

INFLUENCE OF SEX ON SELECTION

I. CONTRIBUTION OF SEX-LINKED GENES

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Summary

Consequences of individual selection and relaxation from selection are examined for genotypes generated by sex-linked genes. Two levels of complexity are studied. At the first level genotypes are derived from an arbitrary number of alleles at one locus. This situation is sufficiently general to include any pattern of dominance parameters. It is shown that the increment responses to selection for the two sexes may be different since they are different functions of genotypic variances and covariances. As a result of selection, the frequencies for the same allele diverge in the two sexes. Hence, on relaxation from selection, both male and female means fluctuate until gene equilibrium is reached.

The second level of complexity concerns populations generated by an arbitrary number of alleles at each of two sex-linked loci. This situation is generalized to include any pattern of dominance and epistatic effects. It is shown that the *immediate* responses to selection involve not only additive and additive \times additive variances, as defined for both sexes, but also covariances for each class of these effects between sexes. Results from relaxation are complicated not only because of the fact that genes at both loci tend to equilibrate, but also because of the decay of the additive \times additive epistatic contributions. Thus, at equilibrium only the additive genetic variances and covariances contribute to the *permanent* gain due to the past history of selection.

I. INTRODUCTION

Interest in population dynamics involving sex-linked inheritance traces back to the early days of modern genetics (Jennings 1916; Robbins 1918). These early works were later followed by more extensive studies involving certain kinds of selection (for example, see Haldane 1924, 1926). The study of Bennett (1963) extended the solutions for equilibria under conditions of random mating and no selection to include an incompletely sex-linked locus and two completely sex-linked loci. Finally, among other contributions, Bohidar (1964) partitioned the genotypic variances for male and female populations and determined the composition of various covariances among relatives for the assumption of both sex-linked and autosomal inheritance. However, it appears that the consequence of applying truncation selection to random-mating populations of genotypes generated by sex-linked genes has not been adequately explored. This paper, then, attempts to deal with this problem.

The problem is attacked at two levels of complexity. At the first level, selection and relaxation from selection are considered for populations of genotypes arising from alleles at a *single* sex-linked locus. At the second level, the genotypes are derived from alleles at *two* sex-linked loci. In this case, the model is extended to include the phenomenon of epistasis as well as dominance.

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For each of the single- and two-locus models, selection responses are derived for the first cycle and for an arbitrary number of consecutive cycles. The procedures necessary to obtain the responses due to selection are illustrated in detail for the first cycle. The results for n cycles are more briefly given. Relaxation from selection is treated in the same way.

II. SELECTION AMONG GENOTYPES GENERATED BY ALLELES AT ONE LOCUS

(a) Definition of Parameters

The following parameters are defined for a random-mating population in equilibrium generated by an arbitrary number of sex-linked alleles, A_1, \dots, A_m , with frequencies, p_1, \dots, p_m .

(i) *Homogametic Sex* (denote individuals as females)

The initial female population may be represented as

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

The genotypic value for $A_i A_j$ is designated as d_{ij} and coded so that

$${}_f\mu_0 = \sum_{ij} p_i p_j d_{ij} = 0.$$

These genotypic values are characterized by the usual gene model,

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

where

$${}_f a_i = \sum_j p_j d_{ij} = \text{additive effect of } A_i \text{ as measured among females,}$$

and

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

The female genotypic variance may be partitioned as follows:

$${}_f \sigma_G^2 = {}_f \sigma_A^2 + {}_f \sigma_D^2,$$

where

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

$${}_f \sigma_A^2 = 2 \sum_i p_i ({}_f a_i)^2 = \text{additive genetic variance,}$$

and

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

(ii) *Heterogametic Sex* (denote individuals as males)

The initial male genotypic array is

$${}_m\Pi_0 = \sum_i p_i (A_i \cdot),$$

where the dot represents the lack of an allele on the Y -chromosome at the particular locus under study.

The genotypic value of $(A_{i\cdot})$ is assumed to be s_i and such that

$${}_m\mu_0 = \sum_i p_i s_i = 0.$$

In order to be consistent with the gene model developed later for genotypes at two loci, let

$$s_i = {}_m\alpha_i,$$

where ${}_m\alpha_i$ = additive effect of A_i as measured among the males.

The male additive genetic variance, then, is defined to be equivalent to the total male genotypic variance, i.e.

$$\sum_i p_i (s_i)^2 = \sum_i p_i ({}_m\alpha_i)^2,$$

or symbolically,

$${}_m\sigma_G^2 = {}_m\sigma_A^2.$$

Finally, an additive genetic covariance needs to be defined for prediction purposes as follows:

$${}_f{}_m\sigma_A = \sum_i p_i ({}_f\alpha_i)({}_m\alpha_i).$$

(iii) Selection Values

Selection values are defined in the usual manner (Kimura 1958) as those values which are proportional to the probability that an individual of a given sex and genotype survives selection. Thus, the selection value for the female $A_k A_l$ is

$${}_fw_{kl} = 1 + (\bar{i}_f/\sigma_f)d_{kl},$$

and for the male $(A_{i\cdot})$ is

$${}_mw_i = 1 + (\bar{i}_m/\sigma_m)s_i,$$

where

$$\bar{i}_f(\bar{i}_m) = \text{standardized selection differential for females (males),}$$

and

$$\sigma_f(\sigma_m) = \text{phenotypic standard deviation for females (males).}$$

(b) Consequences of One Cycle of Selection

The objective of this section is to determine the changes in male and female population means due to one cycle of truncation selection operating on a sex-linked locus with arbitrary and independent intensity in each sex.

The frequency of $(A_{i\cdot})$ following selection in ${}_m\Pi_0$ is

$$p_i({}_mw_i) = p_i[1 + (\bar{i}_m/\sigma_m)s_i].$$

Hence the X -bearing gametic array from selected males is

$$\sum_i ({}_m p_i^1) A_i,$$

where

$$\begin{aligned} {}_m p_i^1 &= p_i [1 + (\bar{i}_m / \sigma_m) s_i] \\ &= \text{frequency of } A_i \text{ resulting from the first cycle} \\ &\quad \text{of selection among males.} \end{aligned}$$

For convenience a simpler notation will be used for this frequency, i.e.

$${}_m p_i^1 = p_i (1 + {}_m \theta_i),$$

where

$${}_m \theta_i = (\bar{i}_m / \sigma_m) s_i.$$

Similarly, the frequency of the gamete A_k produced by selected females is

$${}_f p_k^1 = p_k (1 + {}_f \theta_k),$$

where

$${}_f \theta_k = (\bar{i}_f / \sigma_f) {}_f a_k.$$

The genotypic means for the populations ${}_m \Pi_1$ and ${}_f \Pi_1$ are obtained as follows:

$$\begin{aligned} {}_m \mu_1 &= \sum_k ({}_f p_k^1) s_k \\ &= \sum_k p_k (1 + {}_f \theta_k) s_k \\ &= (\bar{i}_f / \sigma_f) {}_f m \sigma_A, \end{aligned}$$

and

$$\begin{aligned} {}_f \mu_1 &= \sum_{ik} ({}_m p_i^1) ({}_f p_k^1) d_{ik} \\ &\cong \sum_{ik} p_i p_k (1 + {}_m \theta_i + {}_f \theta_k) d_{ik} \\ &= (\bar{i}_m / \sigma_m) {}_f m \sigma_A + \frac{1}{2} (\bar{i}_f / \sigma_f) {}_f \sigma_A^2. \end{aligned}$$

These quantities represent the increment changes in male and female means due to one cycle of mass selection. For further elaboration of assumptions and derivations, the reader is referred to Griffing (1960).

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

In the following presentation it is assumed that, although the selection intensities may be different for the two sexes, they remain the same in successive cycles. The means after n cycles of selection are

$${}_m \mu_n \cong \sum_k ({}_f p_k^n) s_k,$$

and

$${}_f \mu_n \cong \sum_{ik} ({}_m p_i^n) ({}_f p_k^n) d_{ik},$$

where

$${}_m p_i^n \cong p_i [1 + ({}_m A_\lambda) ({}_m \theta_i) + ({}_m B_\lambda) ({}_f \theta_i)],$$

and

$${}_f p_k^n \cong p_k[1 + ({}_f A_\lambda)({}_m \theta_k) + ({}_f B_\lambda)({}_f \theta_k)].$$

In this notation, ${}_m p_i^n$ and ${}_f p_k^n$ represent the frequencies of the gametic A_i and A_k produced by males and females, respectively, after n consecutive cycles of selection. Hence the means are

$${}_m \mu_n \cong (\bar{i}_m/\sigma_m)({}_f A_\lambda)({}_m \sigma_A^2) + (\bar{i}_f/\sigma_f)({}_f B_\lambda)({}_f \sigma_A),$$

and

$${}_f \mu_n \cong (\bar{i}_m/\sigma_m)({}_m A_\lambda + {}_f A_\lambda)({}_f \sigma_A) + (\bar{i}_f/\sigma_f)({}_m B_\lambda + {}_f B_\lambda)\frac{1}{2}({}_f \sigma_A^2).$$

In these formulae, λ denotes "even" or "odd", whichever is appropriate for the value of n . The exact values for the A and B coefficients are obtained by substituting in the expression

$$\{a + \sum_{u=1}^b (\frac{1}{2})^u [1 + d(\frac{1}{2})]\},$$

the following values for a , b , c , and d :

	a	b	c	d
${}_m A_{\text{even}}$	1	$\frac{1}{2}(n-2)$	$2u-1$	$n-2u-1$
${}_m A_{\text{odd}}$	1	$\frac{1}{2}(n-1)$	$2u-1$	$n-2u-1$
${}_m B_{\text{even}}$	0	$\frac{1}{2}n$	$2u-2$	$n-2u$
${}_m B_{\text{odd}}$	0	$\frac{1}{2}(n-1)$	$2u-2$	$n-2u$
${}_f A_{\text{even}}$	0	$\frac{1}{2}n$	$2u-1$	$n-2u$
${}_f A_{\text{odd}}$	0	$\frac{1}{2}(n-1)$	$2u-1$	$n-2u$
${}_f B_{\text{even}}$	0	$\frac{1}{2}n$	$2u-2$	$n-2u+1$
${}_f B_{\text{odd}}$	0	$\frac{1}{2}(n+1)$	$2u-2$	$n-2u+1$

Table 1 gives increment changes in the first five consecutive cycles of selection. However it must be remembered that as n increases the errors of approximation accumulate and predictions become worse.

TABLE 1
INCREMENT CHANGES IN MALE AND FEMALE MEANS DUE TO CONSECUTIVE
CYCLES OF SELECTION (ONE-LOCUS MODEL)

Male Means			Female Means		
	$(\bar{i}_m/\sigma_m){}_m \sigma_A^2$	$(\bar{i}_f/\sigma_f){}_f \sigma_A$		$(\bar{i}_m/\sigma_m){}_f \sigma_A$	$(\bar{i}_f/\sigma_f){}_f \sigma_A^2$
${}_m \mu_0$	0	0	${}_f \mu_0$	0	0
${}_m \mu_1$	0	1	${}_f \mu_1$	1	$\frac{1}{2}$
${}_m \mu_2$	$\frac{1}{2}$	$1\frac{1}{2}$	${}_f \mu_2$	$1\frac{1}{2}$	$1\frac{1}{4}$
${}_m \mu_3$	$\frac{3}{4}$	$2\frac{1}{4}$	${}_f \mu_3$	$2\frac{1}{4}$	$1\frac{7}{8}$
${}_m \mu_4$	$1\frac{1}{8}$	$2\frac{7}{8}$	${}_f \mu_4$	$2\frac{7}{8}$	$2\frac{9}{16}$
${}_m \mu_5$	$1\frac{7}{16}$	$3\frac{9}{16}$	${}_f \mu_5$	$3\frac{9}{16}$	$3\frac{7}{32}$

(d) *Consequences of One Generation of Relaxation following n Cycles of Selection*

With sex-linked inheritance, selection produces different frequencies for the same gene in the two sexes. On relaxation from selection the difference between gene frequencies diminishes until at equilibrium the frequencies in the two sexes are identical. The consequence of these changes in gene frequencies is that the population means also change with relaxation until equilibrium is reached. The objective of this section is briefly to outline the procedure of obtaining this change for the first generation of relaxation. Let

$${}_m\Pi_{n,0} = \sum_k ({}_f p_k^{n,0})(A_k \cdot)$$

represent the male population resulting from n consecutive cycles of selection. Then the array of X -bearing gametes produced by unselected males is

$$\sum_i ({}_m p_i^{n,1}) A_i,$$

where

$${}_m p_i^{n,1} = {}_f p_i^{n,0} = p_i [1 + {}_f A_\lambda ({}_m \theta_i) + {}_f B_\lambda ({}_f \theta_i)].$$

Similarly, when starting with the corresponding female population,

$${}_f \Pi_{n,0} = \sum_{ik} ({}_m p_i^{n,0}) ({}_f p_k^{n,0}) (A_i A_k),$$

the female gametic array, without selection, is

$$\sum_k ({}_f p_k^{n,1}) A_k,$$

where

$$\begin{aligned} {}_f p_k^{n,1} &= \frac{1}{2} ({}_m p_k^{n,0} + {}_f p_k^{n,0}) \\ &= p_k \{1 + \frac{1}{2} [({}_m A_\lambda + {}_f A_\lambda) ({}_m \theta_k) + ({}_m B_\lambda + {}_f B_\lambda) ({}_f \theta_k)]\}. \end{aligned}$$

Hence the means after one cycle of relaxation are

$${}_m \mu_{n,1} = \frac{1}{2} (\bar{i}_m / \sigma_m) ({}_m A_\lambda + {}_f A_\lambda) ({}_m \sigma_A^2) + \frac{1}{2} (\bar{i}_f / \sigma_f) ({}_m B_\lambda + {}_f B_\lambda) ({}_f \sigma_A^2),$$

and

$${}_f \mu_{n,1} = \frac{1}{2} (\bar{i}_m / \sigma_m) ({}_m A_\lambda + 3{}_f A_\lambda) ({}_f \sigma_A^2) + \frac{1}{4} (\bar{i}_f / \sigma_f) ({}_m B_\lambda + 3{}_f B_\lambda) ({}_f \sigma_A^2).$$

(e) *Consequences of t Generations of Relaxation following n Cycles of Selection*

Male and female gene frequencies for populations having a history of n consecutive cycles of selection followed by t cycles of relaxation can be shown to be

$$\begin{aligned} {}_m p_i^{n,t} &\cong p_i \{1 + ({}_m \theta_i) [{}_f A_\lambda + \frac{1}{3} (1 - \langle -\frac{1}{2} \rangle^{t-1}) ({}_m A_\lambda - {}_f A_\lambda)] \\ &\quad + ({}_f \theta_i) [{}_f B_\lambda + \frac{1}{3} (1 - \langle -\frac{1}{2} \rangle^{t-1}) ({}_m B_\lambda - {}_f B_\lambda)]\}, \end{aligned}$$

and

$$\begin{aligned} {}_f p_k^{n,t} &\cong p_k \{1 + ({}_m \theta_k) [{}_f A_\lambda + \frac{1}{3} (1 - \langle -\frac{1}{2} \rangle^t) ({}_m A_\lambda - {}_f A_\lambda)] \\ &\quad + ({}_f \theta_k) [{}_f B_\lambda + \frac{1}{3} (1 - \langle -\frac{1}{2} \rangle^t) ({}_m B_\lambda - {}_f B_\lambda)]\}. \end{aligned}$$

Hence the means for the two sexes are

$$\begin{aligned} m\mu_{n,t} &\cong (\bar{i}_m/\sigma_m)\{fA_\lambda + \frac{1}{3}(1 - \langle -\frac{1}{2} \rangle^t)(mA_\lambda - fA_\lambda)\}(m\sigma_A^2) \\ &\quad + (\bar{i}_f/\sigma_f)\{fB_\lambda + \frac{1}{3}(1 - \langle -\frac{1}{2} \rangle^t)(mB_\lambda - fB_\lambda)\}(f\sigma_A^2), \end{aligned}$$

and

$$\begin{aligned} f\mu_{n,t} &\cong (\bar{i}_m/\sigma_m)\{2(fA_\lambda) + \frac{1}{3}(2 + \langle -\frac{1}{2} \rangle^t)(mA_\lambda - fA_\lambda)\}(f\sigma_A^2) \\ &\quad + (\bar{i}_f/\sigma_f)\{2(fB_\lambda) + \frac{1}{3}(2 + \langle -\frac{1}{2} \rangle^t)(mB_\lambda - fB_\lambda)\}\frac{1}{2}(f\sigma_A^2). \end{aligned}$$

The equilibrium gene frequencies, obtained as the limit when t goes to infinity, are as follows:

$$mP_i^{n,\infty} = fP_i^{n,\infty} \cong p_i\{1 + \frac{1}{3}(mA_\lambda + 2fA_\lambda)(m\theta_i) + \frac{1}{3}(mB_\lambda + 2fB_\lambda)(f\theta_i)\}.$$

Hence, the equilibrium population mean values are

$$m\mu_{n,\infty} \cong \frac{1}{3}\{(\bar{i}_m/\sigma_m)(mA_\lambda + 2fA_\lambda)(m\sigma_A^2) + (\bar{i}_f/\sigma_f)(mB_\lambda + 2fB_\lambda)(f\sigma_A^2)\},$$

and

$$f\mu_{n,\infty} \cong \frac{2}{3}\{(\bar{i}_m/\sigma_m)(mA_\lambda + 2fA_\lambda)(f\sigma_A^2) + (\bar{i}_f/\sigma_f)(mB_\lambda + 2fB_\lambda)\frac{1}{2}(f\sigma_A^2)\}.$$

III. SELECTION AMONG GENOTYPES GENERATED BY ALLELES AT TWO SEX-LINKED LOCI

(a) Definition of Parameters

The following parameters are defined for a random-mating population in equilibrium whose genotypes are generated by an arbitrary number of alleles at each of two sex-linked loci. Let

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

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

and

$$y = \text{recombination value exhibited by females for the two loci.}$$

(i) Homogametic Sex

The initial female population may be obtained as the product of the gametic arrays for the two sexes as follows:

$$f\Pi_0 = \sum_{ijkl} (mf_{ik})(ff_{jl})(A_i^1A_k^2)(A_j^1A_l^2),$$

where

$$mf_{ik} = p_i^1p_k^2 = \text{frequency of the } X\text{-bearing gamete } (A_i^1A_k^2) \text{ produced by males,}$$

and

$$ff_{jl} = p_j^1p_l^2 = \text{frequency of the gamete } (A_j^1A_l^2) \text{ produced by the females.}$$

The genotypic value for the female $(A_i^1A_k^2)(A_j^1A_l^2)$ is $d_{ik,jl}$ and such that

$$f\mu_0 = \sum_{ijkl} (mf_{ik})(ff_{jl})d_{ik,jl} = 0.$$

This genotypic value is characterized by the usual two-locus model (Kempthorne 1957):

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

where the various effects are defined for the female population as follows:

- ${}_f\alpha_u^a$ = additive genetic effect of the A_u^a allele,
- ${}_f\delta_{uv}^a$ = dominance effect associated with the $A_u^a A_v^a$ genotype,
- ${}_f(aa)_{ik}$ = additive \times additive epistatic effect associated with genes A_i^1 and A_k^2 ,
- ${}_f(a\delta)_{ikl}$ = additive \times dominance epistatic effect associated with the gene A_i^1 and the genotype $A_k^2 A_l^2$, and
- ${}_f(\delta\delta)_{ijkl}$ = 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 among females may be partitioned as

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

where

- ${}_f\sigma_G^2$ = total female genotypic variance,
- ${}_f\sigma_A^2$ = additive genetic variance,
- ${}_f\sigma_D^2$ = dominance variance,
- ${}_f\sigma_{AA}^2$ = additive \times additive epistatic variance,
- ${}_f\sigma_{AD}^2$ = additive \times dominance epistatic variance,

and

- ${}_f\sigma_{DD}^2$ = dominance \times dominance epistatic variance.

(ii) *Heterogametic Sex*

The initial genotypic array for males is

$${}_m\Pi_0 = \sum_{jl} ({}_f f_{jl})(A_j^1 A_l^2)(\cdot \cdot),$$

where $(\cdot \cdot)$ indicates the lack of alleles on the Y -chromosome for the loci concerned.

The genotypic value for the male $(A_j^1 A_l^2)(\cdot \cdot)$ is defined to be s_{jl} and coded so that

$${}_m\mu_0 = \sum_{jl} p_j^1 p_l^2 s_{jl} = 0.$$

The following gene model is used to characterize s_{jl} :

$$s_{jl} = {}_m\alpha_j^1 + {}_m\alpha_l^2 + {}_m(aa)_{jl},$$

where

$${}_m\alpha_j^1 = s_{j.} = \sum_l p_l^2 s_{jl},$$

$${}_m\alpha_l^2 = s_{.l} = \sum_j p_j^1 s_{jl},$$

and

$${}_m(aa)_{jl} = s_{jl} - s_{j.} - s_{.l}.$$

The total male genotypic variance may be partitioned as follows:

$${}_m\sigma_G^2 = {}_m\sigma_A^2 + {}_m\sigma_{AA}^2,$$

where

$${}_m\sigma_G^2 = \sum_{jl} p_j^1 p_l^2 (s_{jl})^2$$

$${}_m\sigma_A^2 = \sum_j p_j^1 ({}_m\alpha_j^1)^2 + \sum_l p_l^2 ({}_m\alpha_l^2)^2,$$

and

$${}_m\sigma_{AA}^2 = \sum_{jl} p_j^1 p_l^2 [{}_m(\alpha\alpha)_{jl}]^2.$$

For prediction purposes, certain covariances between male and female effects need to be defined. These are,

$${}_{fm}\sigma_A = \sum_i p_i^1 ({}_f\alpha_i^1)({}_m\alpha_i^1) + \sum_k p_k^2 ({}_f\alpha_k^2)({}_m\alpha_k^2),$$

and

$${}_{fm}\sigma_{AA} = \sum_{ik} p_i^1 p_k^2 [{}_f(\alpha\alpha)_{ik}] \cdot [{}_m(\alpha\alpha)_{ik}].$$

(iii) Selection Values

Selection values are given separately for genotypes of the two sexes. Thus, for the female genotype $(A_i^1 A_k^2)(A_j^1 A_l^2)$ the selection value is

$${}_f w_{ik,jl} = 1 + (\bar{i}_f / \sigma_f) d_{ik,jl},$$

and for the male $(A_r^1 A_t^2)(\cdot \cdot)$ the selection value is

$${}_m w_{rt} = 1 + (\bar{i}_m / \sigma_m) s_{rt}.$$

(b) Consequences of One Cycle of Selection

The frequency of the male genotype $(A_i^1 A_k^2)(\cdot \cdot)$ following selection in ${}_m\Pi_0$ is

$$p_i^1 p_k^2 [1 + (\bar{i}_m / \sigma_m) s_{ik}].$$

The total X-bearing gametic array from selected males is, then,

$$\sum_{ik} ({}_m f_{ik}^1) (A_i^1 A_k^2),$$

where

$${}_m f_{ik}^1 = p_i^1 p_k^2 (1 + {}_m\theta_{ik} + {}_m\phi_{ik}),$$

in which

$${}_m\theta_{ik} = (\bar{i}_m / \sigma_m) ({}_m\alpha_i^1 + {}_m\alpha_k^2),$$

and

$${}_m\phi_{ik} = (\bar{i}_m / \sigma_m) [{}_m(\alpha\alpha)_{ik}].$$

Similarly the total gametic array from selected females is

$$\sum_{jl} ({}_f f_{jl}^1) (A_j^1 A_l^2),$$

where

$${}_f f_{jl}^1 = p_j^1 p_l^2 (1 + {}_f\theta_{jl} + {}_f\phi_{jl}).$$

In this case

$${}_f\theta_{jl} = (\bar{i}_f/\sigma_f)({}_fa_j^1 + {}_fa_l^2),$$

and

$${}_f\phi_{jl} = (\bar{i}_f/\sigma_f)[{}_f(aa)_{jl}].$$

The male and female means resulting from one cycle of selection are then

$$\begin{aligned} m\mu_1 &\cong \sum_{jl} ({}_ff_{jl}^1) s_{jl} \\ &= \sum_{jl} p_j^1 p_i^2 (1 + {}_f\theta_{jl} + {}_f\phi_{jl}) s_{jl} \\ &= (\bar{i}_f/\sigma_f)({}_fm\sigma_A + {}_fm\sigma_{AA}), \end{aligned}$$

and

$$\begin{aligned} {}_f\mu_1 &\cong \sum_{ijkl} ({}_mf_{ik}^1)({}_ff_{jl}^1) d_{ik,jl} \\ &= (\bar{i}_m/\sigma_m)({}_fm\sigma_A + {}_fm\sigma_{AA}) + (\bar{i}_f/\sigma_f)[\tfrac{1}{2}({}_f\sigma_A^2) + \tfrac{1}{4}({}_f\sigma_{AA}^2)]. \end{aligned}$$

(c) Consequences of n Consecutive Cycles of Selection

As in the single-locus case, it is assumed that the selection intensity for one sex remains constant in successive cycles. However, the intensities may differ for the two sexes. Following n cycles of selection the gametic frequencies for the two sexes are:

$${}_mf_{ik}^n \cong p_i^1 p_k^2 [1 + ({}_mA_\lambda)_m \theta_{ik} + ({}_mB_\lambda)_f \theta_{ik} + ({}_mC_\lambda)_m \phi_{ik} + ({}_mD_\lambda)_f \phi_{ik}]$$

and

$${}_ff_{jl}^n \cong p_j^1 p_l^2 [1 + ({}_fA_\lambda)_m \theta_{jl} + ({}_fB_\lambda)_f \theta_{jl} + ({}_fC_\lambda)_m \phi_{jl} + ({}_fD_\lambda)_f \phi_{jl}].$$

Hence the means are

$$\begin{aligned} m\mu_n &\cong \sum_{jl} ({}_ff_{jl}^n) s_{jl} \\ &= (\bar{i}_m/\sigma_m)[({}_fA_\lambda)_m \sigma_A^2 + ({}_fC_\lambda)_m \sigma_{AA}^2] + (\bar{i}_f/\sigma_f)[({}_fB_\lambda)_f \sigma_A + ({}_fD_\lambda)_f \sigma_{AA}], \end{aligned}$$

and

$$\begin{aligned} {}_f\mu_n &\cong \sum_{ijkl} ({}_mf_{ik}^n)({}_ff_{jl}^n) d_{ik,jl} \\ &= (\bar{i}_m/\sigma_m)[({}_mA_\lambda + {}_fA_\lambda)_f \sigma_A + ({}_mC_\lambda + {}_fC_\lambda)_f \sigma_{AA}] \\ &\quad + (\bar{i}_f/\sigma_f)[({}_mB_\lambda + {}_fB_\lambda) \tfrac{1}{2} \sigma_A^2 + ({}_mD_\lambda + {}_fD_\lambda) \tfrac{1}{4} \sigma_{AA}^2]. \end{aligned}$$

As before, λ denotes "even" or "odd", whichever is appropriate for the value of n .

The specific values for the A and B coefficients are those given in the previous section for a single locus. The C 's and D 's are of the form,

$$\left\{ a + \sum_{v=0}^b \sum_{u=v}^c \binom{u}{v} \left(\frac{1-y}{2} \right)^d \right\},$$

where for specific C 's and D 's the substitutions for a , b , c , and d are as follows:

	a	b	c	d
${}_mC_{\text{even}}$	1	$\frac{1}{2}(n-4)$	$n-v-3$	$u+1$
${}_mC_{\text{odd}}$	1	$\frac{1}{2}(n-3)$	$n-v-3$	$u+1$
${}_mD_{\text{even}}$	0	$\frac{1}{2}(n-2)$	$n-v-2$	u
${}_mD_{\text{odd}}$	0	$\frac{1}{2}(n-3)$	$n-v-2$	u
${}_fC_{\text{even}}$	0	$\frac{1}{2}(n-2)$	$n-v-2$	$u+1$
${}_fC_{\text{odd}}$	0	$\frac{1}{2}(n-3)$	$n-v-2$	$u+1$
${}_fD_{\text{even}}$	0	$\frac{1}{2}(n-2)$	$n-v-1$	u
${}_fD_{\text{odd}}$	0	$\frac{1}{2}(n-1)$	$n-v-1$	u

Tables 2 and 3 give the increment changes in male and female means up to the fourth consecutive cycle of selection.

TABLE 2

INCREMENT CHANGES IN MALE MEANS DUE TO CONSECUTIVE CYCLES OF SELECTION
(TWO-LOCUS MODEL)

	$(\bar{v}_m/\sigma_m)_m\sigma_A^2$	$(\bar{v}_f/\sigma_f)_{fm}\sigma_A$	$(\bar{v}_m/\sigma_m)_m\sigma_{AA}^2$	$(\bar{v}_f/\sigma_f)_{fm}\sigma_{AA}$
$m\mu_0$	0	0	0	0
$m\mu_1$	0	1	0	1
$m\mu_2$	$\frac{1}{2}$	$1\frac{1}{2}$	$\frac{1}{2}(1-y)$	$1+\frac{1}{2}(1-y)$
$m\mu_3$	$\frac{3}{4}$	$2\frac{1}{4}$	$[\frac{1}{2}(1-y)+\frac{1}{4}(1-y)^2]$	$[1+(1-y)+\frac{1}{4}(1-y)^2]$
$m\mu_4$	$1\frac{1}{8}$	$2\frac{7}{8}$	$[\frac{1}{2}(1-y)+\frac{1}{2}(1-y)^2+\frac{1}{8}(1-y)^3]$	$[1+(1-y)+\frac{3}{4}(1-y)^2+\frac{1}{8}(1-y)^3]$

TABLE 3

INCREMENT CHANGES IN FEMALE MEANS DUE TO CONSECUTIVE CYCLES OF SELECTION
(TWO-LOCUS MODEL)

	$(\bar{v}_m/\sigma_m)_{fm}\sigma_A$	$(\bar{v}_f/\sigma_f)_f\sigma_A^2$	$(\bar{v}_m/\sigma_m)_{fm}\sigma_{AA}$	$(\bar{v}_f/\sigma_f)_f\sigma_{AA}^2$
$f\mu_0$	0	0	0	0
$f\mu_1$	1	$\frac{1}{2}$	1	$\frac{1}{4}$
$f\mu_2$	$1\frac{1}{2}$	$1\frac{1}{4}$	$[1+\frac{1}{2}(1-y)]$	$\frac{1}{4}[2+\frac{1}{2}(1-y)]$
$f\mu_3$	$2\frac{1}{4}$	$1\frac{7}{8}$	$[1+(1-y)+\frac{1}{4}(1-y)^2]$	$\frac{1}{4}[2+\frac{3}{2}(1-y)+\frac{1}{4}(1-y)^2]$
$f\mu_4$	$2\frac{7}{8}$	$2\frac{9}{16}$	$[1+(1-y)+\frac{3}{4}(1-y)^2+\frac{1}{8}(1-y)^3]$	$\frac{1}{4}[2+2(1-y)+(1-y)^2+\frac{1}{8}(1-y)^3]$

(d) *Consequences of One Generation of Relaxation Following n Cycles of Selection*

In this section the consequences of relaxation following selection are studied. With two loci the additional complication due to additive \times additive epistatic effects occurs.

Starting with the male population

$${}_m\Pi_{n,0} = \sum_{jl} ({}_mf_{jl}^{n,0})(A_j^1A_l^2)(\cdots),$$

the X -bearing gametic array for unselected males is

$$\sum_{jl} ({}_mf_{jl}^{n,1})(A_j^1A_l^2),$$

where

$${}_m f_{jl}^{n,1} = {}_f f_{il}^{n,0} = p_j^1 p_i^2 [1 + ({}_f A_\lambda)_m \theta_{jl} + ({}_f B_\lambda)_f \theta_{jl} + ({}_f C_\lambda)_m \phi_{jl} + ({}_f D_\lambda)_f \phi_{jl}].$$

Similarly, starting with the female population

$${}_f \Pi_{n,0} = \sum_{ijkl} ({}_m f_{ik}^{n,0}) ({}_f f_{jl}^{n,0}) (A_i^1 A_k^2) (A_j^1 A_l^2),$$

the gametic array for unselected females is

$$\sum_{ik} ({}_f f_{ik}^{n,1}) (A_i^1 A_k^2),$$

where

$${}_f f_{ik}^{n,1} = \frac{1}{2}(1-y)[{}_m f_{ik}^{n,0} + {}_f f_{ik}^{n,0}] + \frac{1}{2}y[({}_m f_i^{n,0})({}_f f_k^{n,0}) + ({}_m f_k^{n,0})({}_f f_i^{n,0})].$$

In terms of gene effects this frequency becomes

$$\begin{aligned} {}_f f_{ik}^{n,1} &= p_i^1 p_k^2 \{1 + \frac{1}{2}[({}_m A_\lambda + {}_f A_\lambda)_m \theta_{ik} + ({}_m B_\lambda + {}_f B_\lambda)_f \theta_{ik}] \\ &\quad + \frac{1}{2}(1-y)[({}_m C_\lambda + {}_f C_\lambda)_m \phi_{ik} + ({}_m D_\lambda + {}_f D_\lambda)_f \phi_{ik}]\}. \end{aligned}$$

Relaxation for one generation results, then, in the following means:

$$\begin{aligned} {}_m \mu_{n,1} &\cong \sum_{ik} ({}_f f_{ik}^{n,1}) s_{ik} \\ &= \frac{1}{2}\{(\bar{i}_m/\sigma_m)({}_m A_\lambda + {}_f A_\lambda)_m \sigma_A^2 + (\bar{i}_f/\sigma_f)({}_m B_\lambda + {}_f B_\lambda)_f \sigma_A^2\} \\ &\quad + \frac{1}{2}(1-y)[(\bar{i}_m/\sigma_m)({}_m C_\lambda + {}_f C_\lambda)_m \sigma_{AA}^2 + (\bar{i}_f/\sigma_f)({}_m D_\lambda + {}_f D_\lambda)_f \sigma_{AA}^2], \end{aligned}$$

and

$$\begin{aligned} {}_f \mu_{n,1} &\cong \sum_{ijkl} ({}_m f_{ik}^{n,1}) ({}_f f_{jl}^{n,1}) d_{ik,jl} \\ &= \frac{1}{2}\{(\bar{i}_m/\sigma_m)({}_m A_\lambda + 3{}_f A_\lambda)_f \sigma_A^2 + \frac{1}{2}(\bar{i}_f/\sigma_f)({}_m B_\lambda + 3{}_f B_\lambda)_f \sigma_A^2\} \\ &\quad + (\bar{i}_m/\sigma_m)[\frac{1}{2}(1-y){}_m C_\lambda + \frac{1}{2}(3-y){}_f C_\lambda]_f \sigma_{AA}^2 + (\bar{i}_f/\sigma_f)[\frac{1}{2}(1-y){}_m D_\lambda + \frac{1}{2}(3-y){}_f D_\lambda]_f \sigma_{AA}^2. \end{aligned}$$

(e) Consequences of t Generations of Relaxation following n Cycles of Selection

The final consideration in this study is for a population having had a history of n consecutive cycles of selection followed by t cycles of relaxation.

It can be shown that the gamete frequencies are approximately of the form:

$$\begin{aligned} {}_m f_{ik}^{n,t} &\cong p_i^1 p_k^2 [1 + ({}_m \theta_{ik})[{}_f A_\lambda + \frac{1}{3}(1 - \langle -\frac{1}{2} \rangle^{t-1})({}_m A_\lambda - {}_f A_\lambda)] \\ &\quad + ({}_f \theta_{ik})[{}_f B_\lambda + \frac{1}{3}(1 - \langle -\frac{1}{2} \rangle^{t-1})({}_m B_\lambda - {}_f B_\lambda)] \\ &\quad + \{(1-y)/2\}^{\frac{1}{2}t} \{({}_m \phi_{ik})[({}_m C_\lambda)({}_m E_\tau) + ({}_f C_\lambda)({}_m F_\tau)] + ({}_f \phi_{ik})[({}_m D_\lambda)({}_m E_\tau) + ({}_f D_\lambda)({}_m F_\tau)]\}], \end{aligned}$$

and

$$\begin{aligned} {}_f f_{il}^{n,t} &\cong p_j^1 p_i^2 [1 + ({}_m \theta_{jl})[{}_f A_\lambda + \frac{1}{3}(1 - \langle -\frac{1}{2} \rangle^t)({}_m A_\lambda - {}_f A_\lambda)] \\ &\quad + ({}_f \theta_{jl})[{}_f B_\lambda + \frac{1}{3}(1 - \langle -\frac{1}{2} \rangle^t)({}_m B_\lambda - {}_f B_\lambda)] \\ &\quad + \{(1-y)/2\}^{\frac{1}{2}t} \{({}_m \phi_{jl})[({}_m C_\lambda)({}_f E_\tau) + ({}_f C_\lambda)({}_f F_\tau)] + ({}_f \phi_{jl})[({}_m D_\lambda)({}_f E_\tau) + ({}_f D_\lambda)({}_f F_\tau)]\}]. \end{aligned}$$

In these formulae A , B , C , and D have been defined previously, and λ and τ independently denote "even" or "odd" depending on the values of n and t respectively. The E 's are of the form

$$\sum_{u=0}^a \binom{b}{u} \left(\frac{1-y}{2}\right)^c,$$

where for specific values of E the numbers a , b , and c are

	a	b	c
${}_f E_{\text{even}}$	$\frac{1}{2}(t-2)$	$t-u-1$	$\frac{1}{2}(t-2u)$
${}_f E_{\text{odd}}$	$\frac{1}{2}(t-1)$	$t-u-1$	$\frac{1}{2}(t-2u)$
${}_m E_{\text{even}}$	$\frac{1}{2}(t-2)$	$t-u-2$	$\frac{1}{2}(t-2u-2)$
${}_m E_{\text{odd}}$	$\frac{1}{2}(t-3)$	$t-u-2$	$\frac{1}{2}(t-2u-2)$

The F 's are of the form

$$\sum_{v=0}^a \binom{b}{v} \left(\frac{1-y}{2}\right)^c,$$

where for specific values of F the numbers a , b , and c are

	a	b	c
${}_f F_{\text{even}}$	$\frac{1}{2}t$	$t-v$	$\frac{1}{2}(t-2v)$
${}_f F_{\text{odd}}$	$\frac{1}{2}(t-1)$	$t-v$	$\frac{1}{2}(t-2v)$
${}_m F_{\text{even}}$	$\frac{1}{2}(t-2)$	$t-v-1$	$\frac{1}{2}(t-2v-2)$
${}_m F_{\text{odd}}$	$\frac{1}{2}(t-1)$	$t-v-1$	$\frac{1}{2}(t-2v-2)$

Means for the two sexes are obtained by evaluating the expressions

$${}_m \mu_{n,t} \cong \sum_{jl} ({}_f f_{jl}^{n,t}) s_{jl},$$

and

$${}_f \mu_{n,t} \cong \sum_{ijkl} ({}_m f_{ik}^{n,t}) ({}_f f_{jl}^{n,t}) d_{ik,jl}.$$

As t increases in value, two fundamental processes occur which change the gamete frequencies. Firstly, the contributions due to additive effects adjust to their equilibrium values. Secondly, contributions from the additive \times additive epistatic effects decrease as a function of $\{(1-y)/2\}^{\frac{1}{2}t}$. Hence in the limit (as $t \rightarrow \infty$), the additive effects have equilibrated and the epistatic effects have disappeared completely. In this process the means arrive at the predicted state for independent loci exhibiting no epistasis, i.e.

$${}_m \mu_{n,\infty} \cong \frac{1}{3}[(\bar{i}_m/\sigma_m)({}_m A_\lambda + 2{}_f A_\lambda) {}_m \sigma_A^2 + (\bar{i}_f/\sigma_f)({}_m B_\lambda + 2{}_f B_\lambda) {}_f \sigma_A],$$

and

$${}_f \mu_{n,\infty} \cong \frac{2}{3}[(\bar{i}_m/\sigma_m)({}_m A_\lambda + 2{}_f A_\lambda) {}_f \sigma_A + (\bar{i}_f/\sigma_f)({}_m B_\lambda + 2{}_f B_\lambda) \frac{1}{2} {}_f \sigma_A^2].$$

IV. DISCUSSION

The *immediate* responses to selection involve additive and additive \times additive variances, as defined in both sexes, together with the covariances between sexes for additive and for additive \times additive epistatic effects.

In general, even if the quantities (\bar{i}_m/σ_m) and (\bar{i}_f/σ_f) are equal, the immediate responses to selection for the two sexes may differ. This is due to the fact that the increment changes in means for the two sexes are different functions of genotypic variances and covariances. In fact, this holds true for populations having had a history of selection followed by complete relaxation.

Because the two sexes exhibit different increment changes in means for identical selection intensities, the possibility exists that selection in one sex may be more efficient than in the other sex. However, to explore this possibility it is necessary to examine the consequences of selection when different genetic models are used which relate the monoploid genotypic values of the heterogametic sex with the diploid genotypic values of the homogametic sex. Such a study will be reported at a later date.

Considering genotypes at a single locus, relaxation after selection results in fluctuating means due to the equilibration process of gene frequencies in the two sexes. This phenomenon does not occur with autosomal inheritance.

For more than one locus and when additive \times additive epistatic effects are manifest in either or both sexes, relaxation from selection results in a more complicated phenomenon. In addition to the tendency for gene frequencies to equilibrate, the contributions of additive \times additive effects tend to diminish. This decay of epistatic contributions is also found with relaxation following selection involving autosomal inheritance.

Finally, the various formulae have been given *in extenso* for completeness of presentation. However, it must be realized that errors of approximation accumulate and prediction becomes worse as the number of successive cycles of selection increase.

V. REFERENCES

- BENNETT, J. H. (1963).—Random mating and sex linkage. *J. Theoret. Biol.* **4**: 28–36.
- BOHIDAR, N. R. (1964).—Derivation and estimation of variance and covariance components associated with covariance between relatives under sex-linked transmission. *Biometrics* **20**: 505–21.
- GRIFFING, B. (1960).—Theoretical consequences of truncation selection based on the individual phenotype. *Aust. J. Biol. Sci.* **13**: 307–43.
- HALDANE, J. B. S. (1924).—The mathematical theory of natural and artificial selection. I. *Trans. Camb. Phil. Soc.* **23**: 19–41.
- HALDANE, J. B. S. (1926).—The mathematical theory of natural and artificial selection. III. *Proc. Camb. Phil. Soc.* **23**: 363–72.
- JENNINGS, H. S. (1916).—The numerical results of diverse systems of breeding. *Genetics* **1**: 53–89.
- KEMP THORNE, O. (1957).—“An Introduction to Genetic Statistics,” (John Wiley and Sons, Inc.: New York.)
- KIMURA, M. (1958).—On the change of population fitness by natural selection. *Heredity* **12**: 145–67.
- ROBBINS, R. B. (1918).—Applications of mathematics to breeding problems. II. *Genetics* **3**: 73–92.