AN ASSORTATIVE MATING ENCOUNTER MODEL*

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Received 19.ii.79

1. INTRODUCTION

It has been suggested by a number of theoretical and experimental population geneticists (Karlin, 1968; Scudo and Karlin, 1969; O'Donald, 1978*a*, 1978*b*) that models of sexual selection, and of assortative mating, should be considered in which the mating preferences of one sex (usually the female) are not rigidly expressed, but are to a certain extent influenced by behavioural characteristics and availability of the preferred type. Specifically, one can suppose that a female possessing a preference for one type of male will initially mate only with that type; but if after a certain number of encounters the desired male partner has not been met, then the level of stimulation will have been raised to the point where she will effectively mate at random.

This model is based on a general pattern of female mating behaviour (O'Donald, 1978*a*, 1978*b*, 1979): females are often reluctant to mate at first, but after receiving the stimulation of male courtship, they can respond and mate when a certain threshold has been reached. Thus females will exercise preferences between different types of males if they respond to each type of male at different thresholds. If a female has a lower threshold to one type of male, she will need extra encounters with the other types of male before she has been stimulated sufficiently to mate at random with any type of male. The number of these extra encounters is therefore a parameter of the "encounter models".

In this paper we study the equilibrium configurations in two such models within the following general framework: a population is exhibiting positive assortative mating between classes of individuals determined by the genotype at a certain locus at which two alleles, A and a , are segregating. The following assumptions are incorporated into the model: (a) discrete generations are formed, with each individual participating in only one mating season. (b) The population size is so large that random genetic drift may be neglected, and the changes in genotypic frequencies may be followed deterministically. (c) The sex ratio among the offspring in each generation is one-to-one, so that male and female genotypic frequencies are the same. (d) Mating is polygynous, so that every female finds a mate. (e) No viability selection, nor any mutation or migration takes place.

To each assorting class we need to ascribe two parameters: the " α " parameter, which gives the proportion of females of that class who will prefer to mate with a male of the same class, and the " n " parameter,

* Supported in part by NIH Grant GM10452-15 and NSF Grant MCS76-80624-A01.

which is the number of encounters such a female must have with males before she reaches a level at which she will then mate "at random".

The two genetic models analysed here are as follows:

Model I. A is dominant to a , so that there are two assorting classes:

	AA, Aa	aa
" α " parameter	α	γ
" n " parameter	k	n

Model II. The three genotypes form separate classes:

	AA	Aa	aa
" α " parameter	α	β	γ
" n " parameter	k	m	n

To ease the exposition, this second model is analysed in the case of symmetry between the alleles — i.e., $\alpha = \gamma$, $k = n$, and furthermore only under the extra condition $k = n = 1$. It is expected that the qualitative conclusions apply with more general parameters.

(i) *Remarks.* (i) It is clear that the " α " parameter must satisfy $0 \leq \alpha \leq 1$: increasing α corresponds to a greater tendency to mate assortatively within a phenotypic or genotypic class. (ii) The " n " parameter measures the extent of expression of the assortative preference. As $n \rightarrow \infty$ one approaches the usual model in which an assorting female necessarily chooses a mate of the same type. (iii) The non-assorting females (e.g. $(1-\gamma)$ of aa) are assumed to mate at random from the outset. (iv) Unlike the sexual selection models, we do not have the result that all equilibria will exhibit Hardy-Weinberg proportions (Karlin, 1978). This hinders the determination and analysis of polymorphic equilibria. (v) The corresponding models for sexual selection have been analysed in O'Donald (1978a, 1979), and Karlin and Raper (1979). In these models the " α " parameter is to be interpreted as the proportion of all females who prefer males of that class: in this case we have the restrictions $\alpha + \gamma \leq 1$ and $\alpha + \beta + \gamma \leq 1$, respectively.

2. ANALYSIS AND RESULTS

In both models, let $\mathbf{x} = (u, v, w)$ be the vector of genotypic frequencies; u, v , and w are the population frequencies of the genotypes AA, Aa and aa , so that $u+v+w = 1$. Let $p = u + \frac{1}{2}v$ and $q = w + \frac{1}{2}v$; these are the gene frequencies of the alleles A and a respectively.

(i) *Model 1.*

The frequencies of mating are:

Mating	Frequencies
$AA \times AA$	$u^2 \left[\alpha w \frac{1-w^k}{1-w} + 1 \right]$
$AA \times Aa$	$2uv \left[\alpha w \frac{1-w^k}{1-w} + 1 \right]$
$AA \times aa$	$uw [2 - \alpha(1-w^k) - \gamma\{1 - (1-w)^n\}]$

$$\begin{aligned}
Aa \times Aa & \quad v^2 \left[\alpha w \frac{1-w^k}{1-w} + 1 \right] \\
Aa \times aa & \quad vw[2 - \alpha(1-w^k) - \gamma\{1 - (1-w)^n\}] \\
aa \times aa & \quad w^2 + \gamma\{1 - (1-w)^n\}w(1-w).
\end{aligned}$$

The population state at each generation is described by the variables (p, w) . The recursion relations from one generation to the next are:

$$p' = p \left(1 + \frac{w}{2} f(w) \right), \quad w' = (1-p)^2 + \alpha w \frac{1-w^k}{1-w} p^2 - p w f(w),$$

where $f(w) = \alpha(1-w^k) - \gamma[1 - (1-w)^n]$ as shown in table 1.

TABLE 1
Equilibria and conditions for stability in Model I with dominance

	<i>A</i> -fixation (1, 0, 0)	<i>a</i> -fixation (0, 0, 1)	Polymorphic equilibria (u^*, v^*, w^*)
$\alpha > 0$ $\gamma > 0$	Locally stable	Locally stable	There is a unique unstable polymorphism determined by $0 < w^* < 1$, $f(w^*) = 0$ and $0 < p^* < 1 - w^*$, $h(p^*, w^*) = 0$
$\alpha = 0$ $\gamma > 0$	Unstable	Globally stable	None
$\alpha > 0$ $\gamma = 0$	Globally stable	Unstable	None

$\alpha = \gamma = 0$ The model reduces to the standard random-mating model with a curve of neutrally stable Hardy-Weinberg equilibria.

$$\begin{aligned}
f(w) &= \alpha(1-w^k) - \gamma\{1 - (1-w)^n\} \\
h(p, w) &= p^2 \left[1 + \alpha w \frac{1-w^k}{1-w} \right] - 2p + 1 - w.
\end{aligned}$$

The local stability of (1, 0, 0) (*i.e.* *A*-fixation) is examined by considering the sequence of p -values, p_n .

If $p_0 > 1 - w^*$ and $\alpha > 0$, then $p_n \rightarrow 1$ and $w_n \rightarrow 0$.

The local stability conditions for (0, 0, 1) and the polymorphic equilibrium are obtained through consideration of the eigenvalues of the gradient matrix evaluated at each equilibrium point, respectively.

(ii) *Model II.*

The frequencies of matings with general parameters and with the restriction $k = m = n = 1$ are now as follows:

	<i>Frequency with any values of</i> <i>k, m and n</i>	<i>Frequency when</i> <i>k = m = n = 1</i>
<i>AA</i> × <i>AA</i>	$\alpha u[1 - (1-u)^{k+1}] + u^2(1-\alpha)$	$u^2 + \alpha u^2(1-u)$
<i>AA</i> × <i>Aa</i>	$\alpha u \left(\frac{v}{1-u} \right) (1-u)^{k+1} + \beta v \left(\frac{u}{1-v} \right) (1-v)^{m+1}$ $+ uv(2 - \alpha - \beta)$	$2uv - \alpha u^2 v - \beta uv^2$

<i>Mating</i>	<i>Frequency with any values of k, m and n</i>	<i>Frequency when k = m = n = 1</i>
$AA \times aa$	$\alpha u \left(\frac{w}{1-u} \right) (1-u)^{k+1} + \gamma w \left(\frac{u}{1-w} \right) (1-w)^{n+1} + uw(2-\alpha-\gamma)$	$2uw - \alpha u^2 w - \gamma uw^2$
$Aa \times Aa$	$\beta v [1 - (1-v)^{m+1}] + v^2(1-\beta)$	$v^2 + \beta v^2(1-v)$
$Aa \times aa$	$\beta v \left(\frac{w}{1-v} \right) (1-v)^{m+1} + \gamma w \left(\frac{v}{1-w} \right) (1-w)^{n+1} + vw(2-\beta-\gamma)$	$2vw - \beta v^2 w - \gamma vw^2$
$aa \times aa$	$\gamma w [1 - (1-w)^{n+1}] + w^2(1-\gamma)$	$w^2 + \gamma w^2(1-w)$

In the symmetric case, $\alpha = \gamma$, the population is described by the parameters v and $z = u - w$. The recursion relations are:

$$z' = z \left[1 + \frac{\alpha - \alpha z^2 - v^2(\alpha + 2\beta)}{4} \right], \quad v' = \frac{1}{2} - \frac{z^2}{2} \left(1 - \frac{\alpha}{2} + \alpha v \right) - \frac{\alpha}{4} (1-v)^2;$$

$= 0$ gives any symmetric equilibria: v must then satisfy $v = \frac{1}{2} - \frac{\alpha}{4} (1-v)^2$.

This has exactly one root in $0 \leq v \leq 1$. Local stability conditions are again obtained from the gradient matrix.

Asymmetric equilibria, with $z \neq 0$, must satisfy

$$\alpha - \alpha z^2 - v^2(\alpha + 2\beta) = 0, \quad \text{or} \quad z^2 = 1 - v^2 \left(\frac{\alpha + 2\beta}{\alpha} \right).$$

TABLE 2

Equilibria and conditions for stability in Model II with separate preferences for each of the three genotypes

Parameters	Fixation states	Symmetric equilibria (u^*, v^*, w^*): $u^* = w^*$	Asymmetric equilibria ($\tilde{u}, \tilde{v}, \tilde{w}$): $\tilde{u} \neq \tilde{w}$
		A unique <i>unstable</i> equilibrium, given by	
$\beta < \rho(\alpha)$ $\alpha > 0$	Locally stable	$\frac{1}{v^*} = \sqrt{\frac{2}{2-\alpha}} + 1$ $u^* = w^* = \frac{1}{2}(1-v^*)$	None
$\beta > \rho(\alpha)$ $\alpha > 0$	Locally stable	A unique stable equilibrium as above	Two, symmetrically displaced, unstable equilibria: $\tilde{v} > 0, g(\tilde{v}) = 0$ $(\tilde{u} - \tilde{w})^2 = 1 - \tilde{v}^2 \left(\frac{\alpha + 2\beta}{\alpha} \right)$
$\alpha = 0$ $\beta > 0$	Unstable	A globally stable equilibrium $v^* = \frac{1}{2}, u^* = w^* = \frac{1}{4}$	None
$\alpha = \beta = 0$	No assortment in force: neutrally stable Hardy-Weinberg equilibria		

$$\rho(\alpha) = \frac{\alpha}{2-\alpha} + \alpha \sqrt{\frac{2}{2-\alpha}}$$

$$g(v) = v^2(\alpha + 2\beta) + v \left(\frac{\alpha + 2\beta}{\alpha} - \alpha - \beta \right) - 2$$

For z to be real we must have $v^2 < \frac{\alpha}{\alpha+2\beta}$. Substituting for z^2 into the equation $v = v'$ gives the equation $g(v) = 0$, where the function g is defined in Table 2.

The condition for the existence of a root of g in the range $0 \leq v \leq \sqrt{\frac{\alpha}{\alpha+2\beta}}$ turns out to be $\beta > \rho(\alpha)$, *i.e.* precisely the condition that the symmetric equilibrium should be stable with ρ as defined in table 2. Examination of the eigenvalues of the gradient matrix shows that the asymmetric equilibria are always unstable. Once $\tilde{v}$ is found, there are two possible values for $\tilde{z}$, of opposite sign, hence two asymmetric equilibria placed symmetrically on either side of the line $z = 0$. Tables 1 and 2 give the results of the analysis of the equilibria and stability conditions for the two models.

(iii) *Comments on the results.*

(a) *Model I.* (i) The local stability of the two fixation states is independent of the influence of the encounter process as characterised by the parameters k and n . Fixation of A is locally stable if and only if $\alpha > 0$ — *i.e.* there is some assortative mating in the A -class; fixation of a is locally stable if and only if $\gamma > 0$.

(ii) The asymptotic rate of approach to fixation of a is also independent of k and n , being at a geometric rate of $1 - \frac{1}{2}\gamma$. The approach to A -fixation (when it is stable) is slower at an algebraic rate—as is usual for the fixation of a dominant allele.

(iii) No stable polymorphic equilibrium exists.

(iv) A polymorphic equilibrium exists only in the case when both fixation states are stable: it is, itself, unstable.

(v) k and n do affect the exact location of the polymorphic equilibrium (when $\alpha, \gamma > 0$). When $\alpha, \gamma > 0$ and the fixation states are stable, it is not easy to demarcate precisely the two domains of attraction. It is clear, however, that the unstable polymorphism must lie on the surface separating the domains. Also, it is part of the proof that if the initial value of p is greater than $1 - w^*$ then the population will converge to fixation of A .

(vi) In view of (v), it is of interest to see how the parameters affect the position of the unstable polymorphism, and in particular, the value of w^* . Studying the function f we see that $f(w)$ decreases monotonically from $+\alpha$ to $-\gamma$ as w goes from 0 to 1. Furthermore, increasing α or k increases $f(w)$; but increasing γ or n decreases $f(w)$. This is illustrated in figure 1.

We see that

greater α or k implies a greater value for w^*
greater γ or n implies a smaller value for w^* .

Although the value of w^* does not circumscribe the domains of attraction, the above results appear to indicate the following effect:

Increasing the amount of assortative mating expressed by either class tends to *decrease* the domain of attraction towards fixation of the corresponding allele.

(vii) The results given by Karlin (1968, 1978) for the corresponding model in which assorting females necessarily choose mates of their own class can be obtained by letting k and $n \rightarrow \infty$.

As $k, n \rightarrow \infty$, f takes the form shown in figure 2.

FIG. 1.—Graph of $f(w)$. FIG. 2.—Graph of $f(w)$ for $k, n \rightarrow \infty$.

If $\alpha > \gamma$, then $w^* \rightarrow 1$ as $k, n \rightarrow \infty$, so that in the limit fixation of A is globally stable. Conversely, if $\alpha < \gamma$, then $w^* \rightarrow 0$ and fixation of a is globally stable. Actually, for $\alpha > \gamma$ it suffices that $k \rightarrow \infty$ to make fixation of A globally stable; for $\alpha < \gamma$, $n \rightarrow \infty$ is sufficient to make a -fixation globally stable.

(b) *Model II.* (viii) $m = n = 1$ are fixed in this model, so the only variable parameters are $\alpha = \gamma$ and β , the proportions of assorting homozygotes and heterozygotes, respectively. Note that although AA and aa females have the same parameter α , they still assort separately—viz. AA females select AA males (if they can) and not just homozygotes in general.

(ix) In view of the imposed symmetry, it is not surprising to find that there is always a symmetric equilibrium, and only one. Its position is determined solely by α , the homozygotes' assorting parameter.

(x) The fixation states are locally stable if and only if the homozygotes' parameter α is non-zero. This is the analogue of remark (i) for Model I.

(xi) A result not shown in the table is that the quantity $u - w$ maintains a constant sign from one generation to the next. This is a help in determining the domains of attraction in the case $\beta < \rho(\alpha)$.

(xii) $\rho(\alpha)$ for positive α is an increasing function ranging from $\rho(0) = 0$ to $\rho(1) = 1 + \sqrt{2}$. There is a unique α_0 in the interval $[0, 1]$ with the property that $\rho(\alpha_0) = 1$. (α_0 is given as a root of the equation $\alpha^3 - 4\alpha + 2 = 0$: $\alpha_0 \approx 0.54$).

Since $\beta \leq 1$, $\alpha > \alpha_0$ necessarily implies that $\beta < \rho(\alpha)$. Also, for fixed $\beta > 0$, as α increases from 0 to 1, the symmetric equilibrium changes from being globally stable, to being locally stable and then unstable. Thus, greater values of α enhance the stability of the fixation state while diminishing the stability of the symmetrical equilibrium.

(xiii) On the other hand, for fixed α ($0 < \alpha < \alpha_0$), increasing β tends to make the symmetrical equilibrium *more* stable.

(xiv) Up to three stable equilibria can co-exist. This contrasts with the corresponding model with $m = n = \infty$ where there are no asymmetric equilibria, and the stabilities are given by

	Fixation states	Symmetric equilibrium
$\alpha < \beta$	Unstable	Globally stable
$\alpha > \beta$	Locally stable	Unstable

In this case the symmetric equilibrium has $v^* = \frac{1-\alpha}{2-\alpha}$.

3. DISCUSSION

The most important point to examine is whether these models, with their finite values for the "n" parameters differ qualitatively from the previously analysed models with infinite n 's. To put it another way, is there any qualitative change when the assorting females instead of rigidly choosing males of their own class, search for a male of the desired type for a certain period, and in the event of failing to find one then mate at random?

The most significant difference in this amended model is that the two states of fixation are more likely to be locally stable. In Model I,

both fixations are stable as long as $\alpha, \gamma > 0$, whereas in the corresponding " $k = n = \infty$ " model there is global convergence to fixation of one allele. As the values of k and n are increased, the domain of attraction to one or other of the fixation states becomes wider and wider and ultimately global in the limit. In Model II, both fixations are stable as long as $\alpha > 0$ ($m = n = 1$), whereas for $m = n = \infty$ the stability requirement is the stronger condition $\alpha > \beta$. In other words, there are values of the parameters which give local stability for both fixation states in these models, but which in the " $k, m, n = \infty$ "-models would give global convergence, either to a fixation in I, or to a central equilibrium in II.

This can lead to major re-evaluations of the chances of success for a new allele. Suppose that a population is fixed on the a -allele, and that by mutation or migration or otherwise, a small proportion of A -allele is introduced. It is found (say) that A is dominant to a , and that some assortative mating takes place among the dominant and recessive classes (α and γ positive, respectively), but no other pressures such as viability selection are acting. In the case that $\alpha > \gamma > 0$, the $k = n = \infty$ model would predict that the A allele becomes more frequent and eventually fixes: but with finite values for k and n , $\gamma > 0$ guarantees that fixation of a is locally stable, so that the newly introduced A will become extinct. Only when the values of k and n are very large (numerical computations suggest $k, n > 1000$), will the domain of attraction to $(1, 0, 0)$ be so wide as to include a low initial frequency of A and hence lead to its fixation.

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