

Two-trait Selection and the Genetic Correlation

I. Prediction of Responses in Single-trait and in Two-trait Selection

A. K. Sheridan^{A,B} and J. S. F. Barker^A

^A Department of Animal Husbandry, University of Sydney, Sydney, N.S.W. 2006.

^B Present address: Poultry Research Station, Seven Hills, N.S.W. 2147.

Abstract

Selection using independent culling levels (20% overall selection intensity) was done for the four combinations of high or low third coxal bristle number with high or low sternopleural bristle number in *Drosophila melanogaster*. Single-trait lines from the base population were selected at 20% selection intensity for 10 generations for high or low bristle number. Realized heritabilities and genetic correlations were estimated after 10 and 22 generations of selection in the two-trait lines, and also from the single-trait lines. There was considerable variation among replicate lines within treatments in selection responses, and in realized heritabilities and genetic correlations. Although average estimates of the realized parameters were all less than those made from a diallel analysis of the base population, the average base population genetic correlation and the average realized genetic correlations from single-trait and two-trait selection lines were reasonably similar. Predicted selection responses in both single-trait and two-trait lines using genetic parameters derived from a diallel analysis of the base population were greater than average realized responses. However, predicted selection responses in the two-trait lines using realized genetic parameters from the single-trait lines were in reasonable agreement with average realized responses.

Introduction

The results to be discussed in this paper come from an experiment where simultaneous selection for two traits using independent culling levels was done for 22 generations. The basic aim was to investigate the effect of such two-trait selection on the genetic correlation between the traits, and this aspect is taken up in the second paper in this series (Sheridan and Barker 1974). Here we wish to use the selection results for comparison of predicted and realized responses.

In order to predict responses to two-trait selection it is necessary to take into account the selection intensities, heritabilities and phenotypic variances of the selected traits, the phenotypic and genetic correlations between them, and the number of generations over which selection is to be conducted. When two traits are being selected with equal selection intensities using independent culling levels, the following formula (derived from Young and Weiler 1960) may be used to predict the expected genetic gain per generation in one of the traits:

$$\Delta G_x = [(i_r \sigma_x)/(1 + r_p)](h_x^2 + r_G h_x h_y), \quad (1)$$

where x and y = the two selected traits,

ΔG_x = genetic gain per generation for trait x ,

σ_x = phenotypic standard deviation of trait x ,

r_G = genetic correlation between the selected traits,

r_P = phenotypic correlation between the selected traits,

h_x, h_y = square roots of the heritabilities of traits x and y respectively, and
 i_r = predicted selection differential for trait x in standard units, which is dependent upon the phenotypic correlation, as well as the proportion selected. This value can be obtained from Young and Weiler (1960) and Williams and Weiler (1964).

For the particular case where equal selection intensities are applied to each trait, we have found that i_r is given approximately by $i_r = i_0[(1+r_p/4)(1+r_p)]^{\frac{1}{2}}$, where i_0 is the expected selection differential for trait x in standard units when $r_p = 0$, and depends only on the proportion selected.

On substitution of σ_y for σ_x and h_y^2 for h_x^2 , equation (1) predicts the expected genetic gain per generation in trait y . If r_p and r_G were zero, equation (1) reduces to that used to predict the response to single-trait selection.

The presence of a positive phenotypic correlation between the selected traits will increase the predicted selection differential. Although an increase in the phenotypic correlation between the selected traits can be obtained by generating a positive environmental correlation through keeping the experimental animals under a range of environments, the resulting increases in the selection intensities and phenotypic variances of the selected traits would be more than countered by a reduction in their realized heritabilities.

In the experiment reported here, *Drosophila melanogaster* populations were selected for 22 generations using independent culling levels for the four combinations of high or low third coxal bristle number with high or low sternopleural bristle number. Single-trait selection was also done for both these traits in both directions for 10 generations. As estimates of heritability, phenotypic variances and the genetic and phenotypic correlations have been obtained from variance-covariance analyses of the base population by Sheridan *et al.* (1968), it is possible to compare predicted and realized single-trait and two-trait selection responses.

Experimental Methods

The Canberra strain of *D. melanogaster* (Latter 1964) was used. This stock originated from more than 100 inseminated females captured in Canberra in the summer of 1959. Subsequently it was maintained as a large laboratory stock (approximately 500 pairs per generation) by Dr B. D. H. Latter. Since March 1964 a sample of this stock has been maintained in our laboratory as a cage population averaging 3000–4000 adults. This population has been used in other selection experiments, and considerable genetic variability has been demonstrated (Sheridan *et al.* 1968).

The traits selected were third coxal and sternopleural bristle numbers on the right side only. Four replicates of each of the following treatments were set up:

UU Both traits selected upwards	U— Coxals selected upwards
DD Both traits selected downwards	D— Coxals selected downwards
UD Coxals selected upwards, sternopleurals downwards	—U Sternopleurals selected upwards
DU Coxals selected downwards, sternopleurals upwards	—D Sternopleurals selected downwards
	C Unselected control

The selection lines were maintained for 10 generations at a population size of 20 pairs of parents with 20% selection intensity. The two-trait lines were selected using independent culling levels. Selection was done on a within-bottle basis, selecting 5 out of 25 for each sex. As the closest approximation to equal selection intensities for each trait, 11 of 25 were selected on one trait, then 5 of 11 on the other. The trait selected first was alternated for the two sexes in each bottle, and from each bottle to the next within a line. Unselected controls were set up each generation with 20 pairs chosen at random. At

generation 10 the single-trait lines and the control lines were terminated. The two-trait lines were maintained to generation 22 at half the previous population size (i.e. 10 pairs of parents), but at the same selection intensity.

To initiate the lines, an egg sample was taken by placing five bottles (5-oz cream jars) in the population cage for 24 h. Forty pairs of progeny were collected as virgins from each bottle. Using males and females from different egg-sampling bottles, 10 bottles were set up, each with 20 pairs. These flies were transferred to fresh bottles every 24 h for 6 days. Virgin progeny were collected from each of these 10 mating groups. Each control line was initiated with two pairs of flies from each mating group. Each selection line was initiated with four sets of 25 males and four of 25 females, each of the eight sets for any one selection line being taken from different mating groups. Within each set, five flies were selected. The selected flies then were bulked and randomly assigned in lots of five pairs to new bottles to produce the next generation. In subsequent generations selection was continued on a within-bottle basis. The five pairs of parents placed in each bottle normally were removed on the third day after mating. In a few lines showing reduced reproductive fitness in later generations, parents were left for longer periods. The lines were maintained on a dead yeast fortified medium (medium F of Claringbold and Barker 1961) at $25 \pm 0.5^\circ\text{C}$, 65–70% relative humidity and alternating 12-h periods of light and dark.

Calculations

Means and standard deviations of both traits were calculated for each generation of each line. As standard deviations tended to change in the same direction as the means (32 out of 48 regressions of standard deviation on mean bristle number significantly different from zero, $P < 0.05$), consideration was given to the problem of scale. For many of these regressions the coefficient was significantly different from the value expected (standard deviation \div mean) if variance in log units was constant. Nevertheless, a log transformation seemed likely to be the most appropriate. All calculations of responses and realized genetic correlations therefore were done on both the arithmetic and logarithmic scales. As the realized genetic correlations were essentially identical on the two scales, all results are presented on the arithmetic scale.

For the single-trait lines, direct and correlated selection responses were estimated by linear regression of mean bristle number (averaged over sexes) on generation number. Realized heritabilities were calculated for the single-trait lines by linear regression of mean bristle number on cumulative selection differential (both averaged over sexes). Realized genetic correlations were calculated for the single-trait lines using the formula (Falconer 1960):

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

where

C_y = correlated response in trait y to selection for trait x ,

R_x = direct response in trait x ,

and other symbols are as previously defined. Values of σ_x and σ_y were averaged over generations. In estimating r_G for any one replicate line the realized heritability estimated from that line was used for the selected trait. For the unselected trait, the mean realized heritability from the single-trait lines where it was the selected trait, and being selected for in the same direction, was used. Approximate standard errors of realized genetic correlation estimates were calculated using the following formula (J. W. James, personal communication):

$$\sigma_{r_G} = r_G \left[\frac{V(C_y)}{C_y^2} + \frac{V(R_x)}{R_x^2} + \frac{V(h_x^2)}{(2h_x^2)^2} + \frac{V(h_y^2)}{(2h_y^2)^2} + \frac{1}{2f_x} + \frac{1}{2f_y} \right]^{\frac{1}{2}},$$

where

σ_{r_G} = standard error of r_G ,

$V(C_y), V(R_x)$,

$V(h_x^2), V(h_y^2)$ = variances of C_y, R_x, h_x^2 and h_y^2 respectively (i.e. variances of regression coefficients),

h_x^2, h_y^2 = realized heritabilities for traits x and y respectively,

f_x, f_y = numbers of degrees of freedom for the estimate of the standard deviation for traits x and y respectively (pooled within bottles within generations),

and other symbols are as previously defined. It should be noted that the formula will give an underestimate of the standard error, as no allowance is made for drift variance.

Average realized heritabilities and genetic correlations over replicates, over up and down selection, or over selected traits (r_G only) were calculated as arithmetic means of individual replicate estimates. The standard errors attached to these averages were calculated from the variance of the replicate estimates that contributed to each mean.

Bohren *et al.* (1966) have shown that the genetic covariance can change rapidly under selection, so that prediction of correlated responses or calculation of realized correlations is likely to be valid only over a small number of generations. Therefore, realized heritabilities and genetic correlations were calculated for the data of generations 0–5 only, as well as for generations 0–10. Only the latter estimates are given here, as there were no significant differences between the two sets of estimates, and the standard errors of average realized genetic correlations were lower for those estimated over generations 0–10.

At generation 21 crosses were made between the two-trait selection lines, both within and between selection treatments. Within any one treatment all possible crosses were made. It was necessary to restrict the number of between-treatment crosses, all possible crosses being made 'within replicates'. (As replicates were nested within treatments, this procedure was simply a means of reducing the number of crosses from 96 to 24.) Reciprocal crosses were made, thus doubling the number of matings. Each mating consisted of 10 males and 10 females, the normal mating procedure being adopted (i.e. five pairs per bottle). From each mating 50 male and 50 female offspring were scored for both coxals and sternopleurals, equal numbers being taken from each bottle.

An estimate of the sex-linkage component of the selection responses was obtained from the comparison of reciprocal crosses between the various two-trait selection treatments. The following formula was used: sex linkage = $(M_{yx} - M_{xy}) / (P_x - P_y)$, where P_x and P_y are the mean bristle numbers of males in parental lines, with $P_x > P_y$, M_{yx} is the mean of male progeny from the cross of P_y males with P_x females, and M_{xy} is the corresponding mean for the reciprocal cross.

Results

Control Lines

On the average, these lines showed a small decrease in both traits over the 10 generations. The regression coefficient of mean bristle number on generation number was significantly different from zero ($P < 0.01$) for coxals in one line and for sternopleurals in three lines. However, the total decline in bristle numbers, averaged over the four control lines, was very small, being 0.13 coxal bristles (0.16 standard

deviations) and 0.23 sternopleural bristles (0.22 standard deviations). Selection line responses were not corrected for these changes before calculation of realized genetic parameters.

Single-trait Selection Lines

Selection responses for coxal selection lines are shown in Figure 1 and for sternopleural selection lines in Figure 2. Estimates of realized heritabilities and genetic correlations obtained from these lines are given in Tables 1 and 2 respectively.

Table 1. Realized heritabilities (%) for coxal and sternopleural bristle numbers estimated from generations 0-10 of the single-trait selection lines

Replicate	Coxals		Sternopleurals	
	U—	D—	—U	—D
1	7.6±0.6	16.8±1.4	11.7±0.6	20.6±0.9
2	6.4±0.7	7.8±1.1	19.8±1.7	13.0±0.7
3	12.1±1.1	7.9±1.8	15.1±1.0	12.9±1.0
4	8.7±0.9	7.2±1.2	14.8±1.0	10.2±1.2
Average values	8.7±1.2	9.9±2.3	15.4±1.7	14.2±2.2
	9.3±1.3		14.8±1.4	

Table 2. Realized genetic correlations between coxal and sternopleural bristle numbers estimated from generations 0-10 of the single-trait selection lines

Replicate	Realized genetic correlation for treatment:			
	U—	D—	—U	—D
1	0·12±0·05	0·20±0·09	-0·12±0·06	0·10±0·05
2	0·27±0·08	0·19±0·16	0·57±0·09	0·35±0·09
3	0·13±0·05	1·07±0·38	0·27±0·06	-0·26±0·10
4	-0·12±0·14	0·34±0·10	0·37±0·08	0·36±0·13
Average values	0·10±0·08	0·45±0·21	0·27±0·14	0·14±0·15
	0·28±0·11		0·20±0·10	
	0·24±0·08			

Estimates of realized heritabilities and genetic correlations varied widely between lines, but average values within selection treatments may be taken as the best estimates relevant to the base population. Realized heritabilities for up and down coxal selection and for up and down sternopleural selection were not significantly different, and average realized heritabilities were $9.3 \pm 1.3\%$ for coxals and $14.8 \pm 1.4\%$ for sternopleurals. Average heritability estimates from a diallel analysis of the base population were 17.3% for third coxal bristle number and 18.3% for sternopleural bristle number (Sheridan *et al.* 1968).

Realized genetic correlations were not significantly different for up and down coxal selection, for up and down sternopleural selection, and for coxal and sternopleural selection. The average realized genetic correlation was 0.24 ± 0.08 , whereas the average estimate in the base population was 0.48 (Sheridan *et al.* 1968).

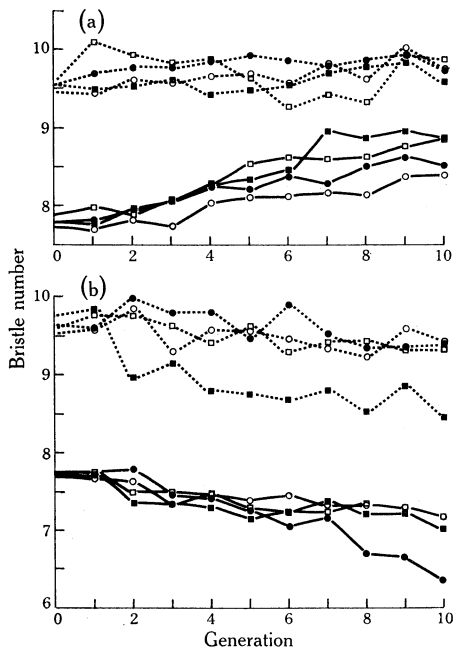


Fig. 1. Selection responses for coxal bristle number (—) and correlated responses for sternopleural bristle number (---) in single-trait lines in which coxals were selected upwards (a; treatment U—) or downwards (b; treatment D—). ●, ○, ■, □: replicates 1, 2, 3 and 4 respectively.

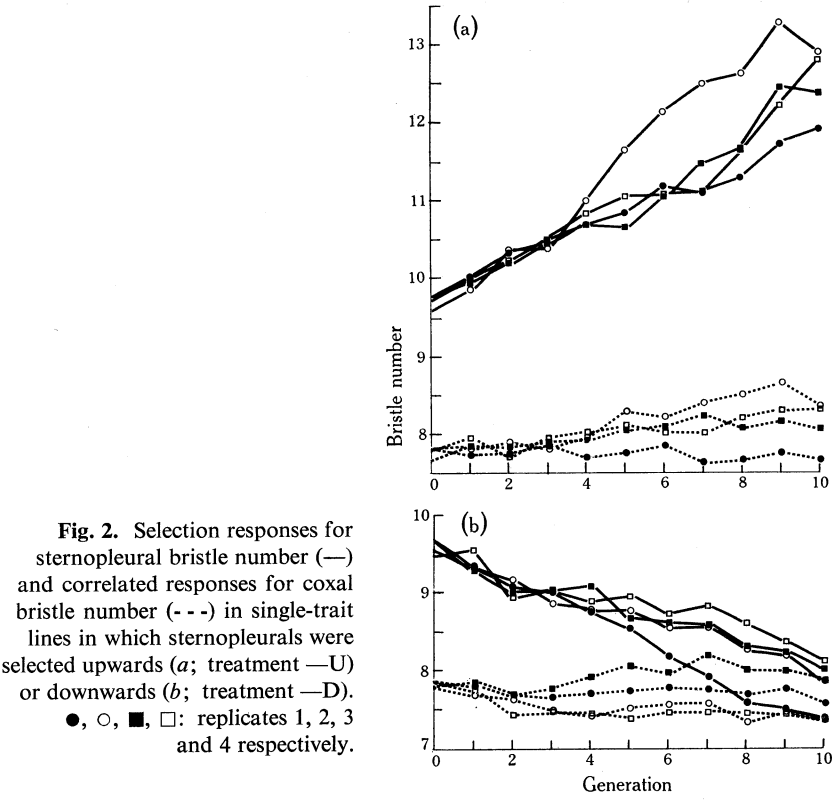


Fig. 2. Selection responses for sternopleural bristle number (—) and correlated responses for coxal bristle number (---) in single-trait lines in which sternopleurals were selected upwards (a; treatment —U) or downwards (b; treatment —D). ●, ○, ■, □: replicates 1, 2, 3 and 4 respectively.

Table 3 lists the comparison between expected and mean realized selection responses for coxal and sternopleural bristle numbers over 10 generations. The expected responses were calculated using the base population parameters of Sheridan *et al.* (1968). There was enormous variability in selection responses between individual lines, with sternopleural selection averaging about 90% and coxal selection about 50% of the predicted response.

Table 3. Expected and realized selection responses for coxal and sternopleural bristle number in the single-trait selection lines over 10 generations

Selection treatment	Expected response	Mean realized response	Range
Coxals selected			
U—	1.82	0.88 ± 0.10	0.68–1.10
D—	1.82	0.88 ± 0.20	0.58–1.46
Mean	1.82	0.88 ± 0.11	
Sternopleurals selected			
—U	2.58	2.81 ± 0.25	2.18–3.32
—D	2.58	1.76 ± 0.17	1.36–2.19
Mean	2.58	2.29 ± 0.15	

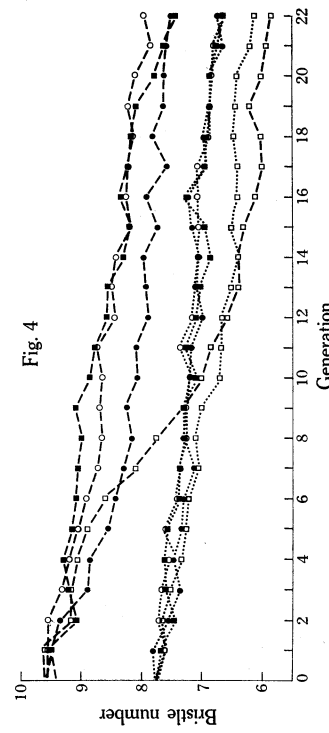
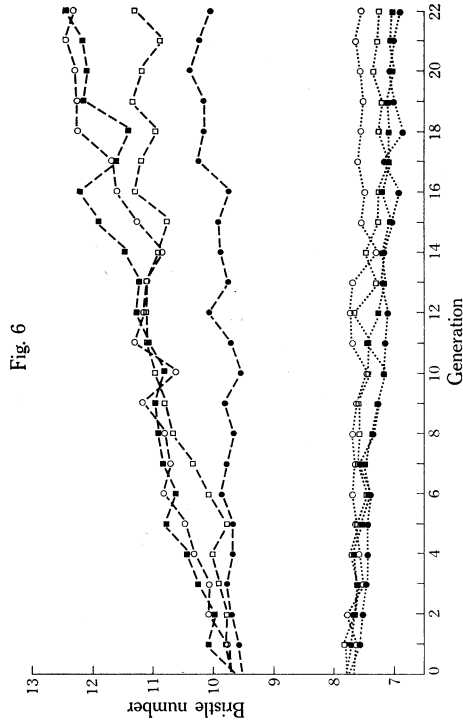
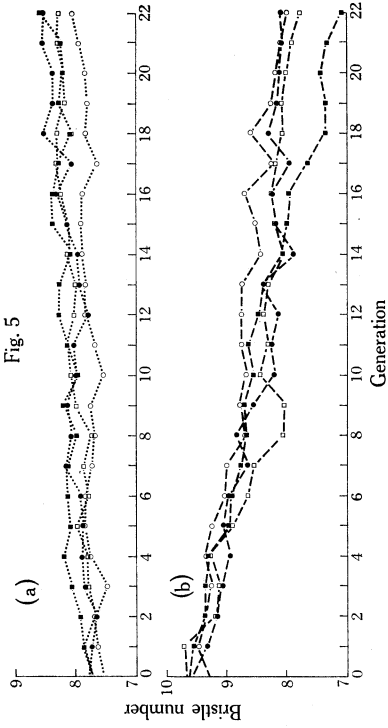
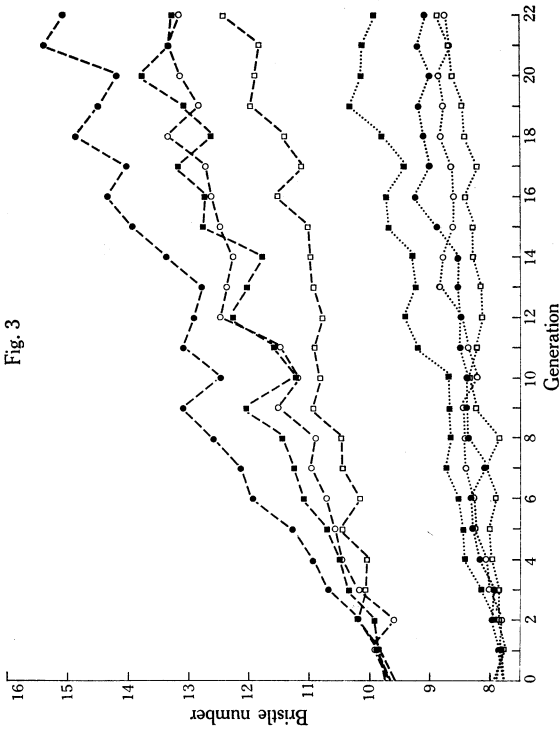
Cumulative selection differentials were calculated for the selected trait over 10 generations. There was no consistent relationship between cumulative selection differentials and either realized heritabilities or realized genetic correlations. Cumulative selection differentials were larger for upward selection, due to the direct relationship between means and standard deviations. This effect was more pronounced in the coxal selection lines.

Two-trait Selection Lines

The responses for each replicate of selection treatments UU, DD, UD and DU are shown in Figs 3–6 respectively. There was considerable variation among replicates within each treatment, the most extreme example being replicate 4 of treatment DD (Fig. 4). In general, cumulative selection differentials to generation 22 for both traits were of similar magnitude for replicates within each treatment. The average observed standardized selection differentials for each trait in each two-trait selection treatment were as follows:

	Coxals	Sternopleurals
UU	0.86	0.89
DD	0.78	0.83
UD	0.79	0.80
DU	0.76	0.82

These values agree closely with the predicted selection differentials (i_r) of 0.88 for the UU and DD treatments and 0.80 for the UD and DU treatments. Therefore variation among replicates in selection response was largely the result of sampling additive genetic variability at the initiation of each line and in each generation during selection.



Figs 3-6. Selection responses for coxal (---) and sternopleural (----) bristle numbers in the two-trait treatments UU (Fig. 3), DD (Fig. 4), UD (Figs 5a, 5b) and DU (Fig. 6). ●, ○, ■, □: replicates 1, 2, 3 and 4 respectively.

Estimates of the phenotypic correlation between the two traits were calculated for each generation of each line. These correlations showed no consistent trends over generations, and the mean estimate was 0.05 ± 0.01 . Using this estimate of the phenotypic correlation and the average realized heritabilities and genetic correlation from the single-trait lines, the environmental correlation was estimated as 0.03.

Estimates of the average realized genetic correlation from comparison of average selection responses of the various treatments to generation 22 have been given by Jones *et al.* (1969), although their separate values derived from changes in sternopleurals and third coxals are incorrect, because heritabilities rather than their square roots were used in the calculations. The correct values estimated from selection responses over generations 0–22 and estimates from other periods of selection in the two-trait lines were as follows:

Generations of selection	0–5	0–10	0–22	10–22
Average realized genetic correlation:				
From coxal responses	0.27	0.31	0.30	0.28
From sternopleural responses	0.28	0.34	0.34	0.37
Average from both responses	0.27	0.33	0.32	0.33

These average estimates are remarkably consistent and agree quite well with the mean realized correlation estimated for the single-trait lines (Table 2).

Realized estimates of the two heritabilities and the genetic correlation can be obtained concurrently by a graphical method. For each two-trait selection treatment, average values of the observed selection response, predicted standardized selection differential and phenotypic standard deviation for sternopleural bristle number, and the phenotypic correlation, were substituted into equation (1). Estimates of the same parameters for coxal bristle number were substituted into the equivalent equation for the second character. By treating these as simultaneous equations and subtracting the second from the first, one can solve for $(h_s^2 - h_c^2)$, i.e. the realized difference between the heritabilities of the two traits, where the subscripts *S* and *C* denote sternopleural and coxal bristle number respectively. Estimates of this average realized difference for each two-trait selection treatment, and the average over all lines, to generations 10 and 22, are given below (heritabilities were expressed as percentages):

Selection treatment	UU	DD	UD	DU	
$(h_s^2 - h_c^2)$ to generation 10	9.69	6.50	10.41	4.18	(av. 7.70)
$(h_s^2 - h_c^2)$ to generation 22	5.89	5.54	6.83	3.38	(av. 5.41)

These average realized differences between the heritabilities for each two-trait selection treatment were used then in the graphical solution. Values for the heritability of coxal bristle number over the range from 2 to 20% were assumed. For each value the corresponding heritability of sternopleural bristle number was obtained by adding the average realized difference. These two values, together with the observed selection response, predicted standardized selection differential and phenotypic standard deviation for sternopleural bristle number, and the phenotypic correlation, were substituted in equation (1) and the genetic correlation estimated. These estimated genetic correlations are graphed against both sternopleural and coxal heritabilities in Fig. 7 for generations 10 and 22. From the region of intersection of the curves for the four different two-trait selection treatments mean estimates were obtained for coxal heritability, sternopleural heritability and the genetic correlation. These estimates were 7.5%, 15.4% and 0.32 respectively for generation 10, and 6.3%, 11.7% and

0.33 respectively for generation 22. The realized heritability estimates for generation 10 agree extremely well with those estimated from the single-trait lines.

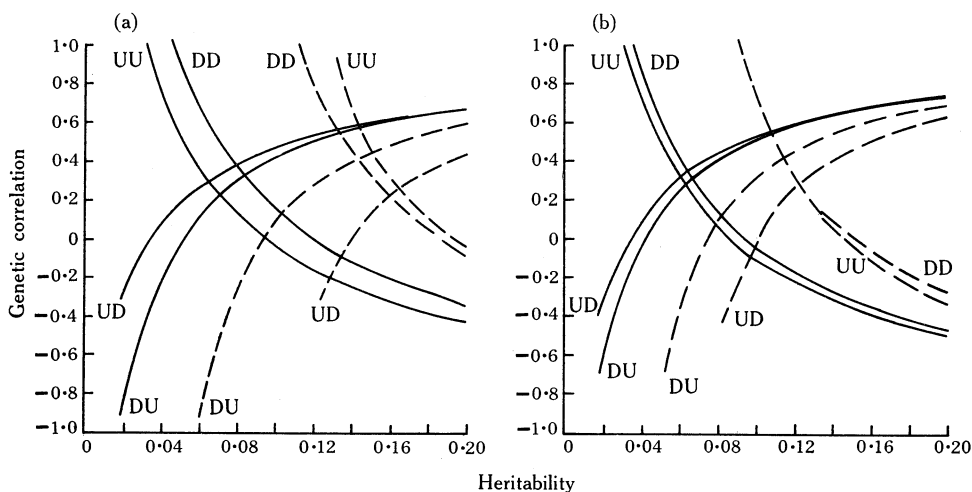


Fig. 7. Estimated genetic correlations for various assumed values of the heritabilities of coxal and sternopleural bristle numbers, given the average difference between the realized heritabilities of the two traits, for each two-trait selection treatment to generations 10 (a) and 22 (b).

— Estimates from coxal bristle responses.
 - - Estimates from sternopleural bristle responses.

Estimated responses for the two traits in each of the two-trait selection treatments were calculated from equation (1), using both base population parameters (Sheridan *et al.* 1968) and realized genetic parameters derived from the single-trait selection lines. The predicted selection differential in standard units (i_r) for each treatment (assuming infinite population size) was derived using the method of Young and Weiler (1960). This was then corrected for finite population size by multiplying by 0.84/0.88, the ratio of the average standardized selection differentials when selecting 11/25 and 5/11 to that for infinite population size at the same average selection intensity. Table 4 compares expected and mean realized selection responses for coxal and sternopleural bristle number in the two-trait lines over 10 and 22 generations of selection. Agreement between mean selection responses over 10 and 22 generations and those predicted from base population parameters was poor except for sternopleural bristle number in the UD and DU selection treatments. The good agreement in these two treatments was due to the combination of a lower sternopleural heritability and a lower genetic correlation. There was reasonable agreement between mean realized selection responses to generation 10 and those predicted using genetic parameters from the single-trait lines, with coxal and sternopleural bristle number showing about 75 and 85% respectively of the predicted response. Mean selection responses to generation 22 for coxals and sternopleurals were about 65 and 75% respectively of those predicted using the single-trait line genetic parameters.

Crosses between Two-trait Lines

The crosses between replicates within two-trait selection treatments had mean bristle numbers similar to mid-parent values. There was a tendency of some regression

towards the base population, the largest amount of regression occurring in the crosses between UU replicates.

The between-treatment crosses also had mean bristle numbers similar to mid-parent values. There tended to be some regression towards the base population mean for lines in which bristle numbers exceeded the base population level. However, most of this regression simply reflected the regression that occurred in the within-treatment crosses. An estimate of the sex-linkage component of the selection responses was obtained from the comparison of reciprocal crosses between the various two-trait selection treatments. On the average, sex linkage accounted for 4% of the selection response for coxals and 11% of that for sternopleurals.

There was no evidence of any maternal effects on either bristle system.

Table 4. Expected and realized selection responses for coxal and sternopleural bristle number in the two-trait selection lines after 10 and 22 generations of selection

Selection treatment	Coxal bristle number			Sternopleural bristle number		
	Expected response ^A	Mean realized response	Range	Expected response ^A	Mean realized response	Range
Generation 10						
UU	1.65 (0.89)	0.55 ± 0.10	0.36–0.80	2.28 (2.03)	1.77 ± 0.33	1.23–2.73
DD	1.65 (0.73)	0.70 ± 0.13	0.52–1.08	2.28 (1.43)	1.37 ± 0.45	0.52–2.59
Mean	1.65 (0.81)	0.63 ± 0.08		2.28 (1.73)	1.57 ± 0.28	
UD	0.59 (0.49)	0.19 ± 0.07	0.00–0.30	0.89 (1.42)	1.07 ± 0.16	0.62–1.37
DU	0.59 (0.40)	0.42 ± 0.10	0.18–0.59	0.89 (1.00)	0.84 ± 0.29	0.02–1.28
Mean	0.59 (0.45)	0.31 ± 0.06		0.89 (1.21)	0.96 ± 0.17	
Generation 22						
UU	3.62 (1.95)	1.31 ± 0.25	0.92–2.03	5.02 (4.46)	3.83 ± 0.53	2.68–5.34
DD	3.62 (1.60)	1.19 ± 0.15	1.02–1.64	5.02 (3.14)	2.32 ± 0.48	1.57–3.74
Mean	3.62 (1.78)	1.25 ± 0.15		5.02 (3.80)	3.08 ± 0.36	
UD	1.31 (1.08)	0.63 ± 0.08	0.49–0.82	1.95 (3.12)	1.78 ± 0.28	1.28–2.52
DU	1.31 (0.88)	0.56 ± 0.17	0.10–0.85	1.95 (2.20)	1.92 ± 0.52	0.55–2.82
Mean	1.31 (0.98)	0.60 ± 0.09		1.95 (2.66)	1.85 ± 0.30	

^A The first value given is the expected selection response estimated using base population parameters, while the value in parentheses is that estimated using realized genetic parameters from the single-trait lines.

Comparison of Estimated and Realized Genetic Parameters for the Base Population

Heritabilities of the two traits and the genetic and phenotypic correlations between them estimated from base population variance and covariance components have been presented by Sheridan *et al.* (1968). These are shown in Table 5, together with the realized estimates from the selection lines. Comparison of the mean values shows that the realized estimates are all less than the base population estimates, but generally the agreement was reasonable.

There was good agreement between mean sternopleural heritability estimates. However, due to the large range of estimates in the single-trait selection lines (10.2–20.6), the mean base population estimate (18.3) was of little value for predicting sternopleural selection response in individual lines. Agreement between mean coxal heritability estimates was poor. Once again, the realized estimates covered a wide range. Possible reasons for this poor agreement include the discontinuous distribution

and sampling variation. It is expected that selection for a discrete variable (such as bristle number) will become less efficient as the number of classes decreases. Coxals had fewer bristle classes than sternopleurals and also showed poorer agreement between diallel analysis and selection estimates of genetic parameters.

The mean realized genetic correlation between coxals and sternopleurals estimated from the single-trait lines was lower than the base population estimate. These realized genetic correlation estimates were extremely variable, the single-trait selection lines yielding estimates ranging from -0.26 to 1.07 (Table 2). The genetic correlation estimate obtained from the two-trait lines was higher than the single-trait selection estimate. The phenotypic correlation between coxals and sternopleurals estimated from within the two-trait lines agreed closely with the diallel analysis estimate.

Table 5. Comparison of estimated and realized genetic parameters for the base population

Parameter	Estimates from diallel analysis ^A		Realized estimates (selection experiment)	
	Mean	Range	Mean	Range
Heritability (%)				
Single-trait lines				
Third coxal	17.3	11.0-26.0	9.3	6.4-16.8
Sternopleural	18.3	12.0-27.0	14.8	10.2-20.6
Two-trait lines ^B				
Third coxal			7.5	
Sternopleural			15.4	
Sex linkage (proportion of response)				
Third coxal			0.04	$-0.29-0.18$
Sternopleural			0.11	$0.06-0.34$
Genetic correlation				
Diallel analysis	0.48	0.21-0.72		
Single-trait lines			0.24	$-0.26-1.07$
Two-trait lines			0.32	
Phenotypic correlation	0.08		0.05	$0.01-0.11$

^A From Sheridan *et al.* (1968).

^B To generation 10.

Discussion

The most outstanding features of these results are the variation among replicate lines in selection responses and in realized heritabilities and genetic correlations, and the generally good agreement between average base population and average realized estimates of genetic parameters, although the latter were always lower.

Base population parameters provided a reasonable estimate of mean sternopleural selection response over 10 generations, but considerably overestimated the coxal selection response. Realized genetic parameters obtained from the single-trait lines provided a reasonable estimate of the mean selection response in the two-trait lines over 10 generations and a fair estimate over 22 generations. Thus the prediction of selection response to two-trait selection is no less reliable than the prediction of response to single-trait selection. However, due to the enormous variation between replicate lines, these genetic parameters were of little use in predicting selection response in individual lines.

Possible causes of variation among replicate lines include selection intensity, population size and the magnitude of the additive genetic variation influencing selected and correlated traits that is included in the foundation samples. Frankham *et al.* (1968) selected for increased abdominal bristle number in *D. melanogaster*, comparing responses over 12 generations for a range of selection intensities (10, 20 and 40%) and population sizes (10, 20 and 40 pairs of parents). The responses on the average agreed well with those expected from the estimated base population heritability, but there was considerable variation among replicate lines. However, as population size was increased, agreement between predicted and observed responses for individual lines tended to improve.

Much of the variation between replicates here presumably was due to differences in the magnitude of additive genetic variance included in the foundation samples. Clayton *et al.* (1957) have discussed some of the factors that could contribute to variation between replicate lines. In addition, Barker (1967) suggested that the base population sampling procedure used in initiating selection lines can contribute to between-replicate variation, where there are desirable genes of low frequency ('rare' genes) in the base population. Rare genes are expected to have least effect when base population samples are either small (most rare genes excluded) or very large (most rare genes included). They would have greatest effect when sample sizes are intermediate. This expectation has been subjected to theoretical examination by James (1971). In our experiments 400 flies were sampled from the base population, so that the minimum possible gene frequency was 0.00125. From their progeny 200 flies were scored to initiate each line. Desirable genes that were rare in the base population thus could have been included in some lines, but not others, accounting for some of the variation between replicates.

Bohren *et al.* (1966) showed that the genetic correlation is very sensitive to changes in gene frequency, so that calculation of realized correlations would be likely to be valid only over a few generations. As changes in gene frequency would arise from random drift as well as selection, wide variation in realized correlations among lines is not surprising. Nevertheless, the average genetic correlation estimated in the base population and the average realized correlations from single-trait and two-trait selection lines were reasonably similar and probably not significantly different.

Acknowledgments

Many of the statistical analyses were done with the cooperation and assistance of Mr F. McCleery, formerly N.S.W. Department of Agriculture, and Mr C. Kirton, N.S.W. Department of Agriculture. The technical assistance of Ms B. Hall and Ms P. Brown is appreciated. Ms J. Shaw, Poultry Research Station, Seven Hills, assisted in the compilation of experimental data. This research was done while one of us (A.K.S.) was on study leave from the N.S.W. Department of Agriculture.

References

- Barker, J. S. F. (1967). Modern problems of population genetics in animal husbandry. *Züchter* **37**, 309–23.
- Bohren, B. B., Hill, W. G., and Robertson, A. (1966). Some observations on asymmetrical correlated responses to selection. *Genet. Res.* **7**, 44–57.
- Claringbold, P. J., and Barker, J. S. F. (1961). The estimation of relative fitness of *Drosophila* populations. *J. theor. Biol.* **1**, 190–203.

- Clayton, G. A., Morris, J. A., and Robertson, A. (1957). An experimental check on quantitative genetical theory. I. Short-term responses to selection. *J. Genet.* **55**, 131–51.
- Falconer, D. S. (1960). 'Introduction to Quantitative Genetics.' (Oliver and Boyd: Edinburgh.)
- Frankham, R., Jones, L. P., and Barker, J. S. F. (1968). The effects of population size and selection intensity in selection for a quantitative character in *Drosophila*. I. Short-term response to selection. *Genet. Res.* **12**, 237–48.
- James, J. W. (1971). The founder effect and response to artificial selection. *Genet. Res.* **16**, 241–50.
- Jones, L. P., Frankham, R., and Sheridan, A. K. (1969). Correlation between bristle systems in *Drosophila melanogaster*. *Aust. J. biol. Sci.* **22**, 1473–84.
- Latter, B. D. H. (1964). Selection for a threshold character in *Drosophila*. I. An analysis of the phenotypic variance on the underlying scale. *Genet. Res.* **5**, 198–210.
- Sheridan, A. K., and Barker, J. S. F. (1974). Two-trait selection and the genetic correlation. II. Changes in the genetic correlation during two-trait selection. *Aust. J. biol. Sci.* **27**, 89–101.
- Sheridan, A. K., Frankham, R., Jones, L. P., Rathie, K. A., and Barker, J. S. F. (1968). Partitioning of variance and estimation of genetic parameters for various bristle number characters of *Drosophila melanogaster*. *Theor. appl. Genet.* **38**, 179–87.
- Williams, J. M., and Weiler, H. (1964). Further charts for the means of truncated normal bivariate distributions. *Aust. J. Statist.* **6**, 117–29.
- Young, S. S. Y., and Weiler, H. (1960). Selection for two correlated traits by independent culling levels. *J. Genet.* **57**, 329–38.