Two-trait Selection and the Genetic Correlation
II.* Changes in the Genetic Correlation
During Two-trait Selection

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With an Appendix by J. W. James

Abstract

Although there is little experimental information on the effect of simultaneous selection for two quantitative characters on the magnitude of the genetic correlation between them, it is apparently generally expected that such selection for the two characters in the same direction will cause a negative change in the genetic correlation, and selection in opposite directions a positive change. Selection using independent culling levels was done for each of the four combinations of high or low third coxal bristle number with high or low sternopleural bristle number in *Drosophila melanogaster* for 22 generations. To estimate changes in the genetic correlation, realized genetic parameters were estimated from single-trait lines started from the base population, and from the two-trait lines after 10 and 22 generations of selection. Changes in the genetic correlation in individual two-trait selection lines were variable and unpredictable. At generation 22 concurrent two-trait selection had resulted in significantly larger realized genetic correlations than divergent two-trait selection, so that results were contrary to the generally accepted expectation.

Introduction

There is very little experimental information on the effect of simultaneous selection for two quantitative characters on the magnitude of the genetic correlation between them. Lush (1948) and Lerner (1950) have suggested that such selection for two characters in the same direction will cause a negative change in the genetic correlation. Genes (or gene blocks) with independent desirable effects on either trait ($+0$ or $0+$ genes) or with desirable pleiotropic effects on both traits ($++$ genes) will be fixed, while allelic genes with undesirable effects (-0, $0-$, or $--$) will be lost. Pleiotropic genes (or gene blocks) with a desirable effect on one trait and an undesirable effect on the other ($+-$ and $-+$ allelic genes) will remain segregating, thus producing the negative change. By the same reasoning, simultaneous selection for two traits in opposite directions will cause a positive change in the genetic correlation, as the only genes left segregating will be pleiotropic ones affecting both traits in the same direction. This prediction assumes that the initial genetic correlation was essentially due to pleiotropy, and that genes with desirable effects on both traits will be fixed or at least reach high frequencies, and so contribute little to genetic variation and covariation. In addition, it predicts the change in the correlation that would occur after several to many generations of selection, as it depends on gene fixation. Changes in the genetic correlation in the short term (i.e. following initial generations of selection) cannot be simply predicted. The change may be positive or negative, depending on the number of loci having $++$ or $+-$ effects, the frequencies

Table 1. *Realized heritabilities (%) for coxal and sternopleural bristle numbers and the realized genetic correlation between them—estimated from single-trait selection lines initiated from replicate lines of each of the two-trait selection treatments at generation 10*

Heritability, treatment UU

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
1	4·2±0·9	7·7±0·9	13·6±1·0	17·2±2·0
2	7·0±0·9	4·6±0·8	13·9±1·0	12·9±1·7
3	9·1±1·3	12·2±1·2	15·3±1·5	15·7±1·9
4	6·4±0·7	3·6±1·0	9·3±1·3	15·1±0·7
Average	6·7±1·0	7·0±1·9	13·0±1·3	15·2±0·9
values	6·9±1·1		14·1±0·8	

Genetic correlation, treatment UU

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
1	-0·58±0·20	0·25±0·10	-0·17±0·09	0·12±0·11
2	0·06±0·13	0·19±0·18	0·36±0·12	0·29±0·15
3	-0·11±0·10	0·59±0·10	0·53±0·12	0·52±0·12
4	-0·25±0·09	0·20±0·22	0·15±0·11	0·28±0·17
Average	-0·22±0·14	0·31±0·10	0·22±0·15	0·30±0·08
values	0·04±0·08		0·26±0·09	
		0·15±0·06		

Heritability, treatment DD

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
3	10·9±0·9	10·1±1·2	11·1±0·9	11·1±1·0
4	4·2±1·0	8·1±1·1	8·5±0·9	19·2±1·1
Average	7·5±3·4	9·1±1·0	9·8±1·3	15·1±4·1
values	8·3±1·8		12·5±2·1	

Genetic correlation, treatment DD

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
3	-0·10±0·09	0·79±0·16	0·36±0·08	0·34±0·10
4	0·83±0·34	0·50±0·14	0·32±0·14	0·56±0·08
Average	0·37±0·46	0·64±0·14	0·34±0·02	0·45±0·11
values	0·50±0·24		0·39±0·06	
		0·45±0·12		

Heritability, treatment UD

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
1	5·7±0·7	9·0±1·5	3·9±1·3	11·8±1·7
2	9·2±1·2	4·7±1·2	8·5±1·7	10·4±1·0
3	4·4±0·8	10·0±0·6	14·3±1·0	19·3±1·4
4	3·9±1·1	4·1±1·5	4·4±1·0	11·5±1·2
Average	5·8±1·2	6·9±1·5	9·0±2·0	13·2±2·0
values	6·4±1·0		11·1±1·4	

Genetic correlation, treatment UD

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
1	0·29±0·17	-0·01±0·35	0·86±0·23	0·68±0·20
2	0·31±0·11	-0·15±0·17	0·24±0·11	-0·20±0·11
3	0·52±0·24	0·73±0·13	0·48±0·13	0·62±0·08
4	0·92±0·44	-0·07±0·15	0·56±0·30	0·12±0·19
Average	0·52±0·13	0·13±0·20	0·53±0·13	0·30±0·21
values	0·32±0·12		0·42±0·12	
		0·37±0·09		

Heritability, treatment DU

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
3	8·9±0·7	7·4±1·1	9·4±1·3	7·9±0·9
4	5·4±1·3	3·2±0·9	21·1±1·3	11·7±1·6
Average	7·1±1·8	5·3±2·1	15·2±5·9	9·8±1·9
values	6·2±1·4		12·5±3·1	

Genetic correlation, treatment DU

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
3	0·74±0·15	0·20±0·08	0·22±0·09	0·32±0·13
4	0·37±0·16	0·52±0·22	0·47±0·11	0·25±0·18
Average	0·55±0·18	0·36±0·16	0·35±0·12	0·28±0·04
values	0·46±0·12		0·32±0·06	
		0·39±0·07		

of the alleles at each locus and the relative magnitude of the effects on each trait. In the very long term, unless the pleiotropic effects on the two traits were equal there must be a net selection pressure for one trait or the other, so that the genetic correlation should tend to zero.

On the other hand, if the genetic correlation between two traits were due to linkage it should tend to zero as linkage equilibrium is attained. But the change in the genetic correlation will be determined by the linkage disequilibrium, which will depend on many factors—selection intensity, gene effects, gene frequency, strength of linkage—and therefore the genetic correlation need not decline directly to zero. Thus simple short-term predictions of the change in the genetic correlation cannot be made. Similarly, no distinction can be made between the expectations where the correlation is due to pleiotropy and where it is due to linkage.

Rendel (1963, 1967) has discussed genetic correlations in terms of developmental processes. Where the developmental processes leading to two characters share the same substrate resources, the genetic correlation between them results from a compromise between two opposing tendencies. The first is caused by factors which influence the total resources available, producing a positive genetic correlation. The second is caused by factors which alter the distribution of these resources between the two characters, producing a negative genetic correlation. On this model, change in the genetic correlation on selection for the two characters depends on whether selection exerts a greater effect on total resources or on the distribution of resources.

Although no experiments have been done specifically to examine the effect of simultaneous selection for two characters on the genetic correlation between them, some results are available. In a flock of White Leghorn chickens selected for increased annual egg production, Dempster *et al.* (1952) found that the genetic correlation between two components of the selected trait (viz. rate of lay and survival to the end of the first laying year) changed from an average of 0·20 over generations 1–3 to 0·49 over generations 8–10, but this increase was not significant. Friars *et al.* (1962) estimated genetic correlations between pairs of traits for each generation in a meat chicken selection flock. Five traits were recorded, the selection pressure applied to any one trait varying from generation to generation. Genetic correlations were estimated by three methods (sire, dam and sire + dam variance and covariance components) for each of six paired character combinations. For eight generations of multi-trait selection, the linear regression of genetic correlation on generation number was negative for 16 of 18 estimates, and significantly different from zero ($P < 0·05$) for four of these. In simultaneous selection for increased abdominal and sternopleural bristle number in *Drosophila melanogaster*, Sen and Robertson (1964) found that the genetic correlation between the traits increased slightly over 12 generations of selection. Burris and Bell (1965) selected for eight generations for each of the four combinations of high or low larval weight with high or low pupal weight in *Tribolium castaneum*. There were no significant trends in the magnitude of the genetic correlation in any of the four treatments (Bell 1972).

In the experiment reported here, *D. melanogaster* populations were selected, using independent culling levels, for each of the four combinations of high or low third coxal bristle number with high or low sternopleural bristle number. The selection in each of these four types of two-trait lines was continued for 22 generations (Sheridan and Barker 1974). In order to estimate changes in the genetic correlation resulting from the different types of two-trait selection, realized genetic parameters

Table 2. Realized heritabilities (%) for coxal and sternopleural bristle numbers and the realized genetic correlation between them—estimated from single-trait selection lines initiated from replicate lines of each of the two-trait selection treatments at generation 22

Left half

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
Heritability, treatment UU				
1	2·0±0·7	1·8±0·8	5·5±0·8	11·9±1·7
2	4·6±0·8	2·2±0·8	12·2±1·0	10·3±1·1
3	4·0±2·4	4·0±1·3	4·4±1·7	32·3±3·7
4	21·2±1·9	7·3±1·3	8·1±1·1	12·4±1·7
Average values	8·0±4·5	3·8±1·3	7·6±1·7	16·7±5·2
Pooled	5·9±2·3		12·1±2·7	
Genetic correlation, treatment UU				
1	1·48±0·72	0·98±0·60	0·45±0·32	1·19±0·37
2	0·00±0·08	0·10±0·16	0·06±0·13	0·14±0·20
3	−0·01±0·24	0·68±0·28	0·38±0·32	0·88±0·27
4	0·71±0·15	1·14±0·29	0·33±0·12	0·07±0·11
Average values	0·54±0·35	0·73±0·23	0·31±0·09	0·57±0·28
Pooled	0·63±0·21		0·44±0·14	
Grand mean		0·54±0·13		
Heritability, treatment DD				
1	5·0±0·7	4·2±1·1	8·5±1·1	12·5±1·9
2	7·7±1·4	0·0±1·4	9·3±1·0	3·0±0·7
3	6·0±1·4	14·7±1·1	10·8±1·5	5·1±1·0
4	17·6±2·7	3·8±0·9	4·4±0·8	4·1±1·2
Average values	9·1±2·9	5·7±3·2	8·3±1·4	6·2±2·2
Pooled	7·4±2·1		7·2±1·3	
Genetic correlation, treatment DD				
1	0·28±0·13	−0·64±0·29	0·46±0·16	1·41±0·40
2	0·82±0·23	—	0·45±0·16	—
3	0·64±0·28	0·78±0·15	−0·05±0·09	0·90±0·23
4	2·34±0·49	0·42±0·22	0·28±0·12	−0·42±0·39
Average values	1·02±0·45	0·19±0·43	0·28±0·12	0·63±0·55
Pooled	0·60±0·31		0·46±0·28	
Grand mean		0·53±0·21		

Right half

Replicate	Coxals selected Up	Coxals selected Down	Sternopleurals selected Up	Sternopleurals selected Down
Heritability, treatment UD				
1	5·1±1·1	5·0±0·9	7·6±1·0	4·7±1·0
2	3·3±1·3	13·3±1·7	6·3±1·3	3·2±1·0
3	4·5±1·5	6·4±1·3	6·8±0·7	22·9±1·5
4	4·3±0·7	15·7±3·5	17·1±0·8	4·6±0·9
Average values	4·3±0·4	10·1±2·6	9·5±2·6	8·8±4·7
Pooled	7·2±1·3		9·1±2·7	
Genetic correlation, treatment UD				
1	0·56±0·22	0·07±0·20	0·61±0·19	0·41±0·18
2	0·07±0·27	0·26±0·25	−0·07±0·22	0·05±0·17
3	0·64±0·27	−0·18±0·12	0·06±0·22	1·21±0·23
4	0·08±0·12	−0·31±0·17	0·27±0·09	−0·06±0·16
Average values	0·34±0·15	−0·04±0·13	0·22±0·15	0·40±0·29
Pooled	0·15±0·10		0·31±0·16	
Grand mean		0·23±0·09		
Heritability, treatment DU				
1	4·7±0·8	2·7±1·8	14·3±1·0	3·7±0·7
2	5·3±0·7	6·8±1·1	21·5±0·9	14·7±2·6
3	1·6±0·8	1·3±0·9	4·1±1·3	27·2±2·4
4	8·2±1·0	3·5±0·5	9·7±1·0	9·2±2·2
Average values	4·9±1·4	3·6±1·2	12·4±3·7	13·7±5·0
Pooled	4·3±0·9		13·0±3·1	
Genetic correlation, treatment DU				
1	0·06±0·13	1·23±1·08	0·23±0·13	0·08±0·27
2	0·16±0·16	0·82±0·30	1·07±0·14	0·58±0·18
3	0·90±0·62	0·70±0·61	0·38±0·42	−0·21±0·21
4	−1·32±0·41	1·00±0·26	0·37±0·12	0·32±0·25
Average values	−0·05±0·46	0·94±0·12	0·51±0·19	0·19±0·17
Pooled	0·44±0·24		0·35±0·13	
Grand mean		0·40±0·14		

were estimated from single-trait selection lines started from the base population, and from single-trait selection lines started from samples of the two-trait lines after 10 and 22 generations of selection.

Materials and Methods

The two-trait selection lines of Sheridan and Barker (1974) comprised four replicates of each of the following four treatments:

<blockquote>
UU   Both traits selected upwards
DD   Both traits selected downwards
UD   Coxals selected upwards, sternopleurals downwards
DU   Coxals selected downwards, sternopleurals upwards
</blockquote>

At generations 10 and 22 of these lines, flies were taken to set up single-trait selection lines for estimation of realized genetic correlations. At generation 10 random samples of flies were taken separately from all replicate lines of treatments UU and UD, and from two replicate lines of each of DD and DU. In these latter, the replicates showing the most (DD4 and DU3) and those showing the least selection response (DD3 and DU1) were chosen. At generation 22, flies were sampled at random from all four replicates of each of the four two-trait selection treatments.

From each two-trait replicate line that was sampled, four single-trait selection lines (coxals up, coxals down, sternopleurals up, sternopleurals down) were initiated. Ten pairs of parents were selected from 50 pairs scored, and selection continued for 10 generations. All experimental procedures and the calculation of realized heritabilities and genetic correlations were as described for the single-trait lines from the base population (Sheridan and Barker 1974), except that in calculating realized genetic correlations the heritability of the unselected trait was taken as that estimated from the single-trait line drawn from the same replicate of the same two-trait selection treatment and selected in the same direction as the selected trait.

Results

Realized heritabilities and genetic correlations for the two-trait treatments UU, DD, UD and DU, estimated from the lines taken off at generations 10 and 22, are given in Tables 1 and 2 respectively.

Although the major interest is in the average realized genetic parameters estimated from these single-trait lines, some comment should be made on their individual patterns of selection response. Particularly for coxal bristle number, the correlated selection response in one line was often as great as the direct response in another line. In some cases correlated responses were even greater than direct responses, while in others correlated responses were in the direction opposite to that expected. Such lines have given estimated realized genetic correlations greater than $1 \cdot 0$ or less than $-1 \cdot 0$. Replicate lines from the same treatment showed considerable variability in direct response, which is reflected in the estimates of realized heritability. In each of the single-trait lines cumulative selection differentials were calculated for the selected trait over the 10 generations of selection. For lines taken from the same two-trait treatment, and selected for the same trait in the same direction, there was very good agreement in the cumulative selection differentials. As noted for the lines from the base population (Sheridan and Barker 1974), cumulative selection differentials tended to be larger for upward than for downward selection for both traits, due to the direct relationship between means and standard deviations.

For most of the single-trait lines taken off the two-trait lines at generation 10, selection responses were fairly regular over the 10 generations studied. However, for the single-trait lines taken off at generation 22, several gave non-linear responses. Some lines showed rapid early selection response, followed by a period of little or no

response, while in other lines the reverse occurred. These cases always involved reverse selection to that in the two-trait treatment. Because of these non-linear responses it may be thought that realized genetic correlations estimated from the early generations of the single-trait lines would be more accurate. All realized genetic parameters were estimated from generations 0–5 of the single-trait lines, as well as from generations 0–10. In general, the average estimates were very similar, and standard errors were lower for the latter estimates. Therefore only these latter are presented. Full details of responses of individual lines, selection differentials, etc. are given by Sheridan (1969).

For all results in Tables 1 and 2, the significance of differences between average realized heritabilities and between average realized genetic correlations for up and down selection on each trait, and between average correlations estimated from each trait, have been determined by the t-test. The only significant difference was for the correlations estimated from coxals up versus down selection in Table 1, treatment UU ($t = 3 \cdot 08$, $P < 0 \cdot 05$). The realized correlations here are clearly asymmetric, with selection either up or down for coxals leading to a correlated decrease in sterno-pleural bristle number. When these correlations were estimated from the responses over generations 0–5 they were even more asymmetric, viz. $-0 \cdot 28 \pm 0 \cdot 39$ and $0 \cdot 70 \pm 0 \cdot 29$, but not significantly different.

Table 3. Average realized heritabilities (%) and realized genetic correlations in the base population, and at generations 10 and 22 of two-trait selection

Treatment	Average heritability:		Average realized genetic correlation
	Coxals	Sternopleurals	
Base population	$9 \cdot 3 \pm 1 \cdot 3$	$14 \cdot 8 \pm 1 \cdot 4$	$0 \cdot 24 \pm 0 \cdot 08$
Generation 10			
UU	$6 \cdot 9 \pm 1 \cdot 1$	$14 \cdot 1 \pm 0 \cdot 8$	$0 \cdot 15 \pm 0 \cdot 06$[A]
DD	$8 \cdot 3 \pm 1 \cdot 8$	$12 \cdot 5 \pm 2 \cdot 1$	$0 \cdot 45 \pm 0 \cdot 12$
UD	$6 \cdot 4 \pm 1 \cdot 0$	$11 \cdot 1 \pm 1 \cdot 4$	$0 \cdot 37 \pm 0 \cdot 09$
DU	$6 \cdot 2 \pm 1 \cdot 4$	$12 \cdot 5 \pm 3 \cdot 1$	$0 \cdot 39 \pm 0 \cdot 07$
Generation 22			
UU	$5 \cdot 9 \pm 2 \cdot 3$	$12 \cdot 1 \pm 2 \cdot 7$	$0 \cdot 54 \pm 0 \cdot 13$
DD	$7 \cdot 4 \pm 2 \cdot 1$	$7 \cdot 2 \pm 1 \cdot 3$[B]	$0 \cdot 53 \pm 0 \cdot 21$
UD	$7 \cdot 2 \pm 1 \cdot 3$	$9 \cdot 1 \pm 2 \cdot 7$	$0 \cdot 23 \pm 0 \cdot 09$
DU	$4 \cdot 3 \pm 0 \cdot 9$[C]	$13 \cdot 0 \pm 3 \cdot 1$	$0 \cdot 40 \pm 0 \cdot 14$

[A] Significantly different from generation 10 (G10) DD, G10 DU, and G22 UU.
[B] Significantly different from base population and G10 UU.
[C] Significantly different from base population.

All pairwise combinations of the overall average realized heritabilities and average realized genetic correlations in Tables 1 and 2, together with the realized estimates from the base population (Tables 1 and 2 of Sheridan and Barker 1974) also were tested for significance of differences. These average estimates are summarized in Table 3. Very few comparisons were significant, but to provide a more comprehensive analysis, a non-orthogonal analysis of variance of all realized genetic correlations was done (Table 4). The correlations were not transformed to z-values prior to analysis (as suggested by Fisher 1948) since some of them were outside the range of $+1 \cdot 0$ to $-1 \cdot 0$. A test of the normality of the distribution revealed that it was both

significantly skewed ($g_1 = 0.51 \pm 0.22$; $0.02 > P > 0.01$) and significantly peaked ($g_2 = 3.19 \pm 0.43$; $P < 0.001$). However, when this distribution was retested after deleting one extreme value ($r_G = 2.34$ in Table 2, treatment DD), the distribution was symmetrical ($g_1 = -0.08 \pm 0.22$; $1.0 > P > 0.5$) but still significantly peaked ($g_2 = 1.49 \pm 0.43$; $P < 0.001$). Although skewness is thought to alter the probability levels of the variance ratios, peakedness is expected to have little effect upon them (Cochran 1947). We have no valid reason for deleting this extreme value and, as the skewness is entirely due to one variable in an array of 126 values, the probability levels are unlikely to be altered to any great extent. The analysis gave no evidence of changes in the correlations from generation 0 to generation 10 to generation 22. However, at generation 22, concurrent two-trait selection had resulted in significantly larger genetic correlations than divergent two-trait selection.

Table 4. **Analysis of variance of realized genetic correlations estimated from the base population and from generations 10 and 22 of the two-trait selection lines**
Only those interactions which were significant are included. G10, G22 signify generations 10 and 22 respectively

Source of variation	D.F.	Mean square
A. Generation and two-trait selection type	8	
(a) Base v. (G10 + G22)	1	0.2767
(b) Among G10	(3)	
(i) UU v. DD	1	0.4561
(ii) UD v. DU	1	0.0027
(iii) (UU + DD) v. (UD + DU)	1	0.5644
(c) Among G22	(3)	
(i) UU v. DD	1	0.4513
(ii) UD v. DU	1	0.3002
(iii) (UU + DD) v. (UD + DU)	1	1.6318**
(d) G10 v. G22	1	0.1651
B. Character selected (single-trait selection)	1	0.0032
C. Direction of selection (single-trait selection)	1	0.0432
Interactions:		
Ac(iii) × B	1	1.0043*
Ac(i) × C	1	1.1233*
Ac(ii) × C	1	1.8629**
Ac(iii) × C	1	0.8579*
Ac(ii) × B × C	1	1.7484**
Ac(iii) × B × C	1	0.9003*
Error	90	0.1971

* $P < 0.05$.   ** $P < 0.01$.

Discussion

This experiment has produced results contrary to the apparently generally accepted expectation (e.g. Falconer 1960; Pirchner 1969) that simultaneous selection for two characters in the same direction will cause a negative shift in the genetic correlation, and in opposite directions a positive shift. We have pointed out in the introduction that this expectation assumes that the initial genetic correlation was due to pleiotropy, and that it predicts the expected change in the correlation after several to many generations of selection.

However, Rendel's (1963, 1967) model of genetic correlations in terms of developmental processes provides a convenient means of further analysing these expectations. The possible relationship between two correlated traits (X and Y) is shown in Scheme 1 as one of the many possible developmental pathways common to the two traits. As the observed relationship between traits X and Y will be a function of the biochemical pathway supplying the substrate in shortest supply, it will be assumed that these two traits require only one substrate and so are influenced by one biochemical pathway. The total substrate resources (T) are shared by traits X and Y in the proportions A and $(1-A)$ respectively. We assume that the amount of substrate resource and its distribution are entirely genetically determined; that is, environmental variation in the traits is independent of and subsequent to determination of T and A.

These assumptions seem reasonable from what is known of bristle development in *Drosophila*. Sondhi (1963) reviewed several theories on gene control and the development of bristle patterns in *Drosophila* and suggested that there are two processes involved in bristle development:

1. Factors controlling the formation of a 'pre-pattern' which determines the bristle sites. (A pre-pattern was defined by Sondhi as a 'distribution of an inducing substance with regions of high and low concentrations'. Bristles would develop at points of high concentration.)
2. Factors influencing the ability of cells to respond to an underlying pre-pattern.

Turing (1952) proposed a simple model for the development of such a pre-pattern. As pre-patterns are thought to be very stable (Sondhi 1963), selection for bristle number would alter the competence of cells to respond to a particular pre-pattern. Whereas some body components (e.g. muscle tissue) can be broken down to supply substrates required for other purposes, bristle growth is a one-way process. Once substrates have been used in the formation of bristles they cannot be reclaimed for other uses. Thus an observed genetic correlation between bristle systems reflects the substrate situation up to and including the formation of the bristles and is uncomplicated by subsequent substrate excesses or deficiencies. Further, the environmental correlation between third coxal bristle number and sternopleural bristle number was effectively zero (Sheridan and Barker 1974).
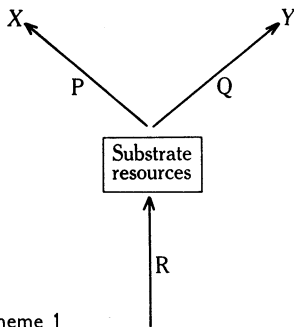
Scheme 1

Scheme 1 shows a model of gene action governing the phenotypes of two traits, X and Y. Genes affecting pathway R control the amount of substrate, while genes affecting pathways P and Q determine the relative proportions of substrate available to X and Y. The genes affecting pathways P, Q and R may be discussed in terms of the frequency of the + allele. For example, an increase in the frequency of R genes will mean that the proportion of + alleles has increased and the proportion of − alleles has decreased. Changes in the frequency of R genes will alter total resources (T) available for the development of X and Y. Thus R genes are effectively + + pleiotropic genes. P and Q genes determine the proportion of the available resources allocated to each trait. Thus, an increase in the frequency of P genes will direct a

greater proportion of substrate toward X. An increase in the frequency of Q genes will similarly favour Y. Of course, P and Q genes are allelic, and pleiotropic with a $+ -$ effect. That is, an allele with a plus effect on X would have a minus effect on Y, and *vice versa*. The model is therefore one of pleiotropy.

Given that there will be variation among individuals in a population in the values of T and A, it is possible to consider their additive genetic variance and covariance, and to determine the effects of selection on them. We are indebted to Dr J. W. James for suggesting the basis of this analysis, the theoretical statement of which is given as Appendix 1. Additive genetic covariances between the two traits have been calculated as:

$$r_G h_x \sigma_{Px} h_y \sigma_{Py},$$

where r_G is the genetic correlation, h_x and h_y are the square roots of the heritabilities of coxal and sternopleural bristle number respectively, and σ_{Px} and σ_{Py} are the phenotypic standard deviations of coxal and sternopleural bristle number respectively. For the two-trait treatment estimates at generations 10 and 22, average estimates of heritabilities and the genetic correlation from the appropriate single-trait lines were used. The phenotypic standard deviations were average estimates from generations 10 and 22 of the two-trait lines. The additive genetic covariance between the two traits in the base population was 0·0233. Results for generations 10 and 22 were as follows:

| | Average additive genetic covariance: | |
Treatment	Generation 10	Generation 22
UU	0·0193	0·0977
DD	0·0304	0·0205
UD	0·0235	0·0135
DU	0·0286	0·0317

The changes recorded above in the additive genetic covariances for the various two-trait treatments do not agree with the expectations given in Appendix 1. However, the theory of the expected changes in the covariance depends on the assumption that the variances of T and A remain unchanged. Although we can make no estimates of the additive genetic variance in T and in A, the heritabilities of both bristle traits have tended to decrease during selection (Table 3). Expectations of changes in the covariance therefore may be valid only in the short term. More frequent estimates of the genetic parameters during the early generations of a selection program would be necessary for an adequate test of the theory. Nevertheless, the covariances at generation 10 as compared with the base population do not disagree with expectations, as the covariance for treatment UU has decreased, that for DD has increased, while those for UD and DU were unchanged.

Of course, the real situation is more complicated than the model given in Scheme 1. Each trait would be likely to have independent substrate supplies as well as the shared resources. The common substrate could be shared not only by third coxals and sternopleurals, but also by second coxals, scutellars, abdominals and presumably other bristle systems. As one example of the effects these may have, suppose that there were genes (denoted I genes) controlling independent substrates for each trait, as well as P, Q and R genes. Further, assume that linkage did not contribute to the initial genetic correlation, so that the correlation depended entirely on the initial state of P, Q and R genes (i.e. number of loci, gene frequencies and magnitude of

gene effects). Now, if I genes had larger average effects and/or if their frequencies were at more intermediate values than the P, Q and R genes, two-trait selection would lead to changes in the frequency of $+$ genes at I loci, with say little change in gene frequency of P, Q or R genes. Thus the additive genetic covariance of the two traits (due to P, Q and R genes) would show little change, but the additive genetic variance of both traits would be decreased. The absolute value of the genetic correlation therefore would be increased—a positive genetic correlation changing towards $+1 \cdot 0$ and a negative one towards $-1 \cdot 0$.

One aspect of possible changes in genetic correlations warrants consideration from the viewpoint of breeding programs. If simultaneous two-trait selection were being done, the genetic parameters ideally should be re-estimated at intervals to allow for any changes in deriving a selection index or in determining independent culling levels. This suggestion is not of immediate practical significance, as to estimate the realized genetic parameters one would need at least two of the four possible types of two-trait selection lines or separate single-trait selection lines. But suppose the latter were being maintained. Then if, as is possible, realized genetic correlations show asymmetry depending on the direction of selection in single-trait lines, it would be more realistic to consider only the correlations estimated from single-trait selection where a particular trait was being selected in the same direction as in the two-trait selection. If these correlations are designated 'effective genetic correlations', then in treatment UD for example the correlation would be estimated from upward coxal selection and downward sternopleural selection. Thus, from Table 2, the effective genetic correlations for treatments UU, DD, UD and DU at generation 22 were $0 \cdot 42 \pm 0 \cdot 18$, $0 \cdot 41 \pm 0 \cdot 35$, $0 \cdot 37 \pm 0 \cdot 16$ and $0 \cdot 72 \pm 0 \cdot 11$ respectively, all larger than the genetic correlation in the base population.

The results of this experiment indicate that changes in the genetic correlation between third coxal and sternopleural bristle numbers in individual two-trait selection lines were variable and unpredictable. Nevertheless, in contrast with the generally accepted expectation, average realized genetic correlations did not decrease under simultaneous selection for the two traits in the same direction.

Acknowledgments

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Appendix 1. Genetic Covariances
Under the Partition of Resources Model

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We consider only a very simple version of the partition of resources model. Two observed traits are involved, denoted by X and Y. The total amount of resources available is denoted by T, while the fraction of resources devoted to trait X is A, the remainder being devoted to Y. The means and variances are $\bar{T}$, $V(T)$ and $\bar{A}$, $V(A)$ for T and A respectively. We assume that T and A are wholly genetically determined and that other contributions to X and Y are E_X and E_Y which are uncorrelated environmental effects. Thus

$$X = AT + E_X,$$

and

$$Y = (1-A)T + E_Y.$$

Then the covariance between X and Y, $\mathrm{Cov}(X, Y)$, is entirely genetic, and arises entirely from the partition of resources. Using standard methods we find

$$\mathrm{Cov}(X, Y) = \mathrm{Cov}[AT, (1-A)T]$$
$$= \bar{A}(1-\bar{A})\,V(T) - \bar{T}^2\,V(A) + \bar{T}(1-2\bar{A})\,\mathrm{Cov}(A, T)$$
$$= \bar{A}(1-\bar{A})\,V(T) - \bar{T}^2\,V(A)$$

if, as we shall assume, A and T are uncorrelated. Similarly,

$$\text{Cov}(X,A) = \bar{T}\,\text{V}(A) \qquad \text{Cov}(Y,A) = -\bar{T}\,\text{V}(A)$$
$$\text{Cov}(X,T) = \bar{A}\,\text{V}(T) \qquad \text{Cov}(Y,T) = (1-\bar{A})\,\text{V}(T)$$

We now suppose that both A and T are controlled by many genes each of small effect, so that changes in $\text{V}(A)$ and $\text{V}(T)$ may be ignored and we may focus attention only on changes in $\bar{A}$ and $\bar{T}$ following different types of selection.

Selection for X

Since both $\text{Cov}(X,A)$ and $\text{Cov}(X,T)$ are positive, $\bar{T}$ and $\bar{A}$ will both increase. If $\bar{A} > 0\cdot5$, $\bar{A}(1-\bar{A})$ decreases and $\bar{T}^2$ increases so $\text{Cov}(X,Y)$ always decreases. If $\bar{A} < 0\cdot5$, $\bar{A}(1-\bar{A})\,\text{V}(T)$ increases and if it increases more rapidly than $\bar{T}^2\,\text{V}(A)$, $\text{Cov}(X,Y)$ may increase for a time, but must begin to decrease once $\bar{A}$ reaches $0\cdot5$, after which $\text{Cov}(X,Y)$ always decreases.

Selection for Y

The results are as in selection for X, except that the condition $\bar{A} > 0\cdot5$ becomes $\bar{A} < 0\cdot5$ and *vice versa*.

Selection for X+Y

Since $\text{Cov}(X+Y,A) = \text{Cov}(X,A)+\text{Cov}(Y,A) = 0$, $\bar{A}$ is expected to remain constant. Since $\text{Cov}(X+Y,T) = \text{V}(T)$ and is always positive, $\bar{T}$ increases steadily and so $\text{Cov}(X,Y)$ always decreases.

Selection for X−Y

Since $\text{Cov}(X-Y,A) = \text{Cov}(X,A)-\text{Cov}(Y,A)$, we have $\text{Cov}(X-Y,A) = 2\bar{T}\,\text{V}(A)$ and similarly $\text{Cov}(X-Y,T) = (2\bar{A}-1)\,\text{V}(T)$. Thus $\bar{A}$ will steadily increase. If $\bar{A} > 0\cdot5$, both $\bar{A}$ and $\bar{T}$ rise steadily and $\text{Cov}(X,Y)$ always decreases. It $\bar{A} < 0\cdot5$, $\bar{T}$ falls while $\bar{A}$ rises. Then $\bar{A}(1-\bar{A})\,\text{V}(T)$ increases while $\bar{T}^2\,\text{V}(A)$ decreases, so $\text{Cov}(X,Y)$ must rise. But after a time $\bar{A}$ reaches $0\cdot5$, and from then on $\text{Cov}(X,Y)$ steadily decreases.

Selection against X

$\bar{T}$ and $\bar{A}$ always decrease. If $\bar{A} > 0\cdot5$, $\bar{A}(1-\bar{A})\,\text{V}(T)$ increases while $\bar{T}^2\,\text{V}(A)$ decreases, so $\text{Cov}(X,Y)$ increases until $\bar{A} = 0\cdot5$.   When $\bar{A} < 0\cdot5$, $\bar{A}(1-\bar{A})\,\text{V}(T)$ decreases, as does $\bar{T}^2\,\text{V}(A)$. The changes in $\text{Cov}(X,Y)$ are then uncertain, since their direction depends on the relative rates of change of $\bar{A}(1-\bar{A})\,\text{V}(T)$ and $\bar{T}^2\,\text{V}(A)$.

Selection against Y

$\bar{A}$ increases while $\bar{T}$ decreases. The results are as in selection against X, except that the conditions $\bar{A} > 0\cdot5$ and $\bar{A} < 0\cdot5$ must be interchanged.

Selection against X+Y

$\bar{A}$ is unchanged while $\bar{T}$ falls steadily so that $\text{Cov}(X,Y)$ always increases.

Selection against X−Y

$\bar{A}$ steadily decreases. If $\bar{A} < 0\cdot5$, $\bar{T}$ steadily rises and $\text{Cov}(X,Y)$ always decreases. If $\bar{A} > 0\cdot5$, $\bar{T}$ first falls, then rises once $\bar{A} = 0\cdot5$. Thus $\text{Cov}(X,Y)$ first increases.

Once $\bar{A} < 0\cdot 5$ the term $\bar{A}(1-\bar{A})\,V(T)$ steadily decreases while $\bar{T}^2\,V(A)$ increases, and therefore $\mathrm{Cov}(X,Y)$ always decreases.

Selection for $\alpha X+\beta Y$

A slightly more detailed analysis along the same lines as above, but estimating the actual rates of change in $\bar{A}$ and $\bar{T}$, can be used to study the change in $\mathrm{Cov}(X,Y)$ following selection for an arbitrary linear function $\alpha X+\beta Y$. Thus

$$\delta\bar{A} = i\,\mathrm{Cov}(A,\alpha X+\beta Y)/[\alpha^2\,V(X)+2\alpha\beta\,\mathrm{Cov}(X,Y)+\beta^2\,V(Y)]^{\frac{1}{2}}$$
$$\delta\bar{T} = i\,\mathrm{Cov}(T,\alpha X+\beta Y)/[\alpha^2\,V(X)+2\alpha\beta\,\mathrm{Cov}(X,Y)+\beta^2\,V(Y)]^{\frac{1}{2}}$$

Also we find that

$$\delta\mathrm{Cov}(X,Y) = (1-2\bar{A})\,V(T)\,\delta\bar{A}-2\bar{T}\,V(A)\,\delta\bar{T},$$

and on making the appropriate substitutions we find that the sign of $\delta\mathrm{Cov}(X,Y)$ is the same as the sign of

$$(1-2\bar{A})(\alpha-\beta)-2\bar{T}[\beta+(\alpha-\beta)\bar{A}].$$

This result may be used to clarify the conclusions for selecting against X when $\bar{A} < 0\cdot 5$, and if we put $\alpha = -1$, $\beta = 0$ we find that the sign of $\delta\mathrm{Cov}(X,Y)$ is that of

$$(1-2\bar{A})(-1)-2\bar{T}(-\bar{A})$$
$$= 2\bar{A}(1+\bar{T})-1.$$

Thus $\mathrm{Cov}(X,Y)$ will increase as long as $\bar{A} > 1/[2(1+\bar{T})]$.