

# Phenotypic plasticity and reaction norms of abdominal bristle number in *Drosophila melanogaster*

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The phenotypic plasticity of abdominal bristle number (segments 3 and 4 in females) was investigated in 10 isofemale lines from a French population, grown at 7 constant temperatures, ranging from 12° to 31°C. Overall concave reaction norms were obtained with a maximum around 20°–21°C. Intraclass correlation (isofemale line heritability) was not affected by temperature. Correlations between segments 3 and 4 strongly contrasted a low within-line phenotypic correlation ( $r = 0.39 \pm 0.04$ ) and a high, between-line genetic correlation ( $r = 0.89 \pm 0.03$ ). A significant decrease of the genetic correlation was observed when comparing more different temperatures. Finally, among 7 other morphometrical traits which were measured on the same set of lines, 3 provided a significant positive genetic correlation with abdominal bristles: thoracic bristles, abdomen pigmentation and thoracic pigmentation.

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## 1. Introduction

Several widespread *Drosophila* species are known to exhibit latitudinal clines for body size, with a general trend of increasing size under colder climates. Investigated species include *Drosophila robusta* (Stalker and Carson 1947), *Drosophila subobscura* (Prevosti 1955; Misra and Reeve 1964), *Drosophila melanogaster* and *Drosophila simulans* (Capy *et al* 1993; James *et al* 1995; Partridge and Coyne 1997; Gibert *et al* 2004), *Drosophila kikkawai* (Karan *et al* 1998) and *Zaprionus indianus* (Karan *et al* 2000). There is a clear analogy with Bergman's rule, which concerns homeothermic species and suggests that a bigger size helps to prevent heat loss under a cold climate (Bergmann 1847; Rensch 1959). In the case of ectotherms, however, this interpretation does not hold, and the adaptive significance of latitudinal clines is far from being clearly understood. Quantitative traits such as body size are not only genetically variable according to climatic conditions, they are also very variable according to

developmental conditions and especially growth temperature (David *et al* 2004). A parallelism exists, for body size, between the geographical clines among populations and plasticity among temperatures, since in both cases bigger flies are observed in colder conditions. This parallelism is often considered as an adaptive argument, a bigger size being better at low temperature, even if we do not understand the precise target of selection (Atkinson 1994; Atkinson and Sibly 1997). Climatic adaptation is not restricted to size. In *D. melanogaster*, several other quantitative traits exhibit latitudinal clines, in spite of the fact that these traits, including bristle numbers, ovariole number and body pigmentation, are not directly related to size (Capy *et al* 1993; Gibert *et al* 2004).

We used the isofemale line technique (ILT), that is the isolation of a set of full-sib families from a natural population, for a detailed analysis of a French natural population, from the vicinity of Bordeaux. ILT is a powerful means for analysing the phenotypic, functional and genetic characteristics of a natural population (Hoffmann

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and Parsons 1988, 1991; David *et al* 2005). Besides uncovering a genetic variability in a population, ILT is also a multipurpose technique, appropriate to a diversity of investigations, including the study of phenotypic plasticity, genetic correlations among traits, or sexual dimorphism (David *et al* 2005).

Ten isofemale lines of the Bordeaux population were grown at temperatures ranging from 12° to 31°C and used to analyse the reaction norms of two size-related traits, wing and thorax length (David *et al* 1994). Other traits have been also measured on the same set of lines, and their phenotypic plasticity has been described over time: ovariole number (Delpuech *et al* 1995), body pigmentation (Gibert *et al* 1996, 1998) and sternopleural bristle number (Moreteau *et al* 2003). In the present paper, we describe the reaction norms of abdominal bristle number on sternites 3 and 4 in females, and analyse the within-line and between-line variability. Genetic correlations with other, previously investigated, traits are also presented.

## 2. Material and methods

Flies from a wild living vineyard population were collected with banana traps in the Grande Ferrade estate, in Pont-de-la Maye, near Bordeaux, France. About 20 females were isolated in culture vials (corneal medium with live yeast) and produced a first laboratory generation, G1, grown at 25°C. Ten lines were then randomly chosen to produce the experimental flies. For this, 10 females and 10 males from each G1 line were used as parents. They oviposited at 20°C on a killed yeast, high nutrient medium (David and Clavel 1965) for about half a day. Vials with eggs were then transferred to one of the 7 experimental constant temperatures, i.e. 12°, 14°, 17°, 21°, 25°, 28° and 31°C. With this procedure larval density was not strictly controlled, and the number of adults emerging from a vial generally ranged between 100 and

200. This is a fairly high density, but the use of a very rich medium for the development prevents significant crowding effects (Karan *et al* 1999). From each line and temperature, 10 females were randomly taken, and the number of mechanosensory bristles on sternites 3 and 4 counted. Data were analysed with the Statistica software (Statsoft 1999).

## 3. Results

### 3.1 Basic statistical data and average reaction norms

Basic statistics for bristle number on sternites 3 and 4 and for their sum are given in table 1. Data were submitted to a 3 way ANOVA (not shown): all the direct effects (temperature, segment and line) were highly significant, as well as two interactions, temperature segment and line segment. There is a slight difference between segments, that is more bristles on segment 4 (average 22.18) than on segment 3 (average 21.71). The line effect corresponds to genetic differences which are analysed below.

The temperature effect was further analysed by considering the response curves (figure 1). These reaction norms were adjusted to quadratic polynomials (David *et al* 1997) according to the formula

$$\text{bristle number} = MV + g_2 (t - TMV)^2,$$

where  $MV$  is the maximum value,  $TMV$  is the temperature of maximum value,  $g_2$  is a curvature parameter and  $t$  is growth temperature. The results of these characteristic values (using a non-linear estimation model, Statsoft 1999) are given in the legend of figure 1, as well as the goodness of fit  $R^2$ .

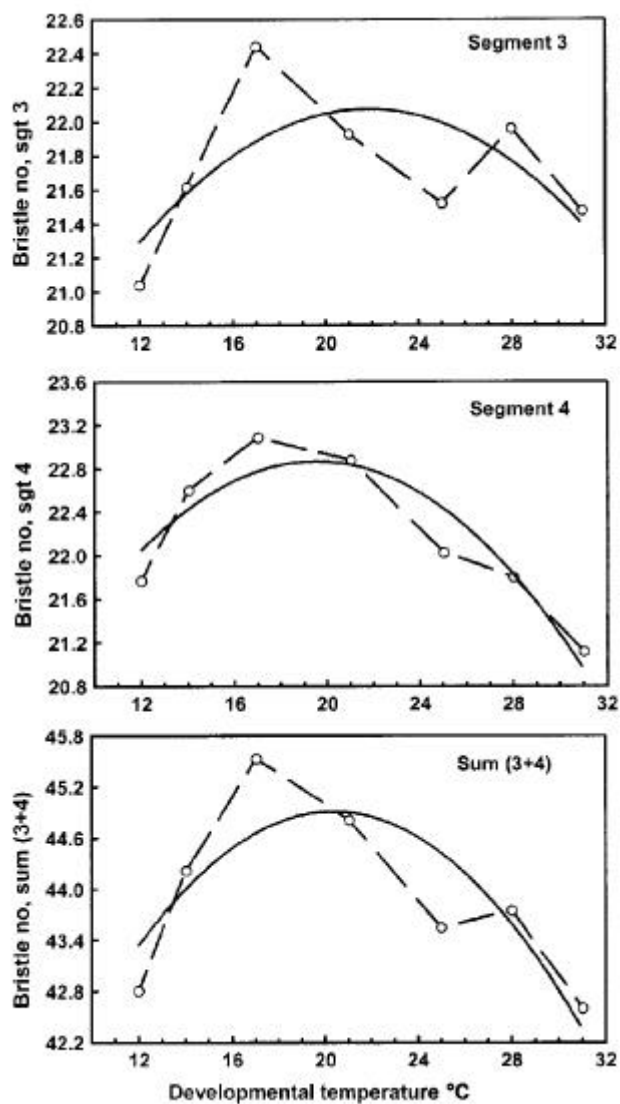
In the three cases, concave reaction norms were obtained, with a maximum in the middle of the thermal range. For segment 3,  $R^2$  is small (0.44), revealing a fairly poor adjustment. Better values are obtained for segment 4 and for the sum.  $TMVs$  are not statistically

**Table 1.** Mean values of abdominal bristle number at different growth temperatures.

Temperature °C	Segment 3	Segment 4	Sum (3 + 4)
12	21.04 ± 0.51	21.77 ± 0.49	42.81 ± 0.96
14	21.62 ± 0.39	22.60 ± 0.35	44.22 ± 0.72
17	22.44 ± 0.39	23.09 ± 0.54	45.53 ± 0.91
21	21.93 ± 0.50	22.88 ± 0.51	44.81 ± 0.99
25	21.52 ± 0.55	22.03 ± 0.42	43.55 ± 0.96
28	21.96 ± 0.47	21.80 ± 0.38	43.76 ± 0.79
31	21.48 ± 0.71	21.12 ± 0.63	42.60 ± 1.33
Mean	21.71 ± 0.17	22.18 ± 0.27	43.90 ± 0.40
CV	2.05	3.16	2.39

Segments 3 and 4: abdominal segments 3 and 4. Each value is the mean (± SE) of 10 isofemale lines.

different between segments 3 and 4, and their mean (20.68°C) is close to the value calculated for the sum (20.34°C). Curvature parameters are negative, as expected for a concave norm and not different between segments 3 and 4.



**Figure 1.** Reaction norms of abdominal bristle number (segments 3, 4 and their sum) as a function of growth temperature. (—○—), Experimental data (mean of 10 isofemale lines) and curve adjusted to a quadratic model. Characteristic values of the curves are:

	$R^2$	MV	TMV (°C)	$g_2 (\times 10^3)$
Sgt 3	0.44	22.07 ± 0.25	21.85 ± 1.46	- 8.04 ± 4.58
Sgt 4	0.86	22.87 ± 0.19	19.50 ± 0.76	- 14.47 ± 3.53
Sum (3+4)	0.71	44.91 ± 0.43	20.34 ± 0.95	- 22.51 ± 7.83

$R^2$ , coefficient of determination; MV, maximum value; TMV, temperature of maximum value;  $g_2$ , curvature parameter.

### 3.2 Within-line variability

We consider here the variability among the 10 flies from each line, expressed as a coefficient of variation (CV) for each segment, and also the covariance between segments 3 and 4, expressed as a correlation coefficient. For 10 lines and 7 temperatures, the whole data set corresponds to 70 values.

Average CVs according to growth temperature are given in table 2. A three way ANOVA (not shown) showed a significant effect of temperature ( $P < 0.01$ ) but not of line nor segment; the interaction line temperature was however significant ( $P < 0.01$ ). The temperature effect was further analysed on the sum. A non-linear adjustment revealed an average convex reaction norm (figure 2), with a minimum value of 7.7 at 21.7°C. However, due to very irregular values and a low  $R^2$  (0.18) these characteristic values are not significant.

The within-line correlation (table 2) was not affected by temperature (ANOVA, not shown, after a  $z$  transformation). The average value ( $0.39 \pm 0.04$ ) is significantly positive, although not very high. For a given segment (3 or 4) the average CV is close to 10. We notice a decrease when the sum is considered (CV about 8). This is due to the fact that the correlation between segments 3 and 4 is quite small (the same CV would be observed for  $r = 1$ ).

### 3.3 Genetic variability among lines

The genetic variability among lines was first examined by calculating the intraclass coefficient of correlation (ICC, table 3) also considered as a special case of heritability (isofemale line heritability, David *et al* 2005). All values were positive, with means of  $0.32 \pm 0.04$  and  $0.25 \pm 0.04$  for segments 3 and 4 respectively. There was no effect either due to sex or segment (ANOVA, not shown). The fact that the mean values are all significantly greater than zero demonstrates a genetic variability among lines. The large heterogeneity which exists among lines is illustrated in figure 3 for the sum.

The genetic CVs (table 3) were not significantly affected by temperature, with an overall mean of 6.3, which is significantly less than the within-line CV (table 2). Finally we calculated the genetic correlation between family means (table 3) and the  $r$  values ranged between 0.74 and 0.97, all significantly greater than zero (threshold value for 10 observations and  $P = 0.05$  is 0.67). The overall mean ( $r = 0.89 \pm 0.03$ ) is much bigger than the average within-line correlation ( $r = 0.39 \pm 0.04$ ). This phenomenon is illustrated in figure 4 for the temperature of 25°C.

### 3.4 Genetic correlations between temperatures

Up to now, we examined only correlations between dif-

ferent traits at the same temperature. But it is also possible to consider the same line at different temperatures. Figure 3 shows that some lines have consistently more bristles than others, so that we may expect a positive correlation between temperatures. With 7 temperatures, we can calculate 21 different correlations, the results of which are given in table 4.

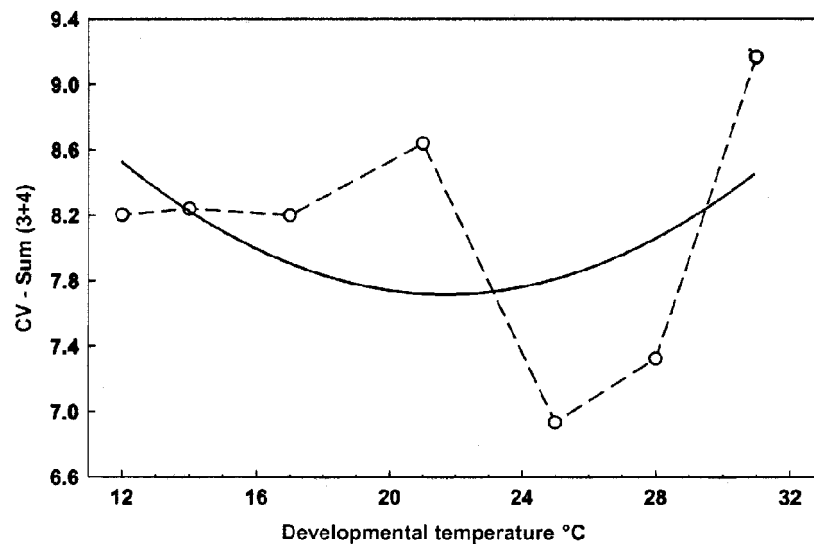
All calculated coefficients are positive and range between 0.10 and 0.89. This confirms that the bristle number genes, which differentiate the lines, are expressed in a similar way at different growth temperature. However we may ask the question: is it possible to find some pattern

within the broad variability visible in table 4? One possible way is to consider the interval between temperatures, as this was already done for wing and thorax length (Karan *et al* 2000). The results of this analysis are presented in figure 5. There is a significant negative regression ( $b = -0.0137 \pm 0.006$ ,  $P < 0.03$ ) between  $r$  and the temperature interval. The correlation decreases when more distant temperatures are considered. In other words, the variability between lines at different temperatures is not exactly determined by the same set of genes, or the expression of the genes is differently modulated by growth temperature.

**Table 2.** Analysis of within-line variability.

Temperature °C	Coefficients of variation			
	Segment 3	Segment 4	Sum (3 + 4)	Correlation 3-4
12	9.10 ± 0.88	10.18 ± 0.75	8.20 ± 0.68	0.39 ± 0.10
14	9.33 ± 0.70	10.17 ± 0.67	8.24 ± 0.69	0.41 ± 0.10
17	9.87 ± 0.72	9.77 ± 0.62	8.20 ± 0.79	0.38 ± 0.13
21	8.97 ± 0.74	11.08 ± 0.86	8.64 ± 0.78	0.45 ± 0.09
25	8.58 ± 0.83	9.32 ± 0.56	6.94 ± 0.52	0.16 ± 0.09
28	7.66 ± 0.56	9.57 ± 0.77	7.33 ± 0.58	0.45 ± 0.08
31	11.08 ± 0.71	10.08 ± 0.77	9.17 ± 0.63	0.50 ± 0.06
Mean	9.23 ± 0.40	10.02 ± 0.21	8.10 ± 0.29	0.39 ± 0.04

Average CVs according to growth temperature ( $m \pm SE$ ;  $n = 10$  lines in each case). The average correlation between segments 3 and 4 is also given.



**Figure 2.** Reaction norm of the within-line variability (mean CV for the sum of segments 3 + 4) as a function of growth temperature. The graph shows the experimental data (—○—) and a curve adjusted to a quadratic polynomial. Due to large irregularities between experimental observations, the overall convex shape of the norm is not significant.

## 3.5 Genetic correlations between different traits

Besides abdominal bristle number, six other quantitative traits were measured on the same set of 10 isofemale lines grown at 7 temperatures, and the results are already published in several papers (see introduction and legend of table 5). The matrix in table 5 was submitted to a two way ANOVA, which evidenced significant variations between traits ( $P < 0.01$ ) but no temperature effects ( $P < 0.44$ ). The differences among traits are visible on the mean correlations averaged over developmental temperatures (table 5). Three correlations involving abdominal bristles are significantly positive and greater than zero, with abdominal pigmentation, trident pigmentation and sternopleural bristles. These significant values range between 0.29 and 0.37, indicating the common genetic basis ( $R^2$ ) is not big, and varies between 0.08 and 0.14.

## 4. Discussion and conclusions

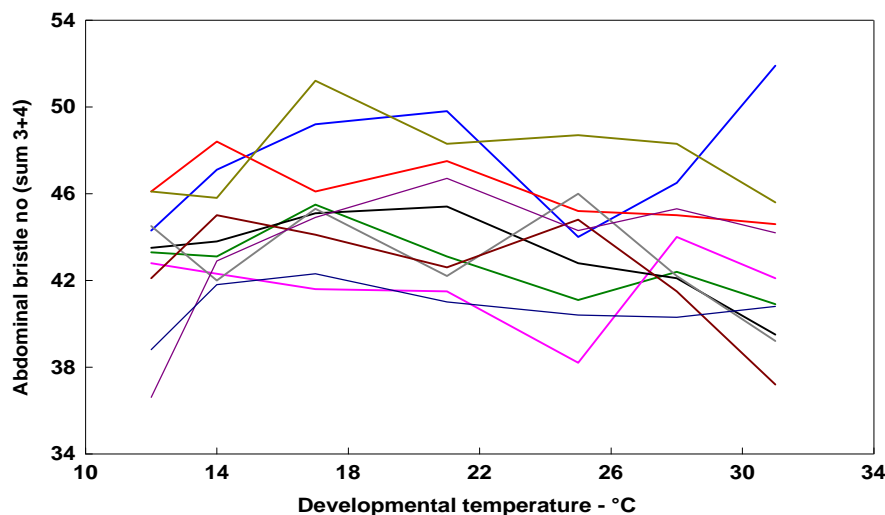
Two meristic traits have been extensively investigated in *D. melanogaster* and can be considered as paradigms in quantitative genetic studies: sternopleural bristle number on both sides of the thorax and abdominal bristle number on abdominal sternites (Falconer and Mackay 1996; Mackay 1995, 1996, 2001). Both concern mechanosensory bristles, the number of which is not known to be directly related to fitness. Some indirect relationship with fitness is however likely, as shown by the occurrence of latitudinal clines which implies a correlation with local climatic conditions (Capy *et al* 1993; Moreteau *et al* 2003; Gibert *et al* 2004).

Sternopleural bristles are defined unambiguously, and all investigators have measured the same trait, on the right and left side of the thorax. By contrast, abdominal

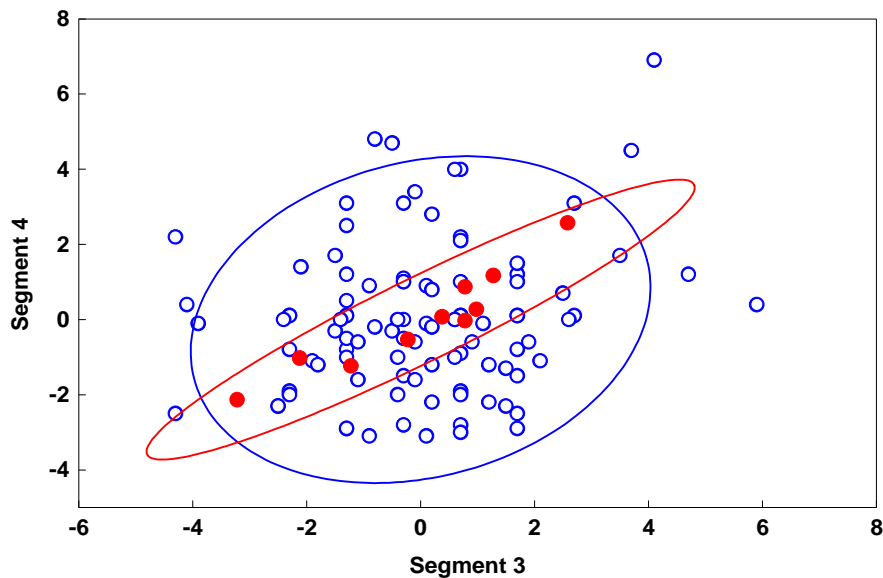
**Table 3.** Genetic variability of abdominal bristle number as a function of growth temperature.

Temperature °C	ICC			CVg			Genetic correlation
	Segment 3	Segment 4	Sum (3 + 4)	Segment 3	Segment 4	Sum (3 + 4)	
12	0.35	0.26	0.37	7.00	6.22	6.54	0.86
14	0.20	0.11	0.21	4.77	3.70	4.37	0.89
17	0.16	0.31	0.31	4.43	6.68	5.72	0.93
21	0.33	0.22	0.33	6.54	6.13	6.37	0.91
25	0.41	0.24	0.46	7.54	5.31	6.59	0.94
28	0.40	0.18	0.33	6.28	4.55	5.20	0.74
31	0.42	0.41	0.49	9.78	8.81	9.38	0.97
Mean	0.32 ± 0.04	0.25 ± 0.04	0.36 ± 0.04	6.62 ± 0.68	5.91 ± 0.62	6.31 ± 0.60	0.89 ± 0.03

ICC, intraclass correlation coefficient; CVg, genetic coefficient of variation (evolvability). The genetic correlation between segments 3 and 4 is also given.



**Figure 3.** Illustration of the variability of abdominal bristle number (sum of segments 3 and 4) among isofemale lines grown at different temperatures.



**Figure 4.** Graphical analysis of the correlation between bristle number on segments 3 and 4, for the developmental temperature of 25°C. Open symbols: variability at the within-line, individual level; close symbols: variability between line means. Data are centred and the overall mean is zero in each case. Note the very low correlation ( $r = 0.16$ ) among individuals from the same line ( $n = 100$ ), but the very high genetic correlation ( $r = 0.94$ ) among line means ( $n = 10$ ). For each graph, ellipses of 90% confidence are shown.

bristles correspond to a modular trait, which can be measured on segments 2 to 7 in females and 2 to 5 in males (Araripe L O, Klaczko L B, Moreteau B and David J R, unpublished results). Most quantitative genetic studies have considered only one or a few of these possible segments, for example segments 3 and 4 (Capy *et al* 1993) or segments 5, 6, 7 (Kopp *et al* 2003). We are aware of only one study in which all segments have been investigated in both sexes, but for a single developmental temperature of 25°C (Araripe L O, Klaczko L B, Moreteau B and David J R, unpublished results).

The need for investigating thermal phenotypic plasticity arises from two main reasons: first the likely selective role of temperature, as evidenced from the observation of latitudinal clines; second, a need of comparative data concerning the phenotypic plasticity of different quantitative traits (David *et al* 2004). Our results on segments 3 and 4 have revealed overall concave reaction norms, with a large amount of genetic variability in the shape of the response curve among lines from the same population, so that it was not possible to make a convenient quadratic adjustment for each line. In this respect, the irregularities observed for abdominal bristles are akin to the irregularities previously found for sternopleural bristles (Moreteau *et al* 2003). Whether these variations reflect significant genetic differences in plasticity among lines requires further investigations.

**Table 4.** Genetic correlations between family means at different temperatures.

	Segment 3	Segment 4	Segment (3 + 4)
12–14	0.56	0.51	0.58
12–17	0.65*	0.37	0.55
12–21	0.24	0.36	0.33
12–25	0.35	0.37	0.39
12–28	0.55	0.10	0.36
12–31	0.26	0.11	0.20
14–17	0.71*	0.56	0.64*
14–21	0.78**	0.75*	0.78**
14–25	0.55	0.50	0.51
14–28	0.68*	0.37	0.59
14–31	0.51	0.62	0.58
17–21	0.77**	0.83**	0.83**
17–25	0.72*	0.78**	0.77**
17–28	0.75**	0.72*	0.77**
17–31	0.59	0.66*	0.63*
21–25	0.62	0.55	0.59
21–28	0.79**	0.69*	0.83**
21–31	0.68*	0.89***	0.81**
25–28	0.46	0.47	0.52
25–31	0.13	0.29	0.21
28–31	0.85**	0.59	0.80**

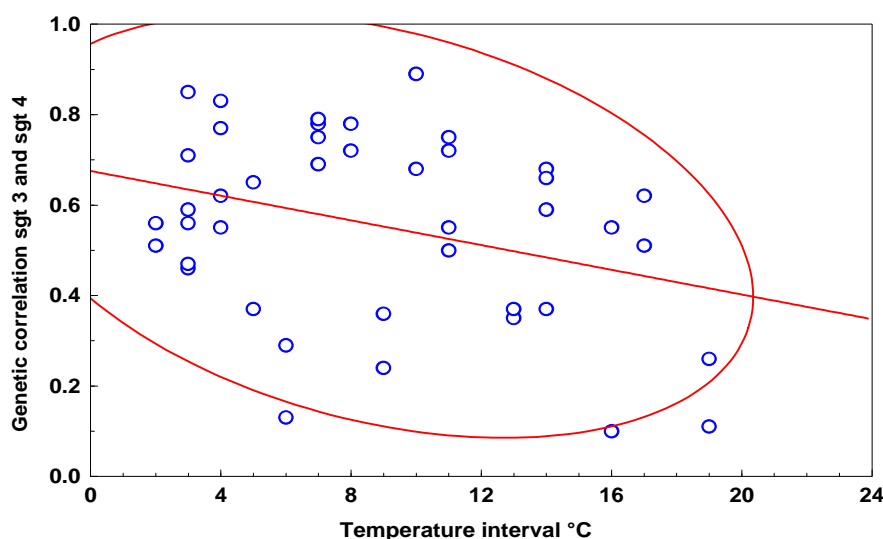
Significance thresholds for  $n = 10$  observations are: \*0.63 ( $P < 0.05$ ); \*\*0.76 ( $P < 0.01$ ); \*\*\*0.87 ( $P < 0.001$ ).

At a given temperature, a significant genetic variability among lines exists and can be quantified by calculating a coefficient of intraclass correlation. The average value of ICC for the sum ( $0.36 \pm 0.04$ ) is close to the value already measured on numerous natural populations at a single temperature of  $25^{\circ}\text{C}$  ( $0.29 \pm 0.02$ ) (Capy *et al* 1993).

The within-line variability (CV) is an interesting parameter which mainly expresses an environmental component (David *et al* 2005). We found an average value close to 10 for each segment (table 2) and to 8 for their sum. These values are similar to those already found for sternopleural bristles (Moreteau *et al* 2003) or ovariole number (Delpuech *et al* 1995), and much higher than those found for size traits (Karan *et al* 1999). Within-line CVs are generally variable according to temperature, with an

increase under extreme, low or high, temperatures. In other words, all traits exhibit a convex reaction norm for their within line variability. We found however a difference between sternopleural and abdominal bristles. In the former trait, the concave reaction norm was very regular (Moreteau *et al* 2003) while for abdominal bristles, there were big irregularities (figure 2). Whether such a divergence is accidental or reflects a real difference between the traits requires further studies.

The analysis of correlations provided also a large amount of interesting information. The correlation between the two successive segments 3 and 4 could be investigated at the individual (phenotypic) and the line (genetic) level, and provided a contrasted, quite unexpected pattern. At the within-line level, the correlation



**Figure 5.** Variation of the genetic correlation, between family means, when more or less different temperatures are considered. There is an overall positive correlation, but the value of  $r$  significantly decreases when more distant temperatures are compared (linear regression:  $b = -0.0137 \pm 0.006$ ,  $P < 0.03$ ,  $r = -0.34$ ). Data for segments 3 and 4 are pooled.

**Table 5.** Genetic correlations between abdominal bristle number (sum of segments 3 + 4) and other quantitative characters measured on the same lines.

Characters	12°C	14°C	17°C	21°C	25°C	28°C	31°C	Mean
Wing length <sup>1</sup>	0.12	-0.09	0.20	0.29	-0.13	0.33	0.26	$0.14 \pm 0.07$
Thorax length <sup>1</sup>	0.12	-0.14	0.18	0.36	-0.26	0.65*	0.62	$0.22 \pm 0.12$
Wing/thorax ratio <sup>1</sup>	0.09	0.02	0.11	0.15	0.07	-0.19	-0.52	$-0.04 \pm 0.09$
Ovariole No. <sup>2</sup>	-0.26	0.36	-0.43	0.19	-0.14	0.11	-0.04	$-0.03 \pm 0.10$
Abd. pigment <sup>3</sup>	0.28	0.45	0.12	0.03	0.41	0.55	0.26	$0.30 \pm 0.07^{**}$
Thoracic trident <sup>4</sup>	0.45	0.27	0.48	0.60	0.29	0.42	0.05	$0.37 \pm 0.07^{**}$
Sternopleural <sup>5</sup>	0.33	0.04	0.27	0.27	0.55	0.50	0.05	$0.29 \pm 0.07^{**}$

Level of significance  $^{**}P < 0.01$ .

Origin of data: <sup>1</sup>David *et al* 1994; <sup>2</sup>Delpuech *et al* 1995; <sup>3</sup>Gibert *et al* 1996; <sup>4</sup>Gibert *et al* 1998; <sup>5</sup>Moreteau *et al* 2003.

was always low (on average  $0.39 \pm 0.04$ ) while it was significantly much higher ( $0.89 \pm 0.03$ ) at the between-line level. This is a further argument in favour of the idea that within- and between-line variability are relatively independent and do not measure the same thing (David *et al* 2005). However, in studies of two size-related traits, wing and thorax length, the wing-thorax correlations were found to be quite similar at the within and between-line level, with average value of 0.69 and 0.78 respectively (David *et al* 2003). Such a contrast is difficult to explain and points to the need of further comparative investigations on different traits.

Genetic correlations can also be investigated by considering the performance of the same line at different temperatures. We have found that the correlation tended to decrease when more distant temperatures were considered. In other words, the degree to which the two traits are controlled by the same genes decreases at extreme temperatures, perhaps due to specific loci affecting the trait at different temperatures. A similar analysis was already performed for body size traits (Karan *et al* 2000). A regular, linear decrease of the correlation as a function of the thermal difference was observed in females, while different results were obtained in males, with a significant quadratic component. Whether a sexual dimorphism also exists for abdominal bristles remains to be investigated.

Finally, we also considered the genetic correlation between abdominal bristles and other quantitative, previously investigated traits (table 5). In this case, values obtained at different temperatures were not significantly different, and could therefore be considered as experimental repeats, providing a better precision for estimating each correlation. Among 7 cases (table 5) we found only 3 correlations significantly greater than zero. Abdominal bristle number is correlated with another abdominal trait, tergite pigmentation ( $r = 0.30 \pm 0.07$ ). This contrasts with the results of Kopp *et al* (2003) who, investigating recombinant inbred lines, failed to find any correlation between bristle number and pigmentation in segments 5 to 7 of females. Abdominal bristle number was also correlated with another bristle trait, sternopleural bristles ( $r = 0.29 \pm 0.07$ ). The third, most significant positive correlation ( $r = 0.37 \pm 0.07$ ) was observed between abdominal bristles and thoracic trident pigmentation. Thoracic trident pigmentation is a trait which is a likely target of natural selection, with clear cut latitudinal clines (Munjal *et al* 1997): darker flies are observed under colder climates, in agreement with the thermal budget adaptive hypothesis. Its relationship with abdominal bristles was, however, completely unexpected, with no obvious functional relationship. We may however recall that any genetic correlation may have two possible origins: either pleiotropy or linkage (Falconer and Mackay 1996). In the

case of the first two correlations, pleiotropy of the same genes is likely, since they concern either similar traits (bristle numbers) or abdomen segments. For the relationship between thoracic trident and bristle number, the linkage hypothesis must be considered. Our data are only valid for a small number (10) of randomly taken lines, and it is possible that a linkage, as evidenced in this sample, would not be found in another sample.

Altogether, our data point to the power of the isofemale line method for working out the genetic architecture of morphometrical traits in natural populations, and to a need for further investigations and comparisons between geographic populations.

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