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Genetic Correlation and Response to Selection in Simulated Populations

III. Correlated Response to Selection[1]

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Summary. One of two quantitative traits was selected and correlated response in the other trait was measured in each of 30 generations for models of additive genes and of complete dominance. Each trait was controlled by 48 loci with equal effects, segregating independently from frequencies of 0.5 in the initial generation. Intensity of selection regulated the number of offspring from randomly mating 24 males and 24 females each generation. Three each of genetic correlations between traits, intensities of selection, and amounts of environmental variation were simulated.

In the additive model correlated responses of the unselected trait to selection of the primary trait agreed closely with responses expected from theoretical considerations. In the model of complete dominance, responses of genotypic means of the unselected trait to selection of the primary trait in opposite directions were quite symmetrical for the first few generations but became distinctly asymmetrical in later generations. With little selection, response was fairly linear but became distinctly curvilinear as intensity of selection increased and environmental variance decreased. Between 15th and 30th generations some gains in the correlated trait to the 15th generation were lost.

Selection applied to one trait may result in correlated changes in other traits not under selection. This correlated response depends on genetic correlation. This paper will examine effects of intensity of selection, environmental variation, and genetic correlation upon the correlated response of traits not selected.

Little has been reported on whether theoretical treatment of correlated response to selection is adequate to explain responses realized in experiments. Falconer (1954) found reasonable agreement between theory and estimates of genetic correlation from correlated response in two-way selection of mice under different environmental conditions for body weight and for tail length. But he concluded the closeness of agreement should not be emphasized since the estimates had rather wide fiducial limits. Estimates of genetic correlation (0.7) between wing and thorax length in *Drosophila melanogaster* in the base population and correlated responses when either was selected separately agreed (Reeve and Robertson, 1953). Clayton et al. (1957) suggested that magnitude of genetic correlation affects the accuracy of predicted response, accidents of genetic sampling in the correlated trait making the response unpredictable for small genetic correlations. In their study with small genetic correlation (0.05 to 0.10 in the base population) between abdominal and sternopleural bristle numbers, correlated response became entirely unpredictable in later generations after moderate agreement earlier while inbreeding was low.

Expectations of correlated response frequently have failed to develop in experiments. Falconer (1960), Bell and McNary (1963), and Yamada and Bell (1963) observed asymmetrical correlated response to selection under two different environments. Siegel (1962) found asymmetrical response when selection was for body weight and breast angle in poultry, and Nordskog and Festing (1962) selecting body and egg weight in poultry observed asymmetry of realized genetic correlations in selection for high and low or between traits under selection. Clayton et al. (1957) also observed asymmetry in response of sternopleural bristle number to selection for increased and decreased abdominal bristle number. They concluded that genetic drift may be important in correlated response when genetic correlation is small.

The frequency of asymmetrical correlated responses seen does suggest some mechanism other than genetic sampling. Asymmetry of correlated response was quite frequent in algebraic studies and simulation of selection by Bohren et al. (1966).

Methods and Procedure

Experimental design and parameters simulated

A detailed description of the experimental design and mechanics of simulation has been presented by Parker *et al.* (1969). Simulated were: (1) Genetic correlations 0.25, 0.50, and 0.75 between quantitative traits X and Y in the initial generation of offspring. (2) Three intensities of selection by upper or lower truncation on the phenotype of X alone, 20, 50, and 80 percent of the offspring each generation. Y was not selected. (3) Three environmental variances, $V(E)$, for X and Y relative to the expected additive genetic variance $V(Ga)$ in the initial generation of offspring. The $V(E)$ were such that $h' =$

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$= V(Ga)/[V(Ga) + V(E)]$ was 0.1, 0.4, and 0.7. When all genetic variance was additive, h' was heritability in the narrow sense. With dominance, h' was larger than heritability in the narrow sense. The four factors each at three levels were considered in all combinations, and each combination or parameter set was replicated, 81 treatment combinations in a 3^4 factorial experiment replicated.

The experiment was conducted separately for two models of gene action:

a) Additive model with genotypic values of 2, 1, and 0 for the $++$, $+-$, and $--$ phases at each locus. Selection was for the $+$ allele.

b) Model of complete dominance with genotypic values of 2, 2, and 0 for the $++$, $+-$, and $--$ phases at each locus. Selection was upward for the dominant allele and downward for the recessive allele.

Each generation 24 male and 24 female parents produced the number of offspring required for the intensity of selection (b), 120 of each sex for 0.2 saved, 48 for 0.5, and 30 for 0.8. Mating was random by sampling with replacement and produced one offspring alternating sexes. Each parameter set was simulated for 30 nonoverlapping generations. Forty-eight loci with no linkage, no epistasis, no interaction between genotype and environment, and initial gene frequencies of 0.5 at each locus affected each trait. Expected genotypic means and variances in the initial generation were 48 and 24 for each trait in the additive model and 72 and 36 for complete dominance. Sufficient environmental variation was simulated to add to the genotypic to produce heritabilities of 0.1, 0.4, and 0.7 initially and was constant over generations. In complete dominance this resulted in heritabilities in the narrow sense of 0.095, 0.33, and 0.52.

Genetic correlation was attributed solely to pleiotropy. All genes affecting both traits affected each one in the same direction. The genetic correlation was set by the number of loci affecting both traits, 12 for 0.25, 24 for 0.50, and 36 for 0.75. The remaining loci of the 48 for each trait affected each trait independently. Genetic correlation was measured in each generation by product-moment correlation between genotypic values.

Simulating the population has been described previously by Parker *et al.* (1959).

Results and Discussion

Additive Model

Results of primary interest were changes in the genotypic mean of X in all combinations of selection intensity and of environmental variation and correlated changes in the genotypic mean of Y at three levels of genetic correlation between the two traits. The changes can be seen in the behaviour of genotypic means plotted against generation for each combination of conditions in Figures 1.1, 1.2, and 1.3. Replicates agreed and correlated response was independent of heritability of the correlated trait so each point on the graph for Y represents the average of six trials, 3 levels of environment replicated. The response of X, directly selected, was independent of both heritability of the correlated trait and genetic correlation and each point in the graph for X represents the average of 18 observations. Results of only every fifth generation are presented.

Trends in Figures 1.1, 1.2, and 1.3 are those expected. Lack of response of Y with small genetic correlation, low heritability, and low selection intensity (bottom of Figure 1.1) was a slight exception. Sampling had more opportunity to be influential in this circumstance, however.

When either intensity of selection was low or heritability was small or both, response to selection was linear over all 30 generations for X and Y for all genetic correlations. As expected, response increased with heritability or selection intensity and became distinctly curvilinear to the selection goal, especially in X (Figures 1.2, and 1.3). Only when heritability was high and selection intense (Figure 1.3, top) was the selection goal for X reached and then at the 30th generation.

To illustrate agreement of the results with those expected, responses in X and Y at 15th and 30th generations of selection have been presented in a different way in Table 1. The response is percent progress toward the goal of selection which differs for direct and indirect selection depending on the genetic correlation.

Table 1. *The response in trait X and correlated response in Y at three levels of genetic correlation, measured as percent of selection goal achieved at the 15th and 30th generation. (Additive model)*

Intensity of selection b	Environment h'_x	Generation	Response to selection as percent of goal X	Y		
				$r_G = 0.25$	0.50	0.75
	0.1	15	13	5	18	15
		30	26	18	34	28
0.8	0.4	15	25	14	22	21
		30	48	41	44	42
	0.7	15	35	34	33	33
		30	63	68	62	59
	0.1	15	30	35	32	31
		30	54	66	62	51
0.5	0.4	15	54	52	55	52
		30	86	92	91	86
	0.7	15	67	65	67	64
		30	96	82	95	94
	0.1	15	53	50	52	53
		30	83	85	82	82
0.2	0.4	15	80	93	84	79
		30	99	118	99	97
	0.7	15	93	97	92	95
		30	100	107	96	100

In selection directly for X, the genotypic mean can be moved from its initial value of 48 to 96 at which time all loci for X would be homozygous for the $+$ allele. This selection on X would move Y toward 60, 72, or 84 when genetic correlation was 0.25, 0.50, or 0.75 and the loci shared with X were homozygous for the $+$ allele.

The table substantiates what already has been observed in the graphs, close agreement between percent response in X and Y when genetic correlation was 0.5 or 0.75, intensity of selection > 0.8, and heritabi-

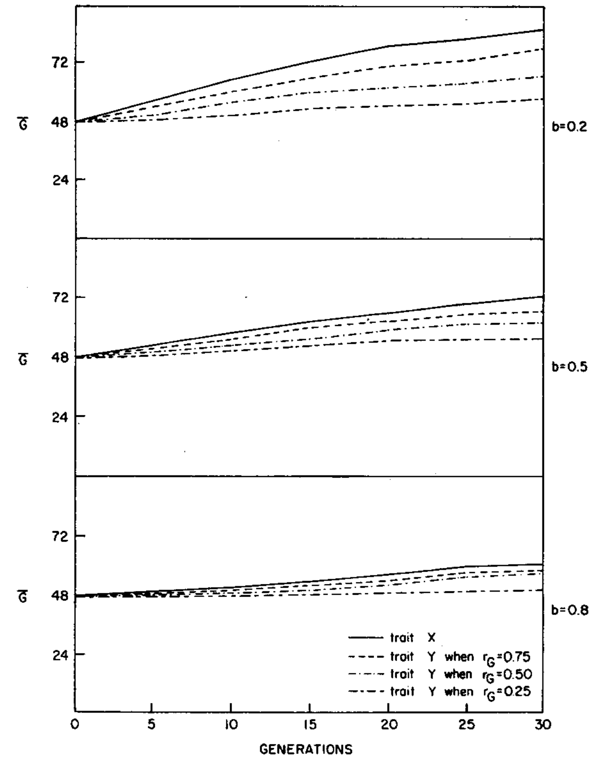

Fig. 1.1. Mean genetic progress at three intensities of selection when $h'_x = 0.1$ (additive model)

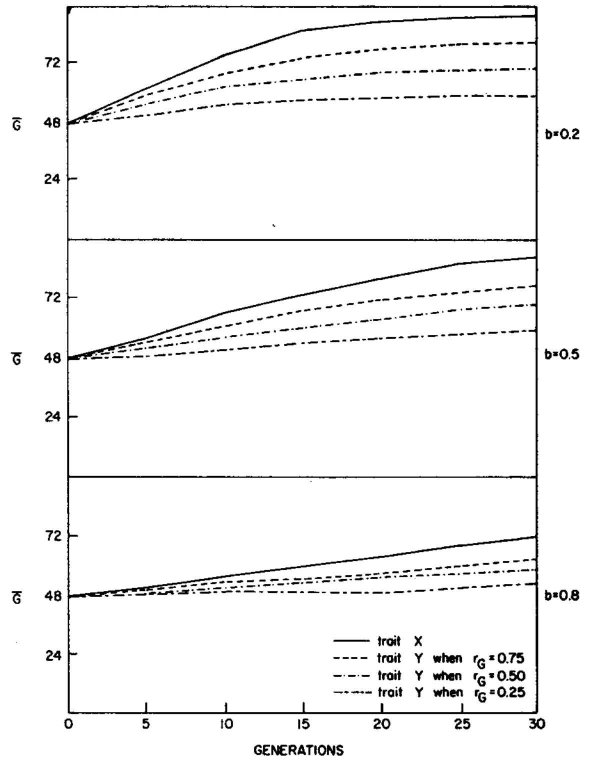

Fig. 1.2. Mean genetic progress at three intensities of selection when $h'_x = 0.4$ (additive model)

lity > 0.1. Less intense selection (fewer offspring to measure) and small genetic correlation (fewer loci in Y affected by selection) allowed larger influence of random sampling as shown by less agreement in response of X and Y, Y actually exceeding its goal occasionally.

Complete Dominance

Change in genotypic mean of X and correlated change in genotypic mean of Y at all treatment combinations are presented graphically over 30 generations in Figures 2.1, 2.2, and 2.3 for both directions of selection, upward for the dominant allele and downward for the recessive allele. As in the additive model, results for the selected X were averaged over replicates, levels of environment of Y, and initial genetic correlations so that each point represents the average of 18 trials. Results for the unselected correlated trait Y were averaged over replicates and levels of environment of Y, each point representing an average of six trials.

For complete dominance the expected maximum advance from selection again differed depending upon whether the trait was selected directly or indirectly and whether by upper or lower truncation. The differing goals for the two traits are in Table 2. The genotypic mean in the initial generation was 72 in every case. The maximum possible advance of the genotypic mean from selection by upper truncation

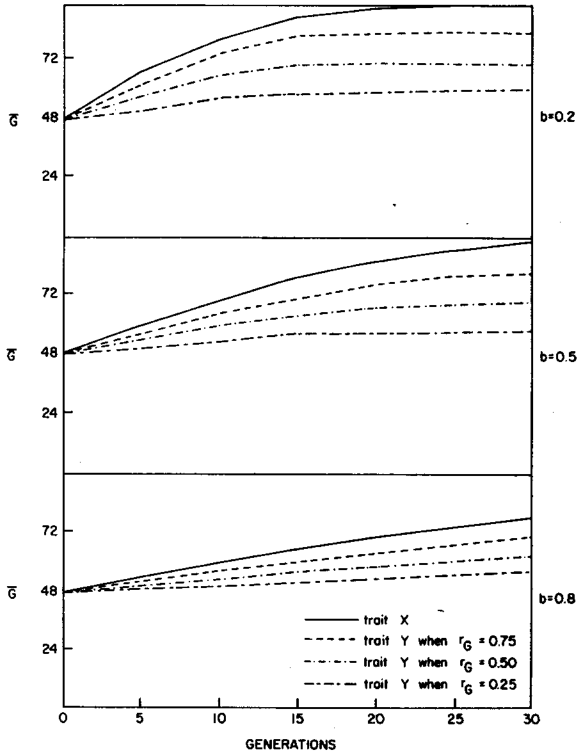

Fig. 1.3. Mean genetic progress at three intensities of selection when $h'_x = 0.7$ (additive model)

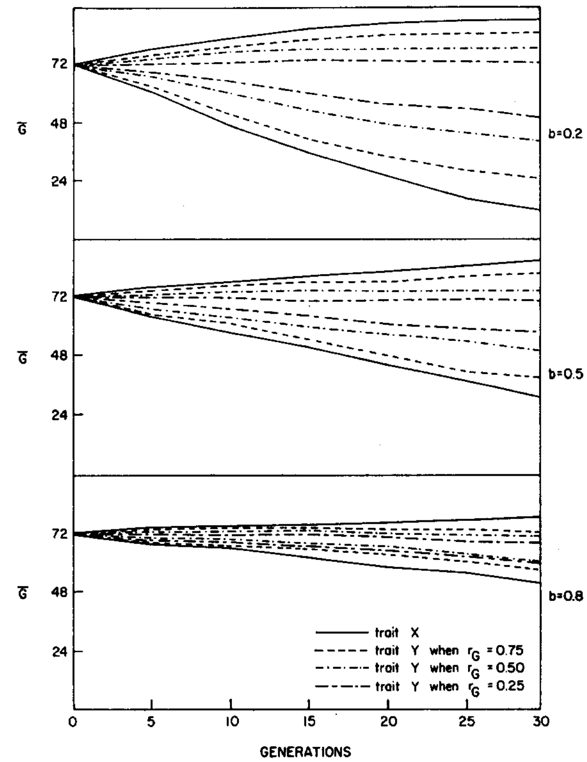

Fig. 2.1. Mean genetic progress at three intensities of selection when $h'_x = 0.1$ (complete dominance). Upper four curves, selection by upper truncation; lower four, selection by lower truncation

Table 2. *Progress possible for genotypic means of X and Y from selecting in different directions with various genetic correlations*

Trait	r_G	Direction of selection			
		Upward		Downward	
		Goal	Maximum advance	Goal	Maximum decline
X		96	24	0	72
Y	.25	78	6	54	18
Y	.50	84	12	36	36
Y	.75	90	18	18	54

was 24 while the maximum possible decline from selection by lower truncation was 72 units. The maximum response possible from downward selection was three times that possible by upward selection.

Asymmetry of response to selection in opposite directions has been observed frequently in selection experiments. In populations simulated here where dominance was complete at each locus and all dominant alleles affected the trait in the same direction, genetic asymmetry of response to selection was expected. Falconer (1960) referred to this as "directional dominance". When the purpose of selection is to move gene frequency of the desired gene from 0.5 to 1, the rate of change of gene frequency is larger

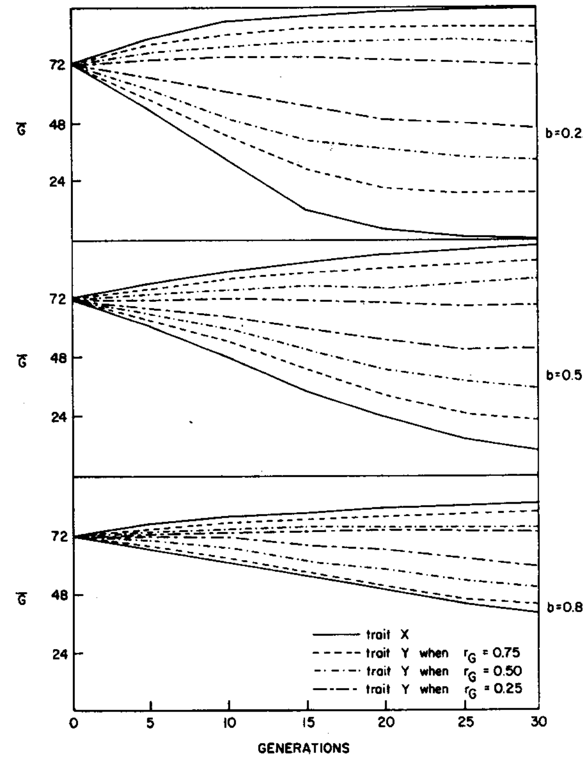

Fig. 2.2. Mean genetic progress at three intensities of selection when $h'_x = 0.4$ (complete dominance). Upper four curves, selection by upper truncation; lower four, selection by lower truncation

Table 3. *Response in trait X and correlated response in Y at three levels of genetic correlation, measured as percent of selection goal achieved at the 15th and 30th generation (Complete dominance, selection by upper truncation)*

Intensity of selection b	Environment h'_x	Generation	Response to selection as percent of goal			
				Y		
			X	$r_G = 0.25$	0.50	0.75
	0.1	15	10	—	6	4
		30	20	—	—	9
0.8	0.4	15	30	—	9	22
		30	53	—	11	43
	0.7	15	41	—	39	31
		30	65	—	55	42
	0.1	15	37	—	24	37
		30	58	—	20	55
0.5	0.4	15	62	—	49	54
		30	87	—	64	75
	0.7	15	75	32	62	75
		30	94	20	61	88
	0.1	15	60	26	51	55
		30	80	17	49	72
0.2	0.4	15	83	42	76	75
		30	95	—	70	87
	0.7	15	92	39	78	81
		30	98	5	59	86

— No progress toward goal.

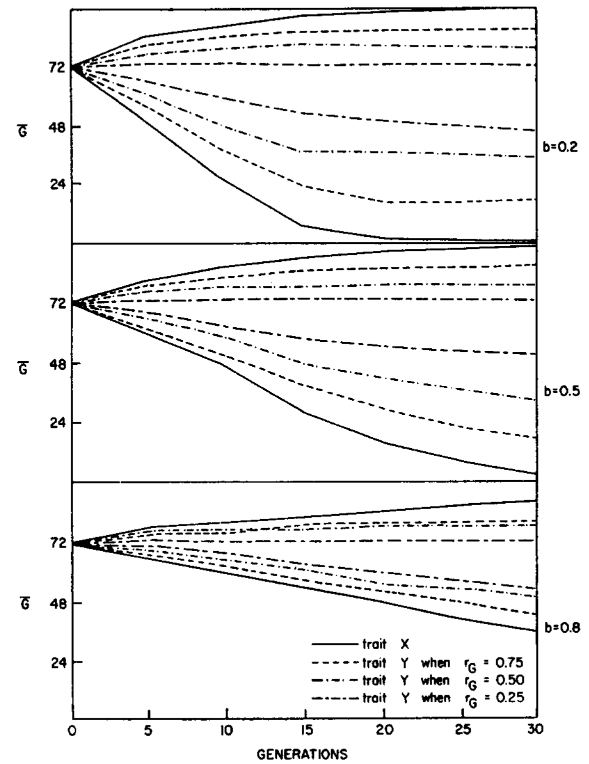

Fig. 2.3. Mean genetic progress at three intensities of selection when $h_x' = 0.7$ (complete dominance). Upper four curves, selection by upper truncation; lower four, selection by lower truncation

Table 4. *Response in trait X and correlated response in Y at three levels of genetic correlation, measured as percent of selection goal achieved at the 15th and 30th generation (Complete dominance, selection by lower truncation)*

Intensity of selection b	Environment h_x'	Generation	Response to selection as percent of goal			
				Y		
			X	r_G = 0.25	0.50	0.75
	0.1	15	14	32	14	13
		30	28	74	33	26
0.8	0.4	15	23	33	29	29
		30	46	64	60	52
	0.7	15	25	54	34	28
		30	53	101	64	56
	0.1	15	29	39	30	29
		30	57	75	59	62
0.5	0.4	15	51	67	58	52
		30	88	112	102	91
	0.7	15	59	80	67	59
		30	96	114	108	99
	0.1	15	51	65	48	57
		30	84	116	89	90
0.2	0.4	15	80	95	87	80
		30	99	144	110	99
	0.7	15	91	110	97	92
		30	100	142	108	104

when selection is for the recessive allele. Lush (1945) illustrated that selection for a dominant allele is most effective when the frequency of that allele is about 0.3 while selection for a recessive allele is most effective when its frequency is about 0.7.

Response to selection in opposite directions was, of course, quite symmetrical for the first few generations, while gene frequencies were still about 0.5 for the desired allele. However, as gene frequencies separated, response to selection for the recessive increased while selection for the dominant allele became much more difficult. When selection was upward for the dominant allele, average gene frequency never rose above 0.95 even with intense selection and small environmental variance. This simply reflects that to remove rare recessive genes by mass selection is difficult.

For little selection ($b = 0.8$), responses were nearly linear at all levels of heritability for both directions of selection. As intensity of selection increased, responses in both directions became asymmetrically curvilinear as they were reduced in later generations when frequencies of desired genes became low.

With upper truncation, correlated responses were less than expected particularly for smaller genetic correlation. At $r_G = 0.25$ unless selection was intense, response was generally negative; sometimes small gains early were lost by the 30th generation. As r_G increased to 0.50 and 0.75, correlated responses followed direct responses increasingly more closely, but most response was achieved by the 15th generation followed by little response or even losses in Y (Figure 2.3 top).

When selection was by lower truncation for recessive alleles, correlated responses of the unselected trait were generally proportional to direct responses and, in most cases, to genetic correlations. In all situations Y changed distinctly with selection downward for X.

Responses to selection in percent of goal of selection illustrate more clearly changes by the various conditions. These ratios for selection in opposite directions at generations 15 and 30 are in Tables 3 and 4. Y failed to respond to selection by upper truncation on X when genetic correlation was small unless selection was intense. Even then more progress had been made toward the selection limit at the 15th generation than at the 30th. Similarly for $r_G = 0.5$, progress toward the selection goal was always less in the correlated trait than in the selected trait; most of this progress had been achieved in the early generations of selection; and some was lost in later generations. For $r_G = 0.75$ percent of selection goal of correlated trait and selected trait agreed more closely, but the correlated trait never quite achieved as much relative progress as the selected trait.

In Table 4 of lower truncation most progress toward the goal of selection of the correlated trait was for genetic correlation 0.25. Possibly the smaller goal of the correlated trait could magnify a small deviation from the response expected; however, the trend was distinct and consistent and occurred to less degree in relative responses of the correlated trait when genetic correlation was 0.5 and 0.75. Progress in the trait correlated 0.75 tended to be slightly larger than in the selected trait, probably more consistently than from random sampling in the unselected part of the correlated trait.

This simulation of simple models reminds that the same population mechanisms and mode of gene action which control amounts and rates of response to direct selection also apply to correlated responses of an unselected trait. For example, in the same way that change becomes more difficult in selecting a dominant allele as the recessive allele becomes rare, a correlated response in an unselected trait is also difficult. This difficulty could be greater in more complex genetic systems of economic species.

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