PHENOTYPIC, GENETIC AND ENVIRONMENTAL CORRELATIONS BETWEEN CHAETA NUMBER AND WING LENGTH IN *DROSOPHILA MELANOGASTER*

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Introduction

There are a number of characteristics in Drosophila that are easily measured and are, therefore, widely used for studies in quantitative inheritance. Among these the bristle number and wing length have been most commonly used. Studies specifically designed to measure different types of correlations between these two characters in a wild stock of *Drosophila melanogaster* have not come to our notice so far. The importance of these correlations is fairly obvious for measuring the response to selection for correlated characters in this species. The experiment reported here was, therefore, undertaken to remedy this deficiency.

Material and Methods

(*a*) *Stock*

The experiment was carried out on *Drosophila melanogaster* that were trapped locally in September 1962. The flies were always raised on Burdick's medium at 25°C (Burdick, 1954). Initially ten pairs were put in each of nine wide mouthed bottles. When the flies emerged, the virgin pairs were collected from each bottle and they were mixed. For this 9 random samples of ten pairs each were drawn and put into separate wide mouthed bottles. Mating was allowed for three days, and on the 4th day the parents were removed. When the offspring emerged 10 male and 10 virgin females were taken from each bottle and were pooled, and nine bottles containing a random sample of ten males and ten females were set up. This constituted the foundation stock for the experiment reported here.

(*b*) *Breeding Lines*

The breeding lines used in these experiments were raised in test tubes. For this, 117 males were taken at random. Each of these males was mated to a random sample of 2 females. On the 4th day each female was transferred to a separate test tube where she laid eggs for 3 days. Then the females were removed. When the offspring emerged a random sample of 4 females was taken for measurement.

(*c*) *Characters measured*

Bristle numbers on the 4th and 5th abdominal segments were counted on each fly. After counting the bristle number the wing was removed and mounted on a slide for

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measuring the wing length. This allowed the measurement of bristles and wing on the same fly. The procedures adopted for counting the bristles and measuring the wing length were essentially the same as described before (Taneja and Negi, 1963, 1964).

(d) Analysis

The mathematical model set out in Table 1 was used for the estimation of components of variances and covariances.

Table 1. *Expected Components of Variances and Covariances*

Source	d.f.	M.S. (1)	Cross product (1, 2)	M.S. (2)
Between sires	$(m-1)$	$\sigma^2_{e_1}+k_2\,\sigma^2_{d_1}+k_3\,\sigma^2_{s_1}$	Cov $e_1e_2+k_2$ Cov $d_1d_2+k_3$ Cov s_1s_2	$\sigma^2_{e_2}+k_2\sigma^2_{d_2}+k_3\sigma^2_{s_2}$
Between dams within sires	$\sum_i (n_i-1)$	$\sigma^2_{e_1}+k_1\,\sigma^2_{d_1}$	Cov $e_1e_2+k_1$ Cov d_1d_2	$\sigma^2_{e_2}+k_1\,\sigma^2_{d_2}$
Between full sibs	$\sum_{ij} (p_{ij}-1)$	$\sigma^2_{e_1}$	Cov e_1e_2	$\sigma^2_{e_2}$

m = number of sires.
n_i = number of dams.
p_{ij} = number of offspring in a sire-dam mating.

The sire and dam components of variances and covariances ($\sigma^2_{s_1}$, Cov s_1s_2, $\sigma^2_{d_2}$ Cov d_1d_2 respectively) were then estimated by substituting values of k_1, k_2 and k_3 which were determined according to the procedure already described (Taneja and Negi, 1963).

It is assumed that the sires were randomly mated to a random sample of females. Then the additive genetic variance represented in σ^2_s, the component of variance within sires, σ^2_d, the component of variance within dams, σ^2_e, the variance between full sibs, is 25, 25 and 50% respectively. However, σ^2_d may also include some variance due to dominance if $\sigma^2_d > \sigma^2_s$. In the present analysis σ^2_d was always less than σ^2_s expect in one case where σ^2_d was extremely large, perhaps because of sampling errors.

In view of this σ^2_s and σ^2_d were combined to obtain 50% of the total additive genetic variance (and non-additive genetic, if any) in the population. Now the genetic and environmental parts of the variation can be described as below:

$$\left.\begin{aligned} \text{Genetic Variance V(G)} &= 2\,(\sigma^2_d+\sigma^2_s) \\ \text{Environmental Variance V(E)} &= \sigma^2_e-(\sigma^2_d+\sigma^2_s) \\ \text{Phenotypic Variance V(P)} &= \sigma^2_s+\sigma^2_d+\sigma^2_e\,. \end{aligned}\right\} \qquad (1)$$

The Covariance terms are completely analogous to the variance terms.

RESULTS

Results in Table 2 show means, variances and coefficients of variation of the characters measured.

Table 2. *Means, Variances, Standard Deviations and Coefficients of Variation of bristle number on 4th and 5th segments, 4th and 5th segments combined, and wing length in* Drosophila melanogaster

Source	Mean	Variance	S.D.	Coeff. of variation %
Bristles on 4th segment	22·742	4·907	2·215	9·739
Bristles on 5th segment	23·559	5·563	2·359	10·013
Total Bristles on 4th and 5th segments	46·301	14·461	3·803	8·213
Wing	1·805	0·00255	0·050	2·770

Results of analysis of variance and covariance are presented in Table 3. The variance between sires was significant for bristle number but it was not significant for wing length. The variances between dams within sires were significant for all the characters.

In order to determine the genetic, environmental and phenotypic variances and covariances as set out in equation (1) the sire and dam components of variances and covariances were estimated from Table 3 and are presented in Table 4. These components are multiplied by the appropriate amount shown in the equation to give the partitioning of variances and covariances as shown in Table 5.

Fig. 1 is a graphical representation of Table 5, following Hazel, Baker and Reinmiller (1943) and sets out the genetic and environmental factors causing variation in the observed phenotypic values. The path coefficients represented by straight lines indicate the quantitative importance of each source in causing variation. The direct influence of the cause to the effect is shown by arrows while the relation between each source in causing variation is represented by correlation coefficients. These are shown by curved double headed arrows.

Each path coefficient measures the importance of a given path of influence from cause to effect. Wright (1921) defined the path coefficient as "the ratio of the standard deviation of the effect when all the causes are constant except the one in question, the variability of which is kept unchanged, to the total standard deviation". Each path is therefore calculated by dividing the square root of the variance for a given source by the square root of phenotypic variance from Table 5. As heritability is the ratio of additive genetic variance to the total phenotypic variance, in this case it can be directly calculated by squaring the individual path coefficients. For example, the path coefficient from G_1 to P_1 is

$$\sqrt{\frac{V(G_1)}{V(P_1)}} = \sqrt{\frac{1{\cdot}910}{4{\cdot}913}} = 0{\cdot}623$$

and the heritability for bristle number on the 4th abdominal segment is 0·39.

Table 3. *Analysis of variance and covariance of 4 characters*† *in* Drosophila melanogaster

Source	D. F.	Variance				Covariance					
		I	II	III	IV	I. II	I. III	I. IV	II. III	II. IV	III. IV
Between sires	116	9·0240**	9·5390*	31·3910**	9·7390	6·4130	15·4380	2·4950	15·9530	2·6690	5·1600
Between dams within sires	107	5·3276*	6·7220**	16·2280**	9·3907**	2·0890	7·4160	1·2060	8·7550	−0·2530	0·9530
Progeny	550	3·9582	4·4990	10·5480	5·0800	1·0450	5·0030	0·3660	5·5550	0·5480	0·9140

†I Bristles on the 4th segment
II „ „ „ 5th „
III Total bristles on 4th and 5th segments
IV Wing length

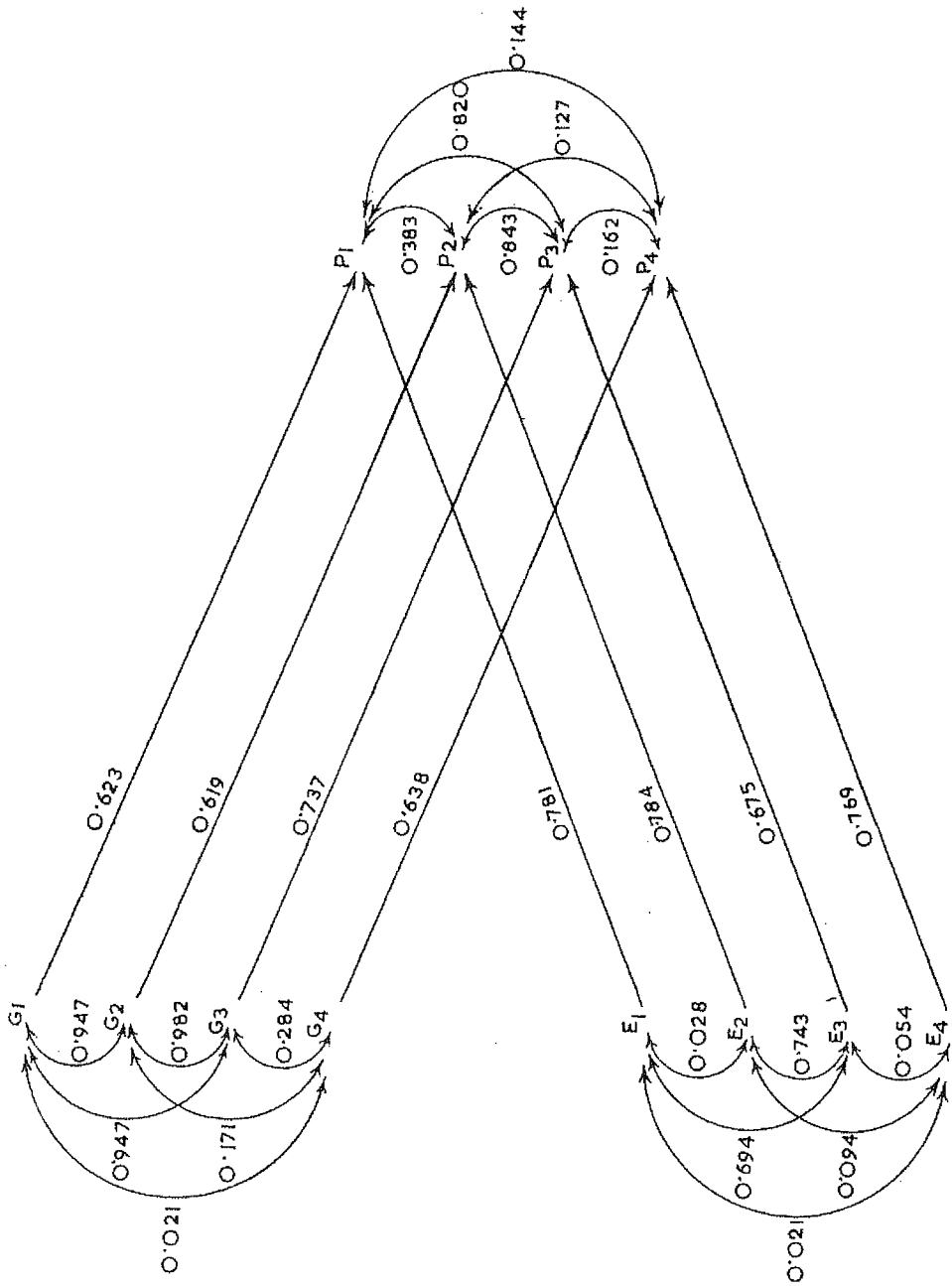

Fig. 1. Path coefficient diagram illustrating the genetic (G), environmental (E) and phenotypic (P) correlations. Suffixes 1, 2, 3 and 4 represent the bristle numbers on 4th segment, 5th segment, 4th and 5th combined and wing length respectively. The path coefficients are represented by straight lines with arrows showing the direct influence of the cause to effect. The correlation coefficients are shown by curved double headed arrows.

Table 4. *Components of Variance and Covariance*

Source	Variance				Covariance					
	I	II	III	IV	I. II	I. III	I. IV	II. III	II. IV	III. IV
Sire	0·547	0·407	2·244	0·105	+0·645	+1·192	+0·188	+1·061	+0·448	+0·641
Dam	0·408	0·662	1·693	1·285	+0·311	+0·719	+0·250	+0·954	−0·238	+0·001
Full sibs (error)	3·958	4·499	10·548	5·080	+1·045	+5·003	+0·366	+5·555	+0·548	+0·914

I Bristles on 4th segment
II „ „ 5th „
III Total bristles on 4th and 5th segments
IV Wing length

Table 5. *Genetic, environmental and phenotypic variances and covariances for the 4 characters* in* Drosophila melanogaster

Source	Variance				Covariance					
	I	II	III	IV	I. II	I. III	I. IV	II. III	II. IV	III. IV
Genetic	+1·910	+2·138	+7·874	+2·600	+1·912	+3·822	+0·876	+4·030	+0·420	+1·284
Environmental	+3·003	+3·430	+6·611	+3·780	+0·089	+3·092	−0·072	+3·540	+0·338	+0·273
Phenotypic	+4·913	+5·568	+14·485	+6·380	+2·001	+6·914	+0·804	+7·570	+0·758	+1·557

*I Bristles on 4th segment
II „ „ 5th „
III Total bristles on 4th and 5th segments
IV Wing length

Figure 1 indicates the following points of interest:

(*a*) *Phenotypic Correlations*

(*i*) There is a significantly positive correlation between the bristle numbers on the 4th and 5th segments.

(*ii*) The correlation between bristle numbers on each of the two segments with wing length is not significant.

(*b*) *Environmental Correlations*

(*i*) There is no significant correlation between bristle numbers on 4th and 5th segments.

(*ii*) There is no significant correlation between wing length and bristle number on each of 4th and 5th abdominal segments.

(*c*) *Genetic Correlations*

(*i*) The positive correlation between bristle number on 4th and 5th segments is very high, approaching unity.

(*ii*) The wing length and bristle number on each of the two segments are positively correlated although the magnitude of this correlation is not as high as that between the two segments.

(*d*) The heritabilities (squares of path coefficients for the characters measured) are as under:

(*i*) Bristle number on 4th segment=0·39

(*ii*) Bristle number on 5th segment=0·38

(*iii*) Bristle number on 4th and 5th segments=0·54

(*iv*) Wing length=0·41

The heritability of 4th and 5th segments combined is higher than the estimates made for each of the segments separately.

DISCUSSION

When the correlations between various traits are calculated on related individuals, the sampling errors decrease as the relationship between them increases. In this study the correlations between various characters measured on the same individual have been obtained, and therefore these values involve relatively more sampling errors which are at present unknown. Nevertheless the general picture presented does give some indication of the pattern of the relationship amongst the characters studied.

The results of this study have shown that the genetic correlation between 4th and 5th segments is very high, almost approaching unity, and the environmental correlation is virtually zero. The high genetic correlation indicates that almost every gene that affects the number of chaetae on the 4th segment also affects the chaeta number on the 5th segment. Reeve and Robertson (1954) similarly recorded very high correlations varying from 0·84 to 1·08 between bristle number on 3rd, 4th, 5th and 6th segments in different stocks of *Drosophila melanogaster*. These authors remarked that high genetic correlation can be interpreted as a measure of the resistance to attempts to create local differentiation among the sternites by selection.

Absence of significant environmental correlation between chaeta numbers on the 4th and 5th segments shows a remarkable independence of these characteristics in relation to environment in spite of their very high genetic association. One would expect that the characters having similar genetic make up would be influenced equally by the environment. Reeve and Robertson (1954) have also reported similar results on their studies in Drosophila. High environmental correlation between each of the 4th and 5th segments with the sum of two segments is obvious because of common factors.

Genetic correlation between chaeta number on each of the 4th and 5th segments with the wing length was found to be 0·393 and 0·171 respectively. These correlations are fairly low when compared to those between bristles on two segments. It is however not clear why the correlation between chaeta number on the 4th segment with the wing length is relatively higher than that between the 5th segment and the wing length. Because of the very high genetic correlation between the two segments, one would expect nearly similar relationship between each of these segments with wing length. Further, since the differences between these two genetic correlations (r=·393, r=·171) cannot be tested statistically for want of information on sampling errors, it is likely these differences have arisen through sampling errors.

The environmental correlation between the chaeta number on each of the two segments and the wing length is nearly zero. It appears that the environmental factors causing variation in these two characters act independently.

Results of this study have shown that selection practised for chaeta number on either of the two segments will be accompanied with almost equal increase in chaeta number on the other segment. The increase in wing length however will be fairly small. Absence of phenotypic correlation between wing length and chaeta number will not permit one to make a precise selection that may subsequently guarantee any correlated response.

The heritability of the sum of the bristles on the 4th and 5th segments is higher than that for each segment. The repeatability is also high (Taneja and Negi, 1963). These peculiarities have often attracted many workers to use the sum of the chaetae on these two segments as a quantitative character instead of the chaetae on a single segment. Estimates of heritability for the characters measured in this study are in agreement with the results reported by other workers (see Falconer 1960, for references).

In conclusion the results of this experiment have shown that the environmental agencies affecting the chaeta in different segments and wing length act independently. The chaeta on the 4th and 5th segments have a very high genetic relationship approaching almost unity.

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SUMMARY

Biometric data on bristle numbers for two segments and wing length of 936 female *Drosophila melanogaster* derived from a wild stock are presented. Heritabilities were about 0·4. The genetic correlation between the two bristle numbers was +·91, the environmental correlation insignificant. The genetic correlations between wing length and the bristle numbers were +·39 and +·17, the environmental correlations again insignificant.

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