more interestingly, different interactions in two sibling *Drosophila* species (Ranz *et al*. 2003). Altogether, the genetics of sexual dimorphism might become a paradigm for the analysis of epistatic interactions, a field of growing significance in quantitative evolutionary genetics (Wolf *et al*. 2000)

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