

CONSEQUENCES OF TRUNCATION SELECTION BASED ON COMBINATIONS OF INDIVIDUAL PERFORMANCE AND GENERAL COMBINING ABILITY

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Summary

The objective of this study is to examine in detail the immediate and long-term consequences of nine combinations of truncation selection. These combinations result from applying one of the following conditions to each sex: (i) no selection, (ii) individual selection, and (iii) general combining ability selection.

Consequences of selection and relaxation from selection are examined for populations of increasing genetic complexity: i.e. for populations generated by alleles at one locus, at two loci, and at an arbitrary number of loci. It is shown that the immediate response to all forms of selection applied to populations involving more than one locus is complicated by the inclusion of certain epistatic variances. In the most general genetic situation the immediate response to selection is formulated in terms of covariances among relatives, the particular covariance depending on the particular form of selection.

It is demonstrated, however, that on relaxation from selection the cumulative epistatic response to selection disappears, leaving as a residual the genetic gains predicted on the basis of independent, non-interacting loci. The rate of disappearance of these epistatic contributions is a function of the linkage parameters.

I. INTRODUCTION

This paper is the third in a series which is devoted to a re-examination of the immediate and long-term responses resulting from different selection schemes when the important phenomena of epistasis and linkage are considered.

The first paper of this series (Griffing 1960*a*) examined the consequences of mass selection in detail. The study was concerned with truncation selection, based on the phenotype of the individual, within the framework of a breeding programme consisting of cycles. The original population was assumed to consist of a random-mating population in equilibrium, and in each cycle the selected individuals were mated at random to provide the population for the next cycle. It was also assumed that the selection differential and recombination frequencies were identical for both sexes. In the second paper (Griffing 1960*b*) the restriction on recombination frequencies was relaxed.

In the present study, a more generalized approach is considered which relaxes the restrictions on both recombination frequencies and selection differentials for the two sexes. More importantly, however, the present approach provides prediction formulae for the nine possible combinations which result when any one of the following three situations is applied to either sex: (i) no selection, (ii) selection of individuals based on their own phenotype, and (iii) selection of individuals based on the performance of their half-sib progeny.

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There are at least two ways in which the evaluation of half-sib progenies may be used in selection. Firstly, entire half-sib families may be selected on the basis of their mean performance. Such family selection has sometimes been termed half-sib selection in the animal breeding literature. Secondly, half-sib families may be used to progeny-test individuals. The selected individuals, then, are mated at random to provide the breeding population for the next cycle. It is this last form of selection, which will be termed general combining ability selection, that is considered in this study.

The analyses are presented for populations having successively higher levels of genetic complexity, i.e. populations generated by alleles at one locus, at two loci, and at an arbitrary number of loci. Most attention is devoted to those populations involving two loci, since the consequences of selection and relaxation following selection can be given in detail in terms of gene effects, linkage parameters, and genotypic variance components. The two-locus analysis is generalized to include (i) any number of alleles at each locus, (ii) any system of dominance and epistatic parameters, and (iii) recombination values which may be different for the two sexes.

This study is of interest because it provides, for very general genetic situations, prediction formulae for selection schemes in which the males may or may not be subjected to the same kind and intensity of selection as that applied to the females. Thus, the theory describes the consequences of mass or general combining ability selection operating on one sex only, of mass or general combining ability selection operating simultaneously (but not necessarily with the same intensity) on both sexes, and, finally, of combinations of mass and general combining ability selection operating on the two sexes.

II. CONSEQUENCES OF SELECTION AMONG GENOTYPES GENERATED BY ALLELES AT ONE LOCUS

(a) *Parameters of the Random-mating Population in Equilibrium*

This section is concerned with selection which starts with a random-mating population in equilibrium generated by an arbitrary number of alleles A_1, A_2, \dots, A_m with frequencies p_1, p_2, \dots, p_m , at a single locus. This population may be represented as

$$\Pi_0 = \sum_{ij} p_i p_j A_i A_j.$$

The male and female genotypic values for $A_i A_j$ are assumed to be identical and are designated as d_{ij} , such that

$$\sum_{ij} p_i p_j d_{ij} = 0.$$

The genotypic value, d_{ij} , is characterized by the usual gene model,

$$d_{ij} = a_i + a_j + \delta_{ij},$$

where

$$a_i = \sum_j p_j d_{ij} = \text{additive effect of } A_i,$$

and

$$\delta_{ij} = d_{ij} - a_i - a_j = \text{dominance effect associated with the genotype } A_i A_j.$$

The total genotypic variance may be partitioned as follows:

$$\sum_{ij} p_i p_j d_{ij}^2 = 2 \sum_i p_i \alpha_i^2 + \sum_{ij} p_i p_j \delta_{ij}^2,$$

which is represented as

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2,$$

where

$$\sigma_G^2 = \sum_{ij} p_i p_j d_{ij}^2 = \text{total genotypic variance},$$

$$\sigma_A^2 = 2 \sum_i p_i \alpha_i^2 = \text{additive genetic variance},$$

and

$$\sigma_D^2 = \sum_{ij} p_i p_j \delta_{ij}^2 = \text{dominance variance}.$$

The half-sib progeny of $A_i A_j$ are generated as

$$\begin{aligned} & \frac{1}{2} (A_i + A_j) \sum_k p_k A_k \\ &= \frac{1}{2} \sum_k p_k (A_i A_k + A_j A_k). \end{aligned}$$

Therefore, the expected half-sib progeny mean of $A_i A_j$ is

$$\gamma_{ij} = \frac{1}{2}(\alpha_i + \alpha_j).$$

(b) Selection Values

The assumptions and detailed argument required for defining the selection value for a particular genotype are given in a previous paper (Griffing 1960a). It is only necessary to state here that the genotypic variability of the characteristic which is being studied is assumed to be controlled by genes, each of small effect, at many loci, and that the phenotypic variability is normally distributed with mean zero and variance σ^2 . Following Kimura (1958), the selection value is defined to be proportional to the probability that an individual of the given genotype survives selection. In the following argument the selection values will be defined for males and females separately and generalized to accommodate the three conditions: (i) no selection, (ii) individual selection, (iii) general combining ability (denoted as g.c.a.) selection. Thus, the selection value for the male $A_i A_j$ is

$${}_m w_{ij} = 1 + \frac{{}_m i_a}{{}_m \sigma_a^2} ({}_m \lambda_{ij}), \quad (1)$$

where

${}_m i_a$ = selection differential for males measured in terms of the phenotypic value used as test criterion (a represents no, individual, or g.c.a. selection),

${}_m \sigma_a^2$ = variance of the phenotypic value used as test criterion.

$$\frac{{}_m i_{\text{no}}}{{}_m \sigma_{\text{no}}^2} ({}_m \lambda_{ij}) = 0 \quad (\text{no selection}),$$

$$\frac{{}_m i_{\text{ind.}}}{{}_m \sigma_{\text{ind.}}^2} ({}_m \lambda_{ij}) = \frac{{}_m i_{\text{ind.}}}{{}_m \sigma_{\text{ind.}}^2} (d_{ij}) \quad (\text{individual selection}), \text{ and}$$

$$\frac{{}_m i_{\text{h.s.}}}{{}_m \sigma_{\text{h.s.}}^2} ({}_m \lambda_{ij}) = \frac{{}_m i_{\text{h.s.}}}{{}_m \sigma_{\text{h.s.}}^2} (\gamma_{ij}) \quad (\text{g.c.a. selection}).$$

The expectation of the variance, ${}_m\sigma_a^2$, will depend not only on the method of selection but, in the case of g.c.a. selection, on the structure of the experimental data giving rise to the half-sib mean values.

For selection based on the individual phenotype, ${}_m\sigma_{\text{ind.}}^2$ is simply the phenotypic variance among individuals, i.e. ${}_m\sigma_{\text{ind.}}^2 = \sigma^2$. For g.c.a. selection, each male is most simply evaluated by taking the mean of n half-sib progeny in a completely randomized experiment. The expected value of the variance of these mean values is then,

$${}_m\sigma_{\text{h.s.}}^2 = 1/n \{ \sigma^2 - [\text{Cov}(\text{HS}) + \sigma_f^2] \} + [\text{Cov}(\text{HS}) + \sigma_f^2],$$

where

$\text{Cov}(\text{HS})$ = half-sib covariance in the random-mating population in equilibrium,

and

σ_f^2 = variance due to the effect common to all members of the same family and uncorrelated with effects common to other families.

The selection value for the female $A_k A_l$ is

$${}_fw_{kl} = 1 + \frac{{}_f\dot{i}_\beta}{{}_f\sigma_\beta^2}({}_f\lambda_{kl}), \quad (2)$$

where the elements in the selection value are defined in a similar manner to those in the male.

(c) Consequences of One Cycle of Selection

The objective of this section is to determine the change in population mean which results with one cycle of truncation selection. The original population, Π_0 , is assumed to be a random-mating population in equilibrium. The population resulting from one cycle of selection is designated as Π_1 and its parameters indicated by a sub- or superscript "1". The elements and variances associated with the gene model are always assumed to be those pertaining to Π_0 .

The frequency of the male $A_i A_j$ following selection from Π_0 is

$$p_i p_j ({}_m w_{ij}) = p_i p_j \left[1 + \frac{{}_m\dot{i}_a}{{}_m\sigma_a^2} ({}_m\lambda_{ij}) \right].$$

Since $A_i A_j$ produces the following gametic array,

$$\frac{1}{2}(A_i + A_j),$$

the total gametic array for all selected males is

$$\begin{aligned} & \sum_{ij} p_i p_j ({}_m w_{ij}) \left[\frac{1}{2}(A_i + A_j) \right] \\ &= \sum_i ({}_m p_i^1) A_i, \end{aligned}$$

where

$$\begin{aligned} {}_m p_i^1 &= p_i \sum_j p_j ({}_m w_{ij}) \\ &= p_i \left[1 + \frac{{}_m\dot{i}_a}{{}_m\sigma_a^2} \sum_j p_j ({}_m\lambda_{ij}) \right] \\ &= p_i \left[1 + \frac{{}_m\dot{i}_a}{{}_m\sigma_a^2} ({}_m\lambda_{i.}) \right]. \end{aligned}$$

Similarly, the frequency for the allele, A_k , among the selected females is

$$f p_k^1 = p_k \left[1 + \frac{f i_{\beta}}{f \sigma_{\beta}^2} (f \lambda_k) \right].$$

Hence, the progeny mean resulting from randomly mating the selected males and females is equal to

$$\sum_{ik} (m p_i^1)(f p_k^1) d_{ik},$$

which is approximately equal to

$$\frac{m i_a}{m \sigma_a^2} \sum_i p_i (m \lambda_i) d_i + \frac{f i_{\beta}}{f \sigma_{\beta}^2} \sum_k p_k (f \lambda_k) d_k,$$

where, for either sex,

$$\lambda_i = a_i \quad (\text{individual selection}),$$

and

$$\lambda_i = \frac{1}{2} a_i \quad (\text{g.c.a. selection}).$$

For a discussion of the approximations which are necessary in the above argument, the reader is referred to the first paper in the series (Griffing 1960a).

The specific results for each of the nine possible selection schemes will be given after the next section which briefly reviews the consequences of n cycles of selection.

(d) Consequences of n Cycles of Selection

The consequences can be determined for n cycles of selection in which the type of selection in either sex may change from one cycle to another. However, for simplicity, consider only the case where the same type of selection is applied to a given sex in n successive cycles. In this case, it can be shown that the mean of Π_n is approximately,

$$\sum_{ik} (m p_i^n)(f p_k^n) d_{ik},$$

where

$$m p_i^n \cong p_i \left[1 + \frac{1}{2}(n+1) \frac{m i_a}{m \sigma_a^2} (m \lambda_i) + \frac{1}{2}(n-1) \frac{f i_{\beta}}{f \sigma_{\beta}^2} (f \lambda_i) \right],$$

and

$$f p_k^n \cong p_k \left[1 + \frac{1}{2}(n+1) \frac{f i_{\beta}}{f \sigma_{\beta}^2} (f \lambda_k) + \frac{1}{2}(n-1) \frac{m i_a}{m \sigma_a^2} (m \lambda_k) \right].$$

Then

$$\mu_n \cong n \left[\frac{m i_a}{m \sigma_a^2} \sum_i p_i (m \lambda_i) d_i + \frac{f i_{\beta}}{f \sigma_{\beta}^2} \sum_k p_k (f \lambda_k) d_k \right].$$

The results of all possible selection schemes are given in Table 1. These results show that the contributions to the increment change in the population mean are independent for the two sexes. The exact contribution for a given sex depends on the form of selection to which the sex is exposed.

If more than one locus is considered and linkage and epistasis ignored, the cumulative effect for all loci is simply the sum of increments over all loci. However, with the possibility of linkage and epistasis, the *immediate* response to selection may be different from that illustrated above with independent and non-interacting loci. These complications are considered in the next section.

TABLE 1
INCREMENT CHANGES IN POPULATION MEANS DUE TO n CYCLES OF SELECTION FOR POPULATIONS
GENERATED BY INDEPENDENT, NON-INTERACTING LOCI

	Females:		
	No Selection	Individual Selection	g.c.a. Selection
Males:			
No selection	0	$\frac{f^{i\text{ind.}}}{f\sigma_{\text{ind.}}^2} \frac{1}{2} n\sigma_A^2$	$\frac{f^{i\text{h.s.}}}{f\sigma_{\text{h.s.}}^2} \frac{1}{4} n\sigma_A^2$
Individual selection	$\frac{m^{i\text{ind.}}}{m\sigma_{\text{ind.}}^2} \frac{1}{2} n\sigma_A^2$	$\frac{m^{i\text{ind.}}}{m\sigma_{\text{ind.}}^2} \frac{1}{2} n\sigma_A^2 + \frac{f^{i\text{ind.}}}{f\sigma_{\text{ind.}}^2} \frac{1}{2} n\sigma_A^2$	$\frac{m^{i\text{ind.}}}{m\sigma_{\text{ind.}}^2} \frac{1}{2} n\sigma_A^2 + \frac{f^{i\text{h.s.}}}{f\sigma_{\text{h.s.}}^2} \frac{1}{4} n\sigma_A^2$
g.c.a. selection	$\frac{m^{i\text{h.s.}}}{m\sigma_{\text{h.s.}}^2} \frac{1}{4} n\sigma_A^2$	$\frac{m^{i\text{h.s.}}}{m\sigma_{\text{h.s.}}^2} \frac{1}{4} n\sigma_A^2 + \frac{f^{i\text{ind.}}}{f\sigma_{\text{ind.}}^2} \frac{1}{2} n\sigma_A^2$	$\frac{m^{i\text{h.s.}}}{m\sigma_{\text{h.s.}}^2} \frac{1}{4} n\sigma_A^2 + \frac{f^{i\text{h.s.}}}{f\sigma_{\text{h.s.}}^2} \frac{1}{4} n\sigma_A^2$

III. CONSEQUENCES OF SELECTION AMONG GENOTYPES GENERATED BY ALLELES AT TWO LOCI WHICH MAY BE LINKED

(a) *Parameters of the Random-mating Population in Equilibrium*

It is assumed that the selection programme commences with a random-mating population in equilibrium which, as before, is designated as Π_0 . The following notation is used (Kempthorne 1957) for this population:

$$\sum_i p_i^1(A_i^1) = \text{allelic array at locus (1),}$$

$$\sum_{ij} p_i^1 p_j^1(A_i^1 A_j^1) = \text{genotypic array at locus (1),}$$

$$\sum_k p_k^2(A_k^2) = \text{allelic array at locus (2),}$$

$$\sum_{kl} p_k^2 p_l^2(A_k^2 A_l^2) = \text{genotypic array at locus (2),}$$

y_m = recombination frequency exhibited by the
males for the two loci,

and

y_f = recombination frequency exhibited by the
females for the two loci.

The initial equilibrium population may be generated as the product of the two genotypic arrays, i.e.

$$\begin{aligned}\Pi_0 &= [\sum_{ij} p_i^1 p_j^1 (A_i^1 A_j^1)] [\sum_{kl} p_k^2 p_l^2 (A_k^2 A_l^2)], \\ &= \sum_{ijkl} p_i^1 p_j^1 p_k^2 p_l^2 (A_i^1 A_j^1 A_k^2 A_l^2),\end{aligned}$$

or, more usefully, as the product of the gametic arrays for the two sexes as follows:

$$\begin{aligned}\Pi_0 &= [\sum_{ik} ({}_m f_{ik}^0) (A_i^1 A_k^2)] [\sum_{jl} ({}_f f_{jl}^0) (A_j^1 A_l^2)] \\ &= \sum_{ijkl} ({}_m f_{ik}^0) ({}_f f_{jl}^0) [(A_i^1 A_k^2) (A_j^1 A_l^2)] \\ &= \sum_{ijkl} p_i^1 p_j^1 p_k^2 p_l^2 (A_i^1 A_j^1 A_k^2 A_l^2),\end{aligned}$$

where

$${}_m f_{ik}^0 = p_i^1 p_k^2 = \text{frequency of the gamete } A_i^1 A_k^2 \text{ produced by the males in } \Pi_0,$$

and

$${}_f f_{jl}^0 = p_j^1 p_l^2 = \text{frequency of the gamete } A_j^1 A_l^2 \text{ produced by the females in } \Pi_0.$$

The genotype value of $(A_i^1 A_k^2) (A_j^1 A_l^2)$ in Π_0 is denoted as $d_{ik, jl}$ such that

$$\sum_{ijkl} p_i^1 p_j^1 p_k^2 p_l^2 d_{ik, jl} = 0.$$

This genotypic value is characterized by the following model (Kempthorne 1957):

$$\begin{aligned}d_{ik, jl} &= \alpha_i^1 + \alpha_j^1 + \alpha_k^2 + \alpha_l^2 + \delta_{ij}^1 + \delta_{kl}^2 + (\alpha\alpha)_{ik} + (\alpha\alpha)_{il} + (\alpha\alpha)_{jk} + (\alpha\alpha)_{jl} \\ &\quad + (\alpha\delta)_{ikl} + (\alpha\delta)_{jkl} + (\delta\alpha)_{ijk} + (\delta\alpha)_{ijl} + (\delta\delta)_{ijkl},\end{aligned}$$

where

- α_u^a = additive genetic effect of the A_u^a allele,
- δ_{uv}^a = dominance effect associated with the $A_u^a A_v^a$ genotype,
- $(\alpha\alpha)_{ik}$ = additive \times additive epistatic effect associated with genes A_i^1 and A_k^2 ,
- $(\alpha\delta)_{ikl}$ = additive \times dominance epistatic effect associated with the gene A_i^1 and the genotype $A_k^2 A_l^2$, and
- $(\delta\delta)_{ijkl}$ = dominance \times dominance epistatic effect associated with the genotypes $A_i^1 A_j^1$ and $A_k^2 A_l^2$.

The total genotypic variance may be partitioned as

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2,$$

where

σ_G^2 = total genotypic variance generated by the two loci,

σ_A^2 = additive genetic variance,

σ_D^2 = dominance variance,

σ_{AA}^2 = additive \times additive variance,

σ_{AD}^2 = additive \times dominance variance,

and

σ_{DD}^2 = dominance \times dominance variance.

The expected half-sib progeny array of the male $(A_i^1 A_k^2)(A_j^1 A_l^2)$ is

$$\sum_{rt} p_r^1 p_t^2 \left[\frac{1}{2}(1-y_m) \{ (A_i^1 A_k^2)(A_r^1 A_t^2) + (A_j^1 A_l^2)(A_r^1 A_t^2) \} + \frac{1}{2}y_m \{ (A_j^1 A_k^2)(A_r^1 A_t^2) + (A_i^1 A_l^2)(A_r^1 A_t^2) \} \right].$$

This array has the following mean value:

$${}_m \gamma_{ik, jl} = \frac{1}{2}(a_i^1 + a_j^1 + a_k^2 + a_l^2) + \frac{1}{2}(1-y_m) \{ (aa)_{ik} + (aa)_{jl} \} + \frac{1}{2}y_m \{ (aa)_{il} + (aa)_{jk} \}.$$

The expected half-sib progeny mean for the female of the same genotype is equal to that given above except that y_f replaces y_m .

(b) Selection Values

In a manner analogous to that outlined in the case of a single locus, the selection value $w_{ik, jl}$ is defined to be proportional to the probability that an individual of the genotype $(A_i^1 A_k^2)(A_j^1 A_l^2)$ survives selection. Thus, the selection value for a male of this genotype is

$${}_m w_{ik, jl} = 1 + \frac{m \dot{i}_a}{m \sigma_a^2} ({}_m \lambda_{ik, jl}) \quad (3)$$

where

$$\frac{m \dot{i}_{no}}{m \sigma_{no}^2} ({}_m \lambda_{ik, jl}) = 0 \quad (\text{no selection}),$$

$$\frac{m \dot{i}_{ind.}}{m \sigma_{ind.}^2} ({}_m \lambda_{ik, jl}) = \frac{m \dot{i}_{ind.}}{m \sigma_{ind.}^2} (d_{ik, jl}) \quad (\text{individual selection}),$$

and

$$\frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} ({}_m \lambda_{ik, jl}) = \frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} (\gamma_{ik, jl}) \quad (\text{g.c.a. selection}).$$

Likewise the selection value for a female of the genotype $(A_r^1 A_t^2)(A_s^1 A_u^2)$ is

$${}_f w_{rt, su} = 1 + \frac{f \dot{i}_\beta}{f \sigma_\beta^2} ({}_f \lambda_{rt, su}). \quad (4)$$

(c) Consequences of One Cycle of Selection

It can be shown that the frequency of the gamete $A_i^1 A_k^2$ from the selected males originating in Π_0 is

$${}_m f_{ik}^1 = f_{ik}^0 \left[1 + (1-y_m) \frac{m \dot{i}_a}{m \sigma_a^2} ({}_m \lambda_{ik, \dots}) + y_m \frac{m \dot{i}_a}{m \sigma_a^2} ({}_m \lambda_{i, \dots k}) \right].$$

Similarly, the frequency of the gamete $A_j^1 A_l^2$ from the selected females is

$${}_f f_{jl}^1 = f_{jl}^0 \left[1 + (1-y_f) \frac{f \dot{i}_\beta}{f \sigma_\beta^2} ({}_f \lambda_{jl, \dots}) + y_f \frac{f \dot{i}_\beta}{f \sigma_\beta^2} ({}_f \lambda_{j, \dots l}) \right].$$

Hence the mean of the progeny which results from mating the selected males and females is approximately equal to

$$\begin{aligned} & \frac{m \dot{i}_a}{m \sigma_a^2} \sum_{ik} p_i^1 p_k^2 [(1-y_m) ({}_m \lambda_{ik, \dots}) (d_{ik, \dots}) + y_m ({}_m \lambda_{i, \dots k}) (d_{ik, \dots})] \\ & + \frac{f \dot{i}_\beta}{f \sigma_\beta^2} \sum_{jl} p_j^1 p_l^2 [(1-y_f) ({}_f \lambda_{jl, \dots}) (d_{jl, \dots}) + y_f ({}_f \lambda_{j, \dots l}) (d_{jl, \dots})]. \end{aligned}$$

To proceed further, it is necessary to evaluate the λ 's for different kinds of selection. The appropriate values may be listed as follows:

	Individual Selection	g.c.a. Selection
$m\lambda_{ik, \dots} = \sum_{jl} p_j^1 p_l^2 (m\lambda_{ik, jl}) =$	$[a_i^1 + a_k^2 + (aa)_{ik}]$	$[\frac{1}{2}(a_i^1 + a_k^2) + \frac{1}{2}(1 - y_m)(aa)_{ik}]$
$m\lambda_{i, \dots k} = \sum_{jl} p_j^1 p_l^2 (m\lambda_{il, jk}) =$	$[a_i^1 + a_k^2 + (aa)_{ik}]$	$[\frac{1}{2}(a_i^1 + a_k^2) + \frac{1}{2}y_m(aa)_{ik}]$

For $f\lambda_{ik, \dots}$ and $f\lambda_{i, \dots k}$, replace y_m by y_f .

With these values it is possible to evaluate μ_1 for the nine possible selection schemes. The results are given in Table 2 and are the immediate theoretical

TABLE 2
INCREMENT CHANGES IN POPULATION MEANS DUE TO A SINGLE CYCLE OF SELECTION FOR
POPULATIONS GENERATED BY TWO LINKED LOCI WHICH EXHIBIT EPISTASIS

	Females:		
	No Selection	Individual Selection	g.c.a. Selection
Males:			
No selection	0	$\frac{f^{i\text{ind.}}A}{f\sigma_{\text{ind.}}^2}$	$\frac{f^{i\text{h.s.}}B_f}{f\sigma_{\text{h.s.}}^2}$
Individual selection	$\frac{m^{i\text{ind.}}A}{m\sigma_{\text{ind.}}^2}$	$\frac{m^{i\text{ind.}}A}{m\sigma_{\text{ind.}}^2} + \frac{f^{i\text{ind.}}A}{f\sigma_{\text{ind.}}^2}$	$\frac{m^{i\text{ind.}}A}{m\sigma_{\text{ind.}}^2} + \frac{f^{i\text{h.s.}}B_f}{f\sigma_{\text{h.s.}}^2}$
g.c.a. selection	$\frac{m^{i\text{h.s.}}B_m}{m\sigma_{\text{h.s.}}^2}$	$\frac{m^{i\text{h.s.}}B_m}{m\sigma_{\text{h.s.}}^2} + \frac{f^{i\text{ind.}}A}{f\sigma_{\text{ind.}}^2}$	$\frac{m^{i\text{h.s.}}B_m}{m\sigma_{\text{h.s.}}^2} + \frac{f^{i\text{h.s.}}B_f}{f\sigma_{\text{h.s.}}^2}$

where

$$A = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2, B_f = \frac{1}{4}\sigma_A^2 + \frac{1}{4}(1 + \delta_f)\frac{1}{4}\sigma_{AA}^2, \text{ and } B_m = \frac{1}{4}\sigma_A^2 + \frac{1}{4}(1 + \delta_m)\frac{1}{4}\sigma_{AA}^2,$$

in which

$$\delta_m = (1 - 2y_m)^2 \text{ and } \delta_f = (1 - 2y_f)^2.$$

responses to one cycle of selection starting from an original random-mating population in equilibrium. These results are different from those given in Table 1 ($n = 1$). Clearly epistatic variances enter into all prediction formulae which involve any form of selection. Also linkage causes a disturbance in those forms of selection involving the evaluation of an individual by its half-sib family mean.

TABLE 3

MALE AND FEMALE GAMETE FREQUENCIES AFTER n CYCLES OF SELECTION FOR POPULATIONS GENERATED BY TWO LINKED LOCI WHICH EXHIBIT EPISTASIS

	Gamete Frequency	Females:		
		No Selection	Individual Selection	g.c.a. Selection
Males:				
No selection	$\left\{ \begin{matrix} m f_{ik}^n \\ f f_{ik}^n \end{matrix} \right\}$	$p_i^1 p_k^2$	$p_i^1 p_k^2 \left(1 + \frac{f^i \text{ind. } X_m}{f^2 \sigma_{\text{ind.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{f^i \text{h.s. } Z_m}{f^2 \sigma_{\text{h.s.}}^2} \right)$
		$p_i^1 p_k^2$	$p_i^1 p_k^2 \left(1 + \frac{f^i \text{ind. } W_f}{f^2 \sigma_{\text{ind.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{f^i \text{h.s. } Y_f}{f^2 \sigma_{\text{h.s.}}^2} \right)$
Individual selection	$\left\{ \begin{matrix} m f_{ik}^n \\ f f_{ik}^n \end{matrix} \right\}$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{ind. } W_m}{m^2 \sigma_{\text{ind.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{ind. } W_m + f^i \text{ind. } X_m}{m^2 \sigma_{\text{ind.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{ind. } W_m + f^i \text{h.s. } Z_m}{m^2 \sigma_{\text{ind.}}^2} \right)$
		$p_i^1 p_k^2 \left(1 + \frac{m^i \text{ind. } X_f}{m^2 \sigma_{\text{ind.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{ind. } X_f + f^i \text{ind. } W_f}{m^2 \sigma_{\text{ind.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{ind. } X_f + f^i \text{h.s. } Y_f}{m^2 \sigma_{\text{ind.}}^2} \right)$
g.c.a. selection	$\left\{ \begin{matrix} m f_{ik}^n \\ f f_{ik}^n \end{matrix} \right\}$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{h.s. } Y_m}{m^2 \sigma_{\text{h.s.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{h.s. } Y_m + f^i \text{ind. } X_m}{m^2 \sigma_{\text{h.s.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{h.s. } Y_m + f^i \text{h.s. } Z_m}{m^2 \sigma_{\text{h.s.}}^2} \right)$
		$p_i^1 p_k^2 \left(1 + \frac{m^i \text{h.s. } Z_f}{m^2 \sigma_{\text{h.s.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{h.s. } Z_f + f^i \text{ind. } W_f}{m^2 \sigma_{\text{h.s.}}^2} \right)$	$p_i^1 p_k^2 \left(1 + \frac{m^i \text{h.s. } Z_f + f^i \text{h.s. } Y_f}{m^2 \sigma_{\text{h.s.}}^2} \right)$
		$W_m = \left[\frac{1}{2}(n+1)(\alpha_i^1 + \alpha_k^2) + \left\{ 1 + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^{n-1}}{1-b} \right) \right\} (\alpha a)_{ik} \right]$	$Y_m = \left[\frac{1}{4}(n+1)(\alpha_i^1 + \alpha_k^2) + \left\{ 1 + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^{n-1}}{1-b} \right) \right\} \left(\frac{1+\delta_m}{4} \right) (\alpha a)_{ik} \right]$	
		$X_m = \left\{ \frac{1}{2}(n-1)(\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^{n-1}}{1-b} \right) (\alpha a)_{ik} \right\}$	$Z_m = \left\{ \frac{1}{4}(n-1)(\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^{n-1}}{1-b} \right) \left(\frac{1+\delta_f}{4} \right) (\alpha a)_{ik} \right\}$	
		where		
		$b = 1 - \frac{1}{2}(y_m + y_f)$, and $\delta_m = (1 - 2y_m)^2$.		
		To obtain W_f , X_f , Y_f , and Z_f interchange all subscripts m and f in the corresponding formulae W_m , X_m , Y_m , and Z_m .		

(d) *Consequences of n Cycles of Selection*

The algebra becomes excessively tedious when an attempt is made to develop prediction formulae for n cycles of selection using the generalized selection values (3) and (4). Hence selection values and prediction formulae are developed separately for each selection scheme. These are summarized for gamete frequencies in Table 3 and for population means in Table 4. In developing these formulae it is assumed that the same kind and intensity of selection is applied in each cycle.

TABLE 4

INCREMENT CHANGES IN POPULATION MEANS DUE TO n CYCLES OF SELECTION FOR POPULATIONS GENERATED BY TWO LINKED LOCI WHICH EXHIBIT EPISTASIS

	Females:		
	No Selection	Individual Selection	g.c.a. Selection
Males:			
No selection	0	$\frac{f^{i\text{ind.}}U}{f\sigma_{f\text{ind.}}^2}$	$\frac{f^{i\text{h.s.}}}{f\sigma_{f\text{h.s.}}^2}V_f$
Individual selection	$\frac{m^{i\text{ind.}}U}{m\sigma_{m\text{ind.}}^2}$	$\frac{m^{i\text{ind.}}}{m\sigma_{m\text{ind.}}^2}U + \frac{f^{i\text{ind.}}}{f\sigma_{f\text{ind.}}^2}U$	$\frac{m^{i\text{ind.}}}{m\sigma_{m\text{ind.}}^2}U + \frac{f^{i\text{h.s.}}}{f\sigma_{f\text{h.s.}}^2}V_f$
g.c.a. selection	$\frac{m^{i\text{h.s.}}}{m\sigma_{m\text{h.s.}}^2}V_m$	$\frac{m^{i\text{h.s.}}}{m\sigma_{m\text{h.s.}}^2}V_m + \frac{f^{i\text{ind.}}}{f\sigma_{f\text{ind.}}^2}U$	$\frac{m^{i\text{h.s.}}}{m\sigma_{m\text{h.s.}}^2}V_m + \frac{f^{i\text{h.s.}}}{f\sigma_{f\text{h.s.}}^2}V_f$

where

$$U = \{\frac{1}{2}n\sigma_A^2 + (\sum_{r=1}^n b^{r-1})\frac{1}{4}\sigma_{AA}^2\},$$

$$V_m = \{\frac{1}{4}n\sigma_A^2 + \frac{1}{4}(1+\delta_m)(\sum_{r=1}^n b^{r-1})\frac{1}{4}\sigma_{AA}^2\},$$

$$b = 1 - \frac{1}{2}(y_m + y_f),$$

and

$$\delta_m = (1 - 2y_m)^2.$$

To obtain V_f change the subscript m to f in V_m .

The conclusion from this section is that complications of linkage and epistasis can cause disturbances to prediction formulae for *immediate* genetic gains.

(e) *Consequences of Relaxation after n Consecutive Cycles of Selection*

The problem of developing prediction equations for the mean of a population which has had a history of n consecutive cycles of individual selection followed by t generations of random mating without selection has been previously examined in detail (Griffing 1960a, 1960b). It was shown that the contributions generated by

linkage and epistasis tend to disappear, leaving as permanent gains only those contributions due to the additive genetic variance, i.e. to those results developed in the first section of this study involving only independent, non-interacting loci.

In this section the results for only one other selection scheme will be examined. This scheme is the one in which both males and females are selected on the basis of their half-sib progeny performance.

The results can be stated briefly as follows: For $t > 0$ the frequency of the male gamete $A_i^1 A_k^2$ from a population which has been subjected to n cycles of selection followed by t generations of relaxation is

$${}_{mj}^{fn,t}{}_{ik} \cong p_i^1 p_k^2 \left\{ 1 + \frac{{}_m i_{h.s.}}{{}_m \sigma_{h.s.}^2} \left[\frac{1}{4} n (\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^n}{1-b} \right) \left(\frac{1+\delta_m}{4} \right) (b^{t-1}) (\alpha\alpha)_{ik} \right] \right. \\ \left. + \frac{{}_f i_{h.s.}}{{}_f \sigma_{h.s.}^2} \left[\frac{1}{4} n (\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^n}{1-b} \right) \left(\frac{1+\delta_f}{4} \right) (b^{t-1}) (\alpha\alpha)_{ik} \right] \right\},$$

where, as before

$$b = 1 - \frac{1}{2}(y_f + y_m).$$

The frequency of the corresponding female gamete is obtained by interchanging the subscripts m and f in ${}_{mj}^{fn,t}{}_{ik}$.

The mean of $\Pi_{n,t}$ is, then,

$$\mu_{n,t} \cong \frac{{}_m i_{h.s.}}{{}_m \sigma_{h.s.}^2} \left[\frac{1}{4} n \sigma_A^2 + \frac{1}{4} (1 + \delta_m) \left(\sum_{r=1}^n b^{r-1} \right) (b^t) \left(\frac{1}{4} \sigma_{AA}^2 \right) \right] \\ + \frac{{}_f i_{h.s.}}{{}_f \sigma_{h.s.}^2} \left[\frac{1}{4} n \sigma_A^2 + \frac{1}{4} (1 + \delta_f) \left(\sum_{r=1}^n b^{r-1} \right) (b^t) \left(\frac{1}{4} \sigma_{AA}^2 \right) \right].$$

Comparing these results with those obtained previously involving individual selection, it appears that the end result of t generations of relaxation is merely to multiply the epistatic contribution found in $\mu_{n,0}$ by a factor (b^t) . This, then, causes the disappearance of the epistatic contribution, as t becomes large. Since this result holds for complete individual and complete g.c.a. selection, one expects, intuitively, that the same results hold for all selection schemes.

It is assumed here, as elsewhere in this study, that natural selection is not operating in any way to modify the pressure applied by artificial selection.

IV. GENERALIZATIONS

The approach used in the previous sections, which utilizes a gamete analysis with a gene interpretation, can be extended to include more than two loci. However, the problem becomes difficult, primarily, because of the increase in the number of linkage parameters. It is for this reason that a different approach must be considered for a completely general situation including any number of alleles at each of any number of loci which are associated in an arbitrary system of linkages.

Briefly, this new approach is possible because the elements in a random-mating population can be generated, not only as the product of male and female gametic arrays, but also as the product of the male and female zygotic arrays. This latter representation provides a family structure which leads to definitions of various useful covariances among relatives. Certain aspects of the prediction problem, then, can be formulated in terms of these covariances in a very general way.

(a) *Definitions*

The following illustrates the two abovementioned methods of generating a random-mating population in equilibrium, and defines the genotypic values and covariances of interest.

In an equilibrium random-mating population the male and female gametic arrays are identical, even if the recombination values are different in the two sexes.

Let

$$\sum_i f_i G_i = \text{gametic array for males and females, and}$$

$$(\sum_i f_i G_i)^2 = \sum_{ij} f_i f_j (H_{ij}) = \text{zygotic array of the random-mating population in equilibrium designated as } \Pi_0,$$

where

$$H_{ij} = \text{zygote formed by the union of } G_i \text{ and } G_j \text{ gametes.}$$

This same population can be generated by forming the product of the male and female zygotic arrays as follows:

$$\begin{aligned} \Pi_0 &= [\sum_{ij} f_i f_j ({}_m H_{ij})] [\sum_{kl} f_k f_l ({}_f H_{kl})] \\ &= \sum_{ijkl} f_i f_j f_k f_l (H_{ij, kl}), \end{aligned}$$

where

$$H_{ij, kl} = \text{full-sib array resulting from the cross } {}_m H_{ij} \times {}_f H_{kl}.$$

In the argument to follow, this latter representation of the equilibrium population which provides full-sib and half-sib families is used. In this argument it is necessary to define the following genotypic mean values:

$$\begin{aligned} {}_m h_{ij} &= \text{genotypic value for } {}_m H_{ij}, \text{ such that } {}_m h_{ij} = {}_f h_{ij} \text{ and } \\ &\quad \sum_{ij} f_i f_j ({}_m h_{ij}) = 0, \\ h_{ij, kl} &= \text{mean genotypic value for the full-sib group } H_{ij, kl} \text{ and such} \\ &\quad \text{that } \sum_{ijkl} f_i f_j f_k f_l (h_{ij, kl}) = 0, \end{aligned}$$

$$h_{ij, ..} = \sum_{kl} f_k f_l (h_{ij, kl}) = \text{mean genotypic value for the half-sib progeny of } {}_m H_{ij}, \text{ and}$$

$$h_{.., kl} = \sum_{ij} f_i f_j (h_{ij, kl}) = \text{mean genotypic value for the half-sib progeny of } {}_f H_{kl}.$$

TABLE 5
INCREMENT CHANGES IN POPULATION MEANS DUE TO ONE CYCLE OF SELECTION FOR POPULATIONS GENERATED BY A COMPLETELY GENERAL GENETIC MODEL

	Females:		
	No Selection	Individual Selection	g.c.a. Selection
Males:			
No selection	0	$\frac{f^i \text{ind. Cov}_f(\text{PO})}{f \sigma_{\text{ind.}}^2}$	$\frac{f^i \text{h.s. Cov}_f(\text{HS})}{f \sigma_{\text{h.s.}}^2}$
Individual selection	$\frac{m^i \text{ind. Cov}_m(\text{PO})}{m \sigma_{\text{ind.}}^2}$	$\frac{m^i \text{ind. Cov}_m(\text{PO}) + f^i \text{ind. Cov}_f(\text{PO})}{m \sigma_{\text{ind.}}^2}$	$\frac{m^i \text{ind. Cov}_m(\text{PO}) + f^i \text{h.s. Cov}_f(\text{HS})}{m \sigma_{\text{ind.}}^2}$
g.c.a. selection	$\frac{m^i \text{h.s. Cov}_m(\text{HS})}{m \sigma_{\text{h.s.}}^2}$	$\frac{m^i \text{h.s. Cov}_m(\text{HS}) + f^i \text{ind. Cov}_f(\text{PO})}{m \sigma_{\text{h.s.}}^2}$	$\frac{m^i \text{h.s. Cov}_m(\text{HS}) + f^i \text{h.s. Cov}_f(\text{HS})}{m \sigma_{\text{h.s.}}^2}$

These mean values are used to define various useful covariances among relatives. These are

$$\text{Cov}_m(\text{PO}) = \sum_{ij} f_i f_j (h_{ij})(h_{ij}, \dots) = \text{male parent-offspring covariance,}$$

$$\text{Cov}_f(\text{PO}) = \sum_{kl} f_k f_l (h_{kl})(h_{\dots, kl}) = \text{female parent-offspring covariance,}$$

$$\text{Cov}_m(\text{HS}) = \sum_{ij} f_i f_j (h_{ij}, \dots)^2 = \text{male half-sib covariance,}$$

and

$$\text{Cov}_f(\text{HS}) = \sum_{kl} f_k f_l (h_{\dots, kl})^2 = \text{female half-sib covariance.}$$

(b) *Consequences of One Cycle of Selection*

Consider the initial population to be Π_0 , a random-mating population in equilibrium, i.e.

$$\Pi_0 = \sum_{ij} f_i f_j (H_{ij}).$$

The frequency of $_m H_{ij}$ following selection is

$$f_i f_j ({}_m w_{ij}) \cong f_i f_j \left[1 + \frac{{}_m i_a}{{}_m \sigma_a^2} ({}_m \lambda_{ij}) \right].$$

Similarly, the frequency of $_f H_{kl}$ following selection is

$$f_k f_l ({}_f w_{kl}) \cong f_k f_l \left[1 + \frac{{}_f i_\beta}{{}_f \sigma_\beta^2} ({}_f \lambda_{kl}) \right].$$

Hence, the mean of the progeny population resulting from random mating the selected males and females is approximately equal to

$$\begin{aligned} & \sum_{ijkl} [f_i f_j ({}_m w_{ij})] [f_k f_l ({}_f w_{kl})] (h_{ij}, {}_{kl}) \\ & \cong \frac{{}_m i_a}{{}_m \sigma_a^2} \sum_{ij} f_i f_j ({}_m \lambda_{ij}) (h_{ij}, \dots) + \frac{{}_f i_\beta}{{}_f \sigma_\beta^2} \sum_{kl} f_k f_l ({}_f \lambda_{kl}) (h_{\dots, {}_{kl}}), \end{aligned}$$

where the λ 's may take on the following values:

	Individual Selection	g.c.a. Selection
${}_m \lambda_{ij}$	h_{ij}	h_{ij}, \dots
${}_f \lambda_{kl}$	h_{kl}	$h_{\dots, {}_{kl}}$

Consequences of the nine possible combinations of selection are given in Table 5. The correspondence between the entries in Table 5 and those of Table 2 becomes immediately apparent. The results in Table 2 are simply the evaluations of the appropriate covariances for the case of two loci.

However, it should be pointed out that for these results to hold, it is necessary to assume that the analysis deals separately with small sub-sets of the total set of loci. The total response is then obtained as the summation over all such small sub-sets.

These results also flow from an approach using the concept of heritability in which the heritability for a given sex is defined as the regression of the g.c.a. of the individual on the phenotypic value of the test criterion with which the individual is selected.

(c) *Consequences of n Cycles of Selection*

The consequences of n cycles of selection are generalized in the following argument. Consider the $(n-1)$ th population which may be represented as

$$\Pi_{n-1} = \sum_{ij} ({}_m f_i^{n-1}) ({}_f f_j^{n-1}) (H_{ij}),$$

where

$${}_m f_i^{n-1} = f_i + \frac{m \dot{i}_a}{m \sigma_a^2} K_1 + \frac{f \dot{i}_\beta}{f \sigma_\beta^2} K_2,$$

and

$${}_f f_j^{n-1} = f_j + \frac{m \dot{i}_a}{m \sigma_a^2} K_3 + \frac{f \dot{i}_\beta}{f \sigma_\beta^2} K_4,$$

and K_1, \dots, K_4 are constants.

The frequency of ${}_m H_{ij}$ following selection is approximately equal to

$$({}_m f_i^{n-1}) ({}_f f_j^{n-1}) ({}_m w_{ij}) = ({}_m f_i^{n-1}) ({}_f f_j^{n-1}) \left[1 + \frac{m \dot{i}_a}{m \sigma_a^2} ({}_m \lambda_{ij}) \right],$$

and the approximate frequency of ${}_f H_{kl}$ following selection is

$$({}_m f_k^{n-1}) ({}_f f_l^{n-1}) ({}_f w_{kl}) = ({}_m f_k^{n-1}) ({}_f f_l^{n-1}) \left[1 + \frac{f \dot{i}_\beta}{f \sigma_\beta^2} ({}_f \lambda_{kl}) \right].$$

Hence, the mean of Π_n is

$$\begin{aligned} &\cong \sum_{ijkl} [({}_m f_i^{n-1}) ({}_f f_j^{n-1}) ({}_m w_{ij})] [({}_m f_k^{n-1}) ({}_f f_l^{n-1}) ({}_f w_{kl})] (h_{ij}, {}_{kl}) \\ &\cong \sum_{ijkl} ({}_m f_i^{n-1}) ({}_f f_j^{n-1}) ({}_m f_k^{n-1}) ({}_f f_l^{n-1}) (h_{ij}, {}_{kl}) + \frac{m \dot{i}_a}{m \sigma_a^2} \sum_{ij} f_i f_j ({}_m \lambda_{ij}) (h_{ij}, \dots) \\ &\quad + \frac{f \dot{i}_\beta}{f \sigma_\beta^2} \sum_{kl} f_k f_l ({}_f \lambda_{kl}) (h_{\dots}, {}_{kl}) \\ &= \mu_{n-1, 1} + \mu_1. \end{aligned}$$

Therefore, the mean of the progeny population which results from random mating selected parents from the previous population is approximately equal to the summation of two parts: (i) the mean of the previous population after it has been allowed to mate at random without selection for one generation, and (ii) the increment advance due to the first cycle of selection. This interesting result was first shown to hold for the special case of individual selection in both sexes. It is now demonstrated to hold for all possible combinations of the different forms of selection in both sexes.

(d) *Consequences of Relaxation after n Consecutive Cycles of Selection*

For an arbitrarily complicated genetic situation, the consequences of relaxation following selection can be discussed only in general terms, unless the genetic system, including linkage parameters, is specified in detail. The following discusses the problem in general terms, and then illustrates the points with a specific two-locus case.

The selected population, $\Pi_{n,0}$, is not in equilibrium if additive \times additive, etc. effects occur in the original population, Π_0 , and contribute to the selection response. For an equilibrium condition, the gamete frequencies must be identically equal to the product of their component gene frequencies. Subjecting a population in disequilibrium, such as $\Pi_{n,0}$, to random mating without selection causes the gametic frequencies to change and hence the population structure to change until equilibrium conditions are reached. As the structure of the population changes, the mean of the population decreases until finally, at equilibrium, the population mean equals that which is predicted on the basis of independent, non-interacting loci.

To illustrate the above argument, consider the previous two-locus example in which the selection of males and females is based on their half-sib progeny mean. In $\Pi_{n-1,0}$ the frequency of the gamete $A_i^1 A_k^2$ among the selected males is

$${}_m f_{ik}^{n,0} = p_i^1 p_k^2 \left(1 + \frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} \left\{ \frac{1}{4}(n+1)(\alpha_i^1 + \alpha_k^2) + \left[1 + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{4}(1+\delta_m)(\alpha\alpha)_{ik} \right\} \right. \\ \left. + \frac{f \dot{i}_{h.s.}}{f \sigma_{h.s.}^2} \left\{ \frac{1}{4}(n-1)(\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^{n-1}}{1-b} \right) \left(\frac{1+\delta_f}{4} \right) (\alpha\alpha)_{ik} \right\} \right).$$

This value is not equal to the product of the component gene frequencies which are

$$\frac{1}{2}({}_m f_i^{n,0} + {}_f f_i^{n,0}) = p_i^1 \left\{ 1 + \frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_i^1) \right] + \frac{f \dot{i}_{h.s.}}{f \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_i^1) \right] \right\} \\ = \text{frequency of } A_i^1 \text{ in } \Pi_{n,0},$$

and

$$\frac{1}{2}({}_m f_k^{n,0} + {}_f f_k^{n,0}) = p_k^2 \left\{ 1 + \frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_k^2) \right] + \frac{f \dot{i}_{h.s.}}{f \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_k^2) \right] \right\} \\ = \text{frequency of } A_k^2 \text{ in } \Pi_{n,0}.$$

Hence the population $\Pi_{n,0}$ is not in equilibrium.

With t generations of random mating without selection, it was shown that the frequency of the gamete $A_i^1 A_k^2$ among males was

$${}_m f_{ik}^{n,t} = p_i^1 p_k^2 \left\{ 1 + \frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^n}{1-b} \right) \left(\frac{1+\delta_m}{4} \right) (b^{t-1})(\alpha\alpha)_{ik} \right] \right. \\ \left. + \frac{f \dot{i}_{h.s.}}{f \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_i^1 + \alpha_k^2) + \left(\frac{1-y_m}{2} \right) \left(\frac{1-b^n}{1-b} \right) \left(\frac{1+\delta_f}{4} \right) (b^t)(\alpha\alpha)_{ik} \right] \right\},$$

which, when t becomes large, approximately equals

$$p_i^1 p_k^2 \left\{ 1 + \frac{m \dot{i}_{h.s.}}{m \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_i^1 + \alpha_k^2) \right] + \frac{f \dot{i}_{h.s.}}{f \sigma_{h.s.}^2} \left[\frac{1}{4}n(\alpha_i^1 + \alpha_k^2) \right] \right\}.$$

This frequency is clearly equal to the product of the component gene frequencies. Thus, with random mating and no selection the population mean, $\mu_{n,0}$, constantly changes until it stabilizes at the equilibrium value, which is given by the analysis involving independent, non-interacting loci. The specific manner in which the equilibrium value is approached cannot be given except in terms of the system of linkage parameters.

V. DISCUSSION

The purpose of this paper is not that of discussing the conditions under which each combination of general combining ability and individual selection may be superior to all others. Some aspects of this problem are given elsewhere (for example, see Dickerson and Hazel 1944, and Lush 1948). The objective of this paper is to examine in detail the immediate and long-term consequences of different combinations of selection when linkage and epistasis are included in the gene model. The selection schemes under study include all possible combinations which result with the application of (i) no selection, (ii) individual selection, or (iii) general combining ability selection to each sex.

It is shown that the immediate response to all forms of truncation selection applied to populations generated by more than one locus is complicated by the inclusion of certain epistatic terms. In the most general genetic situation, the immediate response to selection is formulated in terms of certain covariances among relatives: the particular covariance depending on the particular form of selection. However, it is also demonstrated that on relaxation from selection the epistatic contributions to the genetic gains disappear, leaving as a residual, the genetic gains predicted on the basis of independent, non-interacting loci. The rate of disappearance of these epistatic contributions is a function of the linkage parameters.

The theory, as developed in this paper, depends on various assumptions and approximations, and it is perhaps useful to briefly review these:

- (1) The populations of phenotypic values are considered to be infinite and normally distributed. If, in actual experimental procedures, small samples are taken to represent these populations, the predictability of the theory will be affected.
- (2) Throughout the analyses, approximations are made which involve the assumption that gene effects are small relative to the phenotypic standard deviation. Hence, squares and crossproducts of the ratio of gene effect to phenotypic standard deviation are ignored. Also, when more than one locus is involved, it is assumed that the analysis deals separately with small sub-sets of the total set of loci. In this way, the approximations still hold. The total response is then obtained as the summation over all such small sub-sets. The errors of approximation tend to accumulate in successive cycles so that predictions based on parameters of the original population become worse as selection moves the population mean further from its original position.
- (3) Finally, throughout the study, it is assumed that natural selection is not operating. That is to say, it is assumed that all selected genotypes exhibit the same reproductive potential.

VI. REFERENCES

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