FURTHER ANALYSIS OF NEGATIVE ASSORTATIVE MATING*

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Received October 3, 1967

THE paper "Analysis of models with homozygote $\times$ heterozygote matings" was devoted to the complete mathematical analysis of the equilibrium behavior of some models proposed by SCUDO (1964) and FINNEY (1952) and some of their qualitative implications for population genetics in general. In this paper we repeat this process with certain models described by WORKMAN (1964), NAYLOR (1962) and others. Originally, WORKMAN used the standard methods of linear infinitesimal approximations (see OWEN 1953) to verify local stability of certain equilibria. The inadequacies of local linear analysis were mentioned in the previous paper. As emphasized in the previous paper, a global analysis, whenever possible, provides more information, not only in the strictly mathematical sense but qualitatively as well.

WORKMAN was interested in the fact that models involving (a) exclusively negative assortative mating and (b) mixed self-fertilization and negative assortative mating and (c) mixed random mating and negative assortative mating could explain the maintenance of polymorphic variation in the absence of heterozygote advantage. In this note we will be concerned with those models having exclusively negative assortative mating. Some of the theoretical analysis and implications of the mixed models will be treated elsewhere (BODMER, FELDMAN and KARLIN, manuscript in preparation).

We are concerned with a single locus at which the alleles *A* and *a* occur. The models are specified by the matings which are forbidden: In model I only unlike genotypes may mate; in model II, like homozygotes may not mate but the heterozygotes can mate at random; in model III matings between like members of one homozygote genotype, as well as those between pairs of heterozygotes are forbidden; in model IV only matings between pairs of heterozygotes are prohibited; in model V matings between like members of one homozygote genotype are forbidden.

In the terminology of FINNEY (1952) the models discussed here are of the pollen elimination kind. Zygotes are produced by a union of two gametes, the first one is chosen at random, while the second is chosen at random from among only those individuals with whom mating is permitted. This could be the case in a plant population producing excess pollen, where pollen whose phenotype makes it incompatible fails to germinate. For the biological justification of this type of model the reader is referred to FINNEY (1952), MORAN (1962, Chap. 8)

* Research supported in part under contract NOO14-67-A-0112-0015 and grant NIH 10452 at Stanford University, Stanford, California.

and WORKMAN (1964). NAYLOR (1962) was also interested in how the amount of heterozygosity could be altered from that under random mating. We have included one of his models since it falls under the same general classification as the others treated here and its complete analysis has not previously been given. The analysis is directed toward obtaining the complete equilibrium behavior of the models. By this we mean the equilibria themselves, the rates of approach and domains of attraction of the equilibria. In many cases the full transient behavior (i.e., the manner in which the gene frequencies vary with time) can be determined.

In the first section we discuss the models with reference to their qualitative implications. In the second section the models are reformulated within the framework of what was called by FINNEY (1952) "zygote elimination." This amounts to assuming that certain matings, although they take place, produce inviable offspring. Another interpretation is that these matings have zero fertility. The results appear to be completely analogous if one assigns fertility less than one to these matings. Since in this case matings occur with frequency proportional to the product of the frequencies of the participants, these can be called "mass action" models, in analogy with the physical phenomenon of elastic collision of particles. In considering the two schemes, some interesting comparisons and contrasts emerge as well as certain robust phenomena which have some biological importance. In the last section the mathematical analyses of one of the pollen elimination and one of the zygote elimination models are given. The details of the other zygote elimination models have been omitted but will be presented in BODMER, FELDMAN and KARLIN (manuscript in preparation).

Discussion of Models and Results. Throughout the following we suppose that u_n , v_n and w_n represent the frequencies of the AA, Aa and aa genotypes respectively, with the initial constitution of the population given by u_0 , v_0 and w_0 . For equilibrium frequencies we use the notation u_e , v_e , w_e . In models I-V the recursion relations (or slightly different forms of the same equations) were given in WORKMAN (1964).

Model I. Matings prohibited are AA $\times$ AA, Aa $\times$ Aa and aa $\times$ aa. That is, only unlike genotypes may mate. This type of mating behavior (negative assortative) seems particularly relevant to certain plant populations. See WORKMAN (1964) for examples.

Since all ovules are ultimately fertilized we obtain the recursion relations connecting genotypic frequencies over successive generations:

$$(1) \quad u_{n+1} = \frac{u_n v_n (1 + w_n)}{2(1 - u_n)(1 - v_n)}$$

$$(2) \quad v_{n+1} = \frac{u_n w_n}{2} \cdot \frac{(1 + v_n)}{(1 - u_n)(1 - w_n)} + \frac{1}{2}$$

$$(3) \quad w_{n+1} = \frac{w_n v_n (1 + u_n)}{2(1 - w_n)(1 - v_n)}$$

The equilibrium behavior for this model is dependent on the initial composition

of the population. Specifically, when $u_0 < w_0$ then convergence occurs to the equilibrium $u_e = 0$, $v_e = w_e = 1/2$ at the geometric rate $3/4$ (i.e., for n large enough the frequency u_n decreases by a factor $3/4$ per generation and $|v_n - 1/2| = 0(3/4)^n$). If $u_0 > w_0$ convergence takes place to the equilibrium $u_e = v_e = 1/2$, $w_e = 0$, again at the geometric rate $3/4$. When $u_0 = w_0$, geometric convergence occurs to the equilibrium $u_e = w_e = 1/4(5 - \sqrt{17})$, $v_e = 1/2(-3 + \sqrt{17})$ with rate $(1 - \sqrt{17})/(18 - 2\sqrt{17})$. The last equilibrium is unstable since any small shift destroys the special relation $u_0 = w_0$ and results in ultimate convergence to one of the first two equilibria. The complete equilibrium behavior has therefore been ascertained and shown to depend decisively on the initial conditions.

Model II. The forbidden matings are $AA \times AA$ and $aa \times aa$. Note that the only change from model I is that the mating $Aa \times Aa$ is allowed. The recursion relations are

$$(4) \quad u_{n+1} = 1/2 \frac{u_n v_n}{1 - u_n} + 1/2 u_n v_n + 1/4 v_n^2 ,$$

$$(5) \quad v_{n+1} = 1/2 + 1/2 u_n w_n \frac{(1 + v_n)}{(1 - u_n)(1 - w_n)} ,$$

$$(6) \quad w_{n+1} = 1/2 \frac{w_n v_n}{1 - w_n} + 1/2 w_n v_n + 1/4 v_n^2 .$$

Notice again that $v_n > 1/2$ after one generation. As is usually the case, the equilibrium points themselves are easy to determine. In this case there is a single equilibrium; $u_e = w_e = (5 - \sqrt{17})/4$, $v_e = (-3 + \sqrt{17})/2$ approached at the geometric rate $(1 - \sqrt{17})/(18 - 2\sqrt{17})$. Note that this equilibrium occurred in model I but was unstable there. This is the only one of WORKMAN's models where there is a stable equilibrium in which all genotypes are represented. Such equilibria are usually called "interior." It is, however, non-trivial to show that convergence to this equilibrium always takes place. The arguments are based on the properties of iterates of monotonic functions. (Recently CANNINGS 1967 has also used certain monotonicity properties to prove convergence in a model with sex-linkage and selection.) This type of reasoning may be useful in the treatment of other population models, where previous studies have concentrated only on discerning local stability of the equilibrium in question. The analysis has therefore been included in the last Section. Comparing models I and II, note that allowing the mating $Aa \times Aa$ to take place has led to an increase in the equilibrium heterozygosity. The effect is similar to that occurring under random mating with overdominance. Thus the mating system can be responsible for maintaining variability at levels usually attributed to some degree of heterozygote advantage. A number of the models treated in this paper demonstrate that some cases in which variability is either maintained or lost which have previously been discussed in terms of selection pressures can be explained alternatively as consequences of the mating system.

Model III. We assume here that the matings $AA \times AA$ and $Aa \times Aa$ are

prohibited. (A corresponding analysis obtains for the case where $aa \times aa$ and $Aa \times Aa$ are prohibited.) This model is of added interest since the results are surprising and unintuitive. It demonstrates a very delicate balance between mating system, initial genotype frequencies, and ultimate polymorphism. The recursion relations are

$$(7) \quad u_{n+1} = \frac{u_n v_n (1 + w_n)}{2(w_n + u_n v_n)}$$

$$(8) \quad v_{n+1} = \frac{1 - w_n^2}{2} + \frac{u_n w_n}{2} \left(\frac{2 - u_n}{1 - u_n} \right)$$

$$(9) \quad w_{n+1} = w_n \left[\frac{1}{2} \frac{v_n}{1 - v_n} + \frac{1}{2} v_n + w_n \right].$$

There is one obvious equilibrium, namely $u_e = 0, v_e = 0, w_e = 1$. However, direct inspection of the recursion relations reveals a second equilibrium point $u_e = \frac{1}{2}, v_e = \frac{1}{2}, w_e = 0$, which seems to have been overlooked in WORKMAN's original paper. This probably occurred because the prohibition of the matings $AA \times AA$ and $Aa \times Aa$ would appear to favor the genotype aa , suggesting that, provided all genotypes are initially present, the first of the above equilibria must always be attained. However, the second equilibrium is readily verified to be locally stable thus refuting this intuition. Actually the second equilibrium possesses a domain of attraction; that is, there exists an open set of initial frequency vectors from which there will be convergence to the point $u_e = v_e = \frac{1}{2}, w_e = 0$. An example is given in Table 3. We have not found the precise domains of attraction to the two equilibria. It is very complicated to determine analytically the boundary separating the two regions although it could be approximated by numerical computation. We can show, however, that starting from any initial frequencies obeying the restrictions $u_0 \leq \frac{1}{4}, w_0 \geq \frac{1}{4}$ there will be convergence to $u_e = 0, v_e = 0, w_e = 1$ while for initial frequencies close enough to the equilibrium $(\frac{1}{2}, \frac{1}{2}, 0)$ there will be convergence to this point.

Theoretical considerations make it clear that the domains of attraction must be separated by a curve of the kind described in Figure 1. On this curve there is an unstable interior equilibrium which can be obtained from equations (7) and (9) as the solution, v^* , of the cubic equation $v^3 + 8v^2 - 12v + 4 = 0$, approximately .5442. From (9) the corresponding aa frequency is $w^* = (2 - 4v^* + (v^*)^2) / 2(1 - v^*) = .1309$; with $u^* = .3249$. Starting from a point on the curve there will be convergence to this unstable equilibrium. Thus there is a delicate balance between the mating system, initial frequencies and ultimate equilibrium. It is a formidable and perhaps important task to explain these findings from a biologically intuitive standpoint.

A further surprising feature of this model is that convergence to the point $u_e = 0, v_e = 0, w_e = 1$, when it occurs must proceed very slowly, in fact, at best at an algebraic rate (i.e., the frequency of the heterozygote genotype decreases no faster than $1/n$ as n tends to ∞ ; this means that complete elimination, although certain, is a slow process). The slow rate of approach implies that both

FIGURE 1 (not to scale)—Above the curve the population converges to $w = 1$ while below it there is convergence to $v = 1/2$, $w = 0$. From any interior point on the curve there would be convergence to (v^*, w^*) .

genes will be maintained in the population for an extremely long duration. This raises the question of whether a population observed to contain alleles in low frequencies is in some selectively balanced equilibrium or merely in a state of transition to a situation in which some of the alleles are absent.

It seems to be a general phenomenon that when one allele is destined to disappear because of the intrinsic properties of the mating system, the heterozygote remains in the population for a relatively long time (see KARLIN and FELDMAN 1968). Of course this phenomenon has already been encountered in the classical model of a disadvantageous recessive (see e.g., LI, 1955, p. 252). The slow convergence to $u_e = v_e = 0$, $w_e = 1$ is in striking contrast with the transient behavior of the genotype frequencies in the domain of attraction of $u_e = v_e = 1/2$, $w_e = 0$. The latter equilibrium possesses a relatively small domain of attraction from which convergence occurs geometrically fast with rate $3/4$.

The local linear analysis originally employed to infer the stability of the point $w_e = 1$ is incorrect. The eigenvalues are 0 and 1 and in the presence of an eigenvalue of magnitude 1 the linearization method reveals nothing concerning stability. In fact it is possible to move away from the point $w_e = 1$ in certain directions although the trajectory will then curve back into the equilibrium (see Tables 1 and 2). We have established that at least from the region where the initial genotype frequencies satisfy $u_0 \leq 1/4$, $w_0 \geq 1/4$ there must be convergence to the point $w_e = 1$. The argument is delicate and has been omitted. From an initial state above the curve in Figure 1 there will be convergence to $w_e = 1$ while from starting conditions below the curve there will be convergence to $u_e = v_e = 1/2$, $w_e = 0$.

TABLE 1

An example of Model III in which aa initially decreases but ultimately prevails

Generation	AA u_n	Aa v_n	aa w_n
$n = 0$	.333333	.333333	.333333
1	.166666	.583333	.249999
2	.175000	.514583	.310416
3	.147224	.511905	.340760
4	.121487	.496484	.382027
5	.094224	.476648	.429127
6	.067700	.450462	.481837
$\vdots$	$\vdots$	$\vdots$	$\vdots$
15	.000007	.166290	.833071
$\vdots$	$\vdots$	$\vdots$	$\vdots$
4293	.000000	.000502	.999497

Differences less than 10^{-7} are neglected: although AA disappears extremely quickly, Aa persists, disappearing very slowly.

In general, therefore, the ultimate state of the population is crucially dependent on the initial conditions.

In the last section we prove that when convergence takes place to the equilibrium $w_e = 1$, it does so no faster than algebraically. Some computations have been appended which illustrate the above remarks. Tables 1 and 2 furnish examples in which the genotype frequencies converge to the point $u_e = v_e = 0$, $w_e = 1$. Note that in both cases the frequency of aa first drops then increases to the equilibrium value, but extremely slowly. In Table 3, however, the frequencies converge to $u_e = 1/2$, $v_e = 1/2$, $w_e = 0$ very rapidly. Although the curve Γ is not known in analytic terms it could be determined to a high degree of accuracy by standard numerical techniques.

TABLE 2

Another case of Model III with aa initially decreasing but ultimately prevailing

Generation	AA u_n	Aa v_n	aa w_n
$n = 0$	.020000	.030000	.950000
1	.000615	.067943	.931440
2	.000043	.066782	.933174
3	.000002	.064633	.935363
4	.000000	.062550	.937449
5	.000000	.060594	.939405
6	.000000	.058758	.941241
$\vdots$	$\vdots$	$\vdots$	$\vdots$
15	.000000	.046209	.953790
$\vdots$	$\vdots$	$\vdots$	$\vdots$
4433	.000000	.000449	.999550

Differences less than 10^{-7} are neglected; again the equilibrium is reached extremely slowly.

TABLE 3*

An example of Model III with fast convergence to $(\frac{1}{2}, \frac{1}{2}, 0)$

Generation	AA u_n	Aa v_n	aa w_n
0	.500000	.400000	.100000
1	.366666	.570000	.063333
2	.408023	.527938	.064037
$\vdots$	$\vdots$	$\vdots$	$\vdots$
10	.466228	.514867	.018903
$\vdots$	$\vdots$	$\vdots$	$\vdots$
15	.488876	.505326	.005797
$\vdots$	$\vdots$	$\vdots$	$\vdots$
53	.499999	.500000	.000000

Differences less than 10^{-7} are neglected; the convergence to the previously overlooked fixed point is very fast.

* We are indebted to MR. MARKUS NABHOLZ for assistance with the computations.

Model IIIa. It may appear that the properties of the mating systems treated so far depend on the fact that the heterozygotes and homozygotes are separated as regards prohibited matings. In this model, the matings prohibited are $AA \times AA$, $Aa \times Aa$ and $AA \times Aa$. This case was not treated by WORKMAN. It differs from the other WORKMAN models in that the mating between homozygote AA and heterozygote is prohibited. Equivalently, matings between like dominant phenotypes are prohibited. The recursion relations are

$$(7a) \quad u_n = 0 \quad \text{for all } n$$

$$(8a) \quad v_{n+1} = \frac{v_n}{2} + \frac{w_n v_n}{2}$$

$$(9a) \quad w_{n+1} = \frac{1}{2} + \frac{w_n^2}{2}$$

It is easy to see that $u_e = v_e = 0, w_e = 1$ is the only equilibrium. Examination of the relation (9a) reveals that w_n must converge to 1 at an algebraic rate. Note that the equilibrium $u_e = v_e = 1/2, w_e = 0$ does not appear. The "zygote elimination" modification of this model has the same equilibrium behavior.

Model IV. For WORKMAN's fourth model, matings of the type $Aa \times Aa$ are prohibited. This is similar to the model of random mating with the homozygotes having a selective advantage. The resulting transformations of the genotype frequencies are

$$(10) \quad u_{n+1} = u_n \left[u_n + \frac{1}{2} v_n + \frac{1}{2} \frac{v_n}{1-v_n} \right]$$

$$(11) \quad v_{n+1} = v_n - \frac{v_n^2}{2} + 2u_n w_n$$

$$(12) \quad w_{n+1} = w_n \left[w_n + \frac{1}{2} v_n + \frac{1}{2} \frac{v_n}{1-v_n} \right].$$

There are three possible equilibria; $u_e = v_e = 0, w_e = 1$; $u_e = 1, v_e = w_e = 0$ and $u_e = w_e = 1/4, v_e = 1/2$. If $u_0 < w_0$ there is convergence to the point $u_e = v_e = 0$,

$w_e = 1$. If $u_0 > w_0$ there is convergence to the point $u_e = 1, v_e = w_e = 0$. In both cases the rate of convergence is no faster than algebraic. If $u_0 = w_0$ then $u_n = w_n$ for all n so that $v_n = 1 - 2u_n$ for every n . Substituting this into (11) easily reveals that for $n \geq 1$, $v_n = 1/2$ so that $u_n = w_n = 1/4$ for $n \geq 1$. Thus if $u_0 = w_0$ the third of the equilibrium points is reached after one generation. Once again the equilibria containing only one allele are reached extremely slowly so that for a very long time the population remains diallelic. In this model the initially less frequent homozygote disappears quickly, faster in fact than any geometric rate. However, the heterozygote persists in the population, disappearing at the slow algebraic rate. Considering the analogy with the model of random mating with the homozygotes having the advantage, we can regard the relative fitnesses of the two homozygotes as being determined in some way by their initial relative frequencies.

Model V. Like members of one homozygote genotype are not permitted to mate. We consider the case where $AA \times AA$ matings are prohibited. A corresponding analysis applies when $aa \times aa$ matings are forbidden. This model bears a similarity to the classical situation of random mating with one homozygote at a disadvantage. The transformations in the former case are

$$(13) \quad u_{n+1} = v_n \left[\frac{v_n}{4} + \frac{u_n}{2} + \frac{1}{2} \frac{u_n}{1-u_n} \right]$$

$$(14) \quad v_{n+1} = \frac{1-w_n^2}{2} + \frac{w_n u_n}{2} \left(\frac{2-u_n}{1-u_n} \right)$$

$$(15) \quad w_{n+1} = (w_n + \frac{1}{2} v_n)^2$$

It is trivial to verify that there is only one equilibrium, namely $u_e = v_e = 0, w_e = 1$. The convergence is no faster than algebraic, so that this is another case where an equilibrium state allowing only one allele is attained extremely slowly. Notice that model III which prohibits both $AA \times AA$ and $Aa \times Aa$ matings has quite different equilibrium behavior from that of model V. On the other hand, the "zygote elimination" modification of model III (see next section) behaves similarly to model V.

A Model of NAYLOR. We postulate that heterozygotes mate only with heterozygotes while homozygotes mate at random with homozygotes. The situation can be pictured as a division of the zygotes at the n th generation, into two mating sets. In one set, containing a proportion v_n of zygotes, matings are of type $Aa \times Aa$. In the remaining fraction $1 - v_n$ of the population $AA \times AA$ matings, for example, occur with frequency $u_n^2/(1-v_n)$. The other matings are considered similarly and one arrives at the recursion relations

$$(16) \quad u_{n+1} = \frac{v_n}{4} + \frac{u_n^2}{1-v_n}$$

$$(17) \quad v_{n+1} = \frac{v_n}{2} + \frac{2u_n w_n}{1-v_n}$$

$$(18) \quad w_{n+1} = \frac{v_n}{4} + \frac{w_n^2}{1-v_n}.$$

Note that

$$u_{n+1} - w_{n+1} = u_n - w_n = \dots = u_0 - w_0 = c, \text{ say.}$$

There is a continuum of equilibria in this model, with the precise equilibrium attained depending on the initial conditions. In fact we find the set of equilibria to be

$$u_e = 1/8 + \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}, \quad w_e = 1/8 - \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}, \quad v_e = 3/4 - \frac{\sqrt{1+8c^2}}{4}$$

where $c = u_0 - w_0$. For each c the approach to the equilibrium is geometric with rate $-8c^2/(1 + \sqrt{1+8c^2})^2$. Note that the rate of approach is also dependent on the initial conditions. No matter what the value of c , it is easy to see that $v_e \leq 1/2$.

Table 4 summarizes the information discussed in this section. For the mathematical justification of the results the reader is referred to the section "Analysis of the Models."

Zygote Elimination Modifications. It is possible to investigate fully the zygote elimination analogues of the models described in the previous section. The global analysis of the equilibrium behavior is invariably easier than for the corresponding pollen elimination cases. Table 5 contains the results of the analyses of the zygote elimination models. (The table is given in terms of the matings postulated to be infertile; the modification is indicated by a prime.) In the last section we have included the analysis for the model III', the zygote elimination version of the model III above.

The first general conclusion to be drawn from a comparison of Tables 4 and 5 is that whenever a gene disappears completely it usually does so at an extremely slow rate. The robustness of this phenomenon seems to us to be of considerable practical importance insofar as it questions whether observed polymorphisms are being maintained by a selection balance or are symptomatic of a slow rate of loss of one or more alleles.

From Tables 4 and 5 it is evident that at least half of the models in either scheme are crucially dependent on the initial conditions for their equilibrium behavior. Therefore numerical calculations could result in incorrect interpretations. Models IV and V are independent of whether pollen or zygote elimination is assumed. Models II and II' are intriguing because the equilibria, which in both cases are interior and approached geometrically, are very close together, indicating a degree of independence from the model assumed. The same can be said of models IIIa, III', IIIa', V and V' all of which result in slow convergence to the equilibrium $u_e = v_e = 0$, $w_e = 1$. Model III can be seen to present a striking contrast to this group of models.

The differences between models III and III' are also very interesting. In the case of zygote elimination the transformations (7), (8) and (9) become

$$(19) \quad u_{n+1} = \frac{u_n v_n}{T_n}$$

$$(20) \quad v_{n+1} = \frac{u_n v_n + v_n w_n + 2w_n u_n}{T_n}$$

$$(21) \quad w_{n+1} = \frac{(v_n + w_n) w_n}{T_n}$$

TABLE 4
*Equilibrium conditions, rates of approach and regions of convergence for models involving
 negative assortative mating ("pollen elimination")*

Model (matings prohibited)	Equilibria	Rate of approach	Region of convergence
I AA × AA, Aa × Aa, aa × aa	$ \begin{cases} u_e = 0, v_e = w_e = \frac{1}{2} \\ u_e = \frac{1}{2}, v_e = \frac{1}{2}, w_e = 0 \\ \left\{ \begin{array}{l} u_e = w_e = \frac{5 - \sqrt{17}}{4} \\ v_e = \left(\frac{-3 + \sqrt{17}}{4} \right) \end{array} \right\} \text{(unstable)} \end{cases} $	geometric, rate $\frac{3}{4}$ geometric, rate $\frac{3}{4}$ oscillating geometric, rate $\frac{1 - \sqrt{17}}{18 - 2\sqrt{17}}$	$u_0 < w_0$ $u_0 > w_0$ $u_0 = w_0$
II AA × AA, aa × aa	$ \begin{cases} u_e = w_e = \frac{5 - \sqrt{17}}{4} \\ w_e = \left(\frac{-3 + \sqrt{17}}{2} \right) \end{cases} $	oscillating geometric, rate $\frac{1 - \sqrt{17}}{18 - 2\sqrt{17}}$	see Footnote (i) below
III AA × AA, Aa × Aa	$ \begin{aligned} &u_e = v_e = 0, w_e = 1 \\ &u_e = v_e = \frac{1}{2}, w_e = 0 \\ &u_e = u^*, v_e = v^*, w_e = w^* \\ &\text{(unstable)} \end{aligned} $	slower than algebraic (see footnote (ii) below) geometric, rate $\frac{3}{4}$ probably geometric	see Figure 1 see Figure 1 see Footnote (iv)

IIIa	AA × AA, Aa × Aa, AA × Aa	$u_e = v_e = 0, w_e = 1$	algebraic	
IV	Aa × Aa	$u_e = v_e = 0, w_e = 1$ $u_e = 1, v_e = w_e = 0$ $u_e = w_e = \frac{1}{4}, v_e = \frac{1}{2}$ (unstable)	slower than algebraic slower than algebraic one generation	$u_0 < w_0$ $u_0 > w_0$ $u_0 = w_0$
V	Aa × AA	$u_e = v_e = 0, w_e = 1$	slower than algebraic	
NAYLOR's model, AA × Aa, Aa × aa		$u_e = \frac{1}{8} + \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}$ $v_e = \frac{3}{4} - \frac{\sqrt{1+8c^2}}{8}$ $w_e = \frac{1}{8} - \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}$	geometric, rate $\frac{-8c^2}{(1+\sqrt{1+8c^2})^2}$	see Footnote (iii)

- (i) Where no region of convergence is specified, convergence takes place at least from the whole simplex $u_0 + w_0 + v_0 = 1$ without its boundary.
- (ii) Algebraic convergence means that the distance from the equilibrium decreases no faster than $1/n$ as $n \rightarrow \infty$.
- (iii) $c = u_0 - w_0$ in NAYLOR's model, so the equilibrium is precisely specified by the initial values u_0 and w_0 .
- (iv) v^* is the admissible solution of $v^3 + 8v^2 - 12v + 4 = 0$. $w^* = \frac{2-4v^*+(v^*)^2}{2(1-v^*)}$.

TABLE 5

Equilibrium conditions, rates of approach and regions of convergence for models involving infertile matings ("zygote elimination")

Model (infertile matings)	Equilibria	Rate of approach	Region of convergence
I' AA × AA, Aa × Aa, aa × aa	$u_e = \frac{K}{M}, v_e = \frac{1+K}{2M} + \frac{\sqrt{(1+K)^2 + 8K}}{2M}$ $w_e = \frac{1}{M}$	geometric, rate $\frac{-2K}{(M-1-K)^2}$	see Footnote
II' AA × AA, aa × aa	$u_e = \frac{1-v^*}{2} = w_e, v_e = v^* \ddagger$	geometric, rate $\frac{2-2v^*}{(1+2v^*-v^{*2})^2}$	see Footnote
III' AA × AA, Aa × Aa	$u_e = v_e = 0, w_e = 1$ $u_e = v_e = \frac{1}{2}, w_e = 0$ (unstable)	not faster than algebraic one generation	$w_0 = 0$
IIIa' AA × AA, Aa × Aa, AA × Aa	$u_e = v_e = 0, w_e = 1$	algebraic	
IV' Aa × Aa	$u_e = v_e = 0, w_e = 1$ $u_e = 1, v_e = w_e = 0$ $u_e = w_e = \frac{1}{4}, v_e = \frac{1}{2}$ (unstable)	not faster than algebraic not faster than algebraic equilibrium achieved in one generation	$u_0 < w_0$ $u_0 > w_0$ $u_0 = w_0$
V' AA × AA	$u_e = v_e = 0, w_e = 1$	not faster than algebraic	
NAYLOR's model with zygote elimination: AA × Aa, aa × Aa	$u_e = v_e = 0, w_e = 1$ $u_e = 1, v_e = w_e = 0$ $u_e = w_e = \frac{1}{4}, v_e = \frac{1}{2}$ (unstable)	faster than geometric faster than geometric equilibrium achieved in one generation	$u_0 < w_0$ $u_0 > w_0$ $u_0 = w_0$

In model I', the equilibrium is specified precisely by the initial conditions so the region is omitted. Otherwise the omission of the region denotes convergence at least from the simplex $u_0 + v_0 + w_0 = 1$ without its boundary.

$$+ K = u_0/w_0, M = \frac{3}{2} (1+K) + \frac{1}{2} \sqrt{(1+K)^2 + 8K}.$$

‡ v^* is the root of $v^3 - 2v^2 - v + 1 = 0$ (approximately 0.55).

where $T_n = 1 - u_n^2 - v_n^2$.

The unexpected equilibrium $u_e = v_e = 1/2$, $w_e = 0$ uncovered in model III also appears in model III', but now it possesses no domain of attraction. It is possible to prove for model III' that provided $w_0 > 0$ the vector (u_n, v_n, w_n) tends to $u_e = v_e = 0$, $w_e = 1$ at an algebraic rate. The formal demonstration of this fact is included in the next section. Thus we see that the different type of selection pressure inherent in the mating system of model III' leads to different equilibrium behavior from that of model III. More specifically, selection against AA determined by the prohibition of the matings AA $\times$ AA and Aa $\times$ Aa as in model III is weaker than that inherent in the assumption of model III' that these matings be infertile because in the former case the point $u_e = v_e = 1/2$, $w_e = 0$ has a non-trivial domain of attraction. In both models, when one allele is lost completely the disappearance occurs very slowly. As mentioned previously this phenomenon is characteristic of both zygote and pollen elimination models and also of a number of standard random mating models involving selection.

Analysis of the Models. Model I: From equation (2) it is obvious that for $n \geq 1$, $v_n \geq 1/2$. Notice first that

$$\frac{u_{n+1}}{w_{n+1}} = \frac{u_n}{w_n} \left(\frac{1 - w_n^2}{1 - u_n^2} \right)$$

Hence if $u_0 < w_0$, $\{u_n/w_n\}$ forms a decreasing sequence and has a limit. If this limit is not zero then we infer that $\lim_n (1 - w_n^2)/(1 - u_n^2) = 1$ which is impossible if $\lim_{n \rightarrow \infty} u_n/w_n = \alpha < 1$. Hence $u_n \rightarrow u_e = 0$. Now from (2) $v_n \geq 1/2$ so that $1 - w_n$ is bounded away from zero. Since $u_n \rightarrow 0$ this means that $v_n \rightarrow 1/2$ as $n \rightarrow \infty$. The fixed point is therefore $u_e = 0$, $v_e = 1/2$, $w_e = 1/2$, and convergence has also been established. Similarly, if $u_0 > w_0$, the fixed point is $u_e = v_e = 1/2$, $w_e = 0$.

For the rate of convergence, consider again

$$\frac{u_{n+1}}{w_{n+1}} = \frac{u_n}{w_n} \left(\frac{1 - w_n^2}{1 - u_n^2} \right)$$

In the case where, for example, $u_0 < w_0$, if n is large enough then the factor $(1 - w_n^2)/(1 - u_n^2)$ can be made arbitrarily close to $3/4$. We therefore have u_n/w_n converging to zero geometrically fast with rate $3/4$.

What about the case $u_0 = w_0$? In this case $u_n = w_n$ for all subsequent n , so that $1 + v_n = 2(1 - u_n)$ and (2) reduces to

$$v_{n+1} = \frac{u_n^2}{1 - u_n} + 1/2$$

Then we have from (1) with $v_n = 1 - 2u_n$, $u_{n+1} = [(1 + u_n)(1 - 2u_n)/4(1 - u_n)]$ and, in particular, $u_e = f(u_e) = (1/4)[(1 + u_e)(1 - 2u_e)/(1 - u_e)]$. It is now trivial to find the additional interior fixed point. It is

$$u_e = w_e = (1/4)(5 - \sqrt{17}), \quad v_e = (1/2)(-3 + \sqrt{17})$$

It is not difficult to see that $f'(u) = (u^2 - 2u)/2(1 - u)^2$ which is negative. At the fixed point, $f'(u_e) = (1 - \sqrt{17})/(18 - 2\sqrt{17})$ which is negative and less in absolute value than unity. Therefore when $u_0 = w_0$ there is oscillation into the interior fixed point. (That is, over successive generations the sign of $f(u_n) - u_e$

alternates.) However, the equilibrium is not stable because small shifts from the condition $u_0 = w_0$ cause convergence to one of the other two fixed points.

Model II: Referring to equations (4), (5), (6), we find

$$(22) \quad u_{n+1} - w_{n+1} = (u_n - w_n) \left[\frac{v_n}{2(v_n + u_n w_n)} + \frac{v_n}{2} \right].$$

Now $v_n < 1$ for $n \geq 1$. Hence the multiplier of $u_n - w_n$ on the right hand side of (22) is less than unity. Hence $(u_n - w_n)$ decreases monotonically and must converge to zero since otherwise we may conclude that $v_n \rightarrow 1$; therefore $\lim_n u_n = \lim_n w_n = 0$, and the result $\lim_n (u_n - w_n) \neq 0$ is contradicted. The question of convergence of u_n and w_n remains to be confirmed. We may write the equation for v_{n+1} as follows:

$$(23) \quad \begin{aligned} v_{n+1} &= \frac{1}{2} + \frac{\frac{1}{2} \left[\frac{1}{4} \{ (u_n + w_n)^2 - (u_n - w_n)^2 \} \right] (1 + v_n)}{v_n + \frac{1}{4} \{ (u_n + w_n)^2 - (u_n - w_n)^2 \}} \\ &= \frac{1}{2} + \frac{1}{2} \cdot \frac{(1 - v_n)^2 (1 + v_n) - (1 + v_n) (u_n - w_n)^2}{(1 + v_n)^2 - (u_n - w_n)^2} \end{aligned}$$

From the right hand side of (23) we are led to consider the function

$$f_\xi(v) = \frac{1}{2} + \frac{1}{2} \cdot \frac{(1 - v)^2 (1 + v) - (1 + v) \xi}{(1 + v)^2 - \xi}$$

As a function of ξ alone, direct differentiation reveals that for each fixed v , the function $f_\xi(v)$ decreases as ξ increases. Since $(u_n - w_n)^2 \downarrow 0$, this means that for any $n \geq 0$

$$(24) \quad v_{n+1} \leq f_0(v_n),$$

where $f_0(v_n) = \frac{1}{2} + \frac{1}{2} [(1 - v_n)^2 / (1 + v_n)]$. Note also that $f'_0(v) \leq 0$ and hence that $f_0(v)$ is a decreasing function.

Since v_n is bounded away from 1 for every $n \geq 1$, we have $f'_\varepsilon(v_n) \leq 0$ provided ε is sufficiently small. Hence for every ε , and some $\eta > 0$, $f_\varepsilon(v)$ is a decreasing function for $v \leq 1 - \eta$. Since $|(u_n - w_n)^2|$ decreases as n increases, given any small ε there exists n_0 such that for $n \geq n_0$ we have

$$(25) \quad v_{n+1} \geq f_\varepsilon(v_n).$$

Since f_0 is a decreasing function, and referring to (24) and (25), we deduce that

$$(26) \quad v_{n+2} \leq f_0(v_{n+1}) \leq f_0(f_\varepsilon(v_n)),$$

and then

$$(27) \quad v_{n+3} \geq f_\varepsilon(v_{n+2}) \geq f_\varepsilon(f_0(f_\varepsilon(v_n)))$$

and $v_{n+4} \leq f_0(f_\varepsilon(f_0(f_\varepsilon(v))))$. Hence

$$(28) \quad v_{n_0+2m} \leq (f_0(f_\varepsilon))^{(m)}(v_{n_0}) = g_\varepsilon^{(m)}(v_{n_0})$$

where g_ε is the composed function $g_\varepsilon(x) = f_0(f_\varepsilon(x))$ and $g_\varepsilon^{(m)}$ is the m th iterate of g_ε . From (27) we also infer that

$$(29) \quad v_{n_0+2m+1} \geq (f_\varepsilon(f_0))^{(m)}(f_\varepsilon(v_{n_0})) = h_\varepsilon^{(m)}(f_\varepsilon(v_{n_0}))$$

where $h_\varepsilon(x) = f_\varepsilon(f_0(x))$ and $h_\varepsilon^{(m)}$ is the m th iterate of h_ε .

Again, for n larger than n_0 we have from (25)

$$v_{n+2} \geq f_\varepsilon(v_{n+1}) \geq f_\varepsilon(f_0(v_n)), \quad v_{n+3} \leq f_0(v_{n+2}) \leq f_0(f_\varepsilon(f_0(v_n))).$$

Thus

$$(30) \quad v_{n_0+2m} \geq h_\varepsilon^{(m)}(v_{n_0}), \quad v_{n_0+2m+1} \leq g_\varepsilon^{(m)}(f_0(v_{n_0})).$$

Now direct differentiation reveals that $f_0^{(2)}(v) = f_0(f_0(v))$ is an increasing function and inspection of $f_0^{(2)}(v)$ shows that it has a unique fixed point for $0 \leq v \leq 1$. By continuity, provided $\varepsilon > 0$ is sufficiently small, the same can be said of $g_\varepsilon(v)$ and $h_\varepsilon(v)$ where $v \leq 1 - \eta$.

We have

$$\alpha_\varepsilon = \lim_{m \rightarrow \infty} g_\varepsilon^{(m)}(v), \quad \beta_\varepsilon = \lim_{m \rightarrow \infty} h_\varepsilon^{(m)}(v).$$

Note that α_ε and β_ε are independent of the argument v . From (28), (29) and (30) we may conclude that

$$\begin{aligned} \limsup_{m \rightarrow \infty} v_{n_0+2m} &\leq \alpha_\varepsilon & \liminf_{m \rightarrow \infty} v_{n_0+2m} &\geq \beta_\varepsilon \\ \liminf_{m \rightarrow \infty} v_{n_0+2m+1} &\geq \beta_\varepsilon & \limsup_{m \rightarrow \infty} v_{n_0+2m+1} &\leq \alpha_\varepsilon \end{aligned}$$

As $\varepsilon \downarrow 0$ we have $f_\varepsilon \rightarrow f_0$, $g_\varepsilon \rightarrow f_0^{(2)}$, $h_\varepsilon \rightarrow f_0^{(2)}$. As mentioned above $f_0^{(2)}$ has a unique fixed point in the unit interval. This must be the same as the fixed point of f_0 . Thus

$$\lim_{\varepsilon \downarrow 0} \alpha_\varepsilon = \lim_{\varepsilon \downarrow 0} \beta_\varepsilon,$$

and v_n converges to the fixed point given by the solution of $f_0(v) = v$ namely $(1/2)(-3 + \sqrt{17})$. Hence u_n and w_n converge, both to $(5 - \sqrt{17})/4$. The convergence is geometric with rate given by $f'_0(v_e) = (1 - \sqrt{17})/(18 - 2\sqrt{17})$.

Model III: We show here that the convergence of w_n to the point $w_e = 1$ can occur no faster than at an algebraic rate. Indeed from (9), observe that

$$w_{n+1} = w_n \left[\frac{v_n}{2} \left(\frac{2-v_n}{1-v_n} \right) + w_n \right].$$

Now $\frac{v}{2} \left(\frac{2-v}{1-v} \right)$ is monotonically increasing as a function of v , and since $v_n \leq 1 - w_n$, we obtain after replacing v_n by $(1 - w_n)$,

$$w_{n+1} \leq \left[\frac{1+w_n^2}{2} \right].$$

The function $f(w) = (1+w^2)/2$ is monotonically increasing and has a unique fixed point at $w = 1$. But $f'(1) = 1$, so that as $m \rightarrow \infty$ the rate of approach of $f^{(m)}(w)$ to the point 1 is algebraic. Since $w_{n+1} \leq f(w_n)$, the rate of approach of w_n to $w_e = 1$ is no faster than algebraic.

Model IV. To establish convergence, suppose that $u_0 < w_0$. Then from (10), (11), (12)

$$(31) \quad \frac{u_{n+1}}{w_{n+1}} = \frac{u_n}{w_n} \left[\frac{u_n + \frac{1}{2} v_n + \frac{1}{2} \frac{v_n}{1-v_n}}{w_n + \frac{1}{2} v_n + \frac{1}{2} \frac{v_n}{1-v_n}} \right],$$

so that $u_1/w_1 < u_0/w_0$. Hence $\{u_n/w_n\}$ is a decreasing sequence of positive terms. It therefore converges to some number $\alpha \geq 0$. If $\alpha > 0$ then from (31) we conclude that $\lim_n u_n = \lim_n w_n \neq 0$ which is absurd since $\alpha < 1$. Hence $\alpha = 0$ and we have $u_n \rightarrow 0$.

Now $u_n + w_n = 1 - v_n$. An upper bound for $u_n w_n$ is therefore $(1-v_n)^2/4$. From (11) we have

$$(32) \quad v_{n+1} \leq v_n - \frac{v_n^2}{2} + \frac{(1-v_n)^2}{2} = \frac{1}{2}.$$

Since $u_n \rightarrow 0$, for any small $\varepsilon > 0$ there exists N such that for $n \geq N$ we have

$$v_{n+1} \leq v_n - \frac{v_n^2}{2} + \varepsilon = h_\varepsilon(v_n), \text{ say.}$$

This function $h_\varepsilon(v)$ is monotonic, and strictly increasing when $v < 1$, which by (32) is always the case.

Since h_ε is monotonic, $v_{n+2} \leq h_\varepsilon(v_{n+1}) \leq h_\varepsilon^{(2)}(v_n)$ where $h_\varepsilon^{(m)}$ is the m th iterate of h_ε . Thus $v_{n+r} \leq h_\varepsilon^{(r)}(v_n)$ for every r . Using a simpler variant of the argument employed in the analysis of model II, we deduce the existence of numbers d_ε such that for each ε and every v , $\lim_{n \rightarrow \infty} h_\varepsilon^{(n)}(v) = d_\varepsilon$: It follows, as before, that $\limsup_n v_n \leq d_\varepsilon$. Since $d_\varepsilon \rightarrow 0$ as $\varepsilon \rightarrow 0$ this proves the convergence of v_n to zero.

Now let $k(v) = v - v^2/2$. At the origin this function has slope 1 so that iterates of $k(v)$ converge to the fixed point 0 at an algebraic rate (i.e., like $1/n$ for the n th iterate). But $v_{n+1} \geq k(v_n)$ and since k is monotonically increasing $v_{n+m} \geq k^{(m)}(v_n)$. Thus v_n converges to zero no faster than at an algebraic rate. Note that on the basis of (31), u_n disappears extremely quickly, faster in fact than any geometric rate. In this case $u_n \rightarrow 0$, $v_n \rightarrow 0$, $w_n \rightarrow 1$. Obviously if $w_0 < u_0$ a similar argument establishes that $u_n \rightarrow 1$, $w_n \rightarrow 0$, $v_n \rightarrow 0$. We indicated in the first section the simple proof of the fact that if $u_0 = w_0$, the equilibrium point $u_e = w_e = 1/4$, $v_e = 1/2$ is achieved after one generation.

Model V: Referring to equations (13), (14), (15) we consider the expression

$$w_{n+1} - u_{n+1} = (w_n + \frac{1}{2} v_n)^2 - \frac{v_n^2}{4} - \frac{u_n v_n}{2} - \frac{u_n v_n}{2(1-u_n)}$$

which after elementary manipulations reduces to

$$w_{n+1} - u_{n+1} = (w_n - u_n) + \frac{u_n^2(1-u_n+w_n)}{2(1-u_n)}$$

Hence $(w_n - u_n)$ is an increasing sequence bounded above by 1, so the sequence $(w_n - u_n)$ must converge to some limit, call it α . Thus $(u_n^2(1-u_n+w_n))/2(1-u_n) \rightarrow 0$ as $n \rightarrow \infty$. Now $(u_n^2(1-u_n+w_n))/2(1-u_n) \geq u_n^2/2$. Hence $u_n \rightarrow 0$ as $n \rightarrow \infty$, and since $(w_n - u_n)$ converges to α , we have $w_n \rightarrow \alpha$, $v_n \rightarrow 1 - \alpha$. From (15) we see that $\alpha = ((\alpha+1)/2)^2$ and hence $\alpha = 1$ since $0 < \alpha \leq 1$. Therefore we have proved

the global convergence to the fixed point $(0,0,1)$. It remains to establish the rate of convergence. Return to equation (14). If we substitute $w_n = 1 - u_n - v_n$ into the right hand side of (14) it is not difficult to see that

$$\begin{aligned} v_{n+1} &= v_n - \frac{v_n^2}{2} + \frac{2u_n - 2u_n v_n - u_n^2}{2} + \frac{w_n u_n}{2} \frac{(2-u_n)}{(1-u_n)} \\ &= v_n - \frac{v_n^2}{2} + R(u_n, v_n, w_n) \end{aligned}$$

where $R(u_n, v_n, w_n)$ is positive, and for any ε we can find N such that $n \geq N$ ensures that $R(u_n, v_n, w_n) \leq \varepsilon$. Paraphrasing the argument as used in the analysis of model IV proves that the convergence of v_n to zero is no faster than algebraic.

The Model of NAYLOR: Consider equations (16), (17), (18). From the fact that $u_n + w_n + v_n = 1$ we obtain $u_n = \frac{1}{2}(1-v_n+c)$, $w_n = \frac{1}{2}(1-v_n-c)$. Returning to (17) we have

$$(33) \quad v_{n+1} = \frac{v_n}{2} + \frac{((1-v_n)^2 - c^2)}{2(1-v_n)} = \frac{1-v_n-c^2}{2(1-v_n)} = F(v_n), \text{ say.}$$

From (33) the complete time dependent behavior of v_n can be obtained in analytic terms owing to the fact that $F(v)$ is a linear fractional transformation. The fixed point, the admissible root of $F(v) = v$, that is of the equation $2v^2 - 3v + (1-c^2) = 0$ is

$$v_e = \frac{3}{4} - \frac{\sqrt{1+8c^2}}{4}.$$

Note that $v_e < \frac{1}{2}$. Let $r_1 = \frac{3}{4} - \frac{1}{4}(\sqrt{1+8c^2})$, $r_2 = \frac{3}{4} + \frac{1}{4}(\sqrt{1+8c^2})$. Then the time dependent behavior of the heterozygote frequency is retrievable from the identity

$$\frac{v_n - r_1}{v_n - r_2} = \left(\frac{1 - r_2}{1 - r_1} \right)^n \frac{v_0 - r_1}{v_0 - r_2}.$$

(see Karlin 1966 Chapter 11 for justification). Note that $F'(\xi) = [-c^2/2(1-\xi)^2]$ which is negative. At the point r_1 , $F'(r_1) = [-8c^2/(1+\sqrt{1+8c^2})^2]$ so that $|F'(r_1)| < 1$ and the equilibrium is stable. The limiting values of u_n, w_n can be obtained from $u_e = w_e + c$ and

$$w_e = \frac{1-c-v_e}{2} = \frac{1}{8} - \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}, \quad u_e = \frac{1}{8} + \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}.$$

The convergence to the equilibrium

$$u_e = \frac{1}{8} + \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}, \quad v_e = \frac{3}{4} - \frac{\sqrt{1+8c^2}}{8}, \quad w_e = \frac{1}{8} - \frac{c}{2} + \frac{\sqrt{1+8c^2}}{8}$$

is geometrically fast with rate $-8c^2/(1+\sqrt{1+8c^2})^2$.

Model III'. (zygote elimination modification of model III). Consider the recursion set (19), (20), (21). We have $u_{n+1}/w_{n+1} = (u_n/w_n) \cdot (v_n/v_n+w_n)$. If $w_0 \neq 0$ then u_n/w_n is a decreasing sequence, bounded below by zero; it therefore has a limit, say α . If $\alpha > 0$ then we must have $\lim_n (v_n/v_n+w_n) = 1$. Now $\lim v_n$ and $\lim w_n$ cannot both be zero, and since u_n/w_n is decreasing, this last relation implies that $\lim w_n = 0$. In this event, u_n/w_n cannot be decreasing unless $\lim u_n = 0$ and so $\lim v_n = 1$ which is absurd. Hence $\alpha = 0$.

Now consider

$$\frac{v_{n+1}}{w_{n+1}} = \frac{u_n}{w_n} + \frac{v_n + u_n}{v_n + w_n} = \frac{u_n}{w_n} + \frac{\frac{v_n}{w_n} + \frac{u_n}{w_n}}{\frac{v_n}{w_n} + 1}.$$

Let $u_n/w_n = \gamma_n \rightarrow 0$. Then γ_n is bounded for all n . Obviously $(v_n/w_n)/(1 + v_n/w_n)$ is bounded by 1. Hence v_n/w_n is uniformly bounded (in n) and therefore $w_n/v_n \geq \beta > 0$ for some β .

Now let $z_{n+1} = v_{n+1}/w_{n+1} = \gamma_n + (z_n + \gamma_n)/(1 + z_n)$ then $z_{n+1} \geq z_n/(1 + z_n)$. Now the function $f(u) = u/(1 + u)$ is a monotone increasing function of the "linear fractional" type. Hence $z_1 \geq f(z_0) = \bar{z}_1$ say, and

$$z_2 \geq \frac{z_1}{1 + z_1} \geq \frac{\bar{z}_1}{1 + \bar{z}_1}$$

or, $z_2 \geq f^{(2)}(z_0)$. Hence, in general $z_n \geq f^{(n)}(z_0)$. But the unique fixed point of the iterative scheme $(f^{(n)})$ is zero, and the rate of approach to this fixed point is no faster than algebraic, since $f'(0) = 1$.

Now since $\gamma_n \downarrow 0$ given $\varepsilon > 0$, there exists n_0 such that for $n > n_0$

$$z_{n+1} \leq \varepsilon + \frac{z_n + \varepsilon}{1 + z_n}.$$

Let

$$g_\varepsilon(u) = \varepsilon + \frac{u + \varepsilon}{1 + u}.$$

Then for ε small enough, g_ε is also monotonically increasing. We have $z_{n_0+1} \leq g_\varepsilon(z_{n_0})$ and hence, for any $n \geq n_0$, $z_{n+2} \leq g_\varepsilon(z_{n+1}) \leq g_\varepsilon(g_\varepsilon(z_n)) = g_\varepsilon^{(2)}(z_n)$. By induction we have $z_{n_0+m} \leq g_\varepsilon^{(m)}(z_{n_0})$ for every m . As in model II, there exist numbers p_ε with $\lim_{\varepsilon \downarrow 0} p_\varepsilon = 0$ such that as $n \rightarrow \infty$ $g_\varepsilon^{(n)}(z) \rightarrow p_\varepsilon$ for every z . Hence $\limsup_n z_n \leq p_\varepsilon$. Now as $\varepsilon \downarrow 0$, $g_\varepsilon \rightarrow f$. Thus $\lim_{\varepsilon \downarrow 0} p_\varepsilon = \lim_{n \rightarrow \infty} f^{(n)}(z_0)$ for any initial z_0 . But this last limit is zero and hence $\limsup_n z_n = 0$. This means of course that $z_n \rightarrow 0$, or $v_n \rightarrow 0$, and since $u_n/w_n \downarrow 0$ we have $w_n \rightarrow 1$ with the convergence at best algebraically fast.

CONCLUDING REMARKS

The following are the most important conclusions to be drawn from the models investigated in this paper.

(i) Whenever an allele is certain to disappear, the loss occurs extremely slowly (usually at a rate slower than algebraic). Thus if a wild population is observed to contain alleles in low frequencies, it is possible that some of these alleles are disappearing, but so slowly that they appear to be in a quasi-balanced equilibrium. Since disappearance happens over a considerable span of time, conceivably conditions could change so substantially that the structure of the prevailing mating system and its inherent selection characteristics become inapplicable.

(ii) In many cases the initial conditions play a major role in determining the

ultimate equilibrium behavior. For this reason one has to be very careful in interpreting numerical computations, as special cases could be misleading.

(iii) Usually when there is a stable interior equilibrium, convergence to this equilibrium occurs rapidly, in fact at a geometric rate.

(iv) The effects of the various mating systems parallel those of related selection models with random mating. The comparison can be extended. For example, in the zygote elimination models, postulating that certain matings be infertile is equivalent to imposing a fertility coefficient $f = 0$ for these matings. More generally, in those cases where one allele disappears algebraically, the inclusion of a fertility factor f with $0 < f < 1$ would most likely slow the rate of loss of this allele even further.

Again in models II and II' the mating system leads to a situation of polymorphism resembling that due to over-dominance in fitness. In these models the heterozygote obtains its selective advantage through the prohibition or infertility of matings between like homozygotes. In most of the models treated in this paper similar comparisons can be made and demonstrate that many phenomena usually attributed to some sort of selection pressure have alternative explanations in terms of the mating system.

(v) It is unusual to find model-free phenomena in population genetics but the above properties of the equilibrium behavior, and the relations of the models to corresponding situations of random mating with selection are rather robust. Looking at the equilibrium behavior in particular, the conclusions (i), (ii) and (iii) are pertinent to most of the pollen and zygote elimination models, and also to a broad class of models involving random mating with directed selection.

(vi) Our investigation of the pollen elimination model in which the matings $AA \times AA$ and $Aa \times Aa$ were prohibited produced several surprising conclusions. A previously unnoticed equilibrium $u_e = v_e = \frac{1}{2}$, $w_e = 0$ with a definite although small domain of attraction has been established. Whereas the rate of approach to this new equilibrium is very fast (geometric), the rate of approach to the intuitively obvious equilibrium, $u_e = v_e = 0$, $w_e = 1$, is extremely slow (algebraic). When zygote elimination is assumed the equilibrium $u_e = v_e = \frac{1}{2}$, $w_e = 0$ becomes essentially irrelevant and provided $w_0 > 0$ the genotype frequencies always converge algebraically to $u_e = v_e = 0$, $w_e = 1$. This demonstrates the delicate balance that can exist between the mating system and ultimate configuration achieved. It also indicates that in this model, the mode of selection inherent in the zygote elimination version is stronger than that defined by the pollen elimination case.

We have exhibited methods for the complete analysis of the equilibrium behavior of several incompatibility models. Using the inequalities secured in these analyses it is also possible to approximate the time dependent behavior of the models. The techniques used in the present context could be applicable to other models arising in population genetics. The greater effort involved in rendering a complete analysis is certainly rewarding in view of the more illuminating information obtained.

Many iterative schemes commonly encountered in mathematical investiga-

tions, even those involving only quadratic transformations cannot be analysed in explicit terms and often exhibit weird behavior (see e.g., ULAM 1963). It is a mysterious but fortuitous property of genetically arising systems that many are susceptible to complete analysis. Although there is no single method for accomplishing this analysis we have illustrated several techniques which apply in considerable generality. An essential ingredient of the method involves uncovering particular functions of the frequencies endowed with relevant monotonicity properties. Linear fractional functions arise in a number of places and for these the transient behavior is easily obtained. (For more on this see BODMER, FELDMAN and KARLIN, manuscript in preparation.)

SUMMARY

A group of models of negative assortative mating involving pollen elimination, proposed originally by WORKMAN, is considered. A complete mathematical analysis is carried out to determine the equilibria, domains of attraction and rates of approach. In particular, it is found that whenever an allele is destined to disappear it usually does so at an algebraic or very slow rate. The models are compared with their counterparts involving what was called by FINNEY "zygote elimination", and referred to by other authors as "mass-action" models.

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