

# CORRELATION BETWEEN BRISTLE SYSTEMS IN *DROSOPHILA MELANOGASTER*

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## Summary

The correlation between several bristle systems of *Drosophila melanogaster* was investigated. The changes in sternopleural, second coxal, third coxal, and scutellar bristle numbers were measured in 26 lines selected for increased abdominal bristle number for 46 or 50 generations. The changes in abdominal, second coxal, and scutellar bristle numbers were measured in 16 lines selected with independent culling levels for high or low sternopleural and high or low third coxal bristle numbers for 22 generations.

The changes in these lines indicated positive genetic correlations among abdominal, sternopleural, and second coxal bristle numbers, and among sternopleural and second and third coxal bristle numbers. Abdominal and third coxal bristle numbers were apparently uncorrelated. Scutellar bristle number was positively correlated with abdominal bristle number but its correlation with the other bristle systems was unclear.

Most of the correlated changes were similar on the average to those predicted from base population estimates of genetic parameters, but the realized genetic correlation between second coxals and either abdominals or sternopleurals was in poor agreement with the base population estimate. Genetic correlations between the scores of the characters measured was very different in the different selection lines.

The agreement between estimates of genetic correlations from the base population and those from the selection lines were particularly good considering the number of generations of selection applied.

## I. INTRODUCTION

The mathematical relationships between genetic, phenotypic, and environmental correlations were outlined by Hazel (1943). Since then, this theory has been widely applied in animal and plant breeding, and many estimates of the correlations between various characters are available. Genetic correlations are of primary interest, estimates being used to devise optimum programs in selection for two or more characters, or to predict correlated responses in characters not under selection.

However, estimated genetic correlations have frequently not given reasonable predictions of correlated responses. In individual lines selected for abdominal bristle number in *Drosophila melanogaster* the correlated response in sternopleural bristle number has been quite variable (Mather and Harrison 1949; Rasmuson 1955; Clayton *et al.* 1957). Evidence on the correlation between abdominal and scutellar bristles is also contradictory (Rendel 1963; Young and Sheldon 1965).

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The availability of a large number of selected lines offered valuable material to examine the correlation between different bristle systems. The bristle systems chosen included four systems of microchaetae—abdominals, sternopleurals, second coxals, and third coxals, and one of macrochaetae—scutellars. Scutellar bristle number has been used in canalization studies because of its phenotypic stability. In one experiment, lines were selected for increased abdominal bristle number and the correlated changes in sternopleural, second coxal, third coxal, and scutellar bristle numbers observed. In the other experiment, lines were selected for sternopleural and third coxal bristle number and the correlated changes in abdominal, second coxal, and scutellar bristle numbers measured.

TABLE 1  
EXPERIMENTAL DESIGN, TREATMENT CODE DESIGNATION, AND NUMBER OF  
REPLICATES PER TREATMENT

	Population Size*	Selection Intensity			
		10%	20%	40%	Controls
Code	10	10(10%)†	10(20%)	10(40%)	10(C)
No. of replicates		4	5	4	5
Code	20	20(10%)	20(20%)	20(40%)	20(C)
No. of replicates		2	3	3	3
Code	40	40(10%)	40(20%)	40(40%)	40(C)
No. of replicates		1	2	2	2

\* i.e. pairs of parents.

† Replicates lines within treatments are referred to as, for example, 10(10%)a, 10(10%)b, 10(10%)c, 10(10%)d.

## II. MATERIALS AND METHODS

### (a) The Selection Lines

(i) *Experiment 1.*—These single-trait lines from the Canberra base population were selected for increased abdominal bristle number at intensities (proportion selected) of 10, 20, 40, and 100% (controls), with 10, 20, and 40 pairs of parents per generation. Response in the selected trait during 50 generations was described by Jones, Frankham, and Barker (1968). The same treatment and line codes are used here (Table 1). At generation (G) 46, in addition to the scoring of abdominals, 30 pairs of flies were also scored for the number of sternopleural, second, and third coxal bristles on one side. Scutellar bristle number was scored on between 250 and 1940 pairs of flies at G50.

(ii) *Experiment 2.*—These two-trait lines from the Canberra base population were selected with independent culling for sternopleural and third coxal bristle numbers. Each character was selected at the same intensity, the overall selection intensity being 20%. Each line had 20 pairs of parents for the first 10 generations and 10 pairs thereafter. Selection lines receiving the following treatments were replicated four times:

UU—both characters selected up.

DU—coxals selected down, sternopleurals up.

UD—coxals selected up, sternopleurals down.

DD—both characters selected down.

Twenty pairs of flies were scored for second coxal bristle number (as well as the selected traits) at G20. Selection was suspended after two more generations and the lines maintained as relaxed

lines. Fifty pairs were scored for one abdominal segment after two generations of relaxation, and after five generations of relaxation 92-200 females were scored for scutellar bristle number.

(b) *Methods Used to Compute Realized Genetic Correlations*

To clearly indicate the manner in which a genetic correlation was obtained the terms "realized" and "estimated" genetic correlation, respectively, are used to refer to a genetic correlation estimated from a selection experiment, and to a genetic correlation estimated from base population variance and covariance components.

In single-trait selection the realized genetic correlation between the selected trait ( $x$ ) and the correlated trait ( $y$ ) can be calculated using the formula

$$r_G = (CR_y \cdot h_x \cdot \sigma_x) / (R_x \cdot h_y \cdot \sigma_y),$$

where  $R_x$  is the direct response of trait  $x$ ,  $CR_y$  the correlated response of trait  $y$ ,  $h_x^2$  and  $h_y^2$  the heritabilities, and  $\sigma_x$  and  $\sigma_y$  the phenotypic standard deviations of traits  $x$  and  $y$  (Falconer 1960). Responses were measured as deviations from the mean of all controls.

The average realized genetic correlation over all lines was calculated from the formula:

$$r_G = b_{yx} (h_x \cdot \sigma_x / h_y \cdot \sigma_y),$$

where  $b_{yx}$  is the regression coefficient of line mean of trait  $y$  on line mean of trait  $x$ .

As all combinations of high and low selection for the two traits were carried out in the two-trait selection lines, realized genetic correlations can be estimated from the two-trait selection lines in a manner analogous to that for the single-trait selection lines. Thus the average realized genetic correlation between a selected trait ( $x$ ) and an unselected trait ( $y$ ) was estimated as

$$r_G = \frac{(UU_y + DU_y - UD_y - DD_y) \cdot h_x \cdot \sigma_x}{(UU_x + DU_x - UD_x - DD_x) h_y \sigma_y}$$

The average realized genetic correlation between the two selected traits was estimated from the reduction in response when they were selected in opposite directions. For example, the difference between sternopleurals in treatments UU and DD is due to the direct response plus the correlated response from selection for third coxals. The difference between sternopleurals in treatments DU and UD is due to the direct response minus the correlated response. The genetic correlation can be estimated from the ratio:

$$A = \frac{(UU_x - DD_x - DU_x + UD_x)}{(UU_x - DD_x + DU_x - UD_x)}$$

where the numerator and denominator represent the correlated response of sternopleurals to selection for third coxals and the direct response of sternopleurals respectively. Sheridan (unpublished data) showed that this ratio has the expectation

$$A = \frac{(i_{x+} - i_{x-})(h_x - r_P r_G h_y) + (i_{y+} + i_{y-})(r_G h_y - r_P h_x)}{(i_{x+} + i_{x-})(h_x - r_P r_G h_y) + (i_{y+} - i_{y-})(r_G h_y - r_P h_x)}$$

where  $i_{x+}$ ,  $i_{y+}$  are the selection differentials when  $x$  and  $y$  are selected in the same direction,  $i_{x-}$ ,  $i_{y-}$  the selection differentials when selected in opposite directions, and  $r_P$ ,  $r_G$  the phenotypic and genetic correlations respectively. In the experiments used here, a similar selection intensity was used for each trait and so  $i_{x+} = i_{y+}$ ,  $i_{x-} = i_{y-}$ .

When  $r_P = 0$ ,  $i_{x+} = i_{x-}$  but for  $r_P \neq 0$  this is not the case. When  $r_P = 0$  the expression reduces to

$$A = r_G h_y / h_x.$$

The genetic correlation was estimated in a similar manner from the change in third coxal bristle number.

## III. RESULTS

## (a) Characters in the Base Population

Means and standard deviations of bristle numbers in the base population are shown in the following tabulation:

	Females	Males
Abdominals	21.70 ± 2.02	17.70 ± 1.93
Sternopleurals	9.74 ± 1.04	9.59 ± 1.08
Second coxals	11.39 ± 0.83	11.37 ± 0.85
Third coxals	7.92 ± 0.81	7.72 ± 0.78
Scutellars	4.04	4.01

One segment was scored for abdominals and one side scored for sternopleurals, second, and third coxals. Scutellar bristle number is canalized at four bristles in wild populations of *Drosophila*. Extra scutellars were found on 3.4% of females and 1.1% of males in a base population sample of about 2000 pairs. Flies with three or

TABLE 2  
MEAN BRISTLE NUMBERS OF FEMALES AT G46 IN LINES SELECTED FOR INCREASED ABDOMINAL BRISTLE NUMBER (EXPT. 1)

Line	Abdom- inals	Sterno- pleurals	Second Coxals	Third Coxals	Line	Abdom- inals	Sterno- pleurals	Second Coxals	Third Coxals
10(10%)a	36.87	11.27	11.67	7.77	20(10%)a	42.50	10.63	12.77	8.47
b	47.77	11.97	12.43	7.97	b	38.40	14.97	12.80	7.83
c	32.37	10.00	13.20	8.43	20(20%)a	38.07	10.73	13.03	7.73
d	32.37	13.17	12.70	8.80	b	35.99	11.17	12.87	7.83
10(20%)a	35.93	10.83	12.27	7.83	c	34.63	10.50	11.77	7.87
b	33.23	10.53	13.00	9.90	20(40%)a	36.13	11.80	14.10	10.40
c	28.87	11.07	11.50	8.17	b	29.80	10.20	11.83	7.80
d	33.30	11.47	12.37	8.17	c	33.43	12.80	12.47	7.93
e	31.33	11.27	11.50	7.93	40(10%)	53.62	13.46	14.60	8.18
10(40%)a	28.43	11.83	11.83	7.60	40(20%)a	38.30	11.53	13.07	9.37
b	29.20	9.47	11.20	7.17	b	39.87	12.30	13.93	8.57
d	26.17	10.20	11.53	8.83	40(40%)a	39.00	12.37	13.77	8.10
e	30.93	10.67	12.57	9.07	b	35.23	10.97	12.50	8.50
Controls									
10(C)a	22.77	10.30	11.43	7.87	20(C)a	21.57	9.33	11.73	7.97
b	22.07	9.67	11.70	7.83	b	23.53	9.87	12.00	7.97
c	21.77	8.33	12.30	7.97	c	23.47	10.13	12.13	8.40
d	21.93	9.57	11.33	7.37	40(C)a	22.53	8.63	11.43	7.97
e	22.40	9.60	11.97	7.77					

fewer bristles were very rare in both the base population and the selected lines. Heritabilities and genetic correlations were estimated by several methods (Sheridan *et al.* 1968), and for most characters the estimates varied considerably between methods of estimation. This variation was attributed to a combination of sex linkage and

sampling effects. The following tabulation summarizes what were considered to be the best estimates when averaged over both sexes:

	Heritability	Genetic Correlation		
		Sterno- pleurals	Second Coxals	Third Coxals
Abdominals	0.15	0.19	-0.04	0.08
Sternopleurals	0.19		0.64	0.48
Second coxals	0.20			0.62
Third coxals	0.18			

Heritabilities were similar for most characters, ranging from 15 to 20%. From selection response over several generations, realized heritabilities of 16 (Frankham, Jones, and Barker 1968), 15, and 10% (Sheridan, unpublished data) were obtained

TABLE 3

FEMALE MEAN ABDOMINAL BRISTLE NUMBER, PERCENTAGE OF FEMALES WITH MORE THAN FOUR SCUTELLAR BRISTLES, AND MEAN SCUTELLAR SCORE IN PROBITS RELATIVE TO THE 4-5 THRESHOLD AT G50 IN LINES SELECTED FOR INCREASED ABDOMINAL BRISTLE NUMBER (EXPT. 1)

Line	Abdom- inals	Females with more than 4 Scutellars (%)	Scutellar Probit Score	Line	Abdom- inals	Females with more than 4 Scutellars (%)	Scutellar Probit Score
10(10%)a	38.72	67.64	5.46	20(10%)a	43.68	60.56	5.27
b	47.64	90.37	6.30	b	40.52	12.62	3.86
c	33.57	1.48	2.82	20(20%)a	38.68	20.92	4.19
d	32.55	2.09	2.97	b	36.32	69.63	5.51
10(20%)a	37.48	9.35	3.68	c	34.69	14.34	3.93
b	33.72	0.57	2.47	20(40%)a	37.64	83.14	5.96
c	30.02	4.43	3.29	b	30.04	20.07	4.16
d	33.14	7.95	3.59	c	34.06	5.38	3.39
e	31.32	3.76	3.22	40(10%)	53.52	46.28	4.91
10(40%)a	28.48	10.12	3.72	40(20%)a	40.40	20.36	4.17
b	29.76	4.68	3.32	b	40.74	18.83	4.12
d	27.08	2.50	3.04	40(40%)a	39.34	23.30	4.27
e	32.00	39.50	4.73	b	36.93	18.81	4.12

for abdominal, sternopleural, and third coxal bristle numbers respectively. These values were used in calculating realized genetic correlations. Estimated genetic correlations between the characters were mostly positive. There were low and non-significant genetic correlations between abdominals and either set of coxals (-0.04 with second and 0.08 with third). Sternopleurals and second and third coxals were fairly highly correlated ( $r_G$  between 0.48 and 0.64), while the genetic correlation between sternopleurals and abdominals was 0.19.

(b) *Correlated Responses to Selection*

The means of the females for each bristle system in the experiment 1 lines are listed in Tables 2 and 3. The responses in males were proportionally similar to those

in females so they have not been included. However, all realized genetic correlations were computed from the changes in both sexes. Means of the two selected traits, and second coxal, abdominal, and scutellar bristle number are given in Tables 4 and 5 for the experiment 2 lines.

(i) *Abdominals-Sternopleurals*.—Most lines increased in sternopleurals in experiment 1 (Table 2). The greatest increase in sternopleurals was 5.6 bristles (5.4 standard deviations) above the mean of the controls in either sex in 20(10%)b. Its mean abdominal bristle number was 15.8 bristles (7.8 standard deviations) above the controls. Realized genetic correlations of individual lines ranged from 0.04 in 10(40%)b to 0.7 in 10(40%)a, 10(10%)d, and 20(10%)b. These estimates are not very accurate as only 30 pairs were scored. The average realized genetic correlation (over both sexes) was  $0.24 \pm 0.04$ .

TABLE 4

MEAN OF MALE AND FEMALE BRISTLE NUMBERS OF INDIVIDUAL LINES SELECTED FOR THIRD COXAL AND STERNOPLURAL BRISTLE NUMBERS (EXPT. 2)

Line	Third Coxals	Sterno-pleurals	Second Coxals	Abdom-inals	Line	Third Coxals	Sterno-pleurals	Second Coxals	Abdom-inals
UU 1	9.10	15.45	13.72	21.95	UD 1	8.45	8.08	12.52	18.06
2	8.82	13.65	13.05	20.04	2	8.10	8.12	11.35	20.37
3	11.18	13.85	14.15	21.49	3	8.42	7.50	11.60	22.30
4	8.68	11.90	13.02	20.87	4	8.40	8.08	11.32	18.45
Mean	9.44	13.71	13.48	21.09	Mean	8.34	7.94	11.70	19.80
DU 1	6.78	10.40	10.85	21.27	DD 1	6.72	7.25	10.65	19.80
2	7.58	12.65	12.72	21.16	2	6.88	7.88	11.15	18.77
3	7.28	12.70	11.92	21.29	3	6.98	7.82	11.20	19.95
4	7.10	10.82	11.90	21.28	4	6.18	6.12	9.45	18.97
Mean	7.18	11.64	11.85	21.25	Mean	6.69	7.27	10.61	19.37

In the experiment 2 lines abdominal and sternopleural bristle number generally changed in the same direction, the exception being the rise in abdominals in UD3. The average realized genetic correlation between sternopleurals and abdominals was 0.13.

(ii) *Abdominals-Second Coxals*.—Second coxals increased in most lines but this trend was less consistent than that for sternopleural bristle number. The tendency for second coxal bristle number to increase was more consistent in larger populations. The average realized genetic correlation over all lines calculated from the regression of second coxal on abdominal bristle number was  $0.17 \pm 0.04$ .

Estimates of realized genetic correlations in individual lines ranged from  $-0.18$  for 10(40%)b to 0.50 for 20(40%)a. The 40-pair lines gave estimates between 0.12 for 40(40%)b and 0.32 for 40(40%)a.

(iii) *Abdominals-Third Coxals*.—Third coxal bristle number increased appreciably in only a few experiment 1 lines [20(40%)a, 10(20%)b, and 40(20%)a] and the average realized genetic correlation was effectively zero ( $0.03 \pm 0.04$ ). Estimates for individual lines ranged from  $-0.3$  for 10(40%)b to 0.5 for 10(20%)b and 20(40%)a. Larger populations did not give a more consistent trend of correlated response in third coxal bristle number than smaller populations.

The average realized genetic correlation between abdominals and third coxals for the experiment 2 lines was 0.02.

(iv) *Abdominals-Scutellars*.—Latter (1964) showed that scutellar bristle number can be treated as a quantitative character if the appropriate transformation is made. As the position of extra scutellar bristles was not recorded, it is necessary to use Latter's univariate model. This model assumes a 1:1 correspondence between bristle number and precisely defined intervals on the underlying scale. The population mean in phenotypic standard deviations on the underlying scale, relative to the position of the 4-5 bristle number threshold can be estimated from a table of probit values as a direct function of the percentage of flies having extra bristles. These values are given in Table 3. The regression coefficient of probit value on abdominal bristle number was  $0.10 \pm 0.03$  for females and  $0.13 \pm 0.03$  for males.

TABLE 5  
PERCENTAGE OF FEMALES WITH MORE THAN FOUR SCUTELLAR  
BRISTLES IN LINES SELECTED FOR THIRD COXAL AND STERNO-  
PLEURAL BRISTLE NUMBERS (EXPT. 2)

Line	No. Scored	Females with more than 4 Scutellars (%)	Line	No. Scored	Females with more than 4 Scutellars (%)
UU 1	92	6.5	UD 1	157	34.4
2	143	2.8	2	136	5.9
3	131	6.1	3	175	0.0
4	188	6.4	4	200	1.0
DU 1	88	1.1	DD 1	106	0.0
2	171	0.0	2	141	2.1
3	117	1.7	3	150	0.0
4	200	0.5	4	180	0.0

The average realized genetic correlation, obtained by multiplying the regression coefficient by the phenotypic standard deviation for abdominals was  $0.23 \pm 0.05$  (assuming that the heritability of abdominals and of scutellar probit score were similar as suggested by Latter 1964). However, the regression coefficient was biased upwards by several of the lower lines which did not increase in scutellars. An alternative estimate can be obtained from the average increases in scutellar probit score and abdominal bristle number (in standard deviations). This was 0.13 for females and 0.14 for males. Realized genetic correlations for individual lines ranged from -0.13 in 10(20%)b to 0.46 in 20(40%)a.

(v) *Sternopleurals-Second Coxals*.—The average realized genetic correlation between sternopleurals and second coxals in the experiment 2 lines was 0.23.

(vi) *Sternopleurals-Third Coxals*.—Estimates of the average realized genetic correlation obtained from changes in sternopleurals and third coxals, respectively, were 0.41 and 0.26 (experiment 2 lines).

(vii) *Second Coxals-Third Coxals*.—The average realized genetic correlation between second and third coxals in the experiment 2 lines was 0.53.

(viii) *Sternopleurals-Scutellars and Third Coxals-Scutellars*.—Changes in scutellars in the experiment 2 lines were small (with the exception of UD1), so no attempt was made to estimate realized genetic correlations. There was a tendency for scutellars to increase in the UU lines.

#### IV. DISCUSSION

Table 6 is a summary of estimated genetic correlations and average realized genetic correlations for the various character combinations. Different estimates of genetic parameters in the base population varied considerably and realized genetic correlations varied widely between lines so comparisons of estimated and average realized genetic correlations must be treated with some caution. Realized and estimated genetic correlations for abdominals–sternopleurals (0.24 and 0.13 *v.* 0.19), abdominals–third coxals (0.02 and 0.03 *v.* 0.08) and second coxals–third coxals (0.53 *v.* 0.62) were quite similar. Those for sternopleurals–third coxals (0.41 and 0.26 *v.* 0.48) were not so close. Genetic correlation estimates for abdominals–second coxals (0.17 *v.* –0.04) and sternopleurals–second coxals (0.24 *v.* 0.64) showed poor agreement. It is not clear why second coxals were involved in both cases of poor agreement between estimated and realized genetic correlations. There were few classes for this character so base population estimates of genetic parameters may have been inaccurate (Sheridan *et al.* 1968).

TABLE 6  
SUMMARY OF ESTIMATED AND AVERAGE REALIZED GENETIC CORRELATIONS  
FOR THE VARIOUS CHARACTER COMBINATIONS (SEXES COMBINED)

Character Combination	Estimated $r_G$	Average Realized $r_G$	
		Expt. 1*	Expt. 2†
Abdominals–sternopleurals	0.19	0.24	0.13
Abdominals–second coxals	–0.04	0.17	
Abdominals–third coxals	0.08	0.03	0.02
Abdominals–scutellars		0.23	
Sternopleurals–second coxals	0.64		0.23
Sternopleurals–third coxals	0.48	0.24‡	0.33
Second coxals–third coxals	0.62		0.53

\* Single-trait abdominal bristle selection lines.

† Two-trait lines selected for sternopleural and third coxal bristle numbers.

‡ From single-trait selection lines of Sheridan (unpublished data).

Realized genetic correlations of individual lines varied widely for single-trait lines (they could not be estimated in the individual two-trait selection lines). For abdominals–sternopleurals they ranged from 0.04 to 0.70, for abdominals–second coxals from –0.18 to 0.54, for abdominals–third coxals from –0.3 to 0.5, and for abdominals–scutellars from –0.13 to 0.46. Realized genetic correlations for abdominals–sternopleurals, abdominals–second coxals, and abdominals–scutellars showed less variation and were closer to the average in the 40-pair lines than in the

10-pair lines. This indicates the importance of sampling effects on correlated responses in small populations. The results indicate that the prediction of correlated responses in any individual line is unlikely to be very precise.

Realized genetic correlations from single-trait and two-trait selection lines were in good agreement, being 0.24 and 0.13 respectively for abdominals–sternopleurals, and 0.03 and 0.02 for abdominals–third coxals. Sheridan (unpublished data) obtained an average realized genetic correlation of 0.24 between sternopleurals and third coxals from changes in single-trait selection lines from the Canberra population. This shows reasonable agreement with the estimate of 0.33 from the two-trait selection lines. However, there was large variation among individual single-trait lines, realized genetic correlation estimates ranging from –0.24 to 1.02.

Clayton *et al.* (1957) found that the correlated change in sternopleurals in abdominal bristle selection lines varied widely. They pointed out that genetic drift will be more important for the correlated trait as less change is expected. They and Mather and Harrison (1949) found that the correlated responses were positive in high lines but Rasmuson (1955) found no consistent change.

Changes in second coxal bristle number in our abdominal selection lines were of a similar magnitude to those found by Mather and Harrison (1949) for the sum of second and third coxal bristle numbers. In both their experiments and ours there were large differences between lines.

The formulae of Hazel (1943) were developed from considerations of components of variance and covariance. These components can be expressed in terms of gene frequency and the mode of gene action (Mode and Robinson 1955). Bohren, Hill, and Robertson (1966) showed that the genetic correlation is very sensitive to changes in gene frequency and estimates of genetic correlation should predict changes in unselected traits for only a few generations. As gene frequency changes would arise from random drift as well as selection, wide differences in correlated responses in different lines are not surprising. Estimates of genetic correlation from the base population would predict only the average change of the unselected trait over a number of lines. The average changes in unselected traits were of the order expected for most of the traits. As we studied the change after a long period of time, base population estimates of genetic correlation are unlikely to predict this change with much precision. In fact, the agreement between estimated and realized genetic correlations was remarkably good after so many generations of selection.

To test the usefulness of estimates of genetic correlation to predict changes in unselected traits the following is needed:

- (1) Accurate estimates of genetic parameters in the base population.
- (2) Measurement of changes in the correlated trait at frequent intervals.
- (3) A large number of replicate lines.

A feature of the correlated responses was the spectacular increase in scutellar bristle number in some of our lines. For example, 10(10%)b and 20(40%)a had 90.4 and 83.1% of the females with more than four bristles. Rendel (1963) found that a low positive genetic correlation had developed between abdominal and scutellar bristle numbers in lines selected for high or low abdominal bristle number. Young and

Sheldon (1965) found little change in scutellar bristles in lines selected for high or low abdominal bristle number. However, their results were based on only four lines, and the response in the selected trait was fairly small. Scutellars increased in most of our lines, particularly those with large populations, so there appears to be a strong positive correlation between the two bristle systems.

Rendel (1963) and Young and Sheldon (1965) discussed the correlation in terms of changes in total bristle resources and in the distribution of resources to the particular systems. Genes may affect the amount of material available to several systems and so control total resources or they may affect the distribution of this material to particular systems. A change in total resources generates a positive correlation while a change in the distribution of resources results in a negative correlation. The relative importance of these factors determines the observed correlation. Rendel (1963) found that selection for scutellar bristle number altered both the total resources and distribution to the particular system.

TABLE 7

CHANGE IN ABDOMINAL BRISTLE NUMBER IN PHENOTYPIC STANDARD DEVIATIONS AND SUM OF CHANGES IN STANDARD DEVIATIONS OF STERNOPLEURAL AND SECOND AND THIRD COXAL BRISTLE NUMBERS AND SCUTELLAR PROBIT SCORE (EXPT. 1)

Line	Change in Abdominal Bristle No.*	Sum of Changes in Other Characters	Line	Change in Abdominal Bristle No.*	Sum of Changes in Other Characters
10(10%)a	7.10	3.90	20(10%)a	9.89	5.28
b	12.50	6.53	b	7.86	7.29
c	4.88	2.69	20(20%)a	7.70	3.70
d	4.88	5.75	b	6.59	5.37
10(20%)a	6.64	2.49	c	5.99	1.88
b	5.30	4.43	20(40%)a	6.74	11.08
c	3.14	1.83	b	3.60	1.80
d	5.34	3.56	c	5.40	4.46
e	4.36	1.66	40(10%)	15.40	9.48
10(40%)a	2.92	2.68	40(20%)a	7.81	6.52
b	3.31	-1.27	b	8.59	7.26
d	1.81	1.60	40(40%)a	8.16	6.70
e	4.16	5.29	b	6.29	4.17

\* Selected trait.

Total bristle resources of the lines can be estimated by summing the change in phenotypic standard deviations for each character. These are shown in Table 7 (sexes combined) for the experiment 1 lines. The change was measured as a deviation from the mean of the controls. As insufficient individuals were scored for scutellars in the controls, scutellars were measured as deviations from the base population mean. Selection altered total bristle resources in all lines. This included an increase in the sum of the correlated traits in all lines except 10(40%)b. As the correlation coefficients with other bristle systems were generally well below unity, large changes in distribution of resources occurred.

In experiment 2, selection of sternopleurals and third coxals in the same direction altered total resources. Thus abdominal bristle number, second coxal bristle number, and to a small extent scutellar bristle number have changed in the direction of selection. Selection in opposite directions caused little change in second coxals but abdominals changed in the same direction as sternopleurals. Changes in scutellars were inconsistent.

Correlated changes in unselected traits may be due to linkage or to pleiotropy. The effects of linkage are expected to be temporary while pleiotropy should cause more consistent and permanent changes. However, Hedrick and Comstock (1968) showed that a fairly consistent change in gene frequency of an allele with little or no effect on the selected trait could occur as a result of linkage. However, their selected lines were derived from crosses between two inbred lines. Linkage disequilibrium would be greater in such a population than in lines from an outbred population as used in experiments reported here. The average changes of the correlated trait indicate a pleiotropic effect of genes affecting the different bristle systems. Linkage would contribute to the variation between lines but its effect was not separable from that of genetic drift.

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