WITH SELECTION FOR FECUNDITY THE MEAN FITNESS DOES NOT NECESSARILY INCREASE*

EDWARD POLLAK

Department of Statistics, Iowa State University, Ames, Iowa 50011

ABSTRACT

A population with two alleles at one locus is considered. It is assumed that there is random mating of adults and that matings in which a particular pair of genotypes is involved may have a different mean number of offspring, or fecundity, than other types of matings. There is assumed to be no other selection. It is shown that the genotypic frequencies that maximize the mean fecundity of the population are not necessarily the same as the stable equilibrium frequencies. Thus, examples can be found for which the mean fecundity decreases from one generation to the next, and one such example is presented. An example in which there is no stable equilibrium, and the mean fecundity oscillates, is also given.

IT is likely that selection for fecundity plays a role in the evolution of populations. Evidence that this role may be of some importance in human populations has been given, for example, by FISHER (1958), BAJEMA (1963) and CAVALLI-SFORZA and BODMER (1971). Nevertheless, most of the available theory of selection deals with a situation in which generations do not overlap, individuals of different genotypes may have different probabilities of survival between zygote formation and adulthood, and adults mate at random. BODMER (1965) seems to have been the first author to have set up a general model for a population with two alleles in which there can be selection for fecundity as well as viability. Most of his paper, however, deals with the special case in which the fecundity of mating is a product of two, possibly sex-dependent, factors, one being associated with each of the mates. In this case the calculations are equivalent to those that arise when fecundities are the same for all types of matings and there is viability selection, with viabilities possibly differing in the two sexes.

A particular consequence of the equivalence of the two theories is that if the fecundity factors are not sex-dependent, the mean, among zygotes, of the products of relative viabilities and fecundity factors associated with individuals increases between one generation and the next. At the end of his paper BODMER conjectured that if P, Q and p, q are the gene frequencies of A and a among gametes produced by females and males, respectively, and a, h and b are the relative viabilities of AA, Aa and aa, then the mean viability

$$T = apP + h(pQ + Pq) + bqQ$$

also increases with each generation of selection. This is, however, not always true, as shown by a counterexample given by KEMPTHORNE and POLLAK (1970).

Recently, HADELER and LIBERMAN (1975) have considered a situation in which there is selection only for fecundity in a population with two alleles and the fecundity of a mating is not necessarily factorizable. These authors made a detailed study of the existence and number of equilibria and their stability in the special case in which matings involving AA individuals do not differ in output of offspring from corresponding matings in which aa individuals play a role. ROUX (1977) has studied a general model with any number of alleles and discussed particular cases resulting in fecundity functions factorizable into male and female contributions. He also has considered the genetic structure and equilibrium behavior if the fecundity of a mating is the sum of two terms, one attributable to each mate.

The authors of both of these papers are aware that the mean "fitness" does not necessarily increase when there is fecundity selection, but in neither of the papers is this explicitly studied. My object is to show that with selection only for fecundity, the mean fecundity need not increase. Examples in which the mean fecundity steadily decreases or oscillates will be given. Unlike in the counter-example of KEMPTHORNE and POLLAK (1970), it will not be necessary to assume that there is viability selection, as well as selection for fecundity.

THE MODEL

Let us suppose that the fecundity is influenced by two alleles, A and a, at one locus. The genotypic array among adults in generation t may then be written in the form $P_t AA + 2Q_t Aa + R_t aa$.

If we label genotypes AA, Aa, and aa by 1, 2, and 3, respectively, we may define F_{ij} to be the mean number of offspring, or fecundity, of a mating of a male of type i and a female of type j. Thus, for example, F_{13} will denote the

TABLE 1

Frequencies, fecundities and offspring distributions of the mating types

Mating type Male Female	Frequency	Fecundity	Offspring distribution AA	Aa	aa
$AA \times AA$	P_t^2	F_{11}	1	0	0
$AA \times Aa$	$2P_t Q_t$	F_{12}	1/2	1/2	0
$AA \times aa$	$P_t R_t$	F_{13}	0	1	0
$Aa \times AA$	$2P_t Q_t$	F_{21}	1/2	1/2	0
$Aa \times Aa$	$4Q_t^2$	F_{22}	1/4	1/2	1/4
$Aa \times aa$	$2Q_t R_t$	F_{23}	0	1/2	1/2
$aa \times AA$	$P_t R_t$	F_{31}	0	1	0
$aa \times Aa$	$2Q_t R_t$	F_{32}	0	1/2	1/2
$aa \times aa$	R_t^2	F_{33}	0	0	1

mean number of offspring of a mating of type AA male $\times$ aa female. We now assume that there is no selection for viability, adults mate randomly, and the proportions of various genotypes among the offspring of any particular mating are Mendelian. In addition, the expected proportions of male and female offspring per mating will be assumed to be the same for any mating, so that the genotypic arrays of male and female offspring in any particular generation will be identical. The consequences of the foregoing definitions and assumptions are summarized in Table 1.

By making use of the entries in the table we obtain the recurrence equations

$$\bar{F}_t P_{t+1} = P_t^2 F_{11} + P_t Q_t (F_{12} + F_{21}) + Q_t^2 F_{22} \ ,$$

$$2\bar{F}_t Q_{t+1} = P_t Q_t (F_{12} + F_{21}) + P_t R_t (F_{13} + F_{31}) + 2Q_t^2 F_{22} \tag{1}$$
$$+ Q_t R_t (F_{23} + F_{32}),$$

$$\bar{F}_t R_{t+1} = Q_t^2 F_{22} + Q_t R_t (F_{23} + F_{32}) + R_t^2 F_{33} \ ,$$

where $\bar{F}_t$ is so chosen that $P_{t+1} + 2Q_{t+1} + R_{t+1} = 1$. Equations (1) can be simplified if we set $G_{ij} = (1/2) (F_{ij} + F_{ji}) = G_{ji}$ and $\bar{G}_t = \bar{F}_t$. We then obtain

$$\bar{G}_t P_{t+1} = P_t^2 G_{11} + 2P_t Q_t G_{12} + Q_t^2 G_{22} \ ,$$

$$2\bar{G}_t Q_{t+1} = 2P_t Q_t G_{12} + 2P_t R_t G_{13} + 2Q_t^2 G_{22} + 2Q_t R_t G_{23} \ , \tag{2}$$

$$\bar{G}_t R_{t+1} = Q_t^2 G_{22} + 2Q_t R_t G_{23} + R_t^2 G_{33} \ ,$$

where the mean fecundity in generation t is equal to

$$\bar{F}_t = \bar{G}_t = P_t^2 G_{11} + 4P_t Q_t G_{12} + 2P_t R_t G_{13}$$
$$+ 4Q_t^2 G_{22} + 4Q_t R_t G_{23} + R_t^2 G_{33} \tag{3}$$

We now ask whether $\bar{G}$ is maximized when the frequencies P, $2Q$, and R are stable equilibrium values. If this were true, we would have hope of showing that as $(P_t, 2Q_t, R_t)$ tended toward a stable equilibrium $(P^*, 2Q^*, R^*)$ as t increased, $\bar{G}_t$ would steadily increase toward a value $\bar{G}^*$.

To answer this question, we will find the stationary point of

$$\bar{G} = P^2 G_{11} + 4PQ G_{12} + 2PR G_{13}$$
$$+ 4Q^2 G_{22} + 4QR G_{23} + R^2 G_{33} \tag{4}$$

subject to the constraint

$$P + 2Q + R = 1 \ . \tag{5}$$

This is the same as the stationary point of

$$L = \bar{G} - 2\lambda(P + 2Q + R - 1). \tag{6}$$

Thus, if we take partial derivatives of L with respect to P, Q, and R and then set

them equal to 0, we find that the associated values of P, Q, and R satisfy the equations

$$PG_{1j} + 2QG_{2j} + RG_{3j} = \lambda, \quad j = 1,2,3 . \tag{7}$$

It is evident from (4), (5), and (7) that

$$\lambda = \lambda(P + 2Q + R) = \bar{G} . \tag{8}$$

If the frequencies satisfying (7) are the same as the equilibrium frequencies obtained by setting $P_{t+1} = P_t = P^*$, $Q_{t+1} = Q_t = Q^*$ and $R_{t+1} = R_t = R^*$ in (2), it follows from (2), (7) and (8) that

$$P^*R^*G_{13} = (Q^*)^2 G_{22} . \tag{9}$$

Expression (9) shows that if $(P^*, 2Q^*, R^*)$ is to be both an equilibrium point and a stationary point of $\bar{G}$, the values of G_{13} and G_{22} are subject to constraint. If, for example, P^*, $2Q^*$, and R^* are to be positive, G_{13} and G_{22} would both have to be positive. This suggests that it may be possible to find G_{ij} values for which $\bar{G}$ is not maximized when the population is at a stable equilibrium. Consequently, it may be possible to choose P_0, $2Q_0$, and R_0 is such a way that $\bar{G}_t$ steadily decreases as t increases. An example of this type will be given in the next section.

An example in which $\bar{G}_t$ steadily decreases

Let $G_{12} = 4$, $G_{22} = 8$, and the other G_{ij} values be equal to 0. It then follows from (2) and (3) that

$$\bar{G}_t = 16P_tQ_t + 32Q_t^2 = 16Q_t(1 - R_t),$$

$$2Q_{t+1} = \frac{8P_tQ_t + 16Q_t^2}{16P_tQ_t + 32Q_t^2} = 1/2 ,$$

$$R_{t+1} = \frac{8Q_t^2}{16Q_t(1-R_t)} = \frac{Q_t}{2(1-R_t)} ,$$

for $t = 0, 1, \ldots$ Hence

$$\bar{G}_t = 4(1-R_t) , \tag{10}$$

and

$$R_{t+1} = \frac{1}{8(1-R_t)} , \tag{11}$$

for $t = 1, 2, \ldots$ At equilibrium $R_t = R_{t+1} = R$, where

$$8R^2 - 8R + 1 = 0 .$$

The roots of this quadratic equation are $(2 \pm \sqrt{2})/4$. Since the larger root is inconsistent with having $2Q = 1/2$, the equilibrium is given by

$$R = (2 - \sqrt{2})/4 \doteq 0.14645 ,$$
$$2Q = 1/2 ,$$
$$P = \sqrt{2}/4 \doteq 0.35355 .$$

Expressions (10) and (11) indicate that if it is possible to find a sequence of values $R_1, R_2, \ldots$ such that R_t is increasing toward $R = (2 - \sqrt{2})/4$, then $\overline{G}_t$ will steadily decrease as t increases. We now examine whether this can occur. Thus, we write $R_t = R + d_t$. Then, by (11),

$$\frac{1}{8(1-R)} + d_{t+1} = \frac{1}{8(1-R-d_t)} = \frac{1}{8(1-R)[1-d_t/(1-R)]}$$

and

$$d_{t+1} = \frac{d_t}{8(1-R)^2[1-d_t/(1-R)]} = \frac{d_t}{8(1-R)^2[1-8Rd_t]} = \frac{8R^2 d_t}{1-8Rd_t} .$$

Clearly, $|d_{t+1}| \doteq 8R^2|d_t| < |d_t|$ when d_t is small, so that the equilibrium is locally stable. Also, if $d_t < 0$,

$$0 > \frac{8R^2 d_t}{1+8R^2} > d_{t+1} > 8R^2 d_t > d_t .$$

Hence, if $R_t < R$, then $R_t < R_{t+1} < R$ and $\overline{G}_t > \overline{G}_{t+1} > \overline{G} = 4(1-R)$. In addition $R_t \to R$ and $\overline{G}_t \to \overline{G}$ as $t \to \infty$. Thus, for example, if $R_0 = 0$, $4Q_0 = 1$, we have

t	0	1	2	3	4	∞
R_t	0	1/8	1/7	7/48	6/41	$(2-\sqrt{2})/4$
$\overline{G}_t$	4	3.5000	3.4286	3.4167	3.4146	3.4142

An example in which $\overline{G}_t$ oscillates

HADELER and LIBERMAN (1975) have given an example where, in addition to the two trivial equilibria with only one gene present, there is only one polymorphic equilibrium, and all three equilibria are unstable. This implies that, at least if $\overline{G}$ does not assume a minimum value at the polymorphic equilibrium, it is possible to find a sequence $(P_t, 2Q_t, R_t)$, $t = 0,1,\ldots$, such that $\overline{G}_t$ does not steadily increase with t.

The following example is of a similar type to the one given by HADELER and LIBERMAN, but entails simpler computations. $G_{13} = 36$, $G_{22} = 2$ and all the other G_{ij} values be equal to 0. We then have from (2) and (3) that, for $t = 0,1,\ldots$,

$$\overline{G}_t P_{t+1} = \overline{G}_t R_{t+1} = 2Q_t^2 ,$$
$$2\overline{G}_t Q_{t+1} = 4(18 P_t R_t + Q_t^2) ,$$
$$\overline{G}_t = 8(9 P_t R_t + Q_t^2) .$$

Hence, for $t \geq 1$, $P_t = R_t$, $P_t + Q_t = 1/2$ and $\overline{G}_t = 2 - 8P_t + 80P_t^2$. Thus, if $P_t = R_t$, G_t is minimized when $P = 1/20$.

When there is a polymorphic equilibrium, $P_t = P_{t+1} = \overline{P}$, where

$$(2 - 8\overline{P} + 80\overline{P}^2)\overline{P} = 1/2 - 2\overline{P} + 2\overline{P}^2,$$

and hence

$$160\overline{P}^3 - 20\overline{P}^2 + 8\overline{P} - 1 = (\overline{P} - 1/8)(160\overline{P}^2 + 8) = 0 .$$

This cubic equation has only one real root, $\overline{P} = 1/8$, which is associated with the unique equilibrium that exists in this example for a surviving population.

To explore whether the equilibrium is stable, we set $P_t = 1/8 + d_t$ for $t = 1$, $2, \ldots$. Then, because $Q_t = 3/8 - d_t$, we have that

$$P_{t+1} = \frac{1}{8} + d_{t+1} = \frac{9/32 - (3/2)d_t + 2d_t^2}{9/4 + 12d_t + 80d_t^2}$$

$$= \frac{1/8 - (2/3)d_t + (8/9)d_t^2}{1 + (48/9)d_t + (320/9)d_t^2} \doteq \frac{1}{8} - \frac{4}{3}d_t$$

when d_t is small. The equilibrium is thus locally unstable, with divergent oscillations. Because $\overline{P} = 1/8$ is not the same as $P = 1/20$, the value at which the parabola representing $\overline{G}_t$ for $P_t = R_t$ is minimized, it is evident that $\overline{G}_t$ will oscillate for P_t near $\overline{P}$. If, for example, $P_0 = R_0 = 0.10$ and $2Q_0 = 0.80$, we have the following figures.

t	0	1	2	3	4	5
P_t	0.10	0.16	0.0835	0.1836	0.0621	0.2117
$\overline{G}_t$	2.0000	2.7680	1.8899	3.2269	1.8116	3.8925

In the example given by HADELER and LIBERMAN (1975), $G_{11} = G_{33} = 1$, $G_{12} = G_{23} = 2$, $G_{13} = 55$ and $G_{22} = 4$. At equilibrium $\overline{P} = \overline{R} = 1/7$, which differs from the value $P = 1/28$ at which $\overline{G}_t$ is minimized on the set where $P_t = R_t$. Moreover, it can be shown that the unique polymorphic equilibrium is locally unstable with divergent oscillations, so that $\overline{G}_t$ oscillates for P_t near $\overline{P}$. Thus, the essential qualitative features are the same as in the example that has been discussed above. Therefore this example from HADELER and LIBERMAN (1975) implicitly justifies the assertion they make in their summary that the "fundamental law of population genetics" does not hold.

DISCUSSION

In the usual theory of viability selection at one locus, it is possible to show that $\overline{W}$, the mean of the relative viabilities among zygotes, increases from one generation to the next. Proofs have been given by SCHEUER and MANDEL (1959), MULHOLLAND and SMITH (1959), ATKINSON, WATTERSON and MORAN (1960) and KINGMAN (1961a,b). This theorem seems to be what HADELER and LIBERMAN (1975) mean when they refer to the "fundamental law of population genetics", or "Fisher's fundamental principle".

In this paper we have a situation in which the units that are subjected to selection are not individuals, but mating pairs. Thus, instead of having a relative viability W_{ij}, which is an attribute of individuals with genotype $A_i A_j$, we have a mean fecundity G_{ij}, which is an attribute of mating pairs in which one of the mates is of genotype i and the other is of genotype j. Carrying the analogy further, $\overline{G}$ is then a "natural" measure of the mean fitness of the population, just as $\overline{W}$ is such a measure in the classical viability selection model. With fecundity selection, however, the counterexamples in the last two sections demonstrate that $\overline{G}_t$ is not necessarily larger than $\overline{G}_{t-1}$.

One may object that the "natural" measure of population fitness that has been chosen is not appropriate, and that, after some search, a more suitable function of the G_{ij}'s and P,Q,R could be found, having the desirable property of showing that the population becomes more fit as selection proceeds. I doubt that this is true, for the following reasons. Under viability selection, the merit of a superior individual may not be passed on to its offspring because of genetic segregation. Under fecundity selection, there is an additional hurdle. For, even if a superior mating produces offspring with a potential for entering a superior mating, the realization of this potential is dependent upon the structure of the population. The dynamics of a population under fecundity selection at one locus are then intrinsically more complex than if there were only viability selection at one locus.

Perhaps, then, it is futile to attempt to prove that a population's mean fitness increases with time if any other genetic mechanism than segregation is involved. It is well known (cf., MORAN 1964) that if there is viability selection and recombination at two loci, then $\overline{W}_t$ does not necessarily increase with t. Attempts have been made to find some function $\overline{W}_t'$ that necessarily increases with t, but so far, I believe, without success.

LITERATURE CITED

ATKINSON, F. V., G. A. WATTERSON and P. A. P. MORAN, 1960   A matrix inequality. Quart. J. Math. **11**: 137–140.

BAJEMA, C. J., 1963   Estimation of the direction and intensity of natural selection in relation to human intelligence by means of the intrinsic rate of natural increase. Eugenics Quarterly, **10**: 175–187.

BODMER, W. F., 1965   Differential fertility in population genetics models. Genetics **51**: 411–424.

CAVALLI-SFORZA, L. L. and W. F. BODMER, 1971   *The Genetics of Human Populations.* W. H. Freeman and Company, San Francisco.

FISHER, R. A., 1958   *The Genetical Theory of Natural Selection.* Second Revised Edition. Dover, New York.

HADELER, K. P. and U. LIBERMAN, 1975   Selection models with fertility differences. J. Math. Biol. **2**: 19–32.

KEMPTHORNE, O. and E. POLLAK, 1970   Concepts of fitness in Mendelian populations. Genetics **64**: 125–145.

KINGMAN, J. F. C., 1961a   On an inequality in partial averages. Quart. J. Math. **12**: 78–80.
——, 1961b   A mathematical problem in population genetics. Proc. Camb. Phil. Soc. **57**: 574–582.

MORAN, P. A. P., 1964   On the non-existence of adaptive topographies. Ann. Hum. Genet. **27**: 383–393.

MULHOLLAND, H. P. and C. A. B. SMITH, 1959   An inequality arising in genetical theory. Amer. Math. Monthly **66**: 673–683.

ROUX, C. Z, 1977   Fecundity differences between mating pairs for a single autosomal locus, sex differences in viability and nonoverlapping generations. Theoret. Pop. Biol. **12**: 1–9.

SCHEUER, P. A. G. and S. P. H. MANDEL, 1959   An inequality in population genetics. Heredity **13**: 519–524.