

RESEARCH ARTICLE

# Thermal phenotypic plasticity of body size in *Drosophila melanogaster*: sexual dimorphism and genetic correlations

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## Abstract

Thirty isofemale lines collected in three different years from the same wild French population were grown at seven different temperatures (12–31°C). Two linear measures, wing and thorax length, were taken on 10 females and 10 males of each line at each temperature, also enabling the calculation of the wing/thorax (W/T) ratio, a shape index related to wing loading. Genetic correlations were calculated using family means. The W–T correlation was independent of temperature and on average, 0.75. For each line, characteristic values of the temperature reaction norm were calculated, i.e. maximum value, temperature of maximum value and curvature. Significant negative correlations were found between curvature and maximum value or temperature of maximum value. Sexual dimorphism was analysed by considering either the correlation between sexes or the female/male ratio. Female–male correlation was on average 0.75 at the within line, within temperature level but increased up to 0.90 when all temperatures were averaged for each line. The female/male ratio was genetically variable among lines but without any temperature effect. For the female/male ratio, heritability (intraclass correlation) was about 0.20 and evolvability (genetic coefficient of variation) close to 1. Although significant, these values are much less than for the traits themselves. Phenotypic plasticity of sexual dimorphism revealed very similar reaction norms for wing and thorax length, i.e. a monotonically increasing sigmoid curve from about 1.11 up to 1.17. This shows that the males are more sensitive to a thermal increase than females. In contrast, the W/T ratio was almost identical in both sexes, with only a very slight temperature effect.

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## Introduction

Ever since Darwin (1871), sexual dimorphism has fascinated evolutionary biologists. Morphological differences between sexes correspond either to primary sexual characters, such as gonads and genitalia, which are directly involved in reproduction, or to secondary phenotypic characters which distinguish sexes. The secondary characters may themselves be subdivided into two categories: qualitative and quantitative differences. In *Drosophila melanogaster*, well-known qualitative differences are the male sex combs on the fore tarsus and the black colour of the last two abdominal tergites in males. Quantitative differences, on the other hand, concern most measurable traits, the most obvious being the larger body size of the female.

During the last decade, major progress has been made in unravelling the genetic bases of qualitative sex differences such as sex comb (Randsholt and Santamaria 2008), body pigmentation: (Kopp *et al.* 2000; Williams *et al.* 2008) and wing pigmentation (Carroll *et al.* 2008). Quantitative differences have been analysed with quantitative genetics methods, including heritability, selection and correlations either from a theoretical or an empirical point of view (Frankham 1968; Bird and Schaffer 1972; Lande 1980; Cowley and Atchley 1988; Hedrick and Temeles 1989; Reeve and Fairbairn 1996; David *et al.* 2003; Fairbairn *et al.* 2007; Chakir *et al.* 2008; Gidaszewski *et al.* 2009). Surprisingly, studies which tried to work out quantitative trait loci (QTL) for dimorphic traits have often suggested that the relevant chromosomal regions were not the same in males and females (e.g., Nuzhdin *et al.* 1997; Harbison *et al.* 2004) revealing the complexity of their genetic basis. It is generally

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argued that sex differences have an adaptive significance, arising from various sexual behaviours such as mate recognition and intrasex competition, or from a functional divergence between sexes, linked for example to the well-known difference in parental investment (intra-locus sexual conflict). A general conclusion from such studies is that quantitative sex dimorphism is insufficiently investigated, both at the phenotypic and genetic levels.

In most insect species, temperature is known to play a major role in explaining geographic distributions (Andrewartha and Birch 1954). A strong argument for temperature as a selective agent is the observation of latitudinal clines, for example in various species of *Drosophila* (David and Capy 1988; Capy *et al.* 1993; James *et al.* 1997; Karan *et al.* 1998; David *et al.* 2006a). As a rule, a decrease of size is observed with decreasing latitude, corresponding to an increase in average temperature. In a similar way, studies on phenotypic plasticity in response to a thermal gradient also reveal a decrease of size at higher temperatures (e.g., David *et al.* 2006a). Such a parallelism between phenotypic (short term) and genetic (long term) variations is often called the temperature–size rule (Atkinson 1994; Atkinson and Sibly 1997; Blanckenhorn 2000; Angilletta and Dunham 2003; Angilletta *et al.* 2004; Blanckenhorn and Demont 2004). Several interpretations of this rule have been proposed, one of them being that flight in a cold environment will be favoured by a decrease in wing loading, leading to a specific increase of wing area (Stalker 1980; Pétavy *et al.* 1997). Wing loading can be decreased in two ways, either by decreasing the weight or by increasing wing area. We favour the second alternative, since *D. melanogaster* is native to tropical Africa, where ancestral populations are smaller than temperate ones: during its northward expansion, the species has increased in size but the wing loading has been reduced by a relatively more pronounced increase in wing area. Besides body size, many other traits exhibit latitudinal variations in *D. melanogaster* and its sibling *D. simulans* (see reviews in David *et al.* 2004; Gibert *et al.* 2004), thus revealing the complexity of thermal adaptations.

In a previous paper (David *et al.* 2006a), we analysed the phenotypic plasticity of a French population by considering three different samples, each of 10 isofemale lines collected in three different years. This paper was mostly dedicated to the analysis of the shapes of the reaction norms of two size traits, wing and thorax length, and of their ratio, and to the variability among the three different samples. An interesting conclusion was that the three samples were almost identical, both for their mean values and the shape of their reaction norms. A practical possibility was to pool 30 lines into a single sample, thus improving the power to describe this natural population.

In the present paper, we use the same data set for investigating plasticity in sexual dimorphism (SD). There are many ways of analysing SD, including the female/male ratio, the female–male difference and various correlations. The main conclusion was that SD is indeed a plastic trait responding

to developmental temperature: males and females were more similar in the cold and SD increased as a sigmoid reaction norm with increasing temperature. Surprisingly, however, the wing/thorax ratio (related to wing loading) was practically identical in the two sexes at all temperatures. Significant genetic differences among isofemale lines were found, suggesting that SD could respond to a directional selection. Whether such variations have an adaptive significance remains open to further comparative investigations.

## Material and methods

The data set used in the present paper is the same as in the previous paper (David *et al.* 2006a), in which the shapes of the reaction norms were analysed. Detailed technical information is provided in that paper and only the main features are summarized here. Three wild living samples of *D. melanogaster* adults were collected in the Grande Ferrade estate, near Bordeaux (southern France), in 1992, 1997 and 1999. From each sample, 10 isofemale lines were established and the F<sub>1</sub> flies were used for producing a second laboratory generation. These second generation flies were grown at seven constant temperatures (12, 14, 17, 21, 25, 28, 31°C) encompassing the entire thermal range of species. After emergence, adults were kept for few days at 20–22°C, and then measured with a binocular microscope equipped with an ocular micrometer. Two size-related traits, wing length (W) and thorax length (T) were measured on 10 individuals of each sex for each line and each growth temperature. From these data, the W/T ratio was calculated at the individual and the line level. Special attention was paid to SD which was analysed as a female/male ratio (F/M) (David *et al.* 2003). From these data the genetic variability of SD could be analysed, as well as the shape of the reaction norm, described with a polynomial. The experimental design also permitted the calculation of numerous correlations, and especially of genetic correlations among family means. The previous paper (David *et al.* 2006a) revealed that the three year samples were almost identical. For the sake of simplicity, we have pooled here these three samples, producing a single set of 30 lines.

## Results

We will first consider the correlated variations, either between different traits, or between different environments for the same trait, then the SD is described as a ratio. Note that, within a given environment, the female–male correlation is a means of analysing SD.

### Genetic correlations

**Between wing–thorax correlation:** For each line, temperature and sex, a within-line correlation was calculated for a total of 420 coefficients. Average values are given in

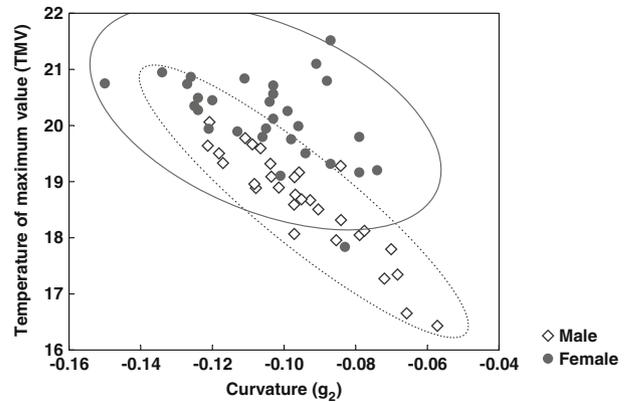
table 1 of electronic supplementary material at <http://www.ias.ac.in/jgenet/> showed that variations among temperatures were reduced (range 0.642–0.797). The results were submitted to ANOVA after a  $z$ -transformation (not shown) and the sole significant effect was due to line. We may conclude that the within-line correlation is fairly stable, with an average ( $\pm$  s.e.) value  $r = 0.708 \pm 0.010$ .

For each sex and temperature, a genetic correlation based on 30 observations (lines) was calculated and data given in table 1 of electronic supplementary material. The overall between-line correlation ( $r = 0.748 \pm 0.008$ ) was slightly, although significantly, greater than the overall within-line value.

**Correlations among temperatures for the same trait:** Significant genetic differences exist among lines and the question is: are these differences expressed similarly in different environments? In other words, is there a significant genotype  $\times$  environment interaction? For each trait, we calculated all possible correlations between any two different temperatures. The temperature difference, or interval, ranged between 2°C (e.g., growth at 12 and 14°C) and 19°C (12 and 31°C). The overall mean ( $\pm$  s.e.) correlation,  $r = 0.517 \pm 0.025$  was very significantly positive but the overall value, which measures a genetic repeatability, may be considered as fairly low.

The whole matrix (two sexes, three traits and 21 differences,  $n = 126$ ) was submitted to ANOVA (not shown) after  $z$ -transformation. The sex effect was not significant, while highly significant variations were due to trait and temperature difference. The trait effect was explained by higher correlations for the wing ( $r = 0.62$ ), as compared to thorax length ( $r = 0.45$ ) and W/T ratio ( $r = 0.48$ ). For the thermal effect, the correlation was slightly larger when the results of closer developmental temperatures were considered. More precisely, for temperature differences in the range 2–7°C, the correlation was  $0.553 \pm 0.031$ , but only  $0.483 \pm 0.037$  for more distant temperatures in the range 8–19°C. Such a difference, although significant, may be considered as very small.

**Correlations among the characteristic values of reaction norms:** The characteristic values of the reaction norms (RNs) of wing and thorax length were calculated in a previous paper (David *et al.* 2006a) but their correlations were not considered. Here we calculated for each line, trait and sex of the three characteristic values of quadratic norms, i.e. the maximum value (MV), the temperature of maximum value (TMV) and the curvature ( $g_2$ ). Very low and non-significant correlations were observed between MV and TMV (average  $r = 0.163 \pm 0.092$ ,  $n = 4$ ). Negative significant values were however observed between  $g_2$  and the two other parameters, MV and TMV (average  $r = -0.410 \pm 0.096$ ,  $n = 8$ ). The relationship between  $g_2$  and TMV for the thorax is illustrated in figure 1. A stronger



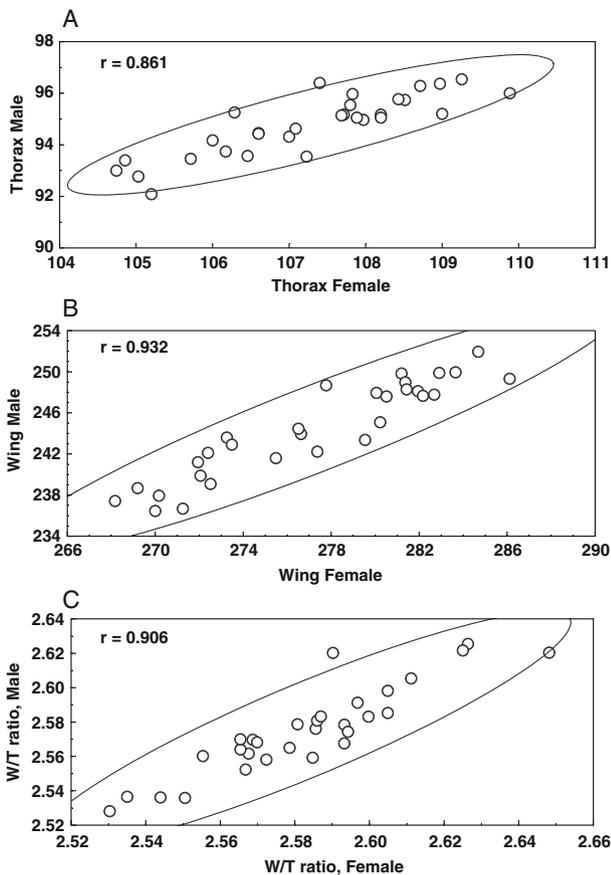
**Figure 1.** Negative correlations between two parameters of the reaction norms of thorax length.  $g_2$ , Curvature; TMV, temperature of maximum value;  $r = -0.91$  for males and  $-0.47$  for females.

(greater absolute value) curvature is associated with a higher TMV.

### Sexual dimorphism

**Female–male genetic correlations:** Values of the female–male correlations at the various temperatures were calculated and the ANOVA (not shown) revealed two significant effects. The average correlation was greater for wing length than for the two other traits:  $r = 0.83$  versus 0.73 and 0.74 for thorax length and W/T ratio, respectively. The significant temperature effect was due to lesser correlations at high temperatures, i.e. 25, 28 and 31°C. We also calculated for each line a mean value for all growth temperatures, then analysed the F–M correlation (figure 2). For the three traits, the correlations were significantly greater than the within temperature correlations ( $r = 0.900 \pm 0.012$ ,  $n = 3$ ). Averaging size traits over temperatures provides a better estimate of the true genetic size of each sex and suggests a higher similarity between females and males. In other words, the sample size of 10 flies which has been used in this work might be too small.

**Genetic variability of SD:** For each trait and temperature, two genetic parameters were calculated (see table 2 of electronic supplementary material): the intraclass correlation (ICC), which is akin to an isofemale line heritability (see David *et al.* 2005) and the genetic coefficient of variation (CVg), which may be called evolvability (Houle 1992). ICC values were submitted to ANOVA (not shown) and no significant effect of either trait or temperature was seen (table 1). The best estimate is the overall ICC:  $0.20 \pm 0.03$  ( $n = 21$ ). Genetic CVs were also submitted to ANOVA and, in that case, significant effects of temperature or trait were seen. For the temperature effect, ( $F_{6,12} = 3.32$ ,  $P = 0.04$ ) no regular trend was observed. Differences among traits ( $F_{2,18} = 5.89$ ,  $P = 0.018$ ) were explained by a lesser evolvability of the W/T ratio, 0.84 versus 1.07 for the two other traits.



**Figure 2.** Female–male correlations for the three traits investigated: A, thorax length; B, wing length; C, wing/thorax ratio. Each point is the mean value of an isofemale line, averaged over the seven growth temperatures. Ellipses of 90% are shown.

**Reaction norms of SD:** Variations of SD in the 30 lines are shown figure 3, and the average curves, the RN, are presented in figure 4. The results were submitted to ANOVA

(table 1). For the two length traits, significant effects due to temperature and lines were observed (figure 4a). Clearly, SD showed a progressive increase at higher temperatures. Males and females are more similar at low temperatures; males react more strongly to the thermal increase. Very different results were obtained for the SD of the W/T ratio (figure 4b). First, the overall value is very close to 1, meaning that for this ratio both sexes remained practically identical. Second, a slight significant temperature effect was observed, but in that case, a curvilinear norm was observed, with a maximum value in the middle of the thermal range.

**Polynomial adjustment of the RN:** Polynomial adjustment is a general method for analysing the shape of a response curve, i.e. a RN. A major problem is the choice of the polynomial degree (David et al. 1997) and the precise shape of a RN may be determined by calculating its derivative (figure 4c). For the W/T ratio, the derivative is decreasing linearly, which means that, for the integral curve (the RN), a quadratic polynomial will be used. For the dimorphism of wing and thorax length, the derivatives are clearly nonlinear, so that a cubic polynomial will be used for analysing the shape of the RNs shown in figure 4a.

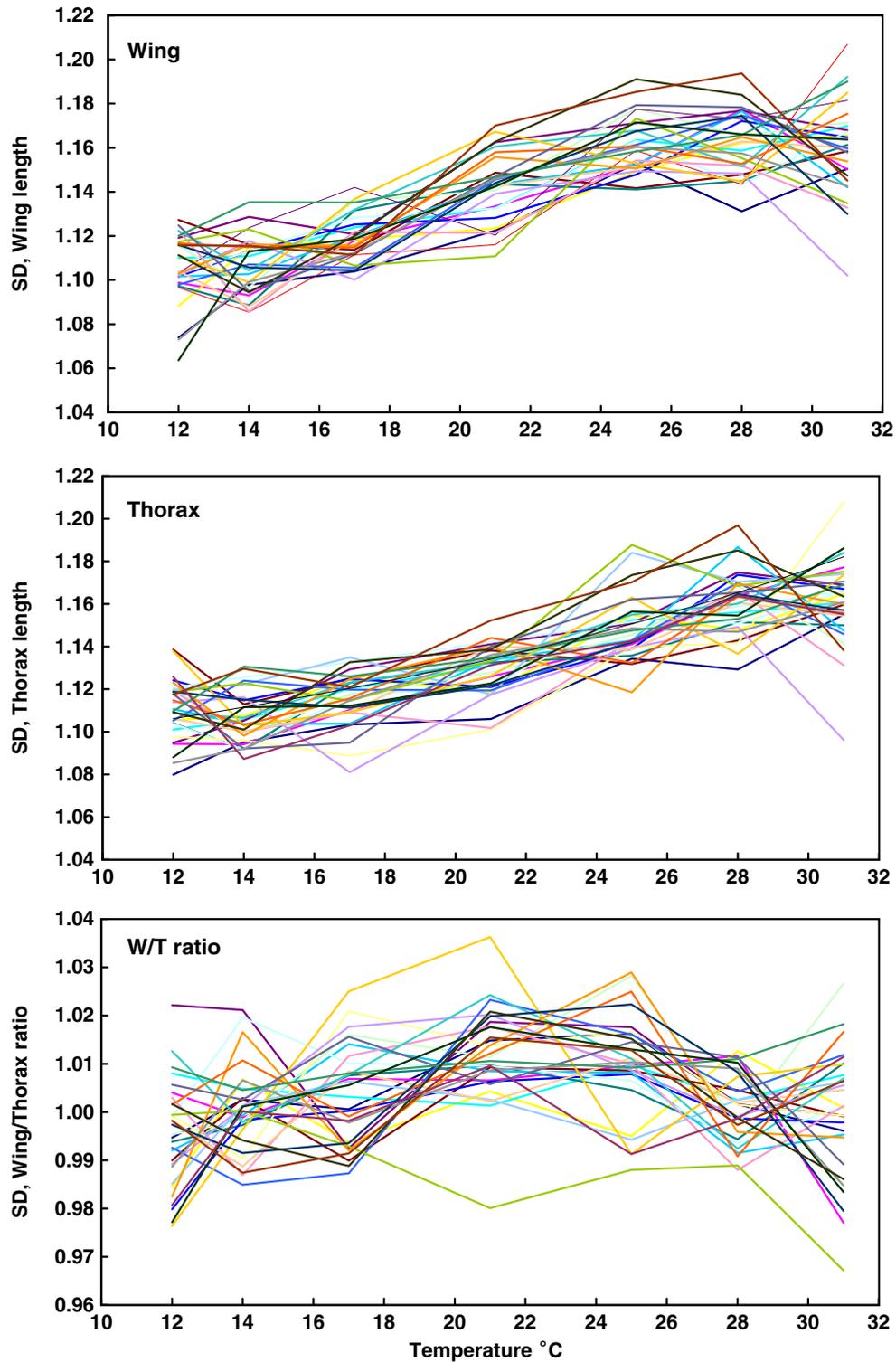
We tried to calculate the characteristic values for each line of the norms but the results were disappointing. In more than a third of the lines, the characteristic values, for example the position of a maximum, were outside the thermal range. Such a result was already observed for other traits, for example, abdomen pigmentation (Gibert et al. 2009). Whether such large variations are due to real genetic differences or merely to statistical imprecision remains a matter for further investigation.

We thus decided to consider only the average curves (figure 4a) for characterizing the plasticity of size SD. Wing and thorax produced similar results: a maximum value of 1.17 was calculated at 29.4°C, and the minimum value of 1.14 was observed at 12.8°C. For the wing/thorax ratio

**Table 1.** Results of ANOVA applied on SD reaction norms shown in figure 4 for the three traits investigated.

	df	MS	F	P level	Variance %
SD wing					
Temp	6	0.020082	102.46	0.00***	72.02
Line	29	0.000438	2.23	0.0008***	7.59
Temp × line (error)	174	0.000196			20.39
SD thorax					
Temp	6	0.017009	93.97	0.00***	70.35
Line	29	0.000397	2.19	0.001***	7.94
Temp × line (error)	174	0.000181			21.71
SD W/T ratio					
Temp	6	0.001034	10.55	0.00***	22.79
Line	29	0.000137	1.41	0.09NS	14.59
Temp × line (error)	174	0.000098			62.62

Temp, temperature; df, degree of freedom; MS, mean square; F, variance ratio; P, probability. \*\*\* <0.001; NS, nonsignificant; variance %, percentage of the total variance explained by each factor.

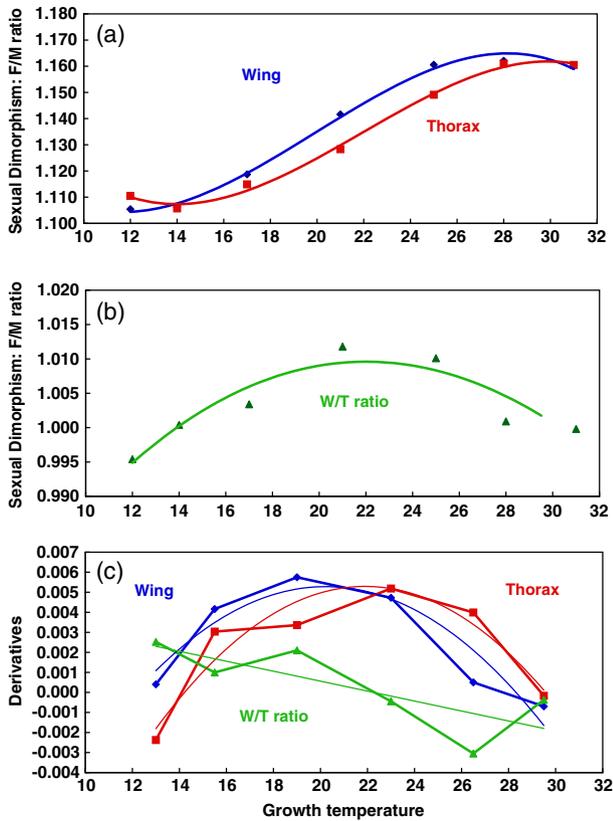


**Figure 3.** Reaction norms of the 30 isofemale lines for the sexual dimorphism (F/M ratio) of the three traits investigated. Note the different scales of the ordinates.

(figure 4b), the relationship was completely different with a maximum in the middle of the thermal range, but the amplitude of the observed variations was very small (range 0.995–1.008) and the overall mean was close to 1.

## Discussion

This work illustrates the power of an isofemale line design for addressing biological problems related to phenotypic



**Figure 4.** Overall shape of the reaction norms of SD for the three investigated traits. A and B, average curves; C, derivatives. Note the similarity of the RNs for wing and thorax length, but a very different shape for the W/T (wing/thorax) ratio.

plasticity (David *et al.* 2005). It also shows how phenotypic ratios that have a clear biological meaning are useful in providing specific information about plasticity; one of them, the SD, being rarely considered in *Drosophila* (David *et al.* 2003).

### Correlations

The experimental design allowed the calculation of numerous correlations, between either the traits or the characteristic values of the RNs. The most interesting correlations are those calculated between family means since they correspond to a genetic correlation (Via 1984; Gibert *et al.* 1998; David *et al.* 2005).

The correlation between wing and thorax length produced consistent results: it is insensitive to growth temperature with an average values of 0.70 within line and 0.75 between lines. An increase of a correlation is expected when mean values are considered (David *et al.* 2005). Interestingly, previous studies in *Drosophila* gave similar values (Chakir *et al.* 2008). This correlation is fairly low ( $R^2 = 0.56$ ), meaning that the genetic bases of wing and thorax size are quite different. The relative independence of these two traits is still more convincingly shown by the fact that their RNs are quite different (David *et al.* 2006a).

Correlations for the same trait among growth temperatures revealed a significant temperature effect. As expected, they were smaller when more distant temperatures were compared, consistent with the suggestion that different genes or genetic networks may be functioning in different environments (DeWitt and Scheiner 2004; Pigliucci and Preston 2004). However, the empirical difference was very small (0.48 versus 0.52) and this shows that the responsible developmental genetic networks function in the same way at all temperatures.

For a given trait, the characteristic values of a RN are used for defining its shape (David *et al.* 1997; 2006a). For the quadratic polynomial adjustments, three parameters are considered, that is the coordinates of a maximum (MV and TMV) and the  $g_2$ . We calculated a third kind of correlation among these parameters with a clear conclusion: MV and TMV are independent. Note that, however, a clear negative relationship would appear if several geographic populations collected along a latitudinal cline were compared (Morin *et al.* 1999).

The curvature parameter  $g_2$  is too variable among lines (David *et al.* 2004) and thus difficult to use in statistical comparisons. An interesting difference of  $g_2$  between males and females was however found for abdomen pigmentation (Gibert *et al.* 2009). For body size, we observed negative correlations between  $g_2$  and both MV or TMV: a greater absolute value of  $g_2$  corresponding to a greater reactivity to temperature is observed in lines with a larger body size or a higher TMV. Whether this relationship would persist if geographic populations were compared deserves further investigations.

### Sexual dimorphism

The most interesting result of this work has been to show that SD expressed as a ratio is a plastic trait. For the two length dimensions, SD increases monotonically with increasing growth temperature and the RN has a sigmoid shape: in other words, males are more similar to females at low temperature. A similar pattern was observed for abdomen pigmentation (Gibert *et al.* 2009). The RN of wing and thorax are very similar and, for example at 25°C, SD is about 1.15, meaning that the linear dimensions are 15% greater in female. Interestingly, the same value was found for a Moroccan population (Chakir *et al.* 2008).

For the W/T ratio, which is related to wing loading and might be the real target of natural selection explaining the latitudinal clines (Pétavy *et al.* 1997) we found the two sexes to be almost identical, which is surprising and seems maladaptive. We know that the female weight shows an important increase in the early days of its life, due to the development of the ovaries, while the weight of the male remains constant (David 1979). In other words, the wing loading increases during the early days of life in females, probably impairing their flight capacity. At first sight, a lower wing loading (i.e., higher W/T ratio) would seem to yield higher fitness in

females. A possible explanation of this sexual identity could be that the W/T ratio has a low genetic variance and a low evolvability. However, such is not the case, either within a population (David *et al.* 2006a) or among populations (Capy *et al.* 1993; Gibert *et al.* 2004). Moreover we found here (see table 2 in electronic supplementary material) that the dimorphism of W/T was also genetically variable and thus could respond to a monosexual selection. Why both sexes have the same W/T ratio remains, for the moment, devoid of any convenient interpretation.

The evolution of SD among drosophilid species was investigated by Pitnick *et al.* (1995) in 42 species of *Sophophora* and *Drosophila* subgenera, and in 20 species of the *obscura* group of *Sophophora* (Moreteau *et al.* 2003; Huey *et al.* 2006). In all cases, larger females were found, but with a large variability of the ratios. For Pitnick *et al.* (1995) the range was 1.014–1.174, and for Moreteau *et al.* (2003) the range was 1.03 (*D. guanche*) and 1.22 (*D. tolteca*). These data show that SD may evolve quite rapidly among related species. At the intraspecific level, interesting data have been obtained in an invasive drosophilid, *Zaprionus indianus*. No significant variations according to growth temperature were found (Karan *et al.* 1999) but this might be due to the fact that female and male are almost the same size. A survey of numerous geographic populations revealed significant latitudinal clines but SD remained very stable and close to 1 (David *et al.* 2006b). The possibility of genetic variations was however suggested by results from old laboratory strains which, presumably due to drift, were found to be too variable. Whether this observation, which suggests some kind of stabilizing selection in nature, exists in *D. melanogaster*, remains to be investigated.

Finally, besides thermal plasticity, SD may also be affected by nutritional effects observed in natural populations. Body size in nature is known to be extremely variable, due to the fact that the larvae grow under very heterogeneous conditions. It has been observed that, in *Zaprionus*, *D. simulans* and *D. melanogaster*, the SD ratio in nature may be quite different from that measured under optimal laboratory conditions (Chakir *et al.* 2007; Yassin *et al.* 2007, 2009). Our present knowledge on SD shows that it is a very interesting trait, which deserves many more studies at the genetic, comparative and ecological levels.

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