Rules for assortative mating in relation to selection for linear merit functions

R. L. Fernando and D. Gianola

Department of Animal Science, 1207 West Gregory Drive, University of Illinois, Urbana, Ill 61801, USA

Summary. This study examined how assortative mating (without selection) based on linear combinations of two traits could be used to change genetic parameters so as to increase efficiency of selection. The efficiency of the Smith-Hazel index for improvement of multiple traits is a function of phenotypic and genetic variances and covariances, and of the relative economic values of the traits involved. Assortative mating is known to change genetic variances and covariances. Recursive formulae were derived to obtain these variances and covariances after t generations of assortative mating on linear combinations (mating rules) of phenotypic values for two traits, with a given correlation between mates. Selection efficiency after t generations of assortative mating without selection was expressed as a function of random mating genetic parameters, economic values, the mating rule, and the correlation between mates. Selection efficiency was maximized with respect to the coefficients in the mating rule. Because the objective function was nonlinear, a computer routine was used for maximizing it. Two cases were considered. When random mating heritabilities for the two traits were $h_X^2 = 0.25$ and $h_Y^2 = 0.50$, the genetic correlation $r_{XY} = -0.60$, and the economic values were $a_X = 3$ and $a_Y = 1$, continued assortative mating based on the optimal mating rule for 31 generations (with a correlation of 0.80 between mates) increased selection efficiency by 29%. Heritabilities changed to 0.38 and 0.66, respectively, and the genetic correlation became -0.79. When $h_X^2 = 0.60$, $h_Y^2 = 0.60$, $r_{XY} = -0.20$, $a_1 = 1$ and $a_2 = 1$, 36 generations of continued assortative mating with the optimal mating rule increased the efficiency of selection by 17%, heritabilities became $h_X^2 = h_Y^2 = 0.71$, and the genetic correlation changed to 0.25. Only three generations of assortative mating were required to change the sign of the genetic correlation.

Introduction

Assortative mating is a process of choosing mates from a population such that a correlation between the phenotypic values of individuals in a mating pair is induced.

Jennings (1916) studied the consequences of assortative mating with a single locus-two alleles model, with and without sex linkage. Wentworth and Remick (1916), working with a single locus-two alleles model, with and without dominance, derived formulae relating gene frequencies at generation n of continued assortative mating to gene frequencies in the randomly mating base population. Fisher (1918) and Wright (1921) examined the consequences of assortative mating for a polygenic trait. While Fisher's (1918) results were asymptotic in the number of loci, Wright (1921) obtained formulae for a finite number of gene pairs assuming equal gene effects and gene frequencies at each locus, and no dominance. Crow and Felsenstein (1968) extended Wright's ideas to include dominance and unequal gene effects and gene frequencies. Bulmer (1980) reproduced Fisher's (1918) results in a much simpler way by using normal distribution theory.

These workers showed that positive assortative mating, starting from a randomly mating population of infinite size, increases the additive genetic variance and the degree of homozygosity. The increase in additive genetic variance is larger than the one accruing under inbreeding. However, the increase in homozygosity is lesser than with inbreeding. This is explained by the fact that while inbreeding causes a positive correlation between homologous genes only, positive assortative mating also induces a positive correlation between nonhomologous genes (Crow and Kimura 1970).

Latter (1965) studied the consequences of assortative mating for a trait X on estimates of heritability of X and of a correlated trait Y, and on the estimated genetic correlation between X and Y. Gianola (1982) further examined the effect of assortative mating on the genetic correlation. He showed

that positive assortative mating increases the absolute value of the equilibrium genetic correlation and negative assortative mating decreases it. Assortative mating for trait X, however, does not change the sign of the equilibrium genetic correlation between X and Y (Gianola 1982). His study also considered "mixed" assortative mating, a system that causes a phenotypic correlation between two different traits in the mating pair. Males and females are ordered on the basis of traits X and Y, respectively, and then mated assortatively. Gianola (1982) showed that "mixed" positive assortative mating increases the genetic correlation and negative assortative mating decreases it.

The objective of this study was to examine consequences of assortative mating (without selection) based on linear combinations of traits (mating rules), and to illustrate how these mating rules could be used to maximize efficiency of selection, after t generations of assortative mating.

Assortative mating on linear combinations of two traits

Consider the linear functions

$$I^M = c_X^M X^M + c_Y^M Y^M,$$

and

$$I^F = c_X^F X^F + c_Y^F Y^F,$$

where (X^M, Y^M) and (X^F, Y^F) are the phenotypic values of traits X and Y measured in each of two individuals in a mating pair; M and F indicate male and female individuals, respectively. The functions I^M and I^F will be referred to as mating rules; the coefficients c_X^M, c_Y^M, c_X^F and c_Y^F are real numbers. Assortative mating on I^M and I^F encompasses "classical" assortative mating ($c_X^M = c_X^F = 1$, $c_Y^M = c_Y^F = 0$) and "mixed" assortative mating ($c_X^M = c_Y^F = 1$, $c_Y^M = c_X^F = 0$).

The consequences of assortative mating based on rules I^M and I^F can be studied in terms of the developments presented by Bulmer (1980) and Gianola (1982). Bulmer (1980) considered a trait determined by a large number of loci without epistasis, and showed that assortative mating does not affect the distribution of dominance or environmental effects. Thus, only the effect of assortative mating on the additive genetic component of variance needs to be examined.

The additive genetic values of an individual for traits X and Y can be written as

$$A_X^0 = \tfrac{1}{2} A_X^M + \tfrac{1}{2} A_X^F + e_X \tag{1}$$

and

$$A_Y^0 = \tfrac{1}{2} A_Y^M + \tfrac{1}{2} A_Y^F + e_Y \tag{2}$$

where:

A_X^0 (A_Y^0) is the additive genetic value of an individual for trait X (trait Y); A_X^M and A_X^F (A_Y^M and A_Y^F) are

the additive genetic values of the individual's parents for trait X (trait Y); and e_X (e_Y) is a random variable that accounts for the within-sibship genetic variance for trait X (trait Y). When the number of loci is large, the joint distribution of A_X^M, A_X^F and e_X approaches multivariate normality, and e_X becomes independent of A_X^M and A_X^F (Bulmer 1980). Further, the variance of e_i ($i = X, Y$) is equal to $\tfrac{1}{2} V_{A(0)}^i$, where $V_{A(0)}^i$ is the additive genetic variance for the ith trait in a randomly mating population (Bulmer 1980). Likewise, $Cov(e_X, e_Y) = \tfrac{1}{2} Cov_{A(0)}^{XY}$, where $Cov_{A(0)}^{XY}$ is the additive genetic covariance between traits X and Y in a randomly mating population (Gianola 1982).

The following recursive relationships can be obtained from (1) and (2)

$$V_{A(t+1)}^i = \tfrac{1}{2} V_{A(t)}^i + \tfrac{1}{2} Cov(A_i^M, A_i^F) + \tfrac{1}{2} V_{A(0)}^i ; \tag{3}$$

and $i = X, Y$

$$Cov_{A(t+1)}^{XY} = \tfrac{1}{2} Cov_{A(t)}^{XY} + \tfrac{1}{4} Cov(A_X^M, A_Y^F)$$
$$+ \tfrac{1}{4} Cov(A_Y^M, A_X^F) + \tfrac{1}{2} Cov_{A(0)}^{XY} \tag{4}$$

where $V_{A(t)}^i$ is the additive genetic variance for the ith trait at generation t of assortative mating and $Cov_{A(t)}^{XY}$ is the additive genetic covariance between traits X and Y at generation t (Bulmer 1980; Gianola 1982). The covariances between A_i^M and A_j^F ($i, j = X, Y$) can be obtained by writing A_i^k as

$$A_i^k = \frac{Cov(A_i^k, I^k)}{Var(I^k)} (I^k - \mu_k) + \varepsilon^k; \quad k = M, F \tag{5}$$

where $\mu_k = E(I^k)$. The two terms in (5) are mutually uncorrelated and, therefore, mutually independent under multivariate normality. Assuming that the covariance between A_i^M and A_j^F ($i, j = X, Y$) is entirely due to assortative mating on the basis of I^M and I^F (see Appendix for further details), we can write

$$Cov(A_i^M, A_j^F)$$
$$= Cov\left[\frac{Cov(A_i^M, I^M)}{Var(I^M)} (I^M - \mu_M), \frac{Cov(A_j^F, I^F)}{Var(I^F)} (I^F - \mu_F)\right]$$
$$= \frac{Cov(A_i^M, I^M) \cdot Cov(A_j^F, I^F)}{[Var(I^M) \cdot Var(I^F)]^{\frac{1}{2}}} \varrho, \tag{6}$$

where $\varrho = Corr(I^M, I^F)$, is the correlation between the values of the mating rule in members of a mating pair. Using (6) in (3) and (4) gives

$$V_{A(t+1)}^i = \frac{1}{2} V_{A(t)}^i$$
$$+ \frac{1}{2} \frac{Cov(A_i^M, I^M) \cdot Cov(A_i^F, I^F)}{[Var(I^M) \cdot Var(I^F)]^{\frac{1}{2}}} \varrho + \frac{1}{2} V_{A(0)}^i ;$$
$$i = X, Y \tag{7}$$

and

$$Cov_{A(t+1)}^{XY} = \frac{1}{2} Cov_{A(t)}^{XY} + \frac{1}{4} \frac{[Cov(A_X^M, I^M) \cdot Cov(A_Y^F, I^F) + Cov(A_Y^M, I^M) \cdot Cov(A_X^F, I^F)]}{[Var(I^M) \cdot Var(I^F)]^{\frac{1}{2}}} \varrho + \frac{1}{2} Cov_{A(0)}^{XY}. \qquad (8)$$

When random mating is practiced, $\varrho = 0$, and the second terms in (7) and (8) become zero.

If random mating, is practiced after t_0 generations of assortative mating, the genetic variance in the next generation would be from (7)

$$V_{A(t_0+1)}^i = \frac{1}{2}[V_{A(t_0)}^i + V_{A(0)}^i]; \quad i = X, Y.$$

Further

$$V_{A(t_0+2)}^i = \frac{1}{2}[V_{A(t_0+1)}^i + V_{A(0)}^i] = \frac{1}{4} V_{A(t_0)}^i + (\frac{1}{2} + \frac{1}{4}) V_{A(0)}^i,$$
$$i = X, Y.$$

Thus, the genetic variance after t_0 generations of assortative mating followed by n generations of random mating is

$$V_{A(t_0+n)}^i = (\frac{1}{2})^n V_{A(t_0)}^i + [\frac{1}{2} + \frac{1}{4} + \ldots + (\frac{1}{2})^n] V_{A(0)}^i.$$

From the above equation, as $n \to \infty$, $V_{A(t_0+n)}^i \to V_{A(0)}^i$. Similarly, as $n \to \infty$, $Cov_{A(t_0+n)}^{XY} \to Cov_{A(0)}^{XY}$. The approach to $V_{A(0)}^i$ and $Cov_{A(0)}^{XY}$ is rapid. For example,

$$V_{A(t_0+4)}^i = \frac{1}{16} V_{A(t_0)}^i + \frac{15}{16} V_{A(0)}^i,$$

and

$$Cov_{A(t+4)}^{XY} = \frac{1}{16} Cov_{A(t_0)}^{XY} + \frac{15}{16} Cov_{A(0)}^{XY}.$$

Construction of rules for assortative mating

In dealing with multiple traits, plant and animal breeders often define an aggregate genotype or merit function. This is usually written as a linear combination of additive genotypic values for individual traits (Smith 1936; Hazel 1943; Henderson 1963). The breeder's objective is to increase the expected value of the merit function, by selection. For the two-trait situation discussed in this research, the unobservable aggregate genotype is defined as

$$T = a_X A_X + a_Y A_Y, \qquad (9)$$

where the coefficients a_X and a_Y are the relative economic values of traits X and Y, respectively.

Cochran (1951) showed that by ordering candidates for selection on the basis of $\hat{T} = E(T|X, Y)$ and then selecting the individuals with $\hat{T} \geq p$, where p is a number such that the proportion selected is α, selection progress is maximized over any other rule that selects a proportion α. Bulmer (1980) has shown under more general conditions that selection on the basis of the conditional mean of the unobservable variable T given vectors x and y maximizes selection progress when a fixed number of candidates is selected. The efficiency of using $\hat{T}$ as a selection rule relative to direct selection

on T is measured by

$$Corr(T, \hat{T}) = [Var(\hat{T})/Var(T)]^{\frac{1}{2}} \qquad (10)$$

(Henderson 1963; Bulmer 1980).

We propose to choose the coefficients $(c_X^M, c_Y^M, c_X^F, c_Y^F)$ in the mating rules I^M and I^F so as to maximize $Corr(T, \hat{T})_t$, the correlation between T and $\hat{T}$ after t generations of continued assortative mating $(t = 0, 1 \ldots)$. Assuming normality, the conditional mean of T given X and Y at generation t of assortative mating is calculated as

$$\hat{T}_{(t)} = b_{X(t)}(X - \mu_X) + b_{Y(t)}(Y - \mu_Y) \qquad (11)$$

where

$$b = \begin{bmatrix} b_{X(t)} \\ b_{Y(t)} \end{bmatrix} = \begin{bmatrix} V_{P(t)}^X & Cov_{P(t)}^{XY} \\ Cov_{P(t)}^{XY} & V_{P(t)}^Y \end{bmatrix}^{-1} \cdot \begin{bmatrix} a_X V_{A(t)}^X + a_Y Cov_{A(t)}^{XY} \\ a_Y V_{A(t)}^Y + a_X Cov_{A(t)}^{XY} \end{bmatrix}. \qquad (12)$$

In (12): $V_{P(t)}^X$ ($V_{P(t)}^Y$) is the phenotypic variance of trait X (trait Y) at generation t of assortative mating; and $Cov_{P(t)}^{XY}$ is the phenotypic covariance between traits X and Y at generation t of assortative mating. Note that when $t = 0$, (12) reduces to the Smith-Hazel selection index. Because assortative mating does not affect the dominance and environmental components of phenotypic variances and covariances, the latter can be calculated at generation t of assortative mating as

$$V_{P(t)}^i = V_{A(t)}^i + V_{P(0)}^i - V_{A(0)}^i; \quad i = X, Y$$

and

$$Cov_{P(t)}^{XY} = Cov_{A(t)}^{XY} + Cov_{P(0)}^{XY} - Cov_{A(0)}^{XY}.$$

The correlation between T and $\hat{T}$ after t generations of assortative mating can be written as

$$Corr(T, \hat{T})_t \qquad (13)$$
$$= \left[\frac{b_{X(t)}^2 V_{P(t)}^X + 2 b_{X(t)} b_{Y(t)} Cov_{P(t)}^{XY} + b_{Y(t)}^2 V_{P(t)}^Y}{a_X^2 V_{A(t)}^X + 2 a_X a_Y Cov_{A(t)}^{XY} + a_Y^2 V_{A(t)}^Y} \right]^{\frac{1}{2}}$$

Because of the form in which the coefficients of the mating rule enter into (13), an explicit solution for the $c_X^M, c_Y^M, c_X^F, c_Y^F$ that maximize (13) cannot be obtained. However, $Corr(T, \hat{T})_t$ can be maximized numerically with respect to $(c_X^M, c_Y^M, c_X^F, c_Y^F)$ using a computer algorithm for optimizing nonlinear functions.

Numerical results

Two hypothetical situations were considered to illustrate the effect of different mating rules on genetic

parameters. Solutions for the optimum rules, in the sense of maximizing $\text{Corr}(T, \hat{T})_t$, were obtained using GRG, a FORTRAN program for optimizing nonlinear functions using the Generalized Reduced Gradient Method (Lasdon et al. 1975).

Case 1

The parameter values assumed for the random mating base population were: heritability of trait X $(h_X^2) = 0.25$; heritability of trait Y $(h_Y^2) = 0.5$, and the genetic correlation between traits X and Y $(r_{XY}) = -0.6$. Relative economic values $a_X = 3$ and $a_Y = 1$ were used to define T, the aggregate genotypic value, in (9). With these parameters, the relative efficiency of $\hat{T}$ as a selection rule with randomly mating parents, is $\text{Corr}(T, \hat{T})_0 = 0.44$. For assortative mating of parents, the correlation between values of the mating rules I^M and I^F in members of a mating pair was taken as $\varrho = 0.8$.

For a given mating rule, recursive application of (7) and (8) was used to obtain equilibrium values for h_X^2, h_Y^2, r_{XY} and $\text{Corr}(T, \hat{T})_t$. Time at equilibrium was arbitrarily defined as the generation t in which $\text{Corr}(T, \hat{T})_{t+10} - \text{Corr}(T, \hat{T})_t < 0.005$. The number of generations to reach equilibrium, the equilibrium genetic parameters $(\hat{h}_X^2, \hat{h}_Y^2, \hat{r}_{XY})$ and the equilibrium efficiency of selection, $\hat{\text{Corr}}(T, \hat{T})$, were calculated for seven different mating rules (A, B, ..., G), for the optimum rule at generation 50 of assortative mating (H), and for the Smith-Hazel index used as a mating rule (I). These mating rules are described in Table 1. Mating rules A and B correspond to positive assortative mating for traits X and Y, respectively. Rules C and D correspond to negative assortative mating for traits X

and Y, respectively. Rules E and F correspond to positive and negative "mixed" assortative mating, respectively. Rule G was for assortative mating on the sum of X and Y. Because the Smith-Hazel index is a function of genetic and phenotypic variances and covariances, rule I was recalculated in every generation.

Positive assortative mating (rules A and B) increased heritability and decreased the genetic correlation as expected (Bulmer 1980; Gianola 1982). Positive assortative mating for trait Y (rule B) increased the heritability of X more than positive assortative mating for trait X (rule A) itself. Rules A and B both increased selection efficiency. However, rule A gave a higher efficiency and led to equilibrium more rapidly than rule B. Although both $\hat{h}_X^2$ and $\hat{h}_Y^2$ were lower with rule A than with rule B, selection efficiency was larger. This is explained by the effect of a lower value of $\hat{r}_{XY}$ for rule B than for rule A, with T defined as $3A_X + A_Y$. However, if the merit function is defined as $T = A_X$, selection efficiency at equilibrium would be about 12% higher with rule B than with rule A. This illustrates that the effect of a mating rule on equilibrium selection efficiency depends on the genetic parameters in the random mating population and on the definition of the aggregate genotype. Negative assortative mating (rules C and D) reduced the heritabilities of the two traits and increased their genetic correlation. Efficiency of selection decreased and equilibrium was reached relatively rapidly.

Positive "mixed" assortative mating (rule E) had effects similar to those of negative assortative mating. This is because under the assumptions of this study a negative genetic correlation between the two traits and a positive correlation between phenotypic values of X

Table 1. Equilibrium values of genetic parameters for traits X and Y, relative selection efficiency and number of generations to equilibrium for seven assortative mating rules[a,b]

	Coefficients of mating rule				Equilibrium values				
	c_X^M	c_Y^M	c_X^F	c_Y^F	$\hat{h}_X^2$	$\hat{h}_Y^2$	$\hat{r}_{XY}$	$\hat{\text{Corr}}(T, \hat{T})$	Generations to equilibrium
A:	1	0	1	0	0.306	0.528	−0.653	0.509	16
B:	0	1	0	1	0.323	0.687	−0.743	0.469	22
C:	1	0	−1	0	0.221	0.486	−0.569	0.408	6
D:	0	1	0	−1	0.233	0.431	−0.547	0.437	2
E:	1	0	0	1	0.227	0.469	−0.522	0.422	3
F:	1	0	0	−1	0.303	0.566	−0.708	0.503	20
G:	1	1	1	1	0.251	0.524	−0.554	0.437	4
H:	1	−0.96	1	−0.96	0.378	0.662	−0.788	0.573	31
I[c]:	−	−	−	−	0.331	0.563	−0.704	0.535	23

[a] Random mating genetic parameters were $h_X^2 = 0.25$, $h_Y^2 = 0.50$, $r_{XY} = -0.60$; relative economic values were $a_X = 3$, $a_Y = 1$; $\text{Corr}(T, \hat{T}) = 0.443$

[b] The correlation between I^M and I^F values of individuals in a mating pair was $\varrho = 0.80$

[c] Coefficients of mating rule I (Smith-Hazel index) were recalculated every generation

and Y in mating pairs cause a negative correlation between phenotypic values of the same trait. Likewise, negative "mixed" assortative mating (rule F) had effects similar to positive assortative mating; $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{Corr}(T, \hat{T})$ were increased, and $\hat{r}_{XY}$ was decreased. The number of generations required to reach equilibrium was as in positive assortative mating.

Assortative mating on the sum of X and Y (rule G) led to increased heritability of X and Y, as it happened in the case of rules A, B and F. However, the genetic correlation increased, the effect being similar to those of rules C, D and E. The equilibrium selection efficiency was lower with rule G than with random mating in spite of the fact that $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{r}_{XY}$ all increased. Equilibrium was reached in 4 generations.

The optimum rule (H) had effects similar to rules A, B and F: $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{Corr}(T, \hat{T})$ increased and $\hat{r}_{XY}$ decreased. Equilibrium was reached only after 31 generations of assortative mating. As expected, the increase in selection efficiency was largest with this rule, a 29% increase over the random mating value. Rule H yielded the highest values for $\hat{h}_X^2$, $|\hat{r}_{XY}|$ and for the number of generations to equilibrium.

As pointed out before, rule I involved using the Smith-Hazel index in (11) for assortative mating. Equilibrium values with rule I were comparable to those obtained with rules A, B, F and H; $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{Corr}(T, \hat{T})$ increased, $\hat{r}_{XY}$ decreased, and equilibrium was reached after 23 generations. Selection efficiency at equilibrium was somewhat lower than in the case of the optimum rule (H), but higher than with the other rules.

Figures 1–4 depict the changes in h_X^2, h_Y^2, r_{XY} and $Corr(T, \hat{T})$ with generations of continued assortative mating for the nine different rules considered in this study. In general, most of the change in these parameters took place within the first 10 generations. For example, rules C, D, E and G reached equilibrium in less than 10 generations. While rule H was the slowest in reaching equilibrium (31 generations), about 85% of the total increase in selection efficiency was attained at generation 10.

As discussed previously, the optimum rule (H) was obtained so as to maximize $Corr(T, \hat{T})_{50}$. In livestock improvement, the breeder may be interested in using a mating rule that maximizes selection efficiency for a smaller value of t. Fig. 5 depicts the change in $Corr(T, \hat{T})$ with generations of continued assortative mating for rule H and two other rules, J and K, that maximize $Corr(T, \hat{T})_5$ and $Corr(T, \hat{T})_2$, respectively. With rules H, J and K the values of $Corr(T, \hat{T})_2$ were, after round-off 0.487, 0.490 and 0.490, respectively. The values of $Corr(T, \hat{T})_5$ for H, J and K were 0.525, 0.535 and 0.526, respectively, and those of $Corr(T, \hat{T})_{50}$ were 0.573, 0.569 and 0.563, respectively. In view of the small differences between these correlations, it appears, at least in the case examined here, that long-term mating rules are also quasi-optimal in the short term.

Case 2

This example illustrates that index assortative mating can alter the sign of a genetic correlation. The random mating genetic parameters used were $h_X^2 = h_Y^2 = 0.60$, and $r_{XY} = -0.20$; the relative economic values of traits X and Y were $a_X = a_Y = 1$. With these values, $Corr(T, \hat{T})_0 = 0.74$. Assuming a correlation between individuals in a mating pair (ϱ) of 0.80, five different mating rules were studied. These represented positive assortative mating (rule A), negative assortative mating (rule B), "mixed" positive assortative mating (rule C), "mixed" negative assortative mating (rule D) and the optimum rule (E). Because the two traits have the same heritability and economic value, positive and negative assortative mating for only one of the two traits needed to be considered. For the same reasons, the Smith-Hazel index and the optimum rule for mating were identical. Further, in this example, maximization of $Corr(T, \hat{T})_t$ yielded the same rule irrespective of the value of t.
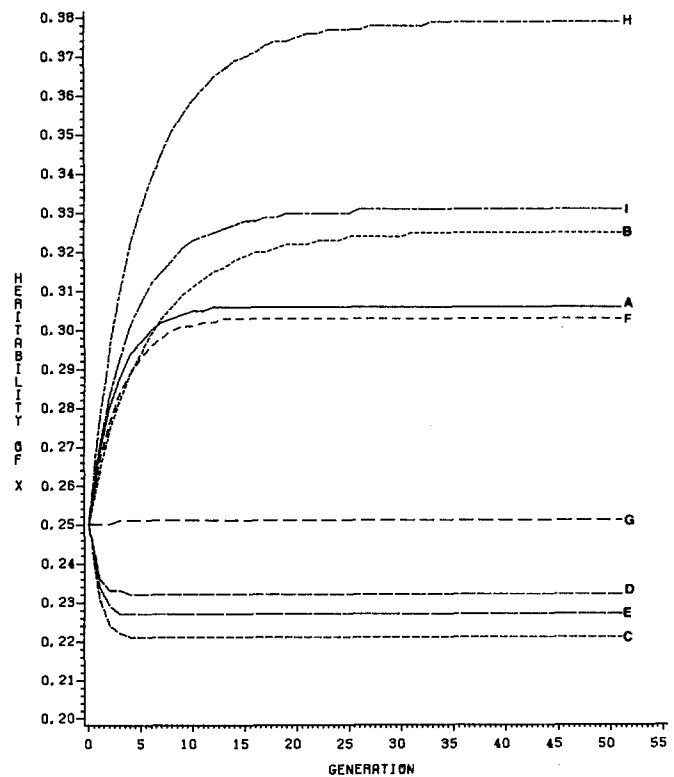

Fig. 1. Change in heritability of trait X under continued assortative mating with mating rules A through I (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.25$, $h_Y^2 = 0.5$ and $r_{XY} = -0.60$; relative economic values were $a_X = 3$ and $a_Y = 1$
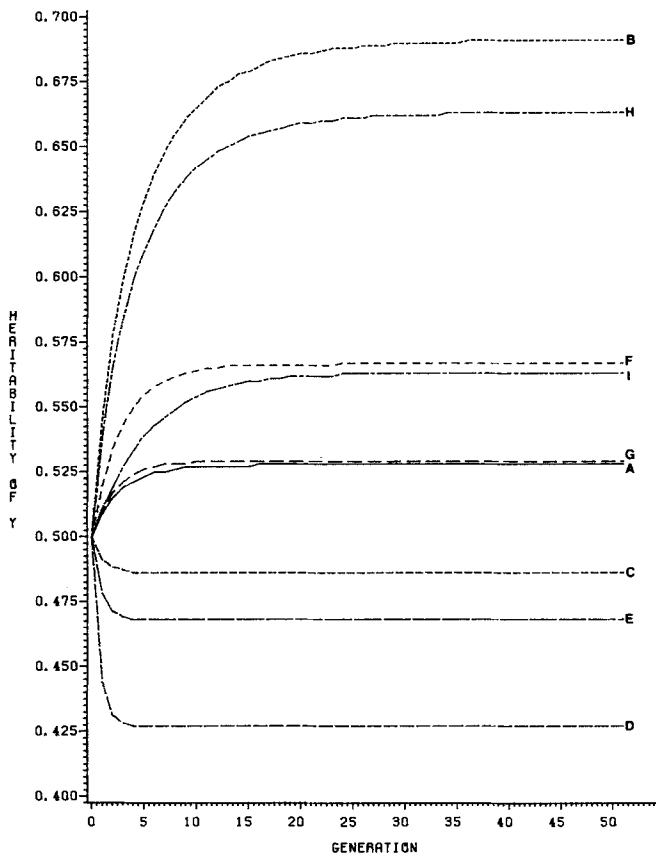
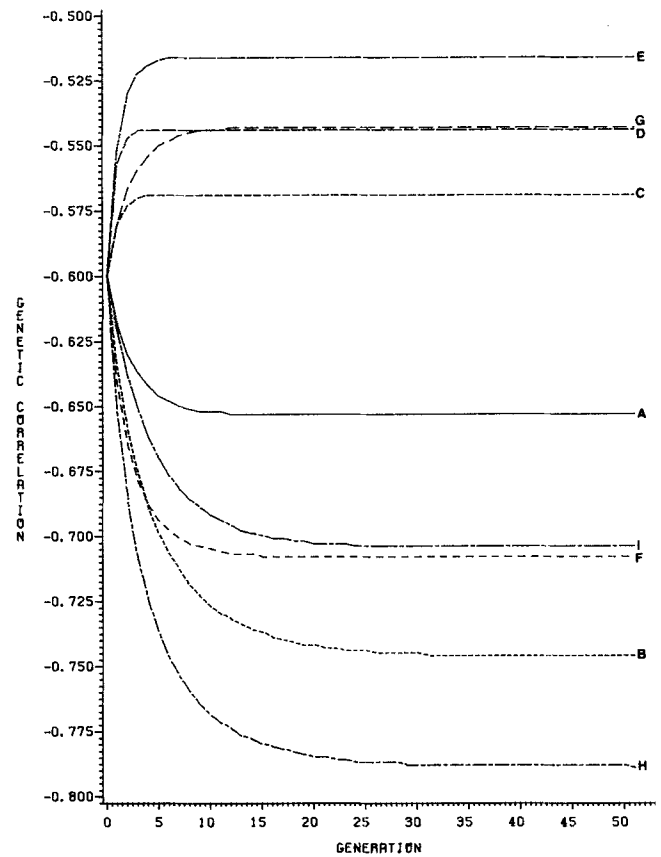**Fig. 2.** Change in heritability of trait Y under continued assortative mating with mating rules A through I (see text); $\varrho = 0.80$. Random mating genetic parameters where $h_X^2 = 0.25$, $h_Y^2 = 0.50$ and $r_{XY} = -0.60$; relative economic values were $a_X = 3$ and $a_Y = 1$

Fig. 3. Change in the genetic correlation between traits X and Y under continued assortative mating with mating rules A through I (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.25$, $h_Y^2 = 0.5$ and $r_{XY} = -0.60$; relative economic values were $a_X = 3$ and $a_Y = 1$

Table 2. Equilibrium values of genetic parameters for traits X and Y, relative selection efficiency and number of generations to equilibrium for five assortative mating rules [a, b]

	Coefficients of mating rule				Equilibrium values				
	c_X^M	c_Y^M	c_X^F	c_Y^F	$\hat{h}_X^2$	$\hat{h}_Y^2$	$\hat{r}_{XY}$	$\hat{C}orr\,(T, \hat{T})$	Generations to equilibrium
A:	1	0	1	0	0.808	0.617	−0.324	0.834	33
B:	1	0	−1	0	0.516	0.597	−0.170	0.720	3
C:	1	0	0	1	0.605	0.605	−0.045	0.785	12
D:	1	0	0	−1	0.662	0.662	−0.464	0.716	10
E:	1	1	1	1	0.705	0.705	0.248	0.866	36

[a] Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$, $\hat{r}_{XY} = -0.20$; relative economic values were $a_X = a_Y = 1$; Corr $(T, \hat{T}) = 0.739$

[b] The correlation between I^M and I^F values of individuals in a mating pair was assumed to be $\varrho = 0.80$

Equilibrium values of genetic parameters and of the relative efficiency of selection and the number of generations to equilibrium are given in Table 2. As in case 1, positive assortative mating (rule A) increased $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{C}orr\,(T, \hat{T})$, and decreased the genetic cor-

relation; 33 generations were required to reach equilibrium. Negative assortative mating (rule B) gave equilibrium results similar to those of case 1: $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{C}orr\,(T, \hat{T})$ decreased, and $\hat{r}_{XY}$ increased; equilibrium was reached in 3 generations. The effects of "mixed"
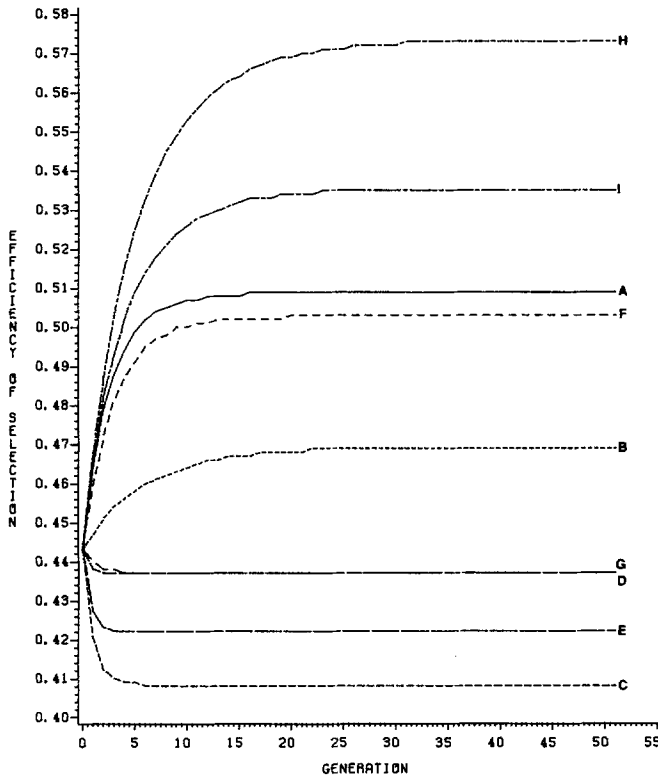
Fig. 4. Change in selection efficiency under continued assortative mating with mating rules A through I (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.25$, $h_Y^2 = 0.5$ and $r_{XY} = -0.60$; relative economic values were $a_X = 3$ and $a_Y = 1$
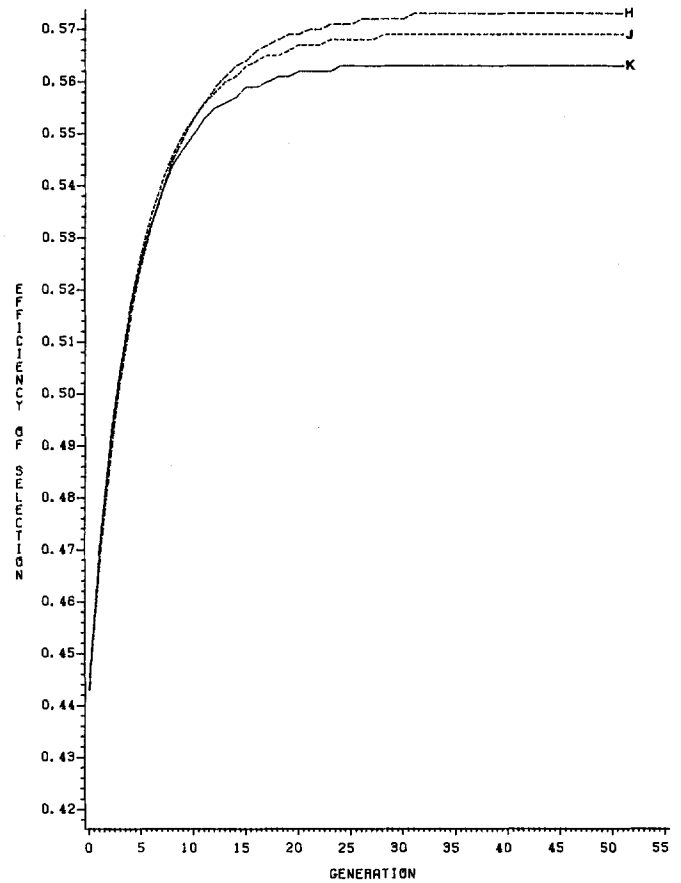

Fig. 5. Change in selection efficiency under continued assortative mating with mating rules H, J and K (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.25$, $h_Y^2 = 0.5$ and $r_{XY} = -0.60$; relative economic values were $a_X = 3$ and $a_Y = 1$

positive assortative mating (rule C) on $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{r}_{XY}$ were different from those of "mixed" positive assortative mating in case 1, and also from those of negative assortative mating in both cases (case 1: rules C and D; case 2: rule B). In case 1, "mixed" positive assortative mating and negative assortative mating led to similar equilibrium values; an explanation for this was given. The main difference was that in case 2 "mixed" positive assortative mating (rule C) changed the sign of the genetic correlation. Table 3 gives the values of h_X^2, h_Y^2, r_{XY} and Corr $(T, \hat{T})$ for generations 0 through 5 under rule C. The genetic correlation, although increasing, remained negative through generation 2, and h_X^2 and h_Y^2 decreased. These trends were similar to those observed with case 1 (rules C, D and E), and case 2 (rule B). However, at generation 3 r_{XY} became positive, and h_X^2 and h_Y^2 started to increase. At this point, because $r_{XY} > 0$, a positive correlation between X and Y phenotypic values in members of a mating pair causes a positive correlation between values of the same trait. Thus, "mixed" positive assortative mating started to have effects similar to those of positive assortative mating. Table 3 also depicts that Corr $(T, \hat{T})$ continued increasing throughout in spite of the fact

Table 3. Values of genetic parameters of traits X and Y and of the efficiency of selection for generations 0 through 5 under "mixed" positive assortative mating (Case 2, rule C)[a]

Generation	Values of genetic parameters			
	h_X^2	h_Y^2	r_{XY}	Corr $(T, \hat{T})$
0	0.600	0.600	−0.200	0.739
1	0.588	0.588	−0.079	0.754
2	0.590	0.590	−0.026	0.764
3	0.593	0.593	0.001	0.770
4	0.597	0.597	0.016	0.775
5	0.599	0.599	0.026	0.778

[a] Random genetic parameters, economic values and ϱ as in Table 2

that h_X^2 and h_Y^2 decreased until reaching a minimum in generation 2. The reason for this is that with $T = A_X + A_Y$, the effect of an increased genetic correlation on Corr $(T, \hat{T})$ was overriding over those of decreased h_X^2 and h_Y^2.

"Mixed" negative assortative mating (rule D) had the same effects as positive assortative mating (rule A) on $\hat{h}_X^2$, $\hat{h}_Y^2$ and $\hat{r}_{XY}$, but the larger decrease in $\hat{r}_{XY}$ caused $\hat{Corr}(T, \hat{T})$ to decrease. The optimum rule (E) was to assortatively mate on the sum of the phenotypic values for the two traits. This produced the largest increase in $\hat{Corr}(T, \hat{T})$, an increase of 17% over random mating. Assortative mating on the optimum rule had the largest effect on the genetic correlation. After 36 generations of continued assortative mating on the optimum selection rule, r_{XY} changed from $- 0.20$ to 0.248.

Figures 6 through 9 depict the change in h_X^2, h_Y^2, r_{XY} and $Corr(T, \hat{T})$ with generations of continued assortative mating for each of the 5 rules in case 2. Again, a large proportion of the change in genetic
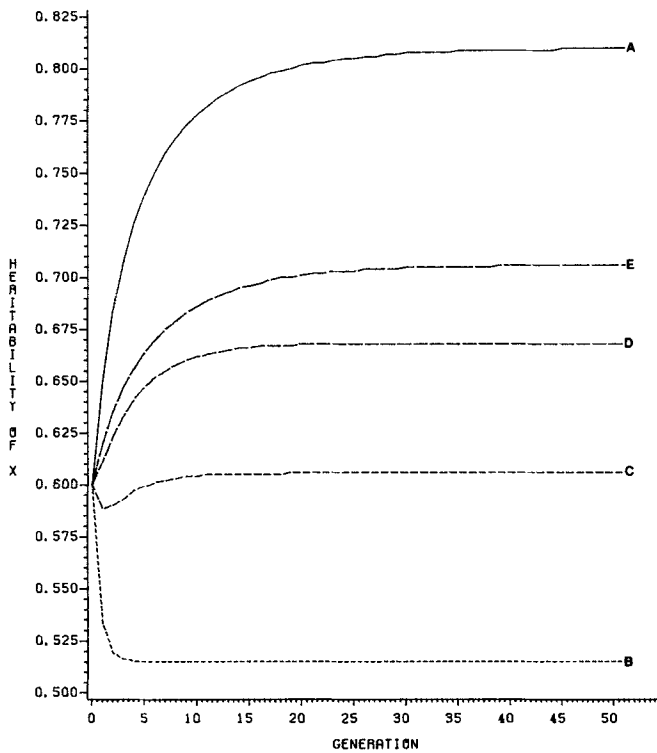

Fig. 6. Change in heritability of trait X under continued assortative mating with mating rules A through E (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = - 0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$
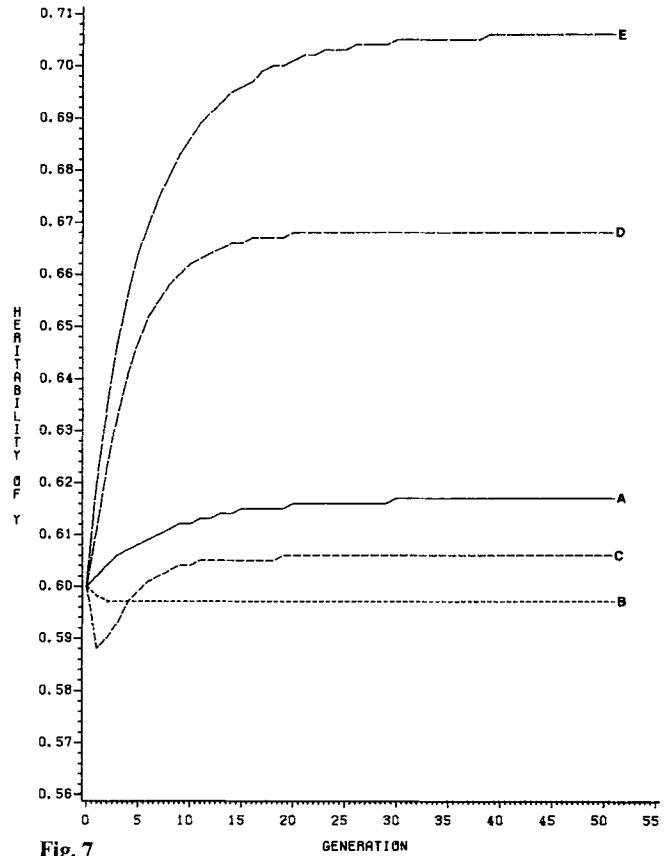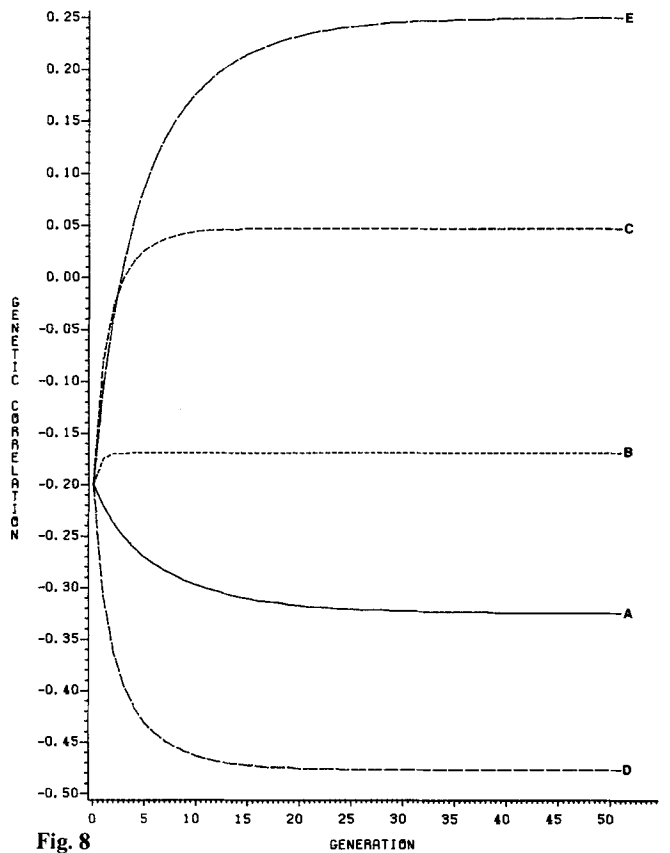
Fig. 7. Change in the heritability of trait Y under continued assortative mating with mating rules A through E (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = - 0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Fig. 8. Change in the genetic correlation between traits X and Y under continued assortative mating with mating rules A through E (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = - 0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Fig. 7

Fig. 8

parameters took place within the first 10 generations. With rules C and E the genetic correlation changed sign in generations 3 and 2, respectively. Although Corr (T, T̂) decreased under rule D compared with random mating, it increased somewhat after generation 6 towards an equilibrium value. This is explained by the antagonistic effects on Corr (T, T̂) of h_X^2 and h_Y^2 increasing and r_{XY} decreasing.

The effects on genetic parameters of increasing the correlation between mates to $\varrho = 0.95$ were examined

under the assumptions of case 2. Results are given in Table 4 and in Figs. 10–13. Changes in value of the genetic parameters were in the same direction as with $\varrho = 0.8$, but larger in magnitude except for rule B. With rule E the genetic correlation changed from − 0.20 to 0.586 in 77 generations; 3 generations were required for the genetic correlation to change sign.
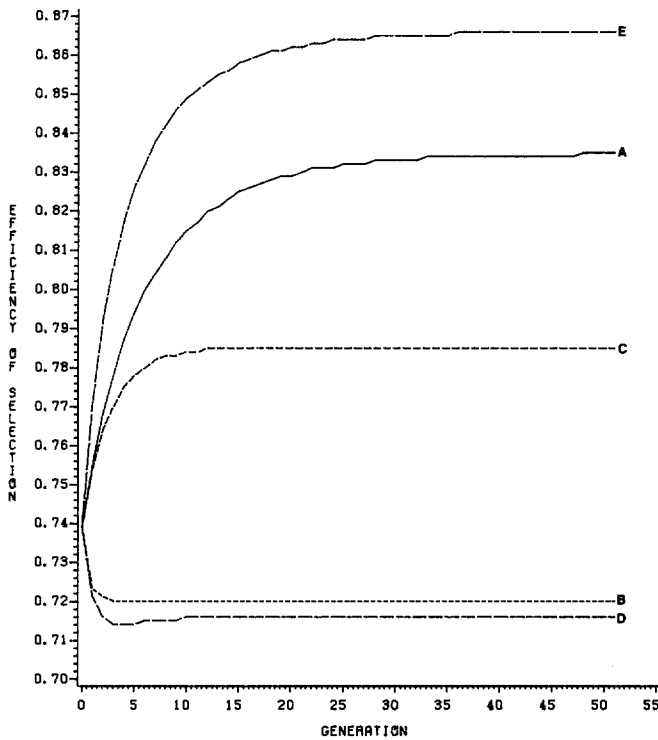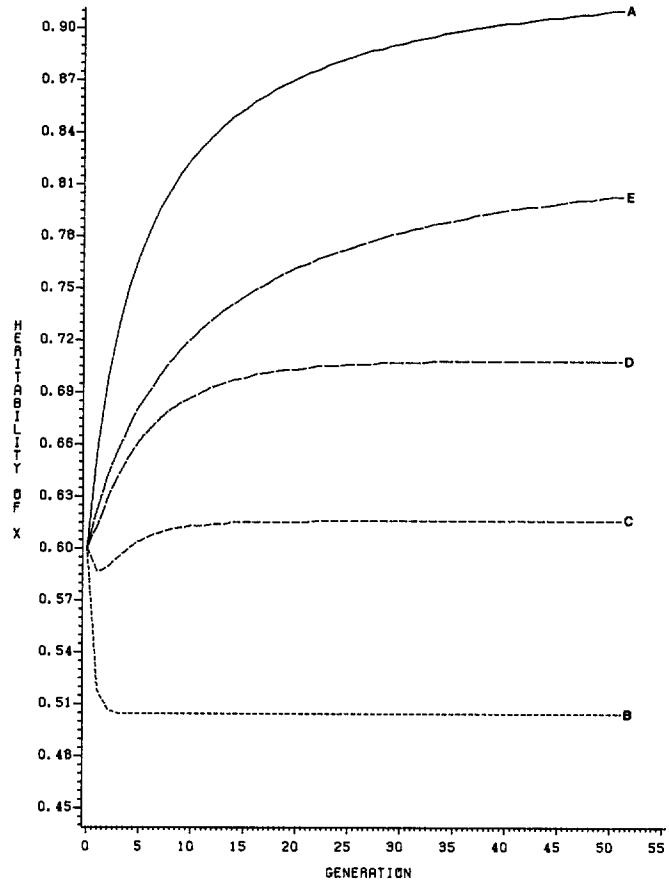

Fig. 9. Change in selection efficiency under continued assortative mating with mating rules A through E (see text); $\varrho = 0.80$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = -0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Fig. 10. Change in heritability of trait X under continued assortative mating with mating rules A through E (see text); $\varrho = 0.95$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = -0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Table 4. Equilibrium values of genetic parameters for traits X and Y, relative selection efficiency and number of generations to equilibrium for five assortative mating rules [a, b]

	Coefficients of mating rule				Equilibrium values				
	c_X^M	c_Y^M	c_X^F	c_Y^F	$\hat{h}_X^2$	$\hat{h}_Y^2$	$\hat{r}_{XY}$	$\hat{C}orr$ (T, T̂)	Generations to equilibrium
A:	1	0	0	1	0.922	0.657	−0.497	0.922	97
B:	1	0	−1	0	0.504	0.597	−0.166	0.718	3
C:	1	0	0	1	0.615	0.615	0.108	0.800	19
D:	1	0	0	−1	0.700	0.700	−0.552	0.715	16
E:	1	1	1	1	0.813	0.813	0.586	0.935	77

[a] Parameters as in Table 2

[b] The correlation between I^M and I^F values of individuals in a mating pair was $\varrho = 0.95$
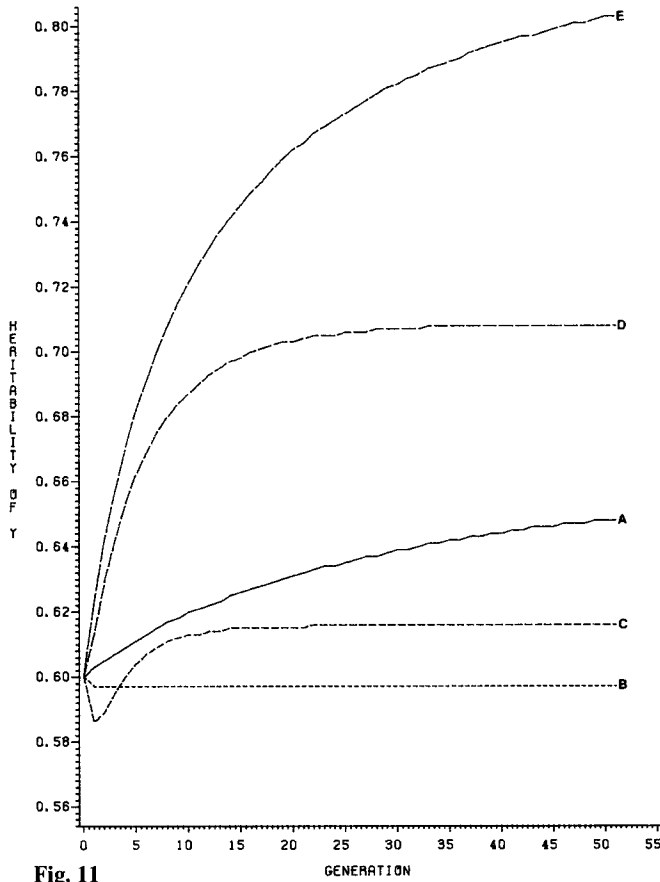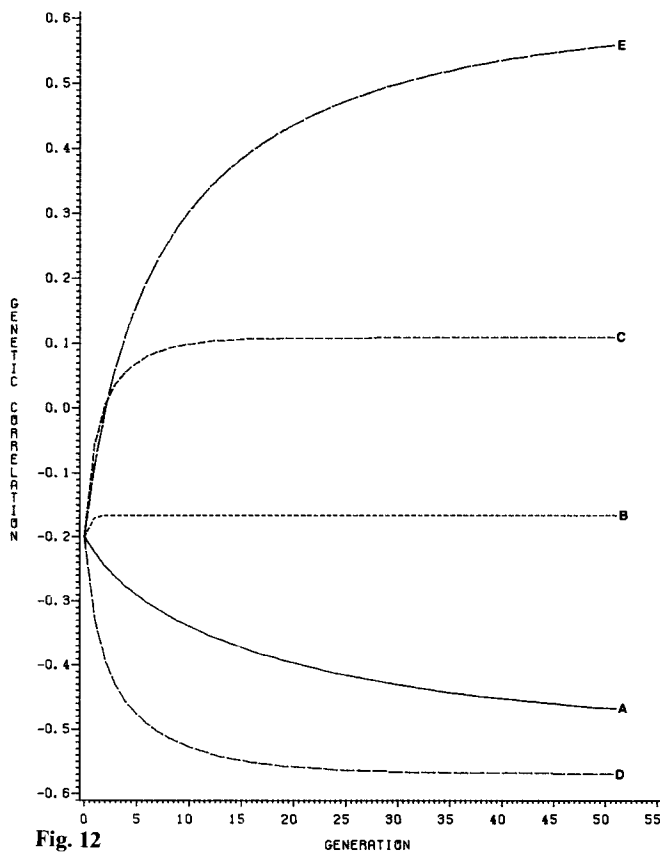
Fig. 11

Fig. 12

Conclusions

As demonstrated by the numerical examples considered in this study, the genetic variance-covariance structure of a population not undergoing selection can be modified by assortative mating. In particular, "mixed" assortative mating and assortative mating based on linear combinations of traits can change the sign of a genetic correlation, e.g., rendering a genetic relationship from unfavorable to favorable, or vice versa. Assortative mating can also be used to increase selection efficiency. The mating rule that maximizes efficiency of selection can be calculated by numerical techniques.
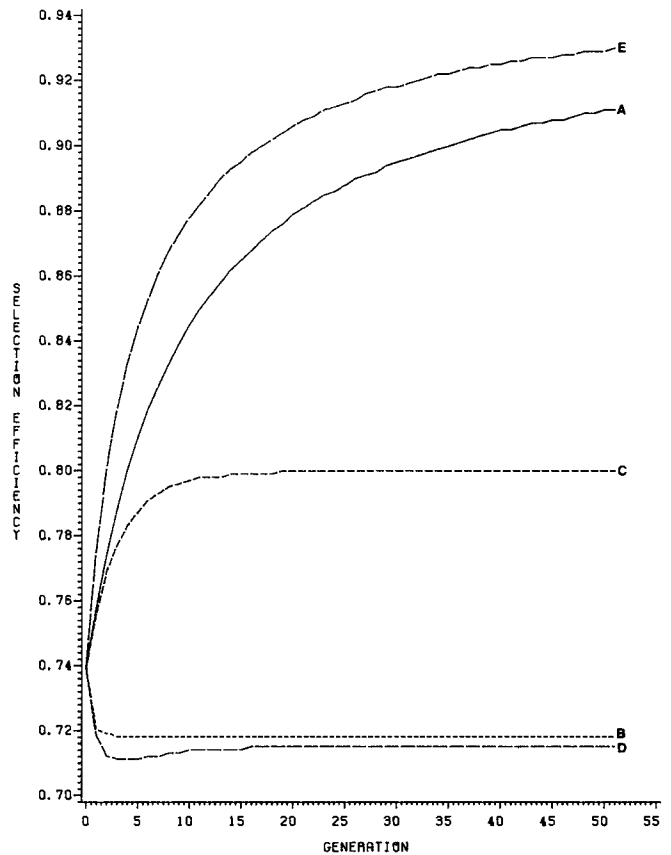

Fig. 13. Change in selection efficiency under continued assortative mating with rules A through E (see text); $\varrho = 0.95$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = -0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Fig. 11. Change in heritability of trait Y under continued assortative mating with mating rules A through E (see text); $\varrho = 0.95$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = -0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Fig. 12. Change in the genetic correlation between traits X and Y under continued assortative mating with rules A through E (see text); $\varrho = 0.95$. Random mating genetic parameters were $h_X^2 = 0.60$, $h_Y^2 = 0.60$ and $r_{XY} = -0.20$; relative economic values were $a_X = 1$ and $a_Y = 1$

Results obtained here may not hold if assortative mating and selection are simultaneous. Baker (1973) studied a single-generation situation and found that if selection intensity was low and heritability high, assortative mating could increase response to selection but not more than 10%. DeLange (1974), in a simulation study, concluded that assortative mating may improve response to selection if heritability is high, the number of loci controlling the trait large and selection intensity low. Work of McBride and Robertson (1963) with *Drosophila melanogaster* was in agreement with DeLange's (1974) findings. More experimental and theoretical work is needed to understand the implications of selection for single and multiple traits in natural or domesticated populations undergoing assortative mating.

Appendix

Bulmer (1980) studied assortative mating under the assumption that the phenotypic values of individuals in a mating pair followed a bivariate normal distribution. This may be a reasonable model to represent the distribution of phenotypic values of mating pairs in natural populations. A further assumption made by Bulmer (1980) was that the covariance between genotypic values of individuals in mating pairs was entirely due to the covariance between their phenotypic values, and that I^M and I^F were uncorrelated to ε^M and ε^F in (5). The validity of this assumption is shown in this Appendix.

In experimental work, assortative mating is practiced by mating males and females according to their ranked phenotypic values. Suppose the unordered phenotypic values of males and females are normally distributed. Once the pairs are ordered, neither the joint nor the marginal distributions of phenotypic values can be considered normal. We now show that I^M and I^F remain uncorrelated to ε^M and ε^F in ordered pairs. Thus, from (5), the covariance between the genotypic values of individuals in mating pairs is entirely due to their phenotypic covariance. Let $\mathbf{m}$ ($\mathbf{f}$) be the vector of I^M (I^F) values, and $\boldsymbol{\varepsilon}_m$ ($\boldsymbol{\varepsilon}_f$) be the vector of ε^M (ε^F) values. In the case of a polygenic trait, before ordering (Bulmer 1980)

$$\mathbf{u} = \begin{bmatrix} \mathbf{m} \\ \mathbf{f} \\ \boldsymbol{\varepsilon}_m \\ \boldsymbol{\varepsilon}_f \end{bmatrix} \sim N \left(\begin{bmatrix} \mu_m \\ \mu_f \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \mathbf{I}\sigma^2 & 0 & 0 & 0 \\ 0 & \mathbf{I}\sigma^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_\varepsilon^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_\varepsilon^2 \end{bmatrix} \right). \quad (A1)$$

The ordering process can be described by

$$\hat{\mathbf{m}} = \mathbf{P}(\mathbf{m})\,\mathbf{m}, \qquad \hat{\mathbf{f}} = \mathbf{P}(\mathbf{f})\,\mathbf{f}, \quad (A2)$$

and

$$\hat{\boldsymbol{\varepsilon}}_M = \mathbf{P}(\mathbf{m})\,\boldsymbol{\varepsilon}_M, \qquad \hat{\boldsymbol{\varepsilon}}_f = \mathbf{P}(\mathbf{f})\,\boldsymbol{\varepsilon}_f, \quad (A3)$$

where $\mathbf{P}(\mathbf{m})$ and $\mathbf{P}(\mathbf{f})$ are random permutation matrices that rank the elements of $\mathbf{m}$ and $\mathbf{f}$, respectively.

Let $\mathbf{u}_1' = [\mathbf{m}', \mathbf{f}']$ and $\mathbf{u}_2' = [\boldsymbol{\varepsilon}_m', \boldsymbol{\varepsilon}_f']$. Now given $\mathbf{u}_1$, $\mathbf{P}(\mathbf{m})$ and $\mathbf{P}(\mathbf{f})$ are not random and

$$E(\hat{\boldsymbol{\varepsilon}}_M \mid \mathbf{u}_1) = \mathbf{P}(\mathbf{m})\, E(\boldsymbol{\varepsilon}_m) = 0, \quad (A4)$$

$$E(\hat{\boldsymbol{\varepsilon}}_f \mid \mathbf{u}_1) = \mathbf{P}(\mathbf{f})\, E(\boldsymbol{\varepsilon}_f) = 0, \quad (A5)$$

$$\text{Var}(\hat{\boldsymbol{\varepsilon}}_m \mid \mathbf{u}_1) = \mathbf{P}(\mathbf{m})\, \mathbf{P}'(\mathbf{m})\, \sigma_\varepsilon^2 = \mathbf{I}\,\sigma_\varepsilon^2, \quad (A6)$$

$$\text{Var}(\hat{\boldsymbol{\varepsilon}}_f \mid \mathbf{u}_1) = \mathbf{P}(\mathbf{f})\, \mathbf{P}'(\mathbf{f})\, \sigma_\varepsilon^2 = \mathbf{I}\,\sigma_\varepsilon^2, \quad (A7)$$

and

$$\text{Cov}(\hat{\boldsymbol{\varepsilon}}_m, \hat{\boldsymbol{\varepsilon}}_f \mid \mathbf{u}_1) = 0 \quad (A8)$$

with (A6) and (A7) following from the orthogonality of permutation matrices (Hohn 1973). It therefore follows that the conditional distribution of $\mathbf{u}_2$ given $\mathbf{u}_1$ is normal with parameters given in (A4) through (A8) above (Bickel and Doksum 1977). Since the distribution of $(\mathbf{u}_2 \mid \mathbf{u}_1)$ does not depend on $\mathbf{u}_1$, it follows that $\mathbf{u}_2$ is independent of $\mathbf{u}_1$. Further, because $\hat{\mathbf{m}}$ and $\hat{\mathbf{f}}$ are a function of $\mathbf{u}_1$, $\mathbf{u}_2$ is independent of $\hat{\mathbf{m}}$ and $\hat{\mathbf{f}}$.

References

Baker RJ (1973) Assortative mating and artificial selection. Heredity 31:231–238

Bickel PJ, Doksum KJ (1977) Mathematical statistics: basic ideas and selected topics. Holden-Day, San Francisco

Bulmer MG (1980) The mathematical theory of quantitative genetics. Clarendon Press, Oxford

Cochran WG (1951) Improvement by means of selection. In: Proc 2nd Berkeley Symp Math Stat Prob, pp 449–470

Crow JF, Felsenstein J (1968) The effect of assortative mating on the genetic composition of a population. Eugen Q 15: 85–97

Crow JF, Kimura M (1970) An introduction to population genetics theory. Harper and Row, New York

DeLange AD (1974) A simulation study of the effects of assortative mating on the response to selection. In: 1st World Congr Genet App Livestock Prod, vol 3. Garsi, Madrid, pp 421–425

Fisher RA (1918) The correlation between relatives on the supposition of Mendelian inheritance. Trans R Soc, Edinburgh 52:339–433

Gianola D (1982) Assortative mating and the genetic correlation. Theor Appl Genet 62:225–231

Hazel LN (1943) The genetic basis for constructing selection indexes. Genetics 28:476–490

Henderson CR (1963) Selection index and expected genetic advance. In: Hanson WD, Robinson HF (eds) Statistical genetics and plant breeding. NAS-NRC 982, Washington DC, pp 141–163

Hohn FE (1973) Elementary matrix algebra Macmillan, New York

Jennings, HS (1916) Numerical results of diverse systems of breeding. Genetics 1:53–89

Lasdon LS, Waren AD, Ratner MW, Jain A (1975) GRG user's guide. Technical Memorandum CIS-75-02, Dept of Operations Research, School of Management, Case Western Reserve University, Cleveland, Ohio

Latter BDH (1965) Quantitative genetic analysis in *Phalaris tuberosa*. 1. The statistical theory of open pollinated progenies. Genet Res 6:360–370

McBride G, Robertson A (1963) Selection using assortative mating in *D. melanogaster*. Genet Res 4:356–369

Smith HF (1936) A discriminant function for plant selection. Ann Eugen 7:240–250

Wentworth EN, Remick BL (1916) Some breeding properties of the generalized Mendelian population. Genetics 1:608–618

Wright S (1921) Systems of mating. Genetics 6:111–178