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Genetic Correlation and Response to Selection in Simulated Populations

II. Model of Complete Dominance [1]

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Summary. Effects of truncation selection of a primary trait upon genetic correlation between the primary trait and an unselected secondary trait were observed during 30 generations. Populations were 24 male and 24 female parents per generation randomly mated with replacement, the number of offspring set by intensity of selection. Each trait was controlled by genes with equal effects and complete dominance segregating independently from starting frequencies of 0.5 at each of 48 loci. Three levels each of genetic correlation, selection, and environmental variation were simulated.

Genetic correlation decreased faster under more intense selection by lower than by upper truncation but behaved similarly in both by remaining near initial level when as many as one-half of the offspring were saved for parents. Truncation selection decreased genetic correlation in the offspring selected to be parents whether selection was by upper or lower truncation. Estimates of genetic correlation from covariances between phenotypes of parent and offspring were erratic for both directions of selection.

In a previous paper, Parker et al. (1969) discussed effects of truncation selection and of environmental variation upon behaviour of genetic correlation in simulated populations for an additive model of gene action. Results of a model of complete dominance are reported here. As in the additive model, cause of genetic correlation was solely pleiotropy.

Methods and Procedure

Experimental design and parameters simulated

The experimental design and mechanics of simulation have been described in the previous paper. Parameters simulated were the same as before except for the model of gene action. Briefly these were: 1) Two traits X and Y with selection by upper or lower truncation on the phenotype of the individual for X alone. Y was not selected, but correlated response was observed. 2) Three genetic correlations, 0.25, 0.50, and 0.75, between X and Y in the initial generation of offspring. 3) Three intensities of selection, 80, 50, and 20 percent of the offspring each generation. 4) Three environmental variances, $V(E)$, for X and Y relative to the expected additive genetic variance in the initial generation of offspring, $V(G_a)$. Levels were chosen that $h' = V(G_a)/[V(G_a) + V(E)]$ was equal to 0.1, 0.4, or 0.7. In complete dominance, when genetic variance other than additive is present, h' will be larger than heritability in the narrow sense.

Genetic correlation, intensity of selection for X, and environmental variation of X and Y were replicated in all combinations, 162 parameter sets. For complete dominance separate experiments selected upward for the dominant allele and downward for the recessive allele. Contributions at each locus to genotypic values were 2, 2, and 0 for the $+\,+$, $+\,-$, and $-\,-$ phases.

Populations were bisexual, diploid, and both sexes expressed the traits. Each generation 24 male and 24 female parents produced a number of offspring determined by intensity of selection desired. Parents were mated at random by sampling with replacement, and each mating produced one offspring alternating sexes. Each parameter set was continued for 30 nonoverlapping generations. Affecting each trait were 48 loci with no linkage, no epistasis, and no interaction between genotype and environment. Gene frequency at each locus was 0.5 in the initial generation to allow for changes in either direction.

In complete dominance the genotypic value was $2(n_1 + n_2)$, where n_1 is number of $+\,+$ phases and n_2 number of $+\,-$ phases in the genotype. The expected genotypic mean and variance in the initial generation (Kempthorne, 1957) were $2nq\,(2-q)$ and $4n[2q(1-q)^3 + q^2(1-q)^2]$ where n is number of loci affecting the trait. With 48 loci affecting each trait, expected mean and variance in the first generation in populations simulated were 72 and 36. When q, gene frequency, was 0.5, genotypic variance was composed of additive variance of 24 and dominance variance of 12.

Simulating environmental variation in ratios (h') of 0.1, 0.4, and 0.7 to the expected additive genetic variance in the first generation of offspring resulted in heritabilities in the narrow sense of 0.095, 0.33, and 0.52. The environmental component was independent of genotype and constant over generations.

Simulation of genetic correlation was given in the previous paper. Genetic correlation was attributed to pleiotropic gene action, and all genes affecting the two traits affected each one in the same direction making a positive covariance. Genetic correlation was measured in each generation by product-moment correlation between genotypic values and also estimated by covariances between phenotypes of parent and offspring (Hazel, 1943).

Mechanics of Simulation

The program to simulate populations was the same as for the additive model (Parker, *et al.*, 1969) except for genotypic evaluation and selection of parents of the next generation. In the additive model, the genotype of an individual could be evaluated simply by summing 1's or 0's over all 48 loci for each X and Y. In complete dominance the number of $+\,+$ and $+\,-$ phases in the 48 loci

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affecting each trait was multiplied by two to give the numerical genotypic value for that trait.

Only the best 24 phenotypes of each sex were selected each generation in the additive model. In complete dominance, however, the best 24 phenotypes of each sex in trait X were chosen in one experiment and the worst 24 were chosen in another, separate experiment.

Results and Discussion

In complete dominance with contributions to genotypic values of 2, 2, and 0 for $++$, $+-$, and $--$ genotypes at each locus, variation between replicates was small, and all statistics presented graphically are averages of two replicates. Statistics were calculated for each of 30 generations of selection in a given parameter set, but results of only every fifth generation are presented. Expected genotypic means and variances in the first generation of offspring were 72 and 36 for both X and Y. Expected genotypic covariances were 9, 18, and 27 for initial expected genetic correlations of 0.25, 0.50, and 0.75. Expected environmental variance for each trait was 10.3, 36, and 216 for $h' = 0.7$, 0.4, and 0.1. Heritability of the two traits in the narrow sense would be less than h' in each case. Results in the first generation of offspring showed close agreement with expected values.

Effect of selection on genetic correlation

Figures 1.1, 1.2, and 1.3 show changes in genetic correlation (product-moment correlation of genotypic

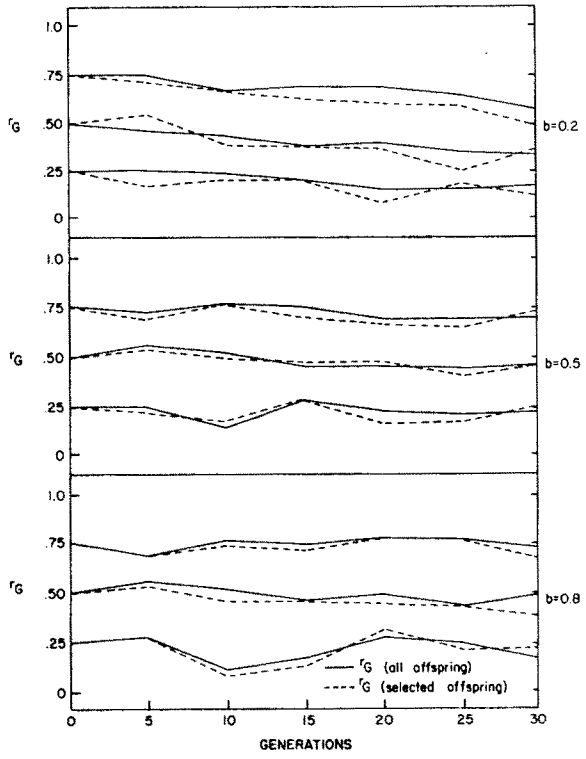

Fig. 1.1. Change in genetic correlation at three intensities of selection by upper truncation when $h'_x = 0.1$ (complete dominance)

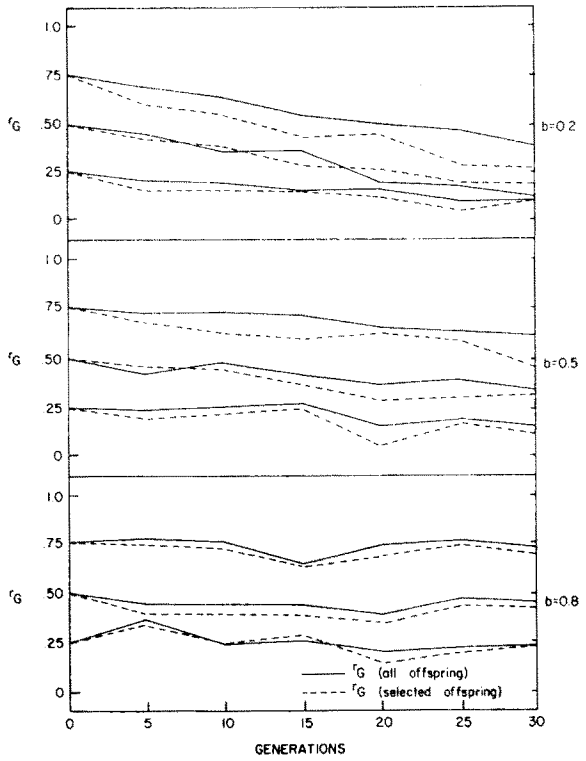

Fig. 1.2. Change in genetic correlation at three intensities of selection by upper truncation when $h'_x = 0.4$ (complete dominance)

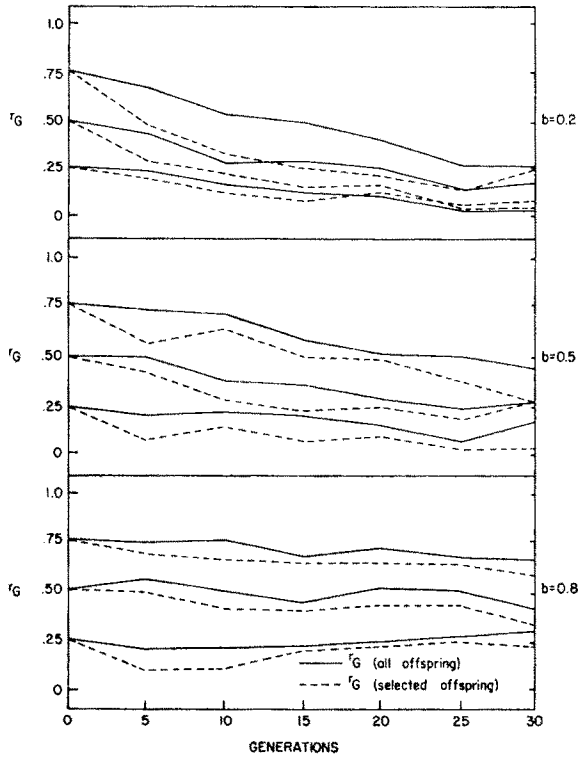

Fig. 1.3. Change in genetic correlation at three intensities of selection by upper truncation when $h'_x = 0.7$ (complete dominance)

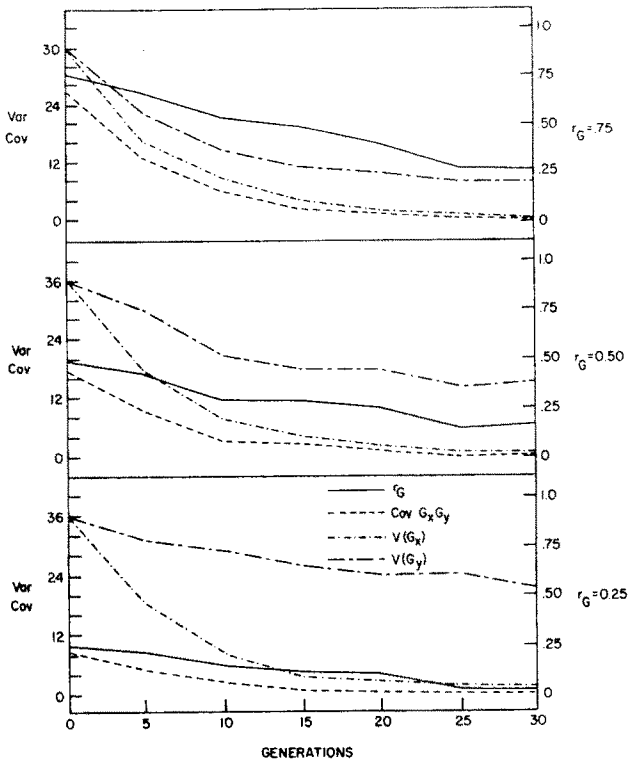

Fig. 2. Relationships between genotypic variances, covariance, and genetic correlation for three initial genetic correlations when $b = 0.2$ and $h_x' = 0.7$ (complete dominance). Selection by upper truncation

values) over 30 generations of selection by upper truncation of phenotypes. The number of individuals upon which r_G is measured is always 48 in the selected group but varies in the unselected offspring with intensity of selection. Correlations include 60 individuals when $b = 0.8$, 96 individuals when $b = 0.5$, and 240 individuals when $b = 0.2$.

Since environmental variation of trait Y, the unselected trait, had no effect on genetic correlation, r_G was averaged over the three environmental variances of Y and, as stated before, over two replicates. Thus, each point on the graphs represents six genetic correlations averaged by transforming to z.

The pattern of results is a remarkable consistency of the genetic correlation in the unselected offspring over the 30 generations of selection at all levels of selection and all initial genetic correlations. Genetic correlation was maintained under little selection or large environmental variance with estimates tending to fluctuate more with initial $r_G = 0.25$ than otherwise. With intense selection ($b = 0.2$) genetic correlation tended to decline over the 30 generations, although the amount of decline was less than shown previously in the additive model (Parker et al., 1969). At intense selection and small environmental variance, for example, (top Figure 1.3), genetic correlation although declining steadily did not become zero even after 30 generations of selection.

The consistency exhibited by all nine graphs indicates that selection must be intense and heritability large before affecting appreciably genetic correlation. Most traits in animals likely are controlled by much more complex genetic systems where genetic correlation should be even less affected by selection.

An accompanied decrease in genotypic variance of one or both traits could offset a decrease in genotypic covariance and maintain the genetic correlation. When both level of selection and heritability were low, genotypic covariance and variances were maintained over the 30 generations of selection. With more intense selection, genotypic covariance decreased more rapidly. Genotypic variances of the selected trait showed a concurrent decrease, however, and acted to maintain genetic correlation near its initial level. At the high level of selection ($b = 0.2$) decay in covariance and variance of the selected trait became quite rapid and distinctly curvilinear (Figure 2). The decrease began immediately and probably was largest in first generations. The curve dropped distinctly between first and fifth generations and then leveled out through the 30th generation. This agrees with expectation of selection for a dominant allele, change in gene frequency by selection becoming more difficult as frequency of the recessive gene becomes less.

Figures 3.1, 3.2, and 3.3 show changes in genetic correlation over the 30 generations of selection by lower truncation for the recessive allele. Behaviour of genetic correlation in the unselected offspring conformed closely in most cases to that already observed in complete dominance when selection was by upper truncation. When selection was intense, however, decrease in genetic correlation was more rapid and r_G reached zero by the 25th generation of selection when heritability was high (Figure 3.3).

Decay in genotypic covariance and variance of the selected trait was quite different for selection by lower truncation (Figure 4). In upper truncation, a rapid decrease occurred in early generations of selection while lower truncation did not change genotypic covariance or variances greatly until after the fifth generation, and then the change became quite rapid. These observations follow quite logically from theory of rate of change in gene frequency under selection when dominance exists. Essentially the same conditions are acting to maintain genetic correlation as in selection by upper truncation.

Genetic correlation in the truncated distribution

The effect of truncation of X on genetic correlation has been graphed for both experiments in the complete dominance model. Broken lines in Figures 1.1 to 1.3 and in Figures 3.1 to 3.3 represent genetic correlation in the group selected to be parents for upward and downward selection.

As in the additive model, truncation caused some decrease in genetic correlation. When selection was

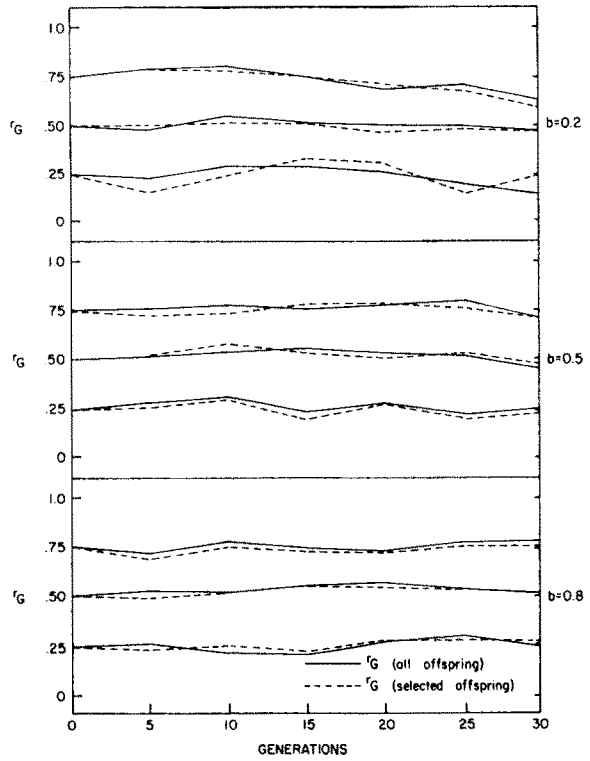

Fig. 3.1. Change in genetic correlation at three intensities of selection by lower truncation when $h_x' = 0.1$ (complete dominance)

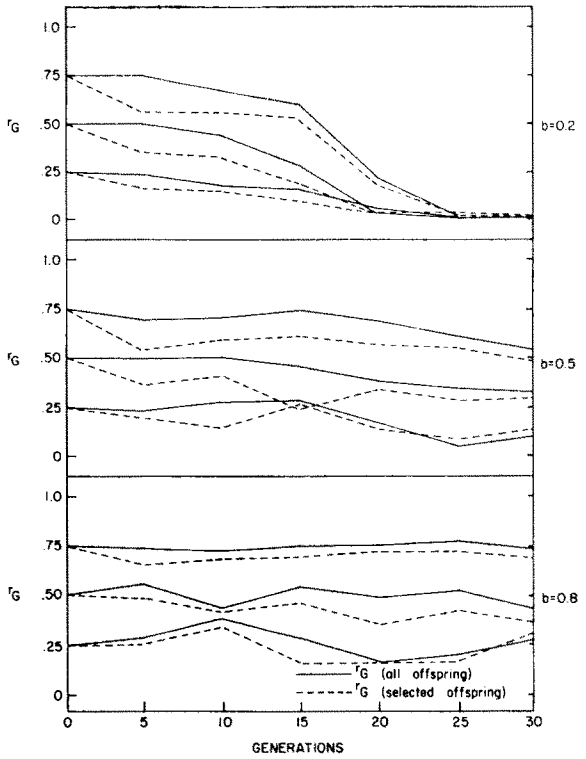

Fig. 3.3. Change in genetic correlation at three intensities of selection by lower truncation when $h_x' = 0.7$ (complete dominance)

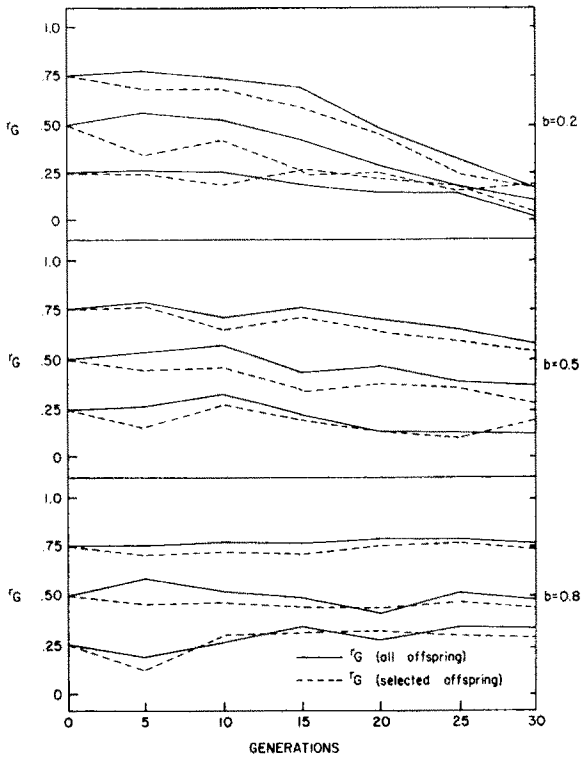

Fig. 3.2. Change in genetic correlation at three intensities of selection by lower truncation when $h_x' = 0.4$ (complete dominance)

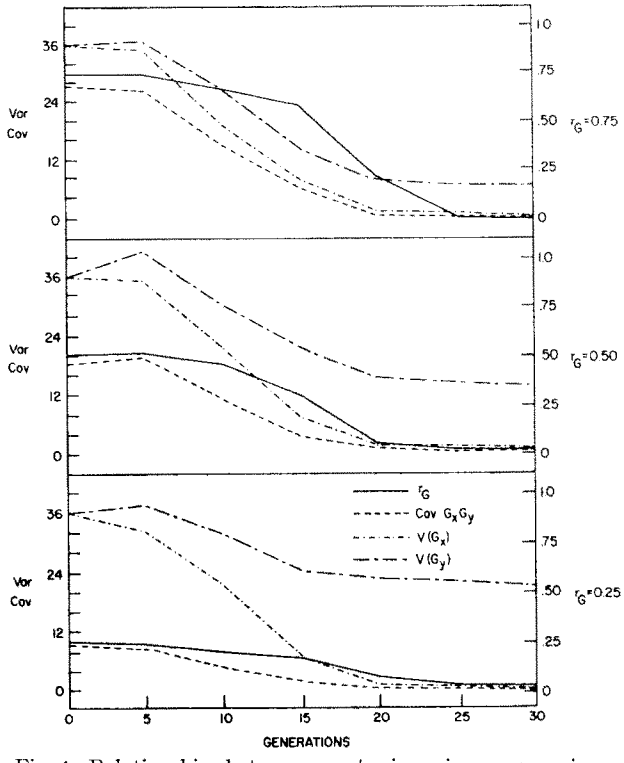

Fig. 4. Relationships between genotypic variances, covariance and genetic correlation at three initial genetic correlations when $b = 0.2$ and $h_x' = 0.7$ (complete dominance). Selection by lower truncation

by upper truncation, reduction in genetic correlation was a function of both heritability and selection. Initial genetic correlation also affected the decrease with a larger and more consistent reduction when initial correlation was 0.75 than when 0.25. When selection was intense ($b = 0.2$) and environmental variance was small (Figure 1.3), the amount of decrease became very large when initial genetic correlation was 0.75. In fact, genetic correlation in the selected group was generally about 0.2 less than correlation in the whole offspring generation. Again, however, when intensity of selection and heritability were both low, reduction in genetic correlation was fairly small as expected.

When selection was by lower truncation (Figures 3.1 to 3.3), results were similar, the amount of reduction increasing as heritability increased. Environment apparently was more important than selection in decreasing correlation in the selected group.

Estimates of genetic correlation from phenotypic covariances between parent and offspring

In complete dominance two estimates of genetic correlation were obtained from covariances between phenotypes of parent and offspring. Erratic results for the additive model prompted rejecting ratios of geometric means if the two covariances in numerator or denominator were of unlike sign in the model of dominance. This condition occurred in the majority of cases. Results of arithmetic means of the two covariances in the numerator were equally as erratic whether selection was by upper or lower truncation as those for the additive model. Where the correlation could be computed by the geometric means in both numerator and denominator, seldom did the correlation by geometric mean agree with that by arithmetic mean.

Random fluctuation prevented observing a predictable pattern of deviations of estimates from r_G. There was, however, the same tendency for the correlation to be underestimated as in the additive model. The results emphasize the wisdom of not being confident of genetic correlations from parent-offspring covariances in a population of the size simulated in this study and when selection is intense.

References

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