

SELECTION IN REFERENCE TO BIOLOGICAL GROUPS

IV.* APPLICATION OF SELECTION INDEX THEORY†

By B. GRIFFING‡

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Summary

Index theory is applied to selection methods which use individuals or randomly associated groups of individuals as basic units of selection. An index is developed which combines "direct" and "associate" phenotypic values in such a way as to invariably ensure a maximum, non-negative change in the population mean. The theory is applicable to populations of groups in each of which individuals may interact in any arbitrary manner, whether such interaction be cooperative or competitive in nature.

I. INTRODUCTION

In this series of studies the genetic model usually used in selection theory is extended to accommodate genotypic interaction (either cooperative or competitive) between genotypes within small groups. It was shown in the first paper of this series (Griffing 1967) that with this more complex, but yet more realistic, genetic model the incongruous situation can occur in which positive individual selection results in a negative change in the population mean. In fact, continued positive mass selection can cause ultimate fixation of the least desirable allele at the locus in question. However, it was shown that this dilemma could be overcome by transferring the basis of selection from that of the individual to that of the entire group, since group selection invariably results in a non-negative genetic change in the mean. In a later paper of the series (Griffing 1968), it was shown that under certain circumstances group selection, although a "safe" procedure, can be a very inefficient form of selection. Hence it is necessary to investigate other selection methods. The methods discussed in this paper are those of selection indices (Smith 1936) with the ultimate objective of combining individual and group selection in such a way as to invariably yield the *maximum* possible non-negative change in the population mean.

In the following study, selection index techniques are applied first to the simplest possible groups, those of order two. The results are then extended to groups of arbitrary size, n . In each case, two different indices are considered. The first and simplest is that applied to individual "direct" values. The second and

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‡ Faculty of Genetics, Ohio State University, Columbus, Ohio, 43210.

more complex index is that which combines "direct" and "associate" values. Several numerical examples are then given to illustrate the efficiency of the index method.

No attempt will be made to review the vast literature on selection index theory. The basic techniques are well known and can be found in a variety of reference books.

II. CONSEQUENCES OF INDEX SELECTION AS APPLIED TO GROUPS OF ORDER TWO

(a) Population Specification

Consider a base population in equilibrium under random mating whose genotypic array is generated by an arbitrary number of alleles at a single locus. Let

$$\sum p_i p_j (A_i A_j) = \text{genotypic array of the base population.}$$

Then the array of groups of size two is obtained as the two-way combinatorial product of the base population, i.e.

$$[\sum p_i p_j (A_i A_j)] \times [\sum p_i p_j (A_i A_j)] = \sum p_{i_1} p_{j_1} p_{i_2} p_{j_2} (A_{i_1} A_{j_1}, A_{i_2} A_{j_2}).$$

The phenotypic value of the individual whose genotype is $A_{i_1} A_{j_1}$, in the couplet $(A_{i_1} A_{j_1}, A_{i_2} A_{j_2})$, can be represented by the model

$${}_{i_1 j_1} \tau_{i_2 j_2} = {}_{i_1 j_1} d_{i_2 j_2} + {}_{i_1 j_1} e_{i_2 j_2},$$

where

$${}_{i_1 j_1} \tau_{i_2 j_2} = \text{phenotype,}$$

$${}_{i_1 j_1} d_{i_2 j_2} = \text{genotypic effect, and}$$

$${}_{i_1 j_1} e_{i_2 j_2} = \text{environmental effect.}$$

The expected values for the elements in the model are as follows:

Mean Values

$$E({}_{i_1 j_1} \tau_{i_2 j_2}) = E({}_{i_1 j_1} d_{i_2 j_2}) = E({}_{i_1 j_1} e_{i_2 j_2}) = 0.$$

Square and Cross Products

$$E({}_{i_1 j_1} \tau_{i_2 j_2})^2 = E({}_{i_2 j_2} \tau_{i_1 j_1})^2 = \sigma_P^2,$$

$$E({}_{i_1 j_1} \tau_{i_2 j_2})({}_{i_2 j_2} \tau_{i_1 j_1}) = \rho \sigma_P^2,$$

and other cross products involving τ 's are zero;

$$E({}_{i_1 j_1} d_{i_2 j_2})^2 = E({}_{i_2 j_2} d_{i_1 j_1})^2 = \sigma_G^2,$$

$$E({}_{i_1 j_1} d_{i_2 j_2})({}_{i_2 j_2} d_{i_1 j_1}) = \sigma_G^2,$$

and other cross products involving d 's are zero;

$$E(i_{1j_1}e_{i_2j_2})^2 = E(i_{2j_2}e_{i_1j_1})^2 = \sigma_E^2,$$

$$E(i_{1j_1}e_{i_2j_2})(i_{2j_2}e_{i_1j_1}) = E\sigma_E,$$

and other cross products involving e 's are zero. Hence the phenotypic variance can be partitioned as follows:

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2,$$

where

σ_P^2 = phenotypic variance among individual values,

σ_G^2 = genotypic variance among individual values, and

σ_E^2 = environmental variance among individual values.

Similarly the covariance between elements within groups can be partitioned as

$$P\sigma_P = G\sigma_G + E\sigma_E,$$

where

$P\sigma_P$ = phenotypic covariance between phenotypes within groups,

$G\sigma_G$ = genotypic covariance between genotypes within groups, and

$E\sigma_E$ = environmental covariance between environmental effects expressed by different phenotypes within groups.

The genotypic effect can be partitioned further. However, to accommodate interactions between genotypes in groups of order two, a two-locus model must be used and direct and associate effects identified (Griffing 1967). Thus the following genetic model is used for $A_{i_1}A_{j_1}$, when its genotypic value is expressed in the couplet ($A_{i_1}A_{j_1}$, $A_{i_2}A_{j_2}$):

$$i_{1j_1}d_{i_2j_2} = a\alpha_{i_1} + a\alpha_{j_1} + a\delta_{i_1j_1} + a\alpha_{i_2} + a\alpha_{j_2} + a\delta_{i_2j_2} + da(\alpha\alpha)_{i_1i_2} + da(\alpha\alpha)_{i_1j_2} + da(\alpha\alpha)_{j_1i_2} \\ + da(\alpha\alpha)_{j_1j_2} + da(\alpha\delta)_{i_1i_2j_2} + da(\alpha\delta)_{j_1i_2j_2} + da(\delta\alpha)_{i_1j_1i_2} + da(\delta\alpha)_{i_1j_1j_2} + da(\delta\delta)_{i_1j_1i_2j_2},$$

where

$$a\alpha_{i_1} = i_1. d \dots = \sum p_{j_1}p_{i_2}p_{j_2}(i_{1j_1}d_{i_2j_2}) \\ = \text{direct additive effect of allele } A_{i_1},$$

$$a\delta_{i_1j_1} = i_{1j_1}d \dots - a\alpha_{i_1} - a\alpha_{j_1} \\ = \text{direct dominance effect of } A_{i_1}A_{j_1},$$

$$a\alpha_{i_2} = \dots d_{i_2}. = \sum p_{i_1}p_{j_1}p_{j_2}(i_{1j_1}d_{i_2j_2}) \\ = \text{associate additive effect of allele } A_{i_2},$$

$$a\delta_{i_2j_2} = \dots d_{i_2j_2} - a\alpha_{i_2} - a\alpha_{j_2} \\ = \text{associate dominance effect of } A_{i_2}A_{j_2},$$

$$da(\alpha\alpha)_{i_1i_2} = i_1. d_{i_2}. - a\alpha_{i_1} - a\alpha_{i_2} \\ = \text{additive} \times \text{additive interaction between alleles } A_{i_1} \text{ and } A_{i_2},$$

$$da(\alpha\delta)_{i_1i_2j_2} = i_1. d_{i_2j_2} - a\alpha_{i_1} - a\alpha_{i_2} - a\alpha_{j_2} - a\delta_{i_2j_2} - da(\alpha\alpha)_{i_1i_2} - da(\alpha\alpha)_{i_1j_2} \\ = \text{additive} \times \text{dominance interaction effect between the direct allele, } A_{i_1}, \text{ and the associate genotype } A_{i_2}A_{j_2},$$

$$\begin{aligned}
 da(\delta\alpha)_{i_1j_1i_2} &= {}_{i_1j_1}d_{i_2} - d\alpha_{i_1} - d\alpha_{j_1} - d\delta_{i_1j_1} - d\alpha_{i_2} - da(\alpha\alpha)_{i_1i_2} - da(\alpha\alpha)_{j_1i_2} \\
 &= \text{dominance} \times \text{additive interaction effect between the direct genotype,} \\
 &\quad A_{i_1}A_{j_1}, \text{ and the associate allele } A_{i_2}, \text{ and} \\
 da(\delta\delta)_{i_1j_1i_2j_2} &= {}_{i_1j_1}d_{i_2j_2} - d\alpha_{i_1} - d\alpha_{j_1} - d\delta_{i_1j_1} - d\alpha_{i_2} - d\alpha_{j_2} - d\delta_{i_2j_2} - da(\alpha\alpha)_{i_1i_2} \\
 &\quad - da(\alpha\alpha)_{i_1j_2} - da(\alpha\alpha)_{j_1i_2} - da(\alpha\alpha)_{j_1j_2} - da(\alpha\delta)_{i_1i_2j_2} - da(\alpha\delta)_{j_1i_2j_2} \\
 &\quad - da(\delta\alpha)_{i_1j_1i_2} - da(\delta\alpha)_{i_1j_1j_2} \\
 &= \text{dominance} \times \text{dominance interaction effect between the direct genotype,} \\
 &\quad A_{i_1}A_{j_1}, \text{ and the associate genotype } A_{i_2}A_{j_2}.
 \end{aligned}$$

The variances associated with the above model involved in selection response are

$$\begin{aligned}
 \sigma_G^2 &= \sum p_{i_1}p_{j_1}p_{i_2}p_{j_2}({}_{i_1j_1}d_{i_2j_2})^2, \\
 da\sigma_A^2 &= 2 \sum p_{i_1}(d\alpha_{i_1})^2, \text{ and} \\
 aa\sigma_A^2 &= 2 \sum p_{i_2}(a\alpha_{i_2})^2.
 \end{aligned}$$

The following covariance between direct and associate additive effects must also be defined:

$${}_{(da)}\sigma_A = 2 \sum p_{i_1}(d\alpha_{i_1})(a\alpha_{i_1}).$$

For further details of the model and its associated parameters see Griffing (1967).

(b) *Selection Index applied to Direct Values*

For the simplest application of selection index theory, consider the selection of $A_{i_1}A_{j_1}$ on the basis of the following index:

$$I_{i_1j_1}^* = \beta({}_{i_1j_1}\tau_{i_2j_2}).$$

The selection value for $A_{i_1}A_{j_1}$ is then taken to be

$$w_{i_1j_1} = 1 + (\bar{i}/\sigma)_I(I_{i_1j_1})$$

where

$I_{i_1j_1} = \beta({}_{i_1j_1}d \dots)$ = mean index value of the subpopulation of individuals whose genotype is $A_{i_1}A_{j_1}$,

\bar{i} = standardized selection differential,

σ = phenotypic standard deviation, and the subscript I indicates that \bar{i} and σ are parameters relating to the index population.

The change in gene frequency can then be shown to be

$$\Delta p_{i_1} = (\bar{i}/\sigma)_I(p_{i_1})[\beta(d\alpha_{i_1})],$$

and the change in the mean is

$$\Delta\mu \simeq (\bar{i}/\sigma)_I(\beta)[da\sigma_A^2 + {}_{(da)}\sigma_A]. \quad (1)$$

This result holds true for any value of β . In particular if β is set equal to 1, the selection value for $A_{i_1}A_{j_1}$ is

$$w_{i_1j_1} = 1 + (\bar{i}/\sigma)_{\text{ind.}}({}_{i_1j_1}d \dots),$$

which leads to the results obtained earlier (Griffing 1967) for the usual concept of individual selection, i.e.

$$\Delta\mu \simeq (\bar{i}/\sigma)_{\text{ind.}}[{}_{ad}\sigma_A^2 + ({}_{da})\sigma_A].$$

In this particular case if $({}_{da})\sigma_A$ is negative and greater in magnitude than ${}_{ad}\sigma_A^2$, positive individual selection causes a negative response in the population mean. As will now be shown this undesirable result can be prevented by proper choice of the value of β .

The general principle in selection index theory is to maximize $\Delta\mu$ for the particular selection procedure in question. This is accomplished by appropriate choice of values for the index coefficients; in this case for the single coefficient, β .

The first step is to evaluate the variance of the index. This variance is given by

$$\sigma_I^2 = \beta^2(\sigma_P^2).$$

Hence equation (1) can be recast as

$$\begin{aligned} \Delta\mu &\simeq (\bar{i})_I(\beta)[{}_{ad}\sigma_A^2 + ({}_{da})\sigma_A]/(\sigma_I^2)^{\frac{1}{2}} \\ &= (\bar{i})_I(\beta)[{}_{ad}\sigma_A^2 + ({}_{da})\sigma_A]/|\beta| \sigma_P. \end{aligned}$$

In this representation, it is clear that the magnitude of β does not affect $\Delta\mu$; however, the sign of β does. Also it is obvious that with positive selection, the quantities $(\bar{i})_I$, $|\beta|$, and σ_P are all non-negative. As mentioned previously the remaining expression $[{}_{ad}\sigma_A^2 + ({}_{da})\sigma_A]$ can be negative. Hence the following rule in the choice of β will invariably result in maximum $\Delta\mu$:

$$(i) \text{ if } [{}_{ad}\sigma_A^2 + ({}_{da})\sigma_A] > 0, \text{ put } \beta = +1,$$

or

$$(ii) \text{ if } [{}_{ad}\sigma_A^2 + ({}_{da})\sigma_A] < 0, \text{ put } \beta = -1.$$

The last situation is the condition in which *negative* selection yields maximum *positive* response in the progeny mean for the procedure which is normally termed individual or mass selection.

(c) Selection Index which Combines "Direct" and "Associate" Values

A more sophisticated and powerful selection index theory is one that utilizes all the information in the group. The following index directs the selection of $A_{i_1}A_{j_1}$, as it occurs in the group $(A_{i_1}A_{j_1}, A_{i_2}A_{j_2})$, so as to consider both the direct phenotypic value, $i_{i_1}\tau_{i_{j_2}}$, and the phenotypic value of its associate member, i.e. $i_{j_2}\tau_{i_{i_1}}$. The index is

$$I_{i_{j_1}}^* = \beta_1(i_{i_1}\tau_{i_{j_2}}) + \beta_2(i_{j_2}\tau_{i_{i_1}}).$$

For the subpopulation of individuals whose genotype is $A_{i_1}A_{j_1}$, the mean index value is

$$I_{i_{j_1}} = \beta_1(i_{i_1}d_{. .}) + \beta_2(. . d_{i_{j_1}}).$$

Hence the selection value of $A_{i_1}A_{j_1}$ is

$$w_{I_{i_{j_1}}} = 1 + (\bar{i}/\sigma)_I(I_{i_{j_1}}).$$

The change in frequency of the allele A_{i_1} can be shown to be

$$\Delta p_{i_1} = (\bar{i}/\sigma)_I(p_{i_1})[\beta_1(a\alpha_{i_1}) + \beta_2(a\alpha_{i_1})].$$

Hence the change in the progeny mean is

$$\Delta\mu \simeq (\bar{i}/\sigma)_I \{ \beta_1 [ad\sigma_A^2 + (da)\sigma_A] + \beta_2 [(da)\sigma_A + aa\sigma_A^2] \}.$$

This result can be put in matrix form as follows:

$$\Delta\mu = (\bar{i})_I [\mathbf{B}' \mathbf{G} \mathbf{1}] / \sigma_I,$$

where

$$\mathbf{B}' = (\beta_1, \beta_2), \quad \mathbf{G} = \begin{pmatrix} ad\sigma_A^2 & (da)\sigma_A \\ (da)\sigma_A & aa\sigma_A^2 \end{pmatrix}, \quad \mathbf{1} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

and

$$\sigma_I = [(\beta_1^2 + \beta_2^2)\sigma_P^2 + 2\beta_1\beta_2(p\sigma_P)]^{\frac{1}{2}},$$

or in matrix notation

$$\sigma_I = [\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}},$$

where

$$\mathbf{P} = \begin{pmatrix} \sigma_P^2 & p\sigma_P \\ p\sigma_P & \sigma_P^2 \end{pmatrix}.$$

Hence

$$\Delta\mu = (\bar{i})_I \frac{[\mathbf{B}' \mathbf{G} \mathbf{1}]}{[\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}}}.$$

The above result is true for any values associated with the β 's. The next step, clearly, is to choose β 's so as to maximize $\Delta\mu$.

(i) *Choosing β 's to Maximize $\Delta\mu$*

For groups of order two, the change in mean can be recast as

$$\Delta\mu = (\bar{i})_I (W/V^{\frac{1}{2}})$$

where

$$W = \beta_1 [ad\sigma_A^2 + (da)\sigma_A] + \beta_2 [(da)\sigma_A + aa\sigma_A^2]$$

and

$$V = (\beta_1^2 + \beta_2^2)\sigma_P^2 + 2\beta_1\beta_2(p\sigma_P).$$

The objective is to choose β 's to maximize $\Delta\mu$, or as it is more convenient, to maximize

$$\ln(\Delta\mu) = \ln(\bar{i})_I + \ln W - \frac{1}{2} \ln V.$$

The normal equations obtained by differentiation are

$$\beta_1(\sigma_P^2) + \beta_2(p\sigma_P) = (V/W)[ad\sigma_A^2 + (da)\sigma_A],$$

and

$$\beta_1(p\sigma_P) + \beta_2(\sigma_P^2) = (V/W)[(da)\sigma_A + aa\sigma_A^2].$$

Since it is only the ratio $\beta_1 : \beta_2$ that is important, set $V/W = 1$. Then in matrix notation these equations become:

$$\mathbf{P} \mathbf{B} = \mathbf{G} \mathbf{1}. \tag{2}$$

Assuming \mathbf{P} is non-singular, the solution for the β 's is

$$\hat{\mathbf{B}} = \mathbf{P}^{-1} \mathbf{G} \mathbf{1}.$$

The genetic gain can now be formulated more simply. Recall that for any set of β 's

$$\Delta\mu = (i)_I \frac{[\mathbf{B}' \mathbf{G} \mathbf{1}]}{[\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}}}. \quad (3)$$

However, on substituting the relationships exhibited by the normal equations (2), which give rise to β 's yielding maximum $\Delta\mu$, the change in mean (3) becomes

$$\begin{aligned} \Delta\mu &= (i)_I \frac{[\mathbf{B}' \mathbf{P} \mathbf{B}]}{[\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}}} \\ &= (i)_I (\sigma_I). \end{aligned}$$

(ii) *A Similar Index*

Parenthetically, it is of interest to note that the index discussed above is equivalent (in the sense of giving the same $\Delta\mu$) to the following index

$$I_{i_1 j_1}^* = \beta_1^* (i_1 j_1 \tau_{i_2 j_2}) + \frac{1}{2} \beta_2^* (i_1 j_1 \tau_{i_2 j_2} + i_2 j_2 \tau_{i_1 j_1}),$$

which, more clearly, combines individual and group selection.

The coefficients for the two indices are related as follows:

$$\begin{aligned} \beta_1 &= \beta_1^* + \frac{1}{2} \beta_2^* \\ \beta_2 &= \frac{1}{2} \beta_2^*. \end{aligned}$$

III. CONSEQUENCES OF INDEX SELECTION AS APPLIED TO GROUPS OF ORDER n

(a) *Population Specification*

The array of groups of order n is obtained as an n -way combinatorial product of the base population, i.e.

$$\begin{aligned} &[\sum p_i p_j (A_i A_j)] \times \dots \times [\sum p_i p_j (A_i A_j)] \\ &= \sum p_{i_1} p_{j_1} p_{i_2} p_{j_2} \dots p_{i_n} p_{j_n} (A_{i_1} A_{j_1}, A_{i_2} A_{j_2}, \dots, A_{i_n} A_{j_n}). \end{aligned}$$

The phenotypic value of the group member whose genotype is $A_{i_1} A_{j_1}$ in the n -tuple

$$(A_{i_1} A_{j_1}, A_{i_2} A_{j_2}, \dots, A_{i_n} A_{j_n})$$

is

$$i_1 j_1 \tau_{i_2 j_2, \dots, i_n j_n} = i_1 j_1 d_{i_2 j_2, \dots, i_n j_n} + i_1 j_1 e_{i_2 j_2, \dots, i_n j_n},$$

where the elements in the model have similar properties to those given for groups of size two. For further details of the representation of the genotypic value $i_1 j_1 d_{i_2 j_2, \dots, i_n j_n}$ in terms of a gene model and its associated variances, see the first paper in this series (Griffing 1967).

(b) *Selection Index Applied to "Direct" Values*

The theory for groups of size n follows essentially that for groups of size two. Hence only the salient features are mentioned.

The index considered for $A_{i_1} A_{j_1}$ is

$$I_{i_1 j_1}^* = \beta (i_1 j_1 \tau_{i_2 j_2, \dots, i_n j_n}),$$

which gives rise to the following selection value for $A_{i_1}A_{j_1}$,

$$\begin{aligned} w_{i_1j_1} &= 1 + (\bar{i}/\sigma)_I(I_{i_1j_1}) \\ &= 1 + (\bar{i}/\sigma)_I(\beta)(i_{i_1j_1}d \dots, \dots). \end{aligned}$$

The change in gene frequency is

$$\Delta p_{i_1} = (\bar{i}/\sigma)_I(p_{i_1})(\beta)_{(aa)\alpha_{i_1}},$$

and the change in mean resulting from selection is

$$\Delta\mu = (\bar{i}/\sigma)_I(\beta)(1/n)[_{aa}\sigma_A^2 + (n-1)_{(da)\sigma_A}].$$

Thus the rule to be employed in order to invariably yield maximum $\Delta\mu$ with individual "direct" selection is:

$$(i) \text{ if } [_{aa}\sigma_A^2 + (n-1)_{(da)\sigma_A}] > 0, \text{ put } \beta = +1,$$

or

$$(ii) \text{ if } [_{aa}\sigma_A^2 + (n-1)_{(da)\sigma_A}] < 0, \text{ put } \beta = -1.$$

(c) *Selection Index Theory which Combines "Direct" and "Associate" Values*

For groups of size n the index for $A_{i_1}A_{j_1}$ in the n -tuple $(A_{i_1}A_{j_1}, A_{i_2}A_{j_2}, \dots, A_{i_n}A_{j_n})$ which combines direct and associate values is taken to be

$$I_{i_1j_1}^* = \beta_1(i_{i_1j_1}\tau_{i_2j_2}, \dots, i_{nj_n}) + \beta_2(i_{i_2j_2}\tau_{i_1j_1}, \dots, i_{nj_n} + \dots + i_{nj_n}\tau_{i_1j_1}, \dots, i_{n-1j_{n-1}})$$

In this representation β_1 is the coefficient for the direct phenotype of the individual selected, and β_2 is the coefficient for the associate phenotypes of the $(n-1)$ remaining members of the group.

The selection value for $A_{i_1}A_{j_1}$ is then

$$w_{I_{i_1j_1}} = 1 + (\bar{i}/\sigma)_I(I_{i_1j_1})$$

where $I_{i_1j_1}$ is the mean index value for individuals of the genotype $A_{i_1}A_{j_1}$ regardless of group origin. More specifically this mean index value is equivalent to

$$I_{i_1j_1} = \beta_1(i_{i_1j_1}d \dots, \dots) + \beta_2(n-1)(\dots d_{i_1j_1}, \dots, \dots).$$

The change in frequency of A_{i_1} is

$$\Delta p_{i_1} = (\bar{i}/\sigma)_I(p_{i_1})[\beta_1(a\alpha_{i_1}) + \beta_2(n-1)(a\alpha_{i_1})],$$

and the change in the progeny mean is

$$\Delta\mu = (\bar{i}/\sigma)_I\{\beta_1(_{aa}\sigma_A^2) + (n-1)(\beta_1 + \beta_2)[_{(da)\sigma_A}] + (n-1)^2(\beta_2)(_{aa}\sigma_A^2)\}.$$

This result can be stated in matrix notation as

$$\Delta\mu = (\bar{i})_I[\mathbf{B}' \mathbf{G} \mathbf{1}]/\sigma_I,$$

where

$$\mathbf{B}' = (\beta_1, \beta_2), \quad \mathbf{G} = \begin{pmatrix} _{aa}\sigma_A^2 & (n-1)[_{(da)\sigma_A}] \\ (n-1)[_{(da)\sigma_A}] & (n-1)^2_{aa}\sigma_A^2 \end{pmatrix}, \quad \mathbf{1} = \begin{pmatrix} 1 \\ 1 \end{pmatrix},$$

and

$$\sigma_I = [\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}},$$

where

$$\mathbf{P} = \begin{pmatrix} \sigma_P^2 & (n-1)(p\sigma_P) \\ (n-1)(p\sigma_P) & [(n-1)(\sigma_P^2) + (n-1)(n-2)(p\sigma_P)] \end{pmatrix}.$$

(i) *Choosing β 's to Maximize $\Delta\mu$*

The change in the population mean can be recast as

$$\Delta\mu = (\bar{i})_i (W/V^{\frac{1}{2}})$$

where

$$W = \beta_1(aa\sigma_A^2) + (n-1)(\beta_1 + \beta_2)[(aa)\sigma_A] + (n-1)^2(\beta_2)(aa\sigma_A^2),$$

and

$$V = [\beta_1^2 + (n-1)\beta_2^2](\sigma_P^2) + [2(n-1)\beta_1\beta_2 + (n-1)(n-2)\beta_2^2](\rho\sigma_P).$$

Then the normal equations for maximization of $\ln(\Delta\mu)$ are

$$\beta_1(\sigma_P^2) + \beta_2[(n-1)(\rho\sigma_P)] = aa\sigma_A^2 + (n-1)[(aa)\sigma_A],$$

and

$$\beta_1[(n-1)(\rho\sigma_P)] + \beta_2[(n-1)\sigma_P^2 + (n-1)(n-2)(\rho\sigma_P)] = (n-1)[(aa)\sigma_A] + (n-1)^2[aa\sigma_A^2],$$

or in matrix form

$$\mathbf{P} \mathbf{B} = \mathbf{G} \mathbf{1}.$$

Hence the solution for the β 's giving maximum genetic gain is given by

$$\hat{\mathbf{B}} = \mathbf{P}^{-1} \mathbf{G} \mathbf{1},$$

assuming that \mathbf{P} is non-singular. On substituting the relationships exhibited by the normal equations, the following expression for the genetic gain

$$\Delta\mu = (\bar{i})_i \frac{[\mathbf{B}' \mathbf{G} \mathbf{1}]}{[\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}}}$$

becomes simply

$$\begin{aligned} \Delta\mu &= (\bar{i})_i [\mathbf{B}' \mathbf{P} \mathbf{B}]^{\frac{1}{2}} \\ &= (\bar{i})_i (\sigma_i). \end{aligned}$$

The matrix representation indicates the general similarity between the above results with those for groups of order two. However, it must be remembered that the matrices, \mathbf{P} and \mathbf{G} are vastly different for the two cases.

IV. ADAPTING THE INDEX THEORY TO ACCOMMODATE A GENE MODEL REPRESENTING AN ARBITRARY NUMBER OF GENETICALLY NON-INTERACTING LOCI

For ease of presentation, the above theory has been developed for a single-locus model. Clearly this is not of practical value with regard to complexly inherited traits. However, the analyses extend naturally to the simplest genetic situation of an arbitrary number of genotypically non-interacting loci. In this case the genotypic variances and covariances and their components which are involved in prediction, i.e. σ_G^2 , $aa\sigma_A^2$, $(aa)\sigma_A$, and $\rho\sigma_G$, are assumed to represent the summation of the independent contributions from each locus. The theory then holds for this specific genetic model. The generalization to more complex models will be made in a subsequent paper of this series.

V. NUMERICAL EXAMPLES

Two numerical examples are given to compare the index method with selection procedures previously discussed in the first three papers of the present series. Selection methods as they apply to groups of size two are used for simplicity. In these examples it is assumed that the genotypic variance components represent the sum of contributions from an arbitrary number of non-interacting loci.

TABLE I
VALUES ASSIGNED TO VARIANCE AND COVARIANCE COMPONENTS FOR NUMERICAL EXAMPLES
ILLUSTRATING VARIOUS KINDS OF SELECTION

Variance Components	Values Assigned		Covariance Components	Values Assigned	
	Example 1	Example 2		Example 1	Example 2
1. Genotypic			1. Genotypic		
(a) Direct			$(da)\sigma_A$	-4	-4
$aa\sigma_A^2$	2	2	$(da)\sigma_D$	-1	-1
$aa\sigma_D^2$	1	1	$(da)\sigma_G = (da)\sigma_A + (da)\sigma_D$	-5	-5
$aa\sigma_G^2 = aa\sigma_A^2 + aa\sigma_D^2$	3	3	Total genotypic covariance for groups of order 2		
(b) Associate			$\sigma_G\sigma_G = 2[(da)\sigma_G]$	-10	-10
$aa\sigma_A^2$	8	8	2. Environmental		
$aa\sigma_D^2$	1	1	$E\sigma_E$	-2	-6
$aa\sigma_G^2 = aa\sigma_A^2 + aa\sigma_D^2$	9	9	3. Total phenotypic		
(c) Total			$P\sigma_P = \sigma_G\sigma_G + E\sigma_E$	-12	-16
$\sigma_G^2 = aa\sigma_G^2 + aa\sigma_G^2$	12	12			
2. Environmental					
σ_E^2	4	20			
3. Total phenotypic					
$\sigma_P^2 = \sigma_G^2 + \sigma_E^2$	16	32			

As can be noted from Table I, the genotypic variance components are identical in the two examples. The only differences in the examples are those due to the relative proportions of the environmental variances and covariances. With regard to the genotypic components, the numerical examples include partial dominance, but for simplicity epistatic variances are taken to be zero. The results from one cycle of selection are given in Table 2. The situation of "no selection" is included as a reference point. In both examples, positive individual selection results in a negative change in the population mean. This undesirable response is corrected by all other selection methods. In both examples, the index applied to individual selection results in a negative selection procedure which yields a positive response in the progeny mean.

In the second example, positive group selection yields the same result as negative individual selection. Although group selection can be inefficient, the first example demonstrates that under certain circumstances it can in fact be more efficient than individual selection.

The best selection procedure is, of course, the index method which most favourably combines individual and group selection for maximum genetic gain.

In the first example the selection index coefficients are $\beta_1 = 2/14$ and $\beta_2 = 5/14$. These values indicate that, for this example, greater attention should be paid to the value of the associate member of the group than to the individual being selected! In the second example the results are even more incongruous. The index coefficients may be taken to be $\beta_1 = 0$ and $\beta_2 = 1$. These coefficients imply that for *maximum* genetic gain in this example, the phenotypic expression of the individual selected should be totally ignored and selection should be based only on the value of the associate member!

TABLE 2
RESULTS OF DIFFERENT KINDS OF SELECTION FOR THE TWO
NUMERICAL EXAMPLES

Selection Procedures	Increment Changes Due to One Cycle of Selection $\times (\bar{x})$	
	Example 1	Example 2
Positive individual selection	-0.5	-0.35
No selection	0.0	0.0
Index selection†	0.5	0.35
Group selection	0.7	0.35
Index selection‡	1.1	0.71

† $I_{i_1j_1}^* = \beta(i_{1j_1}\tau_{i_2j_2})$, where, for $\Delta\mu_{\max}$, $\beta = -1$.

‡ $I_{i_1j_1}^* = \beta_1(i_{1j_1}\tau_{i_2j_2}) + \beta_2(i_{2j_2}\tau_{i_1j_1})$.

These numerical examples are useful in demonstrating how a disastrous course of action due to individual selection can be diverted into any one of several more constructive avenues. Then the examples illustrate how the responses can be progressively improved with different forms of selection, culminating in the results from the selection index method which yields maximum genetic gain for the group structure envisaged in these studies.

VI. DISCUSSION

This study deals with selection procedures which operate and are evaluated with regard to populations of groups. Each group contains n randomly associated individuals from a defined base population. Individuals within groups may interact in any arbitrary manner, whether it be cooperative or competitive in nature. Selection procedures are those based on the individual or the group as a unit, or on some combination of the individual and its associated group.

Under these circumstances selection index methods ensure that (1) change in population mean is invariably non-negative, and (2) a *maximum* change in mean occurs due to selection. Thus for conditions outlined above, index theory provides the most efficient selection procedure possible.

However, production of a selection index in the above context is not the end of the quest for selection methods exhibiting greater efficiency. An entirely different approach may be taken which considers use of groups whose elements are not

randomly associated. An important class of such groups is that in which group members are relatives.

In the case of plants the relationship between group members can be carried to an extreme. For example, with plants that can be separated into propagules, groups can be constituted entirely of the same genotype regardless of the degree of heterozygosity. Furthermore for those plant species from which monpoids can be extracted, groups can be obtained in such a way that each is made up entirely of the same homozygous genotype. In both of these cases, efficiency of selection is greatly enhanced. This new avenue of approach will be explored in future contributions of this series.

VII. REFERENCES

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