Genet. Res., Camb. (1968), **11**, *pp.* 289–301
With 5 *text-figures*
Printed in Great Britain

Fertility differences between homogamous and heterogamous matings

BY C. CANNINGS
Department of Statistics, University of Aberdeen

(*Received* 28 *August* 1967)

1. INTRODUCTION

The investigation of the effect of fertility on population structure requires, for complete generality, that the number of offspring of every pair be specified. The most obvious simplification to introduce when constructing mathematical models of such a population, is that the fertility of a pair depends only on the genotypes of the individuals constituting that pair. Such an assumption enables us to express the genotypic frequencies in a generation in terms of those in the previous one, assuming we know the way in which pairs are formed.

However, even when we confine ourselves to a di-allelic autosomal locus and to a large random mating population the equations appear to be intractable (Bodmer, 1965). Penrose (1949) and Bodmer (1965) considered two special cases, treating the fertility of a pair as the sum and the product respectively of the two individuals' fertilities. Penrose appears to assume that Hardy–Weinberg equilibrium will apply irrespective of fertility differences, which is incorrect. Bodmer concludes that the equations obtained are of the same form as those for an autosomal diallelic locus when the sexes have different viabilities (see Owen, 1953). Purser (1966) proved that whenever there are fertility differences acting (in his sense, though not in ours, this means differential production of gametes between genotypes) then in the subsequent generation there will be an excess of heterozygotes compared with the Hardy–Weinberg equilibrium for the same gene frequency. In the case under consideration a deficiency of heterozygotes can occur. These three papers seem to be the only ones which attempt an analysis of the effects of differential fertility.

A recent study of the mode of inheritance and fitness in the Japanese quail (*Coturnix coturnix japonica*) by Sittmann, Wilson & McFarland (1966) led them to the conclusion that. . .'Judging from three different (although not independent) measures, fertility was consistently higher in homogamic than in heterogamic matings among wild-type and albino quail'. It seems profitable to attempt a mathematical analysis of the effects of such differences in fertility, and to discuss some of the ways in which these might affect both natural and sexual selection.

The mode of inheritance of the albino gene is as a sex-linked recessive, and it should be emphasized that the results in this paper apply only to an autosomal locus. We shall consider only two alleles, and the cases of dominance and no dominance will be discussed.

The model also has an interpretation which is applicable to the study of assortative mating, and the special cases of completely-positive and completely-negative assortative mating are fully treated.

2. AUTOSOMAL DIALLELIC LOCUS WITH DOMINANCE

We restrict our attention to a large random-mating population. The two alleles will be denoted by A and a, A being dominant to a. Since only the ratio of the fertilities is important we will assign the value 1 to heterogamous matings, and x to homogamous ones ($x > 0$). We are assuming that the viabilities are identical for each individual.

Thus each mating AA × AA, AA × Aa, Aa × Aa and aa × aa produces x offspring while AA × aa and Aa × aa produce 1.

If the genotypic frequencies are equal in the two sexes (as they will be after one generation of the model), and are denoted by P, Q, and R for AA, Aa and aa respectively, then in the following generation we have new genotypic frequencies P', Q' and R' where

$$\lambda P' = x(P+\tfrac{1}{2}Q)^2, \tag{1}$$

$$\lambda Q' = 2x(P+\tfrac{1}{2}Q)(\tfrac{1}{2}Q+R)+2(1-x)R(P+\tfrac{1}{2}Q), \tag{2}$$

$$\lambda R' = x(R+\tfrac{1}{2}Q)^2+(1-x)QR, \tag{3}$$

where $P+Q+R = 1$ and λ is such that $P'+Q'+R' = 1$.

If we combine equations (1) and (2) we obtain

$$\lambda\{P'+\tfrac{1}{2}Q'\} = \{P+\tfrac{1}{2}Q\}\{x+(1-x)R\} \tag{4}$$

and from (1), (2) and (3)

$$\lambda = x+2(1-x)R(1-R). \tag{5}$$

Thus at equilibrium (denoted by $\hat{P}$, $\hat{Q}$, $\hat{R}$, and $\hat{\lambda}$) from (4) we have, provided $(\hat{P}+\tfrac{1}{2}\hat{Q}) \neq 0$ (i.e. $\hat{R} \neq 1$),

$$\hat{\lambda} = x+(1-x)\hat{R}, \tag{6}$$

and from (5)

$$\hat{\lambda} = x+2(1-x)\hat{R}(1-\hat{R}). \tag{7}$$

Equations (6) and (7) lead immediately to the relation

$$(1-x)\hat{R} = 2(1-x)\hat{R}(1-\hat{R}). \tag{8}$$

Thus if $x \neq 1$ we have $\hat{R} = 0$, $\hat{R} = \tfrac{1}{2}$ or as obtained previously, $\hat{R} = 1$. (9)

The case $x = 1$ is of course that of no differences in fertilities and leads to Hardy–Weinberg equilibrium.

The three possible equilibria are discussed below.

(i) $\hat{R} = 0$, i.e. $\hat{P} = 1$, $\hat{Q} = 0$. All the members of the population are originally AA, and a is introduced by mutation.

If we examine the generation matrix at this equilibrium we find that the latent roots are zero and one (irrespective of the value of x). In order to determine the exact nature of the equilibria we require to examine second-order effects. One way of doing this is to examine the ratio of the A gene-frequency in successive generations. This is given by

$$\frac{x+(1-x)R}{x+2(1-x)R(1-R)} \quad \text{from (4) and (5).}$$

The limit of this expression as R tends to zero is one, corresponding to the latent root with value one. However, if R is small the expression is less than one, equal to one, or greater than one for $x < 1$, $x = 1$, or $x > 1$ respectively. Thus we have

$x > 1$ stable equilibrium,

$x < 1$ semi-stable equilibrium (Cormack, 1964).

(ii) $\hat{R} = 1$, i.e. $\hat{P} = 0$, $\hat{Q} = 0$. All the members of the population are originally aa, and A is introduced by mutation.

The latent roots of the generation matrix are 0 and $1/x$. Thus we have

$x > 1$ stable equilibrium,

$x < 1$ semi-stable equilibrium.

(iii) $\hat{R} = \frac{1}{2}$ then $\hat{\lambda} = \frac{1}{2}(1+x)$ which can be substituted into equation (3) to give

$$\hat{Q} = \frac{-1+\surd(1+x)}{x} \quad \text{and} \quad \hat{P} = \tfrac{1}{2}+\frac{1-\surd(1+x)}{x}. \tag{10}$$

If we consider $x^2\{\hat{Q}^2-4\hat{P}\hat{R}\}$ as a measure of the heterozygote frequency in comparison with the homozygote frequencies (as a comparison with Hardy–Weinberg result which gives this expression as zero) we obtain

$$x^2\{\hat{Q}^2-4\hat{P}\hat{R}\} = (1-x)\{2+x-2\surd(1+x)\} \tag{11}$$

which is +ve for $x < 1$, and −ve for $x > 1$.

In order to investigate the stability of this equilibrium we set up the generation matrix. This can be derived either from the derivatives of the right-hand sides of (1), (2) and (3), by Taylor's expansion, or by making perturbations ΔP, ΔQ and ΔR from the equilibrium and finding $\Delta P'$, $\Delta Q'$ and $\Delta R'$, the perturbations in the subsequent generation and neglecting second-order terms. If we carry out the necessary manipulation and eliminate ΔQ using $\Delta Q = -\Delta P-\Delta R$ we obtain

$$\begin{pmatrix}\Delta P'\\ \Delta R'\end{pmatrix} = \frac{1}{\hat{\lambda}}\begin{pmatrix} x(\hat{P}+\frac{1}{2}\hat{Q}) & -x(\hat{P}+\frac{1}{2}\hat{Q}) \\ -x\frac{1}{2}\hat{Q}-\frac{1}{2} & x+\hat{Q}-x\frac{1}{2}\hat{Q}-\frac{1}{2}\end{pmatrix}\begin{pmatrix}\Delta P\\ \Delta R\end{pmatrix}. \tag{12}$$

The fact that λ is maximized for $\hat{R} = \frac{1}{2}$ enables us to ignore λ while obtaining equation (12). Since small changes in $\hat{P}$, $\hat{Q}$ and $\hat{R}$ will only cause second-order changes $\hat{\lambda}$ we may neglect these.

For stability we require that $\max\{|\mu_1|, |\mu_2|\} < \hat{\lambda}$ where μ_1 and μ_2 are the roots of the characteristic equation obtained from (12),

$$\mu_2-\mu\{(1-x)(1-\hat{Q})+\tfrac{1}{2}(1+x)\}+\tfrac{1}{2}x(1-\hat{Q})^2(x-1) = 0. \tag{13}$$

It is possible to evaluate the equilibria and compare the moduli of the characteristic roots with λ, but the following analysis is probably a simpler way of obtaining conditions for stability.

Denote the function on the left-hand side of (13) by $F(\mu, x)$. Then

(i) $F(\mu, x)$ has two real roots for $x > 0$,

(ii) $F(\hat{\lambda}, x) = \frac{1}{2}(x-1)(1-\hat{Q})(-x\hat{Q}-1)$ which is < 0 for $x > 1$ and > 0 for $x < 1$, and

(iii) $F(0, x) = \frac{1}{2}x(1-\hat{Q})^2(x-1)$ which is > 0 for $x > 1$ and < 0 for $x < 1$.

These three results enable us to sketch the curves $F(\mu, x)$ for $x > 1$ (Fig. 1) and $x < 1$ (Fig. 2). For $x > 1$ there is always a root greater than $\hat{\lambda}$.

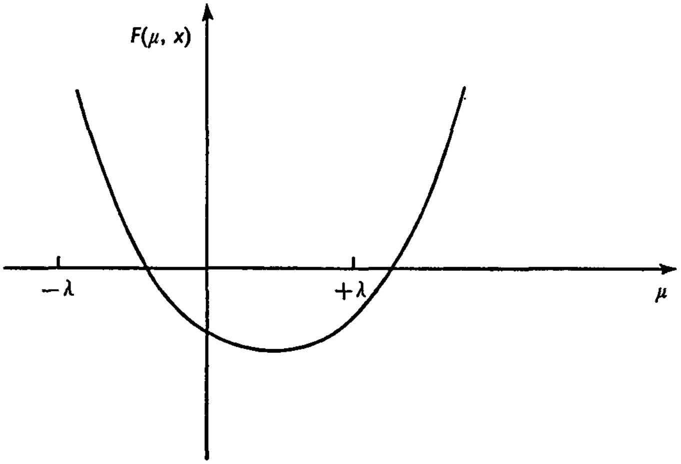

Fig. 1. Function $F(\mu, x)$ defined by left-hand side of (13) plotted against μ; $x > 1$.

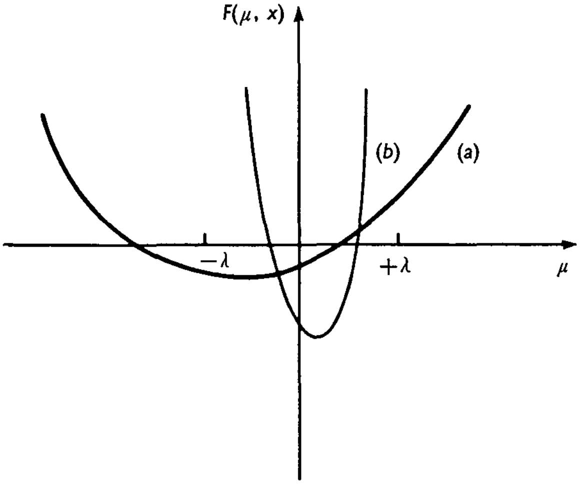

Fig. 2. Function of $F(\mu, x)$ defined by left-hand side of (13) plotted against μ; $x < 1$.

Figure 2 shows that there is one +ve and one −ve root for $x < 1$, and that the +ve root is less than $\hat{\lambda}$. Examination of the coefficient of μ in equation (13), shows us that $F(\mu, x)$ is symmetric about

$$\mu^* = \frac{1}{2}[(1-x)(1-\hat{Q})+\frac{1}{2}(1+x)]$$

and thus $\mu^* > 0$ for $x < 1$. The curve $F(\mu, x)$ for $x < 1$ is therefore of the form (*b*) in Fig. (2) rather than (*a*), and hence the negative root is greater than $-\lambda$.

Our equilibrium is stable if $x < 1$ and unstable if $x > 1$.

Examples

(i) $x = 3$. *Equilibria:*

$(1, 0, 0)$ neutral,
$(\frac{1}{6}, \frac{1}{3}, \frac{1}{2})$ unstable,
$(0, 0, 1)$ stable,
$(\hat{Q}^2 - 4\hat{P}R) = -\frac{2}{9}$.

(ii) $x = \frac{9}{16}$. *Equilibria:*

$(1, 0, 0)$ neutral,
$(\frac{1}{18}, \frac{4}{9}, \frac{1}{2})$ stable,
$(0, 0, 1)$ unstable,
$(\hat{Q}^2 - 4\hat{P}\hat{R}) = \frac{7}{81}$.

In general $(\hat{Q}^2 - 4\hat{P}\hat{R}) > 0$, i.e. $x < 1$ and stable equilibrium, $(\hat{Q}^2 - 4\hat{P}\hat{R}) < 0$, i.e. $x > 1$ and unstable equilibrium. This result is analogous to that for viability differences.

3. ASSORTATIVE MATING

The system considered in §2 was that of random mating with fertility differences between the pairs. The same model can be applied to assortative mating if we assume that given P AA's and R aa's, for example, then the proportion of AA × aa pairs is PR, whereas AA × Aa pairs are formed not in proportion PQ but in proportion xPQ. Thus if $x > 1$ there is positive assortative mating and for $x < 1$ negative assortative mating and the above analysis of §2 is immediately applicable.

There are two situations which are unreasonable as far as fertilities are concerned but not unreasonable for assortative mating; $x = 0$ and $x \to \infty$. These two cases are that of complete negative assortative mating and of complete positive assortative mating respectively.

(i) *Complete negative assortative mating;* $x = 0$

This situation has been fully treated by Li (1955) in connexion with self incompatibility in Primrose (Fig. 3). The equilibrium position is $\hat{P} = 0$; $\hat{Q} = \frac{1}{2}$; $\hat{R} = \frac{1}{2}$.

(ii) *Complete positive assortative mating* $x \to \infty$

The equations (1), (2) and (3) become

$$\lambda P' = (P + \tfrac{1}{2}Q)^2, \tag{14}$$

$$\lambda Q' = Q(P + \tfrac{1}{2}Q), \tag{15}$$

$$\lambda \hat{R}' = \tfrac{1}{4}Q^2 + R^2. \tag{16}$$

The result of this type of mating system is very simple to evaluate if we consider the population split into two distinct subpopulations. These subpopulations will consists of $\bar{\mathrm{A}}$ phenotypes and $\bar{\mathrm{a}}$ phenotypes respectively. In the first of these the genotype aa has effectively a viability of zero (although it may join the other $\bar{\mathrm{a}}$ phenotypes).

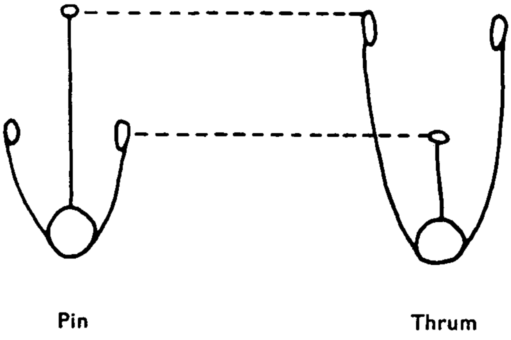

Fig. 3. Distyly as in Primrose.

The final situation is one in which we have two distinct populations of AA's and of aa's.

This case has been treated by Cormack (1964) and is included for completeness only.

4. AUTOSOMAL DI-ALLELIC LOCUS WITH NO DOMINANCE

The only change required from §2 is that the mating AA × Aa, which was previously considered as homogamous, is now heterogamous.

Therefore

$$\lambda P' = xP^2+PQ+xQ^2/4, \tag{17}$$

$$\lambda Q' = 2PR+PQ+QR+xQ^2/2, \tag{18}$$

$$\lambda R' = xR^2+RQ+xQ^2/4, \tag{19}$$

where

$$P+Q+R = 1 \quad \text{and} \quad P'+Q'+R' = 1.$$

W use the notation $\hat{P}$, $\hat{Q}$, and $\hat{R}$ for equilibrium as before. Multiplying both sides of (17) by $\hat{R}$, both sides of (19) by $\hat{P}$ and combining we have

$$x\hat{P}\hat{R}^2+\hat{P}\hat{Q}\hat{R}+\frac{x\hat{R}\hat{Q}^2}{4} = x\hat{P}\hat{R}^2+\hat{P}\hat{Q}\hat{R}+\frac{x\hat{P}\hat{Q}^2}{4}$$

provided $\hat{P} \neq 0$ and $\hat{R} \neq 0$.

For $x \neq 0$ this reduces to

$$4\hat{P}\hat{R} = \hat{Q}^2, \tag{20}$$

or

$$\hat{P} = \hat{R}. \tag{21}$$

We now consider the four possible equilibria defined above.

(i) $\hat{P} = 0$, i.e. $\hat{Q} = 0$, $\hat{R} = 1$. This is identical to the situation discussed in §2 (ii) and thus we have:

$x > 1$ stable equilibrium,

$x < 1$ semi-stable equilibrium.

(ii) $\hat{P} = 1$, $\hat{Q} = 0$, $\hat{R} = 0$. Similar to (i) above:

$x > 1$ stable equilibrium,
$x < 1$ semi-stable equilibrium.

(iii) $Q^2 = 4\hat{P}\hat{R}$.

From equation (17) we obtain

$$\hat{\lambda} = x\hat{P} + \hat{Q} + x\hat{R}, \tag{22}$$

and from (18)

$$\hat{\lambda} = \tfrac{1}{2}\hat{Q} + \hat{P} + \hat{R} + \tfrac{1}{2}x\hat{Q},$$

which can be rearranged to give

$$\hat{\lambda} = 1 - \tfrac{1}{2}\hat{Q}(1-x). \tag{23}$$

Equating (22) and (23) gives

$$(1-x) = \tfrac{3}{2}\hat{Q}(1-x).$$

Thus either $x = 1$ (for which we know $\hat{Q}^2 = 4\hat{P}\hat{R}$) or $\hat{Q} = \tfrac{2}{3}$ which is impossible when $\hat{Q}^2 = 4\hat{P}\hat{R}$, leading to $\hat{P}$ and $\hat{R}$ with complex values.

We already know that $x = 1$ yields a neutral equilibrium.

(iv) $\hat{P} = \hat{R}$.

Substitution of $\hat{P} = \hat{R}$ and $(\hat{P} + \tfrac{1}{2}\hat{Q}) = (\tfrac{1}{2}\hat{Q} + \hat{R}) = \tfrac{1}{2}$ into (17) and (18) gives

$$\hat{\lambda}\hat{P} = \tfrac{1}{4}x - (x-1)\hat{P}\hat{Q} = \hat{\lambda}\hat{R}, \tag{24}$$

$$\hat{\lambda}\hat{Q} = \tfrac{1}{2} + (x-1)\tfrac{1}{2}\hat{Q}^2. \tag{25}$$

(17), (18) and (19) are added to obtain

$$\hat{\lambda} = x + 2(1-x)\hat{P}(2-3\hat{P}). \tag{26}$$

Then further manipulation of (24), (25) and (26) yields

$$6\hat{P}^3(x-1) - 6\hat{P}^2(x-1) + \hat{P}(2x-1) - \tfrac{1}{4}x = 0, \tag{27}$$

and an alternative expression follows

$$x = \frac{6\hat{P}^3 - 6\hat{P}^2 + \hat{P}}{6\hat{P}^3 - 6\hat{P}^2 + 2P - \tfrac{1}{4}}$$

which can be used to build up a table of $\hat{P}$ against x (see below).

A cubic equation has either one real root or three real roots. The nature of these roots can be determined in the usual manner, (Abromonitz & Stegun, 1964). In this case the number of real roots is determined by the sign of

$$F = \frac{(24)^2 + 18(x-1)(x-4)^2}{(18)^3(x-1)^3(24)^2}. \tag{29}$$

The numerator of F is +ve for all $x > 0$, and the denominator is +ve for $x > 1$, −ve for $x < 1$.

Thus if $x > 1$, $F > 0$ and there is only one real root;
if $x < 1$, $F < 0$ and there are three real roots.

We denote the roots of (27) by P_1, P_2, and P_3 then

$$P_1 + P_2 + P_3 = 1, \tag{30}$$

$$P_1P_2P_3 = \frac{x}{24(x-1)}, \tag{31}$$

i.e. $P_1P_2P_3 < 0$ for $x < 1$ which implies that one root is negative and two positive, or all three are negative. Equation (30) eliminates the second possibility, and so if we consider P_1 to be the negative root, (P_2+P_3) must exceed 1. However, $\hat{P} = \hat{R}$ and $\hat{P}$ is therefore $< \frac{1}{2}$ in the actual genetic situation. We can conclude that for $x < 1$ there is one negative root, one root between 0 and $\frac{1}{2}$ which is possible and one root greater than $\frac{1}{2}$ which is impossible. There is thus only one acceptable root for both $x < 1$ and $x > 1$; a unique non-degenerate equilibrium always exists. Table 1 contains some of the values of $\hat{P}$ and x, which can be obtained from equation (28).

Table 1. *The equilibrium value of the frequency of AA for various values of* x

$\hat{P}$	x
0·225	0·2939
0·230	0·4186
0·235	0·5520
0·240	0·6938
0·245	0·8433
0·250	1·0000
0·260	1·3317
0·270	1·6825
0·290	2·4151
0·350	4·0600
⋮	
0·500	'∞'

Stability of the equilibrium

It has been demonstrated that for $x > 0$ $(x \neq 1)$ there is a unique non-degenerate equilibrium. Although an explicit expression for $\hat{P}$ in terms of x has not been derived we are still able to investigate the stability. We consider the generation matrix near equilibrium and examine the latent roots, considered as functions of $\hat{P}$ and x.

The generation matrix near equilibrium is

$$\frac{1}{\hat{\lambda}}\begin{pmatrix}(1-\frac{1}{2}x)-5\hat{P}(1-x)+6\hat{P}^2(1-x) & \frac{1}{2}x-3\hat{P}(1-x)+6\hat{P}^2(1-x)\\ \frac{1}{2}x-3\hat{P}(1-x)+6\hat{P}^2(1-x) & (1-\frac{1}{2}x)-5\hat{P}(1-x)+6\hat{P}^2(1-x)\end{pmatrix}, \tag{32}$$

where $\hat{Q}$ has been eliminated $(\hat{Q} = 1-2\hat{P})$, and $\hat{P}$ substituted for $\hat{R}$. Since the matrix is doubly symmetric we may represent the characteristic equation by the determinant

$$\frac{1}{\hat{\lambda}}\begin{pmatrix}a-\hat{\mu} & b\\ b & a-\hat{\mu}\end{pmatrix} = 0 \tag{33}$$

which leads immediately to

$$\hat{\mu}^2-2a\hat{\mu}+(a^2-b^2) = 0.$$

Stability occurs if the two roots $\hat{\mu}_1 = a+b$ and $\hat{\mu}_2 = a-b$ are such that

$$|\hat{\mu}_1| < |\hat{\lambda}| \quad \text{and} \quad |\hat{\mu}_2| < |\hat{\lambda}|.$$

We thus compare

$$\hat{\mu}_1 = (1-x)(1-6\hat{P})(1-2\hat{P})$$

and $$\hat{\mu}_2 = 2\hat{P}(x-1)+1$$

with $$\hat{\lambda} = x+2\hat{P}(1-x)(2-3\hat{P}).$$

We require the following 3 results:

(i) $\hat{\lambda} = x(1-4\hat{P}+6\hat{P}^2)+2\hat{P}(2-3\hat{P}) > 0$ since $\hat{P} < \frac{1}{2}$.

(ii) $\hat{\mu}_1 = (1-x)(1-6\hat{P})(1-2\hat{P})$ and $\frac{1}{6} < \hat{P} < \frac{1}{2}$ and so

$$\begin{aligned}\hat{\mu}_1 &< 0 \quad \text{if} \quad x < 1\\ &= 0 \quad \text{if} \quad x = 1\\ &> 0 \quad \text{of} \quad x > 1.\end{aligned}$$

(iii) $\hat{\mu}_2 = 2\hat{P}x+(1-2\hat{P}) < 0$ since $\hat{P} < \frac{1}{2}$.

We now consider the two cases $x < 1$ and $x > 1$ separately.

(i) $x < 1,\ \hat{\lambda} > 0,\ \hat{\mu}_1 < 0,\ \hat{\mu}_2 > 0.$

$$\begin{aligned}|\hat{\lambda}|-|\hat{\mu}_1| &= \hat{\lambda}+\hat{\mu}_1\\ &= x+(1+x)(1-4\hat{P}+6\hat{P}^2)\\ &> 0 \quad \text{for all } \hat{P} \text{ and } x < 1.\end{aligned}$$

$$\begin{aligned}|\hat{\lambda}|-|\hat{\mu}_2| &= \hat{\lambda}-\hat{\mu}_2\\ &= (x-1)(1-6\hat{P}+6\hat{P}^2) \qquad (34)\\ &> 0 \quad \text{for all } x > 0 \text{ and } \hat{P}.\end{aligned}$$

See following section for proof that $(1-6\hat{P}+6\hat{P}^2) < 0$ for all $x > 0$.

Thus $|\hat{\lambda}| > |\hat{\mu}_1|$ and $|\hat{\lambda}| > |\hat{\mu}_2|$, hence for $0 < x < 1$ the equilibrium is stable.

(ii) $x > 1,\ \hat{\lambda} > 0,\ \hat{\mu}_1 > 0,\ \hat{\mu}_2 > 0.$

$$\begin{aligned}|\hat{\lambda}|-|\hat{\mu}_1| &= \hat{\lambda}-\hat{\mu}_1\\ &= x+(x-1)(1-12\hat{P}+18\hat{P}^2)\\ &> 0 \quad \text{for } x > 1 \text{ and all } \hat{P}.\end{aligned}$$

$$|\hat{\lambda}|-|\hat{\mu}_2| = \hat{\lambda}-\hat{\mu}_2$$

which therefore leads to equation (34) again. Thus if $x > 1$, $|\hat{\lambda}| > |\hat{\mu}_2|$.

The equilibrium is therefore semi-stable, Cormack (1964),

$$|\hat{\lambda}| > |\hat{\mu}_1| \quad \text{and} \quad |\hat{\lambda}| < |\hat{\mu}_2| \quad \text{for} \quad x > 1.$$

We have thus proved that the condition for stability is that $x < 1$ which was also the condition when there was dominance.

Another property which carries over from §2 is that relating stability to an excess of heterozygotes. Since $\hat{P}$ increases with x and is equal to $\frac{1}{4}$ for $x = 1$ there is an excess of heterozygotes for $x < 1$ and a deficiency for $x > 1$.

5. ASSORTATIVE MATING WITH NO DOMINANCE

The introductory remarks made in §3 are equally applicable here, although the mathematical treatment needed is more complex.

(i) *Complete negative assortative mating, i.e.* $x = 0$

Fisher & Mather (1943) considered the possible modes of inheritance of *Lythrum salicaria*. This plant is tristylic (Fig. 4) and although the style length is not determined by as simple a genetic mechanism as that treated here, it illustrates a way in which complete negative assortative mating might occur when three distinct genotypes exist. Sheppard (1952) observed partial negative assortive mating between the three phases of the moth *Panaxia*. Putting $x = 0$ in equations (17), (18) and (19) we have

$$\lambda P' = PQ,$$

$$\lambda Q' = 2PR+PQ+QR$$

and

$$\lambda R' \equiv RQ.$$

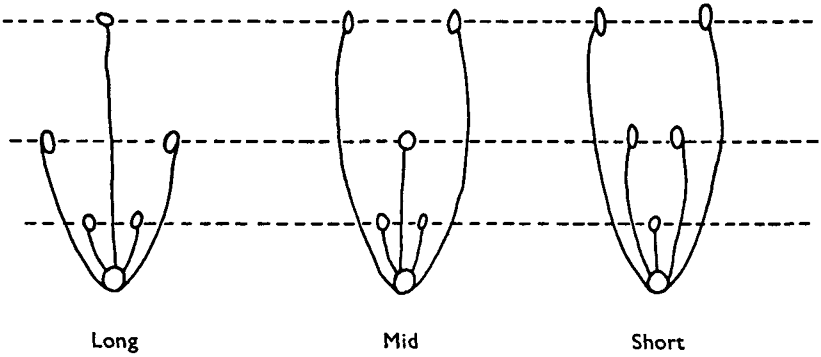

Fig. 4. Tristyly as in *Lythrum salicaria*.

We omit λ, and noting that P/R is a constant k say, where k is positive, from generation to generation we can replace the equations above by

$$P' = kQ,$$

$$R' = Q$$

and

$$Q' = 2kR+(1+k)Q.$$

If we now denote the nth generation by a suitable subscript we have

$$Q_{n+2} = 2kQ_n+(1+k)Q_{n+1}. \qquad (35)$$

These equations contain all the necessary information for finding our modified P, Q and R in any generation.

Equation (35) is a generalized Fibonacci sequence and we can investigate the behaviour of Q_n by evaluating α and β in a relation of the form

$$(Q_{n+2}-\alpha Q_{n+1}) = \beta(Q_{n+1}-\alpha Q_n) \qquad (36)$$

so that it is equivalent to (35). Thus there are two pairs of solutions (α_1, β_1) and (α_2, β_2), where

$$\alpha_1 = \beta_2 = \frac{(1+k)+\sqrt{(1+10k+k^2)}}{2}$$

and

$$\alpha_2 = \beta_1 = \frac{(1+k)-\sqrt{(1+10k+k^2)}}{2}.$$

For simplicity we shall consider only the situation when $0 < k < 1$, and we can then deduce the behaviour for $k > 1$. When we thus restrict k, β_1 lies in $(-1, 0)$ and so

$$(Q_{n+2}-\alpha_1 Q_{n+1}) \to 0 \quad \text{as} \quad n \to \infty.$$

Thus

$$\frac{Q_{n+2}}{Q_{n+1}} \to \alpha \quad \text{as} \quad n \to \infty.$$

Since

$$\frac{Q_{n+1}}{Q_{n+1}+(1+k)Q_n}$$

represents the genotypic frequency of the heterozygote we must now consider this, and

$$\frac{Q_{n+1}}{Q_{n+1}+(1+k)Q_n} \to \frac{\alpha_1}{\alpha_1+(1+k)} \quad \text{as} \quad n \to \infty.$$

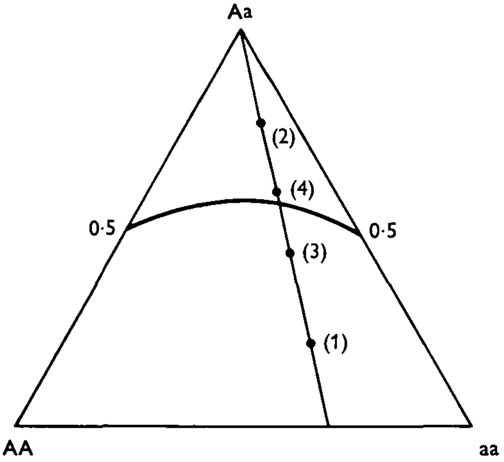

Fig. 5. Possible equilibria for varying values of k: thick line. Successive generations numbered (1), (2), (3), (4).

This gives us all the information required, i.e. that the proportion of heterozygotes in the population approaches the value

$$\frac{(1+k)+\sqrt{(1+10k+k^2)}}{3(1+k)+\sqrt{(1+10k+k^2)}}$$

is an oscillatory manner.

It is clear from the treatment above that the equilibrium position is stable when displacements from it leave P/R unaltered. When P/R changes, from k_1 to k_2 say, then a new equilibrium position is reached (see Fig. 5).

The convergence of the heterozygote frequency has been demonstrated above and we now derive an expression for this frequency in the nth generation. From (36) and (37) we have that

$$(Q_{n+2}-\alpha_1 Q_{n+1}) = \beta_1^{n+1}(Q_1-\alpha_1 Q_0)$$

and

$$(Q_{n+2}-\alpha_2 Q_{n+1}) = \beta_2^{n+1}(Q_1-\alpha_2 Q_0).$$

Thus

$$Q_{n+2} = \frac{(\alpha_2\beta_1^{n+1}-\alpha_1\beta_2^{n+1})Q_1+\alpha_2\alpha_1(\beta_1^{n+1}-\beta_2^{n+1})Q_0}{\alpha_2-\alpha_1}$$

and from this we can calculate Q_{n+2} in any generation and hence the heterozygote frequency.

When $k = 0$ (or $\to \infty$) the AA genotype (or the aa genotype) is absent and so an equilibrium is attained in one generation at $\hat{P} = 0$, $\hat{Q} = \frac{1}{2}$, $\hat{R} = \frac{1}{2}$ (or $\hat{P} = \frac{1}{2}$, $\hat{Q} = \frac{1}{2}$, $\hat{R} = 0$).

(ii) *Complete positive assortative mating, i.e.* $x \to \infty$

If the population originally has genotypic array P_0 AA $+ Q_0$ Aa $+ R_0$ aa then in the next generation

$$P_1 = P+\tfrac{1}{4}Q, \quad Q_1 = \tfrac{1}{2}Q \quad \text{and} \quad R_1 = R+\tfrac{1}{4}Q,$$

and in the nth generation

$$P_n = P_0+\tfrac{1}{2}Q_0(1-\tfrac{1}{2}n),$$

$$Q_n = Q_0/2^n$$

and

$$R_n = R_0+\tfrac{1}{2}Q_0(1-\tfrac{1}{2}n).$$

There is only one equilibrium for any set of initial values given by

$$\hat{P} = P_0+\tfrac{1}{2}Q_0, \quad \hat{R} = R_0+\tfrac{1}{2}Q_0,$$

i.e. the gene frequency is unchanged, as in fact it is from generation to generation. The system must converge to this equilibrium and hence stability is assured.

6. DISCUSSION

(i) One of the questions which population geneticists have been considering for some years is why so many polymorphisms exist. The mechanism for maintaining a polymorphism which has been investigated more than any other is that of differential viabilities for the genotypes. This leads to a stable equilibrium whenever heterosis (higher viability of the heterozygote), or some modification of it, occurs, Kingman (1961); Mandel (1959). It is interesting to note that not only does the present work suggest another simple mechanism for maintaining a polymorphism but it also indicates a possible extension of the idea of heterosis. In §§2 and 4 it was found that a necessary and sufficient condition for stability was that the heterogamous matings had higher fertilities than the homogamous ones. Thus higher viability for an individual heterogeneous in its gene complement is paralleled by higher fertility for a pair heterogeneous in its genotypic composition.

Another feature which carries over, and which is almost certainly related to the above heterogeneity condition, is the excess of heterozygotes at a stable equilibrium, over the Hardy–Weinberg value for an identical gene frequency.

(ii) Sittmann *et al.* (1966) found that the homogamous matings in the Japanese quail had a higher fertility. This presumably was balanced by the viability effects. An attempt to incorporate viabilities into the present model would lead to a more complex mathematical model and has therefore been omitted.

(iii) Any extension to a multiallelic locus will require a carefully defined dominance structure, and many different cases will need to be considered.

(iv) The effect of these fertility differences on the evolution of assortative mating might be considerable. In the case of higher fertility for the heterogamous matings it will be advantageous to individuals to choose a mate unlike themselves, effectively changing the value of x in the model. Negative assortative mating will evolve.

If we have higher fertilities for homogamous matings in the case of dominance, and recurrent mutation of A to a then a balance may be reached which will make positive assortative mating advantageous to the individual. The term 'advantageous' is used simply to imply an increase in the number of offspring produced.

SUMMARY

The effect of fertility differences between homogamous and heterogamous matings are considered. The equilibria are evaluated and their stability determined. Completely positive and completely negative assortative mating with two, and with three forms, are investigated as special cases of the above fertility structure. In these cases convergence of the genotype frequencies has been demonstrated.

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