

INFLUENCE OF SEX ON SELECTION

II. CONTRIBUTIONS OF AUTOSOMAL GENOTYPES HAVING DIFFERENT VALUES IN THE TWO SEXES

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[Manuscript received January 17, 1966]

Summary

Consequences of mass and general combining ability selection are examined for characteristics subject to the phenomenon of sex-influenced inheritance. This form of inheritance is due to autosomal genes whose expressions are different in the two sexes.

Two different approaches are made to the problem of predicting genetic advance. Firstly, an analysis is made for an autosomal two-locus model which gives prediction equations in terms of genotypic variances and covariances. Secondly, a generalized analysis is given in terms of covariances among relatives.

In both mass and general combining ability selection, the *immediate* response to selection involves additive and additive \times additive epistatic effects. On relaxation from selection the epistatic contributions tend to disappear, leaving as a residual *permanent* gain only those contributions due to additive gene effects. The complication introduced by sex-influenced inheritance is that the immediate and permanent responses to selection are made in terms of genotypic *covariances* as well as *variances*. This complication results in the sexes exhibiting different responses for the same selection pressure. Such differences may be confused with those due to sex-linked inheritance.

I. INTRODUCTION

The present series of papers, of which this is the second, has to do with the various indirect ways that sex may influence the response to selection. In Part I of the series (Griffing 1965), the results due to selection operating on sex-linked genes were examined. In the present paper, the results of selection operating on autosomal loci whose effects are "sex-influenced" are considered. This phenomenon implies that a given autosomal genotype is associated with different genotypic values in the two sexes.

The analyses are presented for two different levels of genetic complexity: (1) a two-locus model which yields results in terms of genotypic variances and covariances, and (2) a generalized model which yields results in terms of covariances among relatives. For each of these analyses, results are given for mass selection and for general combining ability (hereafter abbreviated to g.c.a.) selection. The term "g.c.a. selection" implies the use of half-sib progeny to evaluate an individual's selective value.

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II. ANALYSES BASED ON AN AUTOSOMAL TWO-LOCUS MODEL

This section, dealing with an autosomal two-locus model, may be viewed as an extension of an earlier study (Griffing 1962). In that study the model included (1) any number of alleles at each of two linked autosomal loci, (2) any system of dominance and epistatic parameters, and (3) recombination values which may be different for the two sexes. In the present study the above model is extended to include the additional generalization that a genotype may have different values in the two sexes.

1. λ -SEX PARAMETERS OF THE INITIAL RANDOM-MATING POPULATION

It is assumed that the selection program is initiated with random-mating populations in equilibrium. However, since the genotypic values may be different for the two sexes, the male and female populations need to be treated separately. Because the analyses deal with autosomal genotypes only, the parameters and selection results for either sex can be given most economically for a "dummy" or λ -sex. Then the male-sex values are obtained by replacing λ by the word "male" or, in the case of subscripts, by the letter m . Parameters for the female sex are obtained by substituting the word "female", or the letter f , for λ as the situation demands.

Since it is assumed that the initial populations are in equilibrium, gene frequencies, gamete frequencies, and genotypic arrays are identical for the two sexes. In order to specify exactly these aspects of the populations, let

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

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

$$\sum_{i,k} (f_{ik})(A_i^1 A_k^2) = \text{gametic array produced by either sex from the initial equilibrium population in the absence of forces changing gene frequencies,}$$

where, for convenience,

$$f_{ik} = p_i^1 p_k^2 = \text{frequency of gamete } (A_i^1 A_k^2), \text{ and}$$

$$\sum_{i,j,k,l} (f_{ik})(f_{jl})(A_i^1 A_k^2)(A_j^1 A_l^2) = \text{genotypic array for either sex.}$$

Differentiation between male and female populations occurs when genotypic values are assigned. The genotypic value for the λ -sex genotype $(A_i^1 A_k^2)(A_j^1 A_l^2)$ is denoted as $\lambda_{ik,jl}$ and is coded so that

$$\sum_{i,j,k,l} (f_{ik})(f_{jl})\lambda_{ik,jl} = 0.$$

This genotypic value is characterized by the following gene model:

$$\begin{aligned} \lambda_{ik,jl} = & \lambda a_i^1 + \lambda a_j^1 + \lambda a_k^2 + \lambda a_l^2 + \lambda \delta_{ij}^1 + \lambda \delta_{kl}^2 + \lambda (aa)_{ik} + \lambda (aa)_{il} \\ & + \lambda (aa)_{jk} + \lambda (aa)_{jl} + \lambda (a\delta)_{ikl} + \lambda (a\delta)_{jkl} + \lambda (\delta a)_{ijk} + \lambda (\delta a)_{ijl} + \lambda (\delta\delta)_{ijkl}, \end{aligned}$$

where λa_u^a = additive genetic effect of the A_u^a allele,

$\lambda \delta_{uv}^a$ = dominance effect associated with the $A_u^a A_v^a$ genotype,

$\lambda (aa)_{ik}$ = additive \times additive epistatic effect associated with genes A_i^1 and A_k^2 ,

$\lambda (a\delta)_{ikl}$ = additive \times dominance epistatic effect associated with the gene A_i^1 and the genotype $A_k^2 A_l^2$, and

$_{\lambda}(\delta\delta)_{ijkl}$ = dominance \times dominance epistatic effect associated with the genotypes $A_i^1A_j^1$ and $A_k^2A_l^2$.

The total genotypic variance may be partitioned as

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

where the variances may be denoted by either of the two following notations,

$_{\lambda}\sigma_G^2 = _{\lambda}\sigma_G$ = total genotypic variance generated by the two loci,

$_{\lambda}\sigma_A^2 = _{\lambda}\sigma_A$ = additive genetic variance,

$_{\lambda}\sigma_D^2 = _{\lambda}\sigma_D$ = dominance variance,

$_{\lambda}\sigma_{AA}^2 = _{\lambda}\sigma_{AA}$ = additive \times additive variance,

$_{\lambda}\sigma_{AD}^2 = _{\lambda}\sigma_{AD}$ = additive \times dominance variance, and

$_{\lambda}\sigma_{DD}^2 = _{\lambda}\sigma_{DD}$ = dominance \times dominance variance.

Besides these variances, certain covariances need to be defined. These are:

$$_{fm}\sigma_A = 2\sum_i(p_i^1)(_{f}a_i^1)(_{m}a_i^1) + 2\sum_k(p_k^2)(_{f}a_k^2)(_{m}a_k^2),$$

$$_{fm}\sigma_{AA} = 4\sum_{i,k}(p_i^1)(p_k^2)[_{f}(aa)_{ik}][_{m}(aa)_{ik}].$$

Another way in which the sexes may differ is the magnitude of the recombination value for the two loci under consideration. Hence, to complete the array of parameters of the λ -sex population, let y_{λ} designate its recombination frequency.

In the following it will be often necessary to specify parameters associated with both sexes in the same equation. This is done by introducing $\bar{\lambda}$ which is the symbol for the sex complementary to that of λ ; i.e. in a specific case if λ represents male, then $\bar{\lambda}$ represents female.

2. MASS SELECTION

In defining the selection value $_{\lambda}w_{ik,jl}$ for the genotype $(A_i^1A_k^2)(A_j^1A_l^2)$ of the λ -sex, it is assumed that the genotypic variability of the characteristic under consideration is controlled by genes, each of small effect, at many loci. The phenotypic variability is assumed to be normally distributed with mean zero and variance $_{\lambda}\sigma_{\text{ind}}^2$. Following Kimura (1958), the selection value $_{\lambda}w_{ik,jl}$ is defined to be proportional to the probability that a λ -sex individual of the genotype $(A_i^1A_k^2)(A_j^1A_l^2)$ survives selection. Hence, for mass selection

$$_{\lambda}w_{ik,jl} = 1 + (\bar{i}_{\lambda}/_{\lambda}\sigma_{\text{ind}})(\lambda_{ik,jl}),$$

where \bar{i}_{λ} = standardized selection differential for the λ -sex. It is assumed that this value is constant for the λ -sex throughout the period of selection, but may be different in the two sexes.

(a) Consequences of n Consecutive Cycles of Selection

In this section the specific case in which individuals of both sexes are subject to mass selection will be considered first. This is followed by a brief summary giving the independent sex increments to gamete frequencies and progeny means due to mass selection operating in one sex irrespective of the mode of selection operating in the other sex. These latter results permit the inclusion of mass selection terms in prediction equations for complex selection programs which involve mass as well as other forms of selection.

(i) *A Specific Mass-selection Program*

In this program it is assumed that individuals of each sex are subject to n consecutive cycles of mass selection.

Among the genetic effects which characterize a genotype in the two-locus model, only the additive effects and the additive \times additive epistatic effects contribute to the increment change in gamete frequency due to selection. It is convenient to deal with these two classes of effects separately in deriving the recurrence equations which relate gamete frequencies of the n th selection cycle with those of the previous cycle. The recurrence equations for the λ -sex are given as follows. For additive effects only,

$${}_{[\lambda, \bar{\lambda}]}f_{ik}^n = \frac{1}{2}({}_{[f, m]}f_{ik}^{n-1} + {}_{[m, f]}f_{ik}^{n-1}) + p_i^1 p_k^2 (\lambda \theta_{ik}),$$

and for additive \times additive effects only,

$${}_{[\lambda, \bar{\lambda}]}f_{ik}^n = c_\lambda ({}_{[f, m]}f_{ik}^{n-1} + {}_{[m, f]}f_{ik}^{n-1}) + p_i^1 p_k^2 (\lambda \phi_{ik}),$$

where ${}_{[\lambda, \bar{\lambda}]}f_{ik}^n$ = gamete frequency: the subscript $[\lambda, \bar{\lambda}]$ denotes that the frequency is associated with a λ -sex gamete (indicated by the fact that λ occurs in the first position) from a population in which both λ and $\bar{\lambda}$ are subject to mass selection,

$$\begin{aligned} \lambda \theta_{ik} &= (\bar{v}_{\lambda/\lambda} \sigma_{\text{ind.}})(\lambda \alpha_i^1 + \lambda \alpha_k^2), \\ \lambda \phi_{ik} &= (\bar{v}_{\lambda/\lambda} \sigma_{\text{ind.}})[\lambda (\alpha \alpha)_{ik}], \text{ and} \\ c_\lambda &= \frac{1}{2}(1 - y_\lambda). \end{aligned}$$

If these recurrence relationships are utilized, it is possible to determine the composition of the gamete frequency for the n th cycle in terms of the parameters of the initial populations, i.e.

$$\begin{aligned} {}_{[\lambda, \bar{\lambda}]}f_{ik}^n &= p_i^1 p_k^2 \left\{ 1 + \frac{1}{2}(n+1)(\lambda \theta_{ik}) + \frac{1}{2}(n-1)(\lambda \bar{\lambda} \theta_{ik}) \right. \\ &\quad \left. + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] (\lambda \phi_{ik}) + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) (\lambda \bar{\lambda} \phi_{ik}) \right\}, \end{aligned}$$

where

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

The gamete frequencies can be used to obtain the increment advance in the λ -sex population mean due to n consecutive cycles of selection:

$$\begin{aligned} {}_{[\lambda, \bar{\lambda}]} \times {}_{[\bar{\lambda}, \lambda]} \mu_n &= \frac{1}{2}n[(\bar{v}_{\lambda/\lambda} \sigma_{\text{ind.}})(\lambda \lambda \sigma_A) + (\bar{v}_{\bar{\lambda}/\bar{\lambda}} \sigma_{\text{ind.}})(\lambda \bar{\lambda} \sigma_A)] \\ &\quad + \frac{1}{4} \left(\frac{1-b^n}{1-b} \right) [(\bar{v}_{\lambda/\lambda} \sigma_{\text{ind.}})(\lambda \lambda \sigma_{AA}) + (\bar{v}_{\bar{\lambda}/\bar{\lambda}} \sigma_{\text{ind.}})(\lambda \bar{\lambda} \sigma_{AA})]. \end{aligned}$$

The subscript $[\lambda, \bar{\lambda}] \times [\bar{\lambda}, \lambda]$ denotes that the associated progeny mean is that for the λ -sex population (since the λ -gamete symbol, $[\lambda, \bar{\lambda}]$, occurs first) resulting from crossing gametes from populations in which both sexes are subject to mass selection.

(ii) *Independent Sex Increments due to Mass Selection*

Since the contributions of the two sexes are independent, it is possible to give the increments to both gamete frequencies and progeny means which are due to mass selection operating in one sex only. The necessary increments to *gamete* frequency are as follows:

(1) The contribution of mass λ -sex selection to the λ -sex gamete frequency is

$$p_i^1 p_k^2 \left\{ \frac{1}{2}(n+1)(\lambda\theta_{ik}) + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] (\lambda\phi_{ik}) \right\}.$$

(2) The contribution of mass λ -sex selection to the $\bar{\lambda}$ -sex gamete frequency is

$$p_i^1 p_k^2 \left\{ \frac{1}{2}(n-1)(\lambda\theta_{ik}) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) (\lambda\phi_{ik}) \right\}.$$

Contributions to the λ -sex *mean* are arranged in a hierarchical order as follows:

(A) Contributions from λ -sex individuals drawn from a population in which

(1) the λ -sex is subject to mass selection:

$$(\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n+1)(\lambda\lambda\sigma_A) + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{4}(\lambda\lambda\sigma_{AA}) \right\}.$$

(2) the $\bar{\lambda}$ -sex is subject to mass selection:

$$(\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n-1)(\lambda\bar{\lambda}\sigma_A) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{4}(\lambda\bar{\lambda}\sigma_{AA}) \right\}.$$

(B) Contributions from $\bar{\lambda}$ -sex individuals drawn from a population in which

(1) the λ -sex is subject to mass selection:

$$(\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n-1)(\lambda\lambda\sigma_A) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{4}(\lambda\lambda\sigma_{AA}) \right\}.$$

(2) the $\bar{\lambda}$ -sex is subject to mass selection:

$$(\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n+1)(\lambda\bar{\lambda}\sigma_A) + \left[1 + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{4}(\lambda\bar{\lambda}\sigma_{AA}) \right\}.$$

Use of these independent sex increments can be illustrated by deriving the prediction equation given earlier for the specific selection program in which both sexes are subject to mass selection. In this case the desired mean is represented symbolically as $_{[\lambda, \bar{\lambda}] \times [\bar{\lambda}, \lambda]} \mu_n$. The elements in the subscript, which occur in the order λ , $\bar{\lambda}$, $\bar{\lambda}$, and λ , are associated with the increments given for (A)(1), (A)(2), (B)(2), and (B)(1) respectively. Hence

$$\begin{aligned} _{[\lambda, \bar{\lambda}] \times [\bar{\lambda}, \lambda]} \mu_n &= (\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n+1)(\lambda\lambda\sigma_A) + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{4}(\lambda\lambda\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n-1)(\lambda\bar{\lambda}\sigma_A) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{4}(\lambda\bar{\lambda}\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n+1)(\lambda\bar{\lambda}\sigma_A) + \left[1 + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{4}(\lambda\bar{\lambda}\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}}) \left\{ \frac{1}{4}(n-1)(\lambda\lambda\sigma_A) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{4}(\lambda\lambda\sigma_{AA}) \right\} \\ &= (\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}}) \left\{ \frac{1}{2}n(\lambda\lambda\sigma_A) + \frac{1}{4} \left(\frac{1-b^n}{1-b} \right) (\lambda\lambda\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}}) \left\{ \frac{1}{2}n(\lambda\bar{\lambda}\sigma_A) + \frac{1}{4} \left(\frac{1-b^n}{1-b} \right) (\lambda\bar{\lambda}\sigma_{AA}) \right\}. \end{aligned}$$

An example which combines mass and g.c.a. independent sex increments will be given after the section on g.c.a. selection.

(b) *Consequence of t Cycles of Relaxation following n Cycles of Selection*

In this section the consequences of t cycles of relaxation are considered only for those populations resulting from the specific program in which both sexes are subject to mass selection.

The recurrence equations relating the λ -sex gamete frequencies of the t th and $(t-1)$ th cycles are as follows. For additive effects only,

$$_{[\lambda, \bar{\lambda}]}f_{ik}^{n,t} = \frac{1}{2}({}_{[f,m]}f_{ik}^{n,t-1} + {}_{[m,f]}f_{ik}^{n,t-1}),$$

and for additive \times additive effects only,

$$_{[\lambda, \bar{\lambda}]}f_{ik}^{n,t} = c_{\lambda}({}_{[f,m]}f_{ik}^{n,t-1} + {}_{[m,f]}f_{ik}^{n,t-1}).$$

If these relations are used, the gamete frequency for the t th cycle may be given in terms of the effects of the initial population, i.e.

$$_{[\lambda, \bar{\lambda}]}f_{ik}^{n,t} = p_i^1 p_k^2 \left\{ 1 + \frac{1}{2}n({}_f\theta_{ik} + {}_m\theta_{ik}) + c_{\lambda}(b^{t-1}) \left[\left(\frac{1-b^n}{1-b} \right) ({}_f\phi_{ik} + {}_m\phi_{ik}) \right] \right\}.$$

Finally, these gamete frequencies may be used to determine the mean of the λ -sex population which has had a history of n consecutive cycles of mass selection operating in both sexes, followed by t generations of relaxation. This mean is

$$\begin{aligned} {}_{[\lambda, \bar{\lambda}] \times [\bar{\lambda}, \lambda]} \mu_{n,t} &= \frac{1}{2}n[(\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}})(\lambda\sigma_A) + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}})(\lambda\bar{\lambda}\sigma_A)] \\ &\quad + \frac{1}{4}b^t \left(\frac{1-b^n}{1-b} \right) [(\bar{i}_{\lambda}/\lambda\sigma_{\text{ind.}})(\lambda\lambda\sigma_{AA}) + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{\text{ind.}})(\lambda\bar{\lambda}\sigma_{AA})]. \end{aligned}$$

It is clear that the additive \times additive contributions tend to disappear with relaxation since $\frac{1}{2} \leq b < 1$ for loci exhibiting a recombination value greater than zero. Thus the *permanent* gain due to selection is a function only of the additive variances and covariances.

3. GENERAL COMBINING ABILITY SELECTION

With g.c.a. selection, evaluation of the breeding value of an individual is based on the performance of its half-sib progeny. These progeny can be of either sex. Hence λ -sex individuals can be tested on the basis of their τ -sex progeny [denote as a $\lambda(\tau)$ g.c.a. test] and individuals of the $\bar{\lambda}$ -sex tested on the basis of their η -sex progeny (denote as a $\bar{\lambda}(\eta)$ g.c.a. test). The expected half-sib mean associated with the genotype $(A_i^1 A_k^2)(A_j^1 A_l^2)$, subject to a $\lambda(\tau)$ g.c.a. test, is

$$_{\lambda(\tau)}\gamma_{ik,jl} = \frac{1}{2}(\tau\alpha_i^1 + \tau\alpha_j^1 + \tau\alpha_k^2 + \tau\alpha_l^2) + c_{\lambda}(\alpha\alpha)_{ik} + {}_{\lambda}(\alpha\alpha)_{jl} + (1-c_{\lambda})[{}_{\lambda}(\alpha\alpha)_{il} + {}_{\lambda}(\alpha\alpha)_{jk}].$$

These half-sib means may be used to define selection values. Thus, for the λ -sex the selection value for $(A_i^1 A_k^2)(A_j^1 A_l^2)$, which is subject to a $\lambda(\tau)$ g.c.a. test, is

$$_{\lambda(\tau)}w_{ik,jl} = 1 + (\bar{i}_{\lambda}/\lambda\sigma_{\text{h.s.}})(_{\lambda(\tau)}\gamma_{ik,jl}),$$

where

$\lambda\sigma_{\text{h.s.}}$ = phenotypic standard deviation of the half-sib means used to test the λ -sex individuals.

(a) *Consequences of n Consecutive Cycles of Selection*

As with mass selection, the consequences of n consecutive cycles of g.c.a. selection will be given in terms of (1) a specific class of programs and (2) the independent sex increments due to g.c.a. selection in one sex irrespective of the mode of selection in the other sex.

(i) *Specific g.c.a. Selection Programs*

This section is generalized to include all those programs in which the λ -sex is subject to $\lambda(\tau)$ g.c.a. test and the $\bar{\lambda}$ -sex is subject to a $\bar{\lambda}(\eta)$ g.c.a. test. More specifically, there are four such g.c.a. programs which can be obtained by appropriate substitution of symbols.

The recurrence equations relating the n th and the $(n-1)$ th gamete frequencies for the λ -sex are as follows. For additive effects only,

$$[\lambda(\tau), \bar{\lambda}(\eta)]f_{ik}^n = \frac{1}{2} \{ [\lambda(\tau), \bar{\lambda}(\eta)]f_{ik}^{n-1} + [\bar{\lambda}(\eta), \lambda(\tau)]f_{ik}^{n-1} \} + p_i^1 p_k^2 (\lambda(\tau)\theta_{ik}),$$

and for additive \times additive effects only,

$$[\lambda(\tau), \bar{\lambda}(\eta)]f_{ik}^n = c_\lambda \{ [\lambda(\tau), \bar{\lambda}(\eta)]f_{ik}^{n-1} + [\bar{\lambda}(\eta), \lambda(\tau)]f_{ik}^{n-1} \} + p_i^1 p_k^2 (\lambda(\tau)\phi_{ik}),$$

where

$$\lambda(\tau)\theta_{ik} = \frac{1}{2}(\bar{i}_{\lambda/\lambda}\sigma_{h.s.})(\tau a_i^1 + \tau a_k^2)$$

and

$$\lambda(\tau)\phi_{ik} = \frac{1}{4}(\bar{i}_{\lambda/\lambda}\sigma_{h.s.})(1 + \delta_\lambda)[\tau(\alpha\alpha)_{ik}],$$

in which

$$\delta_\lambda = (1 - 2y_\lambda)^2.$$

These recurrence relationships determine the composition of the gamete frequency for the λ -sex in the n th cycle as a function of the effects in the initial population, i.e.

$$[\lambda(\tau), \bar{\lambda}(\eta)]f_{ik}^n = p_i^1 p_k^2 \left\{ 1 + \frac{1}{2}(n+1)(\lambda(\tau)\theta_{ik}) + \frac{1}{2}(n-1)(\bar{\lambda}(\eta)\theta_{ik}) \right. \\ \left. + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) (\lambda(\tau)\phi_{ik}) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) (\bar{\lambda}(\eta)\phi_{ik}) \right] \right\}.$$

Finally, the mean of the λ -sex after n consecutive cycles of g.c.a. selection, in which the λ -sex is tested with its τ -sex progeny and the $\bar{\lambda}$ -sex is tested with its η -sex progeny, is

$$[\lambda(\tau), \bar{\lambda}(\eta)] \times [\bar{\lambda}(\eta), \lambda(\tau)]\mu_n = \frac{1}{4}n \{ (\bar{i}_{\lambda/\lambda}\sigma_{h.s.})(\lambda\tau\sigma_A) + (\bar{i}_{\bar{\lambda}/\bar{\lambda}}\sigma_{h.s.})(\lambda\eta\sigma_A) \} \\ + \frac{1}{4} \left(\frac{1-b^n}{1-b} \right) \left\{ (\bar{i}_{\lambda/\lambda}\sigma_{h.s.}) \frac{1}{4}(1 + \delta_\lambda)(\lambda\tau\sigma_{AA}) \right. \\ \left. + (\bar{i}_{\bar{\lambda}/\bar{\lambda}}\sigma_{h.s.}) \frac{1}{4}(1 + \delta_{\bar{\lambda}})(\lambda\eta\sigma_{AA}) \right\}.$$

Use of the above notation permits an efficient method of deriving results simultaneously for a variety of g.c.a. schemes. However, it is worth while to give the end results for the male and female means of the four specific g.c.a. selection methods. These are listed in Tables 1 and 2.

(ii) *Independent Sex Increments due to g.c.a. Selection*

The increments of gamete frequencies due to g.c.a. selection in one sex irrespective of selection in the other sex may be summarized briefly as follows:

(1) The contribution of $\lambda(\tau)$ g.c.a. test to the λ -sex gamete is

$$p_i^1 p_k^2 \left\{ \frac{1}{2}(n+1)(\lambda_{(\tau)}\theta_{ik}) + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] (\lambda_{(\tau)}\phi_{ik}) \right\}.$$

(2) The contribution of $\bar{\lambda}(\eta)$ g.c.a. test to the λ -sex gamete is

$$p_i^1 p_k^2 \left\{ \frac{1}{2}(n-1)(\bar{\lambda}_{(\eta)}\theta_{ik}) + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) (\bar{\lambda}_{(\eta)}\phi_{ik}) \right\}.$$

The independent sex increments for the λ -sex *mean* are arranged in a hierarchical order as follows:

(A) Contributions from λ -sex individuals drawn from a population in which

(1) the λ -sex is subject to a $\lambda(\tau)$ g.c.a. test:

$$(\bar{i}_\lambda/\lambda\sigma_{h.s.}) \left\{ \frac{1}{8}(n+1)(\lambda_\tau\sigma_A) + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{16}(1+\delta_\lambda)(\lambda_\tau\sigma_{AA}) \right\}.$$

(2) the $\bar{\lambda}$ -sex is subject to a $\bar{\lambda}(\eta)$ g.c.a. test:

$$(\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.}) \left\{ \frac{1}{8}(n-1)(\lambda_\eta\sigma_A) + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{16}(1+\delta_{\bar{\lambda}})(\lambda_\eta\sigma_{AA}) \right\}.$$

(B) Contributions from $\bar{\lambda}$ -sex individuals drawn from a population in which

(1) the λ -sex is subject to a $\lambda(\tau)$ g.c.a. test:

$$(\bar{i}_\lambda/\lambda\sigma_{h.s.}) \left\{ \frac{1}{8}(n-1)(\lambda_\tau\sigma_A) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{16}(1+\delta_\lambda)(\lambda_\tau\sigma_{AA}) \right\}.$$

(2) the $\bar{\lambda}$ -sex is subject to a $\bar{\lambda}(\eta)$ g.c.a. test:

$$(\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.}) \left\{ \frac{1}{8}(n+1)(\lambda_\eta\sigma_A) + \left[1 + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{16}(1+\delta_{\bar{\lambda}})(\lambda_\eta\sigma_{AA}) \right\}.$$

Finally, use of these increments is illustrated by deriving the mean

$$[\lambda(\tau), \bar{\lambda}(\eta)] \times [\bar{\lambda}(\eta), \lambda(\tau)] \mu_n.$$

As before, the subscript elements in the order $\lambda(\tau)$, $\bar{\lambda}(\eta)$, $\bar{\lambda}(\eta)$, and $\lambda(\tau)$ are associated with the increments given for (A)(1), (A)(2), (B)(2), and (B)(1), respectively. Hence

$$\begin{aligned} [\lambda(\tau), \bar{\lambda}(\eta)] \times [\bar{\lambda}(\eta), \lambda(\tau)] \mu_n &= (\bar{i}_\lambda/\lambda\sigma_{h.s.}) \left\{ \frac{1}{8}(n+1)(\lambda_\tau\sigma_A) + \left[1 + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{16}(1+\delta_\lambda)(\lambda_\tau\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.}) \left\{ \frac{1}{8}(n-1)(\lambda_\eta\sigma_A) + c_\lambda \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{16}(1+\delta_{\bar{\lambda}})(\lambda_\eta\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.}) \left\{ \frac{1}{8}(n+1)(\lambda_\eta\sigma_A) + \left[1 + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \right] \frac{1}{16}(1+\delta_{\bar{\lambda}})(\lambda_\eta\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_\lambda/\lambda\sigma_{h.s.}) \left\{ \frac{1}{8}(n-1)(\lambda_\tau\sigma_A) + c_{\bar{\lambda}} \left(\frac{1-b^{n-1}}{1-b} \right) \frac{1}{16}(1+\delta_\lambda)(\lambda_\tau\sigma_{AA}) \right\} \\ &= (\bar{i}_\lambda/\lambda\sigma_{h.s.}) \left\{ \frac{1}{4}n(\lambda_\tau\sigma_A) + \frac{1}{16} \left(\frac{1-b^n}{1-b} \right) (1+\delta_\lambda)(\lambda_\tau\sigma_{AA}) \right\} \\ &\quad + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.}) \left\{ \frac{1}{4}n(\lambda_\eta\sigma_A) + \frac{1}{16} \left(\frac{1-b^n}{1-b} \right) (1+\delta_{\bar{\lambda}})(\lambda_\eta\sigma_{AA}) \right\}. \end{aligned}$$

TABLE 1
FEMALE MEANS FOR POPULATIONS SUBJECT TO n CONSECUTIVE CYCLES OF G.C.A. SELECTION

Females: η -sex Testers			
	m	f	
m	$[f(m), m(m)] \times [m(m), f(m)] \mu_n$ $= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_m \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_m}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_m \sigma_{AA}) \right\}$ $+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_m \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_f}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_m \sigma_{AA}) \right\}$	$[f(f), m(m)] \times [m(m), f(f)] \mu_n$ $= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_f \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_m}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_f \sigma_{AA}) \right\}$ $+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_f \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_f}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_f \sigma_{AA}) \right\}$	
f	$[f(m), m(f)] \times [m(f), f(m)] \mu_n$ $= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_f \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_m}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_f \sigma_{AA}) \right\}$ $+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_m \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_f}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_m \sigma_{AA}) \right\}$	$[f(f), m(f)] \times [m(f), f(f)] \mu_n$ $= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_f \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_m}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_f \sigma_{AA}) \right\}$ $+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{2} n (r_f \sigma_A) + \frac{1}{4} \left(\frac{1 + \delta_f}{4} \right) \left(\frac{1 - b^n}{1 - b} \right) (r_f \sigma_{AA}) \right\}$	

Males: r -sex Testers

TABLE 2
MALE MEANS FOR POPULATIONS SUBJECT TO *n* CONSECUTIVE CYCLES OF DIFFERENT COMBINATIONS OF G.C.A. SELECTION

Males: 7-sex Testers		Females: 7-sex Testers	
<i>m</i>	<i>m</i>	<i>m</i>	<i>f</i>
<i>m</i>	<i>m</i>	$\begin{aligned} & [m(m), f(m)] \times [f(m), m(m)] \mu_n \\ &= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (mm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_m}{4} \right) \left(\frac{1-b^n}{1-b} \right) (mm\sigma_{AA}) \right\} \\ &+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (mm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_f}{4} \right) \left(\frac{1-b^n}{1-b} \right) (mm\sigma_{AA}) \right\} \end{aligned}$	$\begin{aligned} & [m(m), f(f)] \times [f(f), m(m)] \mu_n \\ &= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (mm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_m}{4} \right) \left(\frac{1-b^n}{1-b} \right) (mm\sigma_{AA}) \right\} \\ &+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (fm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_f}{4} \right) \left(\frac{1-b^n}{1-b} \right) (fm\sigma_{AA}) \right\} \end{aligned}$
	<i>f</i>	$\begin{aligned} & [m(f), f(m)] \times [f(m), m(f)] \mu_n \\ &= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (fm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_m}{4} \right) \left(\frac{1-b^n}{1-b} \right) (fm\sigma_{AA}) \right\} \\ &+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (mm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_f}{4} \right) \left(\frac{1-b^n}{1-b} \right) (mm\sigma_{AA}) \right\} \end{aligned}$	$\begin{aligned} & [m(f), f(f)] \times [f(f), m(f)] \mu_n \\ &= \left(\frac{\bar{z}_m}{m\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (fm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_m}{4} \right) \left(\frac{1-b^n}{1-b} \right) (fm\sigma_{AA}) \right\} \\ &+ \left(\frac{\bar{z}_f}{f\sigma_{h.s.}} \right) \left\{ \frac{1}{4} n (fm\sigma_A) + \frac{1}{4} \left(\frac{1+\delta_f}{4} \right) \left(\frac{1-b^n}{1-b} \right) (fm\sigma_{AA}) \right\} \end{aligned}$

(b) *Consequences of t Cycles of Relaxation following n Cycles of Selection*

Only the end result of t cycles of random mating without selection following n consecutive cycles of $\lambda(\tau)$ and $\bar{\lambda}(\eta)$ g.c.a. selection will be given. Thus, the λ -sex mean is

$$\begin{aligned} [\lambda(\tau), \bar{\lambda}(\eta)] \times [\bar{\lambda}(\eta), \lambda(\tau)] \mu_{n,t} = & \frac{1}{4}n[(\bar{i}_{\lambda}/\lambda\sigma_{h.s.})(\lambda\tau\sigma_A) + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.})(\lambda\eta\sigma_A)] \\ & + \frac{1}{16}b^t\left(\frac{1-b^n}{1-b}\right)[(\bar{i}_{\lambda}/\lambda\sigma_{h.s.})(1+\delta_{\lambda})(\lambda\tau\sigma_{AA}) \\ & + (\bar{i}_{\bar{\lambda}}/\bar{\lambda}\sigma_{h.s.})\frac{1}{4}(1+\delta_{\bar{\lambda}})(\lambda\eta\sigma_{AA})]. \end{aligned}$$

As with mass selection it is clear that contributions from additive \times additive epistatic effects diminish as t increases. This leaves as the *permanent gain* due to selection only the variance and covariance contributions from the additive effects.

III. A GENERALIZED ANALYSIS BASED ON COVARIANCES AMONG RELATIVES

In this section prediction formulae for one cycle of selection are developed in terms of covariances among relatives rather than in terms of specific gene models and their associated parameters. A relationship can be established between these two approaches for any specific genetic situation. However, for a given population the covariances among relatives are estimable and thus prediction equations can be solved without recourse to an evaluation of the complexities of the genetic system. On the other hand, analyses based on the gene model are useful in that they provide a genetic interpretation of the various covariances among relatives as well as a detailed dynamic picture of the changes in population structure for a sequence of selection cycles. The results in this section are given entirely in the form of independent sex increments of predicted means due to selection in one sex.

I. PARAMETERS OF THE INITIAL RANDOM-MATING POPULATIONS

In the following argument, it is convenient to represent the initial random-mating population in two ways: (1) in terms of the genotypic array, i.e. by enumerating all possible different genotypes without reference to family structure, and (2) in terms of the full-sib array, i.e. by enumerating all possible different full-sib, and consequently, half-sib families.

(a) λ -sex Population Parameters

The λ -sex genotypic array can be obtained as the product of the gametic arrays from the two sexes. More specifically let

$\sum_i f_i G_i$ = gametic array, which is identical in an equilibrium population for both males and females,

${}_{\lambda}H_{ij}$ = λ -sex genotype resulting from the union of G_i and G_j ,

${}_{\lambda}h_{ij}$ = genotypic value of ${}_{\lambda}H_{ij}$, measured as a deviation from the λ -sex population mean.

Then

$$\sum_{i,j} f_i f_j ({}_{\lambda}H_{ij}) = \lambda\text{-sex genotypic array,}$$

and

$${}_{\lambda}\mu_0 = \sum_{i,j} f_i f_j ({}_{\lambda}h_{ij}) = 0 = \lambda\text{-sex population mean.}$$

Next, consider a representation of this same initial λ -sex population in terms of family structure. Let

$${}_{\lambda}H_{ij,kl} = \lambda\text{-sex full-sib genotypic array resulting from the cross } {}_mH_{ij} \times {}_fH_{kl},$$

$${}_{\lambda}h_{ij,kl} = \text{genotypic mean for } {}_{\lambda}H_{ij,kl}, \text{ measured as a deviation from the } \lambda\text{-sex population mean,}$$

$${}_{\lambda}h_{ij..} = \sum_{k,l} f_k f_l ({}_{\lambda}h_{ij,kl}) = \lambda\text{-sex half-sib mean associated with the sire, } {}_mH_{ij},$$

$${}_{\lambda}h_{..,kl} = \sum_{i,j} f_i f_j ({}_{\lambda}h_{ij,kl}) = \lambda\text{-sex half-sib mean associated with the dam, } {}_fH_{kl},$$

$$\sum_{i,j,k,l} f_i f_j f_k f_l ({}_{\lambda}H_{ij,kl}) = \lambda\text{-sex full-sib array,}$$

and

$${}_{\lambda}\mu_0 = {}_{\lambda}h_{..} = \sum_{i,j,k,l} f_i f_j f_k f_l ({}_{\lambda}h_{ij,kl}) = 0 = \lambda\text{-sex population mean.}$$

(b) Definitions of Covariances among Relatives

The covariances of parent and offspring necessary for prediction purposes are defined to be

$$\begin{aligned} \text{Cov}_{m(m,\lambda)}(\text{PO}) &= \sum_{i,j} f_i f_j ({}_m h_{ij}) ({}_{\lambda} h_{ij} ..), \\ &= \text{covariance of the sire with his } \lambda\text{-sex half-sib offspring,} \end{aligned}$$

and

$$\begin{aligned} \text{Cov}_{f(f,\lambda)}(\text{PO}) &= \sum_{k,l} f_k f_l ({}_f h_{kl}) ({}_{\lambda} h_{..,kl}), \\ &= \text{covariance of the dam with her } \lambda\text{-sex half-sib offspring.} \end{aligned}$$

The necessary covariances among the half-sib means are

$$\text{Cov}_{(m,\xi)(m,\nu)}(\text{HS}) = \sum_{i,j} f_i f_j ({}_{\xi} h_{ij} ..) ({}_{\nu} h_{ij} ..),$$

and

$$\text{Cov}_{(f,\xi)(f,\nu)}(\text{HS}) = \sum_{k,l} f_k f_l ({}_{\xi} h_{..,kl}) ({}_{\nu} h_{..,kl}),$$

where each of the subscripts ξ and ν may represent male or female independently, thus giving rise to a total of eight different covariances among half-sib values.

2. MASS SELECTION

The increments due to one cycle of mass selection operating on individuals of one sex irrespective of the mode of selection operating on the other sex are given in terms of parent-offspring covariances. The genetic interpretations of these increments are also given. These interpretations are made in terms of the previously described sex-influenced two-locus model.

(A) The contribution to the λ -sex mean due to mass selection of males is

$$\begin{aligned} &(\bar{i}_m / m \sigma_{\text{ind.}}) [\text{Cov}_{m(m,\lambda)}(\text{PO})] \\ &= (\bar{i}_m / m \sigma_{\text{ind.}}) \left[\frac{1}{2} (\lambda, m \sigma_A) + \frac{1}{4} (\lambda, m \sigma_{AA}) \right]. \end{aligned}$$

(B) The contribution to the λ -sex mean due to mass female selection is

$$\begin{aligned} & (\bar{i}_f/\sigma_{\text{ind.}})[\text{Cov}_{f(f,\lambda)}(\text{PO})] \\ &= (\bar{i}_f/\sigma_{\text{ind.}})[\tfrac{1}{2}(\lambda, f\sigma_A) + \tfrac{1}{4}(\lambda, f\sigma_{AA})]. \end{aligned}$$

3. GENERAL COMBINING ABILITY SELECTION

Again contributions to genetic advance due to selection in each sex are given separately as follows:

$(\bar{i}_{\lambda/\lambda}\sigma_{\text{h.s.}})[\text{Cov}_{(\lambda,v)(\lambda,f)}(\text{HS})]$ = contribution to the female progeny mean due to selection of λ -sex on the basis of its τ -sex progeny,

and

$(\bar{i}_{\lambda/\lambda}\sigma_{\text{h.s.}})[\text{Cov}_{(\lambda,v)(\lambda,m)}(\text{HS})]$ = contribution to the male progeny mean due to selection of λ -sex on the basis of its τ -sex progeny.

The genetic interpretations of these covariances on the basis of the previous two-locus model are

$$\text{Cov}_{(\lambda,v)(\lambda,f)}(\text{HS}) = \tfrac{1}{4}(f\tau\sigma_A) + \tfrac{1}{16}(1+\delta_\lambda)(f\tau\sigma_{AA}),$$

and

$$\text{Cov}_{(\lambda,v)(\lambda,m)}(\text{HS}) = \tfrac{1}{4}(m\tau\sigma_A) + \tfrac{1}{16}(1+\delta_\lambda)(m\tau\sigma_{AA}).$$

The following equations relate the results given in terms of covariances among relatives with those given for the two-locus model (see Tables 1 and 2 in which $n = 1$), for the four g.c.a. selection methods:

Female Means

$$\begin{aligned} [f(m), m(m)] \times [m(m), f(m)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,m)(m,f)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,m)(f,f)}(\text{HS})], \\ [f(f), m(m)] \times [m(m), f(f)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,m)(m,f)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,f)(f,f)}(\text{HS})], \\ [f(m), m(f)] \times [m(f), f(m)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,f)(m,f)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,m)(f,f)}(\text{HS})], \\ [f(f), m(f)] \times [m(f), f(f)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,f)(m,f)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,f)(f,f)}(\text{HS})]. \end{aligned}$$

Male Means

$$\begin{aligned} [m(m), f(m)] \times [f(m), m(m)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,m)(m,m)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,m)(f,m)}(\text{HS})], \\ [m(m), f(f)] \times [f(f), m(m)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,m)(m,m)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,f)(f,m)}(\text{HS})], \\ [m(f), f(m)] \times [f(m), m(f)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,f)(m,m)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,m)(f,m)}(\text{HS})], \\ [m(f), f(f)] \times [f(f), m(f)] \mu_1 &= (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,f)(m,m)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{h.s.}})[\text{Cov}_{(f,f)(f,m)}(\text{HS})]. \end{aligned}$$

Prediction equations for combinations of mass selection in one sex with g.c.a. selection in the other sex can be obtained as a function of the appropriate covariances. For example, consider the prediction equation for the female progeny mean resulting from crossing dams, which have been mass selected, with sires selected on the basis of their daughter's performances. In this case, the genetic advance predicted for the female progeny is

$$[f, m(f)] \times [m(f), f] \mu_1 = (\bar{i}_m/m\sigma_{\text{h.s.}})[\text{Cov}_{(m,f)(m,f)}(\text{HS})] + (\bar{i}_f/f\sigma_{\text{ind.}})[\text{Cov}_{f(f,f)}(\text{PO})].$$

Finally, the covariance analysis of this section has been developed on the assumption of autosomal inheritance. Hence, the genetic interpretations of these covariances are based on an autosomal model. An extension to include both sex-linked and autosomal inheritance will be considered in Part III of this series (Griffing 1966).

IV. DISCUSSION

For a characteristic subject to sex-influenced inheritance, the responses to identical selection pressures may be different for the two sexes. There are at least two consequences arising from such a differential response. Firstly, the possibility exists that selection is more efficient in one sex than in the other. This has practical implications which have been exploited in animal breeding. Secondly, the differential response due to sex-influenced inheritance may be confounded with that due to sex-linked inheritance. The problem of separating these disturbances, as well as those due to maternal effects, will be discussed in a later paper of this series.

Although the characteristics under consideration are associated with sex, the patterns of response to selection and relaxation from selection cause the frequencies of a sex-influenced gene to diverge for the two sexes. However, these frequencies equilibrate as a result of one generation of random mating without selection. Such immediate equilibration of gene frequencies is a typical manifestation of autosomal inheritance. On the other hand, divergent sex-linked gene frequencies do not equilibrate immediately, but rather approach the equilibrium value in an oscillatory manner with successive generations of relaxation.

Finally, for completeness of presentation, results for the two-locus model have been given for an arbitrary number of selection cycles. However, it must be remembered that errors of approximation accumulate and prediction becomes worse as the number of successive cycles of selection increases.

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