ASSORTATIVE MATING BASED ON PHENOTYPE: II.
TWO AUTOSOMAL ALLELES WITHOUT DOMINANCE

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IN the preceding paper (SCUDO and KARLIN 1969), several one-locus models for assortment based on the phenotypes with complete dominance were analyzed. Complete dominance is common for assortment on traits like color and pattern. Some cases are known, however, where some mating choice is based on chromatic traits determined by a single locus with other forms of interaction (SHEPPARD 1952). Assortment is also known to occur for other morphological and behavioral traits. The genetics of such traits is, however, not well developed up to the present time.

This paper will be mainly concerned with assortment based on a pair of alleles where the heterozygote can be distinguished from both homozygotes. As in the first paper, we delimit a model by specifying the effects of a tendency to assort on the individual reproductive behavior and the fertility. We further restrict our consideration to the case in which the preference is manifested only in one sex. In most cases it does not matter which sex assorts but, for definiteness (reflecting the most common case in nature), the female is stipulated to be the assorting sex.

Paralleling the development of the preceding paper, we shall be mainly interested in the direct evolutionary effects of assortment; the production of gene substitutions or the maintenance of partial genetic isolation between two populations. In contrast to the case of dominance, assortment for autosomal traits without dominance can also produce stable polymorphisms.

Formulation of the Models

We consider first a particular case in which the heterozygote behaves differently from both homozygotes. To account for assortment in a general formulation would involve six parameters. Corresponding to each genotype it would be necessary to prescribe the fractions of individuals who refuse to mate with the other two genotypes.

Instead of examining the model in its most general form we assume that individuals assort only on the basis of the genotype being different. In other words, assorting individuals would just prefer a partner of their own genotype. The propensity for assortment for the three genotypes, AA, AA' and A'A' is described by the parameters α, β and γ, respectively: That is, a fraction α of the females of genotype AA "tend to" mate with their own kind while the complementary

fraction mates at random. Similarly for β and γ. The frequencies of the genotypes in the nth generation will be denoted by X_n, Y_n and Z_n, respectively, and generally by X, Y, and Z.

As in the preceding paper, our models attempt to take into account factors like the availability of proper mates, the timing of mating, the relative contributions of the assorting and nonassorting individuals to the next generation, the chance of encounter, and the ability of males to fertilize different numbers of females.

The first two models apply to animals forming permanent bonds whose populations have an effective 1:1 sex ratio. If assorting occurs first and later all remaining females (with frequencies $(1-\alpha)X$, $(1-\beta)Y$ and $(1-\gamma)Z$ of the AA, AA′ and A′A′ kinds, respectively) pair at random, we obtain the frequencies of mating types and recursion relations as given in Table 1. Analogously to the case of dominance, two contrasting assumptions can be made concerning the relative fertilities of the assorting and the random-mating females. The first, (Case 1), introduced earlier by O'DONALD (1960), assumes that there is no impairment of fertility in assorting *versus* random-mating individuals. For the second, we assume that the delay in mating reduces the average relative fertility of the random mating females to $R^* = 1 - \alpha X - \beta Y - \gamma Z$ (Case 2).

An alternative model to account for the effects of the timing postulates that females practicing random mating pair earlier than the assorting females. Consequently, the following fractions of male and female individuals are available for assortative pair bonding:

genotypes	available males	assorting females
AA	$X(\alpha X + \beta Y + \gamma Z)$	αX
AA′	$Y(\alpha X + \beta Y + \gamma Z)$	βY
A′A′	$Z(\alpha X + \beta Y + \gamma Z)$	γZ

TABLE 1

Population array and recursion formulae in the case of permanent pairs and 1:1 sex ratio. Assorting occurs prior to random mating

Mating types	Assorting	Frequencies Random mating
AA × AA	αX	$[(1-\alpha)X]^2/R$
AA × AA′		$2(1-\alpha)X \cdot (1-\beta)Y/R$
AA × A′A′		$2(1-\alpha)X \cdot (1-\gamma)Z/R$
AA′ × AA′	βY	$((1-\beta)Y)^2/R$
AA′ × A′A′		$2(1-\beta)Y \cdot (1-\gamma)Z/R$
A′A′ × A′A′	γZ	$[(1-\gamma)Z]^2/R$

Recursion relations connecting genotype frequencies in successive generations.

$$NX' = \alpha X + \tfrac{1}{4}\beta Y + [(1-\alpha)X + \tfrac{1}{2}(1-\beta)Y]^2/R \qquad (1.1)$$

$$NY' = \tfrac{1}{2}\beta Y + 2[(1-\alpha)X + \tfrac{1}{2}(1-\beta)Y][(1-\gamma)Z + \tfrac{1}{2}(1-\beta)Y]/R \qquad (1.2)$$

$$NZ' = \gamma Z + \tfrac{1}{4}\beta Y + [(1-\gamma)Z + \tfrac{1}{2}(1-\beta)Y]^2/R \qquad (1.3)$$

where

Case 1: no difference in fertility
$$R = R^*; \ N = 1 \qquad (R^* = 1 - \alpha X - \beta Y - \gamma Z).$$

Case 2: the average fertility of random mating females reduces to R^*.
$$R = 1; \ N = 1 - R^*(1 - R^*); \quad (R^* = 1 - \alpha X - \beta Y - \gamma Z)$$

TABLE 2

As in Table 1 but assortment occurs after random mating
For simplicity the symmetrical case $\alpha = \gamma$ is considered. When $\alpha = \gamma > \beta$, and proper partners are available only to the fraction $f = \alpha(1-Y) + \beta Y$ of the assorting AA and A'A' females. The remaining ones do not contribute to the following generation.

| | | Frequencies | |
Mating type	Random mating		Assorting
AA × AA	$(1-\alpha) X^2$		fX
AA × AA'	$(2-\alpha-\beta) XY$		
AA × A'A'	$(1-\alpha) 2XY$		
AA' × AA'	$(1-\beta) Y^2$		βY
AA' × A'A'	$(2-\alpha-\beta) ZY$		
A'A' × A'A'	$(1-\alpha) Z^2$		fZ

$N = 1 - (\alpha-\beta)Y(1-Y)$
$f = \alpha(1-Y) + \beta Y$

$$NX' = Xf + \frac{Y}{4}\beta + (1-\alpha) X\left(X+\frac{Y}{2}\right) + (1-\beta)\frac{Y}{2}\left(X+\frac{Y}{2}\right) \tag{2.1}$$

$$NY' = \frac{Y}{2}\beta + (1-\alpha)\left[\frac{Y(1-Y)}{2} + 2XZ\right] + (1-\beta)\frac{Y}{2} \tag{2.2}$$

$$NZ' = Zf + \frac{Y}{4}\beta + (1-\alpha) Z\left(Z+\frac{Y}{2}\right) + (1-\beta)\frac{Y}{2}\left(Z+\frac{Y}{2}\right) \tag{2.3}$$

Assorting continues until all possible pairs of phenotypically alike individuals are formed while those remaining do not contribute to the next generation. All the AA assorting females will be fertilized if and only if $\alpha X \leq X(\alpha X+\beta Y+\gamma Z)$ or equivalently $\alpha \leq (\beta Y+\gamma Z)/(Y+Z)$; corresponding relations apply for the other two genotypes.

We shall confine attention to the simpler symmetrical case in which $\alpha = \gamma$. We find that if $\alpha = \gamma > \beta$ all AA' assorting females can pair while proper male partners will be available only to a fraction $f = \alpha(1-Y) + \beta Y$ of the assorting AA and A'A' females. The remaining $(\alpha-\beta) Y(1-Y)$ females will not contribute to the next generation. Verification of the entries of Table 2 should now be clear.

In the case $\alpha = \gamma < \beta$ analogous rationale and justifications lead to the quantities and recursion relations connecting genotype frequencies displayed in Table 3.

Table 4 gives the relevant formulae for the "mass action" case, which accounts for the "opportunity of encounter" in a scattered population. The chance of a given type of mating is assumed to be proportional to the product of the densities of the two kinds of individuals which can perform the mating. In this model, as in the next one, no effect of assortment on the timing of mating has been explicitly considered.

Finally we may account for some excess of males by the "asymmetric model" (Table 5), which assumes that the tendency to assort does not appreciably reduce the average fertility of females. The limitations implicit in this model have been discussed in the previous paper.

TABLE 3

As in Table 2, but for $\alpha = \gamma < \beta$

In this case $f = \alpha(1-Y) + \beta Y$ is the fraction of heterozygous assorting females for which a proper partner is available

	Frequencies	
Mating type	Random mating	Assorting
AA × AA	$(1-\alpha)\,X^2$	αX
AA × AA′	$(1-\alpha)XY + (1-\beta)\,XY$	
AA × A′A′	$(1-\alpha)\,2XZ$	
AA′ × AA′	$(1-\beta)\,Y^2$	fY
AA′ × A′A′	$(1-\alpha)\,ZY + (1-\beta)\,ZY$	
A′A′ × A′A′	$(1-\alpha)\,Z^2$	αZ

$N = 1 - (\beta-\alpha)\,Y(1-Y)$ where $f = \alpha(1-Y) + \beta Y$

$$NX' = \alpha X + f\frac{Y}{4} + (1-\alpha)\,X\left(X+\frac{Y}{2}\right) + (1-\beta)\frac{Y}{2}\left(X+\frac{Y}{2}\right) \tag{3.1}$$

$$NY' = \qquad f\frac{Y}{2} + (1-\alpha)\left[\frac{Y}{2}(1-Y)+2XZ\right] + (1-\beta)\frac{Y}{2} \tag{3.2}$$

$$NZ' = \alpha Z + f\frac{Y}{4} + (1-\alpha)\,Z\left(Z+\frac{Y}{2}\right) + (1-\beta)\frac{Y}{2}\left(Y+\frac{Z}{2}\right) \tag{3.3}$$

TABLE 4

Recursion formulae for the mass action model

$N = 1 - \alpha X(1-X) - \beta Y(1-Y) - \gamma Z(1-Z)$

$$NX' = \alpha X^2 + \beta\frac{Y^2}{4} + (1-\alpha)\,X\left(X+\frac{Y}{2}\right) + (1-\beta)\frac{Y}{2}\left(X+\frac{Y}{2}\right) \tag{4.1}$$

$$NY' = \qquad \beta\frac{Y^2}{2} + (1-\alpha)\,X\left(\frac{Y}{2}+Z\right) + (1-\beta)\frac{Y}{2} + (1-\gamma)\,Z\left(X+\frac{Y}{2}\right) \tag{4.2}$$

$$NZ' = \gamma Z^2 + \beta\frac{Y^2}{4} + (1-\gamma)\,Z\left(\frac{Y}{2}+Z\right) + (1-\beta)\frac{Y}{2}\left(Z+\frac{Y}{2}\right) \tag{4.3}$$

TABLE 5

Recursion formulas for the "asymmetric model"

$N = 1$

$$NX' = \alpha X + \beta\frac{Y}{4} + (1-\alpha)\,X\left(X+\frac{Y}{2}\right) + (1-\beta)\frac{Y}{2}\left(X+\frac{Y}{2}\right) \tag{5.1}$$

$$NY' = \qquad \beta\frac{Y}{2} + (1-\alpha)\,X\left(\frac{Y}{2}+Z\right) + (1-\beta)\frac{Y}{2} + (1-\gamma)\,Z\left(X+\frac{Y}{2}\right) \tag{5.2}$$

$$NZ' = \gamma Z + \beta\frac{Y}{4} + (1-\gamma)\,Z\left(\frac{Y}{2}+Z\right) + (1-\beta)\frac{Y}{2}\left(Z+\frac{Y}{2}\right) \tag{5.3}$$

RESULTS

I. *Model of Table 1:* In the first model, where no reduction in fertility occurs among the random-mating females (Case 1 in Table 1) it is easily verified that the gene frequency, $p_n = 1 - q_n = X_n + Y_n/2 = X_0 + Y_0/2 = p$ is invariant over time. Using this fact, the analysis of the system (1.1) to (1.3) reduces to the study of the single recursion relation

$$Y' = \frac{\beta}{2} Y + \frac{2\{(1-\alpha)p + \frac{\alpha-\beta}{2} Y\} \{(1-\gamma)q + \frac{\gamma-\beta}{2} Y\}}{1 - \alpha p - \gamma q + Y\left(\frac{\alpha+\gamma}{2} - \beta\right)} \equiv g(Y) \qquad (1.4)$$

Let $Y_n = g^{(n)}(Y)$ where $g^{(n)}(\cdot)$ is the nth iterate of $g(\cdot)$. It can be proved, that Y_n converges at a geometric rate to the unique root in $(0,1)$, $\hat{Y}$, of the quadratic equation $g(Y) - Y = 0$. Obviously $\hat{Y}$ generates a family of equilibria depending on the initial gene frequency, p_0.

When an appropriate reduction in fertility is assumed for the random-mating females (Case 2) gene frequencies are no longer invariant over time. At first we restrict our discussion to the special case $\alpha = \gamma$. Symmetry considerations suggest that the quantity $X - Z$ is the most convenient for analysis; its recursion relaiton is

$$X' - Z' = (X-Z) \frac{1 - (1-\alpha)(1-R^*)}{1 - R^*(1-R^*)} \text{ where } R^* = 1 - \alpha X - \beta Y - \gamma Z \quad (1.5)$$

It follows that the magnitude of these differences decreases when $\alpha < \beta$; and increases if $\alpha > \beta$.

It is easy to verify that the recursion relations connecting genotype frequencies admit a single polymorphic equilibrium

$$\hat{X} = \hat{Z} = \frac{1 - \hat{Y}}{2} \qquad (1.6)$$

where $\hat{Y}$ is the unique root in $(0,1)$ of the equation

$$(\alpha-\beta)^2 Y^3 + (\alpha-\beta)\left(1 - \frac{5}{2}\alpha + \frac{\beta}{2}\right) Y^2$$

$$+ \left\{1 - \alpha(1-\alpha) + \frac{\beta}{2} - (\alpha-\beta)(1-\alpha)\right\} Y - \frac{1}{2}(1-\alpha)^2 = 0 \qquad (1.7)$$

The global stability properties of the system (1.1)–(1.3) (Case 2), can be ascertained with the following results:

i) When $\alpha < \beta$ for any nontrivial initial values, X_0, Y_0 and Z_0, the genotype frequencies at the nth generation, X_n, Y_n and Z_n converge as $n \to \infty$ to the stable polymorphic equilibrium (1.6) at a geometric rate.

ii) When $\alpha > \beta$ for any nontrivial genotype frequencies satisfying $X_0 < Z_0$ convergence takes place to the pure A' state, i.e., $X_n \to 0$, $Y_n \to 0$ and $Z_n \to 1$ as

$n \to \infty$, at a geometric rate; when $X_0 > Z_0$ convergence occurs to the pure A state also at a geometric rate. Thus the boundary between the domains of attraction of the two trivial solutions is the straight line $X = Z$. Starting from a point on this line, $X_0 = Z_0$, convergence takes place to the unstable polymorphic equilibrium (1.6).

iii) When $\alpha = \beta = \gamma$, $Z_1 - X_1 = Z_0 - X_0 = C$ so that $Z_n - X_n$ is invariant over time; the associated family of equilibria is completely determined by α and C. The complete time-dependent behavior can be worked out in terms of a single recursion.

A complete analysis in the general case is not feasible; however the local stability structure of the trivial equilibria probably reflects an accurate qualitative picture of the global properties of the system (1.1)–(1.3), (Case 2). It turns out that the pure A state $(X = 1, Y = Z = 0)$ is stable if

$$\{1 - \alpha(1-\alpha)\}^2 - \{1 - \alpha(1-\alpha)\} \left\{\gamma + \frac{\beta}{2} + (1-\alpha)(1-\beta)\right\}$$

$$+ \frac{\beta\gamma}{2} + \gamma(1-\alpha)(1-\beta) - \frac{\beta}{2}(1-\alpha)(1-\gamma) > 0 \qquad (1.8)$$

When $\alpha = \gamma$ a little algebra reveals that this inequality is equivalent to $\alpha > \beta$, as it should be. Similarly, the pure A′ state will be locally stable if

$$\{1 - \gamma(1-\gamma)\}^2 - \{1 - \gamma(1-\gamma)\} \left\{\alpha + \frac{\beta}{2}(1-\gamma)(1-\beta)\right\}$$

$$+ \frac{\alpha\beta}{2} + \alpha(1-\gamma)(1-\beta) - \frac{\beta}{2}(1-\alpha)(1-\gamma) > 0 \qquad (1.9)$$

Thus the following stability situations can occur in the general case:

i) If both (1.8) and (1.9) are strictly satisfied an interior unstable polymorphism exists and either A or A′ will be fixed according to the initial frequencies.

ii) If the reverse of both inequalities (1.8) and (1.9) is strictly satisfied, then for any nontrivial initial frequencies convergence will take place to a stable polymorphic solution.

iii) If (1.8) is strictly satisfied and the opposite inequality of (1.9) holds, then no interior polymorphism exists and for any nontrivial initial set of frequencies convergence towards fixation of A will take place.

iv) If the opposite of (1.8) is strictly satisfied and (1.9) holds, then no interior equilibrium exists and only the pure A′ state is stable.

II. *Model of Tables 2 and 3:* Consider now the model for permanent bonding, when nonassorting females mate first. Two situations need to be distinguished according to whether the number of AA′ assorting females exceeds the desired number of available males or vice versa. In the latter case ($\alpha = \gamma < \beta$, Table 3), manipulation of the recursion relations yields

$$X' - Z' = (X - Z) \frac{1 - \dfrac{\beta - \alpha}{2} Y}{1 - (\beta - \alpha) Y(1 - Y)} \qquad (2.4)$$

which implies that $X - Z$ is strictly increasing in magnitude if and only if $Y < \frac{1}{2}$. But

$$Y' = \frac{\frac{Y}{2}\{\alpha + (\beta - \alpha)Y\} + (1 - \alpha)\{\frac{Y}{2}(1 - Y) + 2XZ\} + (1 - \beta)\frac{Y}{2}}{1 - (\beta - \alpha)Y(1 - Y)} \tag{2.5}$$

and therefore, since $4XZ \leq (1 - Y)^2$, we have

$$Y' \leq \frac{\frac{Y}{2}\{\alpha + (\beta - \alpha)Y\} + (1 - \alpha)\frac{1 - Y}{2} + (1 - \beta)\frac{Y}{2}}{1 - (\beta - \alpha)Y(1 - Y)} = f(Y)$$

for all Y in $(0,1)$. In this interval, $f(Y)$ is monotonically increasing. It follows that the frequency of heterozygotes after n generations, Y_n, satisfies

$$Y_n \leq f^{(n)}(Y_0)$$

From the general theory of iteration of functions it can be inferred that $f^{(n)}(Y)$ converges, as $n \to \infty$, to the unique solution $\hat{Y}$ in $(0,1)$ of the equation

$$(\beta - \alpha)Y^3 - \frac{3}{2}(\beta - \alpha)Y^2 + \left(1 - \alpha + \frac{\beta}{2}\right)Y - \frac{1 - \alpha}{2} = 0 \tag{2.6}$$

Direct examination of this equation verifies that $\hat{Y} < \frac{1}{2}$; therefore, for n sufficiently large we will have $Y_n < \frac{1}{2}$ which implies that ultimately $|X_n - Z_n|$ will be continually increasing.

Thus for $\alpha = \gamma < \beta$ fixations are the only stable equilibria and the domains of attraction of the trivial equilibria are separated by the straight line $X = Z$. More precisely,

   i)   If $X_0 > Z_0$ then $X_n \to 1$, $Y_n \to 0$ and $Z_n \to 0$ as $n \to \infty$;

         if $X_0 > Z_0$ then $X_n \to 0$, $Y_n \to 0$ and $Z_n \to 1$ as $n \to \infty$;

The approach of Y_n to 0 is geometrically fast at the rate $1 - \beta/2$; convergence of X_n and Z_n to their limits occurs at a faster rate.

   ii) If $X_0 = Z_0$ then $Y_n \to \hat{Y}$ and $X_n = Z_n \to (1 - \hat{Y})/2$ at the geometric rate $|f'(\hat{Y})|$.

In the case $\alpha = \gamma > \beta$ (Table 2) the analysis is analogous to that of the model associated with Table 3; the conclusions are as follows:

   i)   If $X_0 > Z_0$ then $X_n \to 1$, $Y_n \to 0$ and $Z_n \to 0$ as $n \to \infty$;

         if $X_0 > Z_0$ then $X_n \to 0$, $Y_n \to 0$ and $Z_n \to 1$ as $n \to \infty$;

convergence of Y_n being geometrically fast at the rate $1 - \alpha/2$.

   ii) If $X_0 = Z_0$ then $Y_n \to \hat{Y}^*$, $X_n = Z_n \to (1 - \hat{Y}^*)/2$ where $\hat{Y}^*$ is the unique solution in $(0,1)$ of the equation

$$(\alpha - \beta)Y^3 - (\alpha - \beta)Y^2 + \left(1 - \frac{\alpha}{2}\right)Y - \frac{1 - \alpha}{2} = 0$$

and it is again easy to verify that $\hat{Y}^* < 1/2$.

Thus, in contrast to the first model, the present model yields the same qualitative result as in the case of partial assortative mating for dominant traits: an unstable polymorphism exists independently of the relative magnitude of $\alpha = \gamma \neq \beta$. A local analysis for the stability of the nontrivial solutions in the general case $\alpha \neq \gamma$ leads to inequalities on the parameters which determine the existence of the unique unstable polymorphism.

For ease of exposition in the mass action model of Table 4, we restrict ourselves to the special case $\alpha = \gamma$. We find the unique interior equilibrium

$$\hat{Z} = \hat{X} = \frac{1-\hat{Y}}{2} \tag{4.4}$$

where $\hat{Y}$ can be computed as the unique solution in $(0,1)$ of the equation

$$(2\beta+\alpha)\,Y^3 - 3\beta Y^2 + (\beta+2-2\alpha)\,Y - (1-\alpha) = 0 \tag{4.5}$$

It can be shown that, regardless of the comparative magnitudes of α and β, the equilibrium (4.4) is always locally unstable. If $X_0 > Z_0$, fixation of the pure A state takes place at a geometric rate; if $X_0 < Z_0$ convergence to A' occurs at a geometric rate.

The analysis of the asymmetric model in Table 5 can be carried out in the general case. There results at most one nontrivial equilibrium, given by

$$\hat{X} = \frac{(L+\gamma-\alpha)\,(\gamma-\beta)\,(2-\alpha-\beta)}{L\{L(4-\alpha-\gamma) - (\gamma-\alpha)^2\}}\,, \quad \hat{Y} = \frac{(L+\gamma-\alpha)\,(L+\alpha-\gamma)\,(2-\alpha-\gamma)}{L\{L(4-\alpha-\gamma)-(\gamma-\alpha)^2\}}$$

$$\hat{Z} = \frac{(L+\alpha-\gamma)\,(\alpha-\beta)\,(2-\gamma-\beta)}{L\{L(4-\alpha-\gamma) - (\gamma-\alpha)^2\}} \tag{5.4}$$

where

$$L = (1-\alpha)\,(\gamma-\beta) + (1-\gamma)\,(\alpha-\beta) \tag{5.5}$$

The point (5.4) is an admissible set of frequencies if and only if

$$(L+\gamma-\alpha)\,(L+\alpha-\gamma) > 0 \tag{5.6}$$

The stability behavior of the system can be summarized as follows:

i) The pure A state is locally stable if and only if

$$L+\alpha-\gamma > 0.$$

ii) The pure A' state is locally stable if and only if

$$L+\gamma-\alpha > 0.$$

iii) The polymorphic equilibrium is valid if (5.6) is satisfied and is stable if and only if

$$L+\gamma-\alpha < 0 \quad \text{and} \quad L+\alpha-\gamma < 0\,,$$

convergence taking place at a geometric rate; it is unstable if these inequalities are strictly reversed.

Some particularizations of this model are worth mentioning:

i) If $\gamma < \beta < \alpha$ then necessarily $L + \alpha - \gamma > 0$ and $L + \gamma - \alpha < 0$ and it

follows that fixation of A is the only stable condition; if $\gamma > \beta > \alpha$, then there is fixation in A'.

ii) In the symmetric case $\alpha = \gamma < \beta$ the interior equilibrium simplifies to $\hat{X} = \hat{Z} = 1/2(2-\alpha)$, $\hat{Y} = (1-\alpha)/(2-\alpha)$ which is independent of β and globally stable, convergence taking place again at a geometric rate.

iii) When $\alpha = \gamma > \beta$ the equilibrium $\hat{X} = \hat{Z} = 1/2(2-\alpha)$, $\hat{Y} = (1-\alpha)/(2-\alpha)$ is unstable and the domains of attraction of the fixations are separated by the straight line $X = Z$.

VARIOUS EXTENSIONS

As mentioned before the general case of assortment without complete dominance could be specified by 6 parameters and then the analysis becomes exceedingly cumbersome. Other meaningful specifications in terms of three parameters are possible. One such is obtained by assuming "sex symmetry" in the choice as in the following table:

♂ ♂ \ ♀ ♀	AA	AA'	A'A'
AA	1	$1-\delta$	$1-\varepsilon$
AA'	$1-\delta$	1	$1-\eta$
A'A'	$1-\varepsilon$	$1-\eta$	1

where, as usual, $0 \leq \delta < 1$, $0 \leq \varepsilon < 1$, $0 \leq \eta < 1$. Plainly stated, AA' females "dislike" AA males as much as AA females dislike AA' males, and this is measured by a fraction δ of females tending to avoid such matings.

The relevant formulae for the mass action model are given in Table 7. Comparison with Table 4 shows that the two systems differ only in the definition of the parameters. Thus 6 is converted into 4 by the substitution

$$2\delta = \alpha + \beta, \quad 2\varepsilon = \alpha + \gamma \quad \text{and} \quad 2\eta = \beta + \gamma .$$

We shall now formulate another class of models applying to animal populations in which the duration of courtship is sufficiently long and where the beginning of courtship is well synchronized.

As a rough representation of such mating systems we can assume that a first round of "encounters" occurs simultaneously and at random. Then a fraction of females will terminate the courtship with males of different phenotype at some stage before copulation. (A similar situation has been observed in some gulls (GRIFFITH SMITS 1967).) With the gene interaction introduced above, this will occur for a proportion of $X(\delta Y + \varepsilon Z)$ AA females, $Y(\delta X + \eta Z)$ AA' females and $Z(\varepsilon X + \eta Y)$ A'A' females. A class of models arises by making assumptions on the types of mating and the average fertility of such females.

Assuming, for instance, that the remaining females will be fertilized by males of the same genotype, with no loss in fertility, we derive the entries in Table 6.

Inspection of the recursion relations reveals that the quantity $X-Z$ is invariant over time, i.e., $X_n - Z_n = X_0 - Z_0 \equiv C$, as for the first model in the special case,

TABLE 6

Model for a population in which part of the pairs, formed at random, break off before copulation
Asymmetric Case

Mating Types	Frequencies of	
	Modified Random Mating	Assortative Mating
AA × AA	X^2	$X(\delta Y + \varepsilon Z)$
AA × AA'	$2(1-\delta)XY$	
AA × A'A'	$2(1-\varepsilon)XZ$	
AA' × AA'	Y^2	$Y(\delta X + \eta Z)$
AA' × A'A'	$2(1-\eta)YZ$	
A'A' × A'A'	Z^2	$Z(\varepsilon X + \eta Y)$

$$X' = \left(X + \frac{Y}{2}\right)^2 + \varepsilon XZ + \frac{Y}{4}\,(\delta X + \eta Z) \tag{6.1}$$

$$Y' = 2\left(X + \frac{Y}{2}\right)\left(\frac{Y}{2} + Z\right) - 2\varepsilon XZ - \frac{Y}{2}\,(\delta X + \eta Z) \tag{6.2}$$

$$Z' = \left(Z + \frac{Y}{2}\right)^2 + \varepsilon XZ + \frac{Y}{4}\,(\delta X + \eta Z) \tag{6.3}$$

$\alpha = \beta = \gamma$. Using this relation the system reduces to a single recursion relation

$$Y' = \frac{\delta + \eta - 2\varepsilon}{4}\,Y^2 - \left\{\frac{\delta}{4}\,(1+C) + \frac{\eta}{4}\,(1-C) - \varepsilon\right\}Y + \frac{1-C^2}{2}\,(1-\varepsilon) = u(Y).$$

Iteration yields that $Y_n = u^{(n)}(Y_0)$ converges to the unique root in $(0,1)$, $\hat{Y}$, of the equation $u(Y) - Y = 0$. This root depends on the initial frequencies only through C, thereby generating a family of equilibria. Although gene frequencies are not invariant over time, the equilibria span a curve of neutral type. This case is thus of little evolutionary consequence.

A simple alternative to the assumption that all assorting females mate with the preferred phenotype, with no loss in fertility, would be that they do not contribute at all to the next generation. This gives the "mass action" model in Table 7 which is formally the same as the mass action model of Table 4.

TABLE 7

Mass action model in the case of a generic "sex symmetrical" interaction

$$N = 1 - 2(\delta XY + \varepsilon XZ + \eta YZ)$$

$$NX' = \left(X + \frac{Y}{2}\right)^2 - \delta XY \tag{7.1}$$

$$NY' = 2\left(X + \frac{Y}{2}\right)\left(\frac{Y}{2} + Z\right) - 2\varepsilon XZ - \delta XY - \eta YZ \tag{7.2}$$

$$NZ' = \left(Z + \frac{Y}{2}\right)^2 - \eta YZ \tag{7.3}$$

DISCUSSION AND CONCLUSIONS

In this paper we deduced some of the consequences of partial assortative mating based on the phenotypes of an autosomal pair where gene interactions other than complete dominance are involved. This case would entail, in the most general formulation, six parameters. A simplified version with three parameters is obtained by assuming that the females (males) of a genotype equally dislike those of a different genotype. The analogs of the models previously studied for the case of dominance have been examined. We underscore the principal conclusions with special emphasis on contrasting the results for the no dominance and dominance analogs of all the models.

We discuss first the two models for permanent bonding in animals having a 1:1 sex ratio at maturity. As in the case of dominance, when individuals practicing assortment mate prior to those mating at random we obtain a neutral family of equilibria if the relative fertility of the random-mating females is not affected. However, if fertility is affected by the timing of matings the resulting ultimate changes of genotype frequencies do not exclusively produce one or the other fixation as in the case of dominance. In fact, if the intensity of assorting in the heterozygote is large enough compared to the tendency for assortment in both homozygotes, a stable polymorphism will result. When both homozygotes assort with the same intensity, the condition for polymorphic stability is simply that of a larger assortment intensity in the heterozygote. This result is analogous to overdominance in the case of natural selection.

Consider the second alternative for permanent bonding, i.e., assorting occurs after random mating and all "mismatched" females do not contribute to the next generation. Now the results are qualitatively much the same as for dominance; either one of the fixations is the only stable situation or an unstable polymorphism exists and both fixations are stable. Thus, timing is more crucial in the case of no dominance than in that of dominance.

When assortment affects only the chance of encounter in a scattered population (mass action model) we get the same qualitative result as in the case of dominance, i.e., always an unstable polymorphism. The asymmetric model, accounting for some excess of males, has the same properties as the first case of permanent pairs; a stable polymorphism will result if the assorting intensity in heterozygotes is large enough compared to the assorting intensity in both homozygotes.

We can conclude that, barring very unlikely circumstances (like exact equality of all assorting parameters, etc.) assorting for traits without dominance will produce, as for dominant ones, some significant evolutionary effects. The type of possible equilibria differs from the dominant case in that stable polymorphisms can be established. A further analogy of assortment with natural selection is that fixation (initial increase) of dominant alleles occurs at an algebraic rate, while in the absence of dominance a geometric rate is the rule.

We also discussed an alternative formulation of a model of assortment with three parameters by assuming "sex symmetry" in the choice. This leads to approximately the same conclusion as for the previous case.

A new class of models arises by assuming that a first attempt at pairing, lasting for some time, occurs at random. A fraction of the females will reject partners of unlike phenotype at some later stages of courtship, prior to copulation. Specific models will then result by making assumptions on the type of mating and the fertility of the remaining females. When they are applied to the "sex symmetric" case they give a neutral solution in the asymmetric case.

SUMMARY

The models of the preceding paper are examined in the context of assortment for an autosomal pair of genes without dominance. While the most general formulation would involve six parameters, two specifications involving only three parameters have been considered. In striking contrast to the case of dominance, for some circumstances of the parameters and depending on the mechanism of fertilization, stable polymorphisms can result even for autosomal traits. The effect of assortment in these cases is somewhat similar to that of overdominance in the case of natural selection.—Another class of models is studied where we assume that a first attempt to pair occurs at random and then some of the pairing between individuals of different phenotypes disassociates at a later stage prior to copulation.

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