SELECTION FOR MIGRATION MODIFICATION*

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ABSTRACT

Simple models for the genetic control of the tendency to migrate are considered. It is shown that migration from a more favorable regime to a less favorable regime is selected against. The ramifications for general modifier theory are discussed.

IN recent papers, FELDMAN (1972) and FELDMAN and BALKAU (1973a and 1973b) have examined a series of models in which the recombination between two loci was under the control of a third and selectively neutral locus. The outline of the model used was that of NEI (1967), although the mathematical conception was somewhat different. The results of our above-mentioned work can be stated as follows: If a mutant, selectively neutral modifier arises when the modified loci are in linkage disequilibrium, it will increase in frequency only if it reduces recombination between the modified loci. If the modified loci are in linkage equilibrium no such advance is possible.

In this note we consider a locus which modifies the migration rate between two populations, or between parts of a subdivided population. At one gene locus the populations are assumed to be in equilibrium under migration and selection. Mutation occurs at a locus which controls the extent to which the individuals migrate. We ask what is the fate of the migration-modifying mutant. This situation may occur when the deletion of flagella reduces the amount of motion of a protozoan. Similarly, the strength with which hydra may be attached to substrata (and in consequence their motility) may be under genetic control (KANAEV 1952). DR. UZI RITTER brought the problem to our attention with reference to hydra.

Model and Analysis

We give a detailed specification of the model for the haploid case. Suppose the individuals are originally of the types A or a at the first locus but only B at the second. There are two populations, I and II, between which individuals migrate at the rate m. Suppose that in population I the fitnesses of AB and aB are $1+s$ and 1, respectively, while in population II these fitnesses are reversed. Let x and y be the AB frequencies in populations I and II, respectively. Suppose selec-

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tion occurs, then migration; then the recursion system giving the frequencies x', y' in the next generation is

$$x' = \frac{(1-m)(1+s)x}{(1+s)x + (1-x)} + \frac{my}{y + (1+s)(1-y)} \qquad 1a$$

$$y' = \frac{m(1+s)x}{(1+s)x + (1-x)} + \frac{(1-m)y}{y + (1+s)(1-y)} \qquad 1b$$

The non-trivial equilibrium is readily seen to be given by the positive root, $\hat{x}$, of the quadratic

$$x^2s + x(2m+ms-s) - m = 0 \qquad 2$$

with $\hat{y} = 1-\hat{x}$. The equilibrium is locally stable for $s > 0$ and $m > 0$.

Suppose that the two populations are in equilibrium ($\hat{x}$, $1-\hat{x}$) and that mutation occurs at the previously monoallelic locus *B* to a new allele *b*. Whereas *b* has no effect on the fitness of its carriers, it alters their migration rate from m to m^*. Suppose that r is the recombination fraction between the two loci. We now denote the frequencies of *AB*, *Ab*, *aB* and *ab* in populations I and II by x_1, x_2, x_3, x_4 and y_1, y_2, y_3, y_4, respectively. Suppose recombination, selection and migration occur in that order. Then we have

$$x'_1 = \frac{(1+s)(1-m)(x_1-rD_x)}{(1+s)(x_1+x_2) + (x_3+x_4)} + \frac{m(y_1-rD_y)}{(y_1+y_2) + (1+s)(y_3+y_4)}$$

$$x'_2 = \frac{(1+s)(1-m^*)(x_2+rD_x)}{(1+s)(x_1+x_2) + (x_3+x_4)} + \frac{m^*(y_2+rD_y\ \ )}{(y_1+y_2) + (1+s)(y_3+y_4)} \qquad 3$$

etc., where $D_x = x_1x_4 - x_2x_3$, $D_y = y_1y_4 - y_2y_3$. To determine the fate of the migration modifier *b* we determine the local stability conditions in the neighborhood of the original *AB*, *aB* equilibrium. If this equilibrium is unstable in the higher (i.e., six-) dimensional sense (having been stable in the two-dimensional sense) then *b* will increase in frequency. The local stability is, of course, determined by linearizing (3) in the neighborhood of

$$\begin{aligned} x_1 &= \hat{x}, x_2 = x_4 = 0, x_3 = (1-\hat{x}) \\ y_1 &= 1-\hat{x}, y_2 = y_4 = 0, y_3 = \hat{x} \end{aligned} \qquad 4$$

where $\hat{x}$ is obtained from (2). If the largest eigenvalue of the resulting matrix transformation is greater than one in absolute value, (4) is unstable and *b* will increase, i.e. migration will be modified.

RESULTS

The local stability matrix reduces to dimension 4 and the resulting characteristic polynomial factors into two quadratics. The resulting four eigenvalues can all be shown to be less than unity in absolute value if $m^* > m$, but the largest is greater than unity if $m^* < m$. *Therefore, if* b *reduces the migration rate of its carriers, it will increase in frequency.*

Diploid Models

The problem as structured above for the haploid case has been extended to the diploid case. Here the original genotypes are *AABB*, *AaBB* and *aaBB*. A number of migration-selection balances are known for diploids (Moran 1959 and Eyland 1971) with the most complete treatment by Karlin and McGregor (1972). We have studied a number of the cases considered by these authors. For a complete specification of the model in the diploid case we postulate that the original migration rate for *BB* is $m < 1/2$, that the modifier heterozygote *Bb* have migration rate m^* and *bb* migrate at the rate m^{**}. Clearly the initial evolution of *b* should be determined by the relation between m and m^*. A typical case is where the fitnesses of AA, Aa, aa in population I are $1+s$, 1, $1-s$ and in population II $1-s$, 1, $1+s$. Another would be where both populations have fitnesses 1, $1-s$, 1, i.e. disruptive selection. The general theory of such models was elaborated by KARLIN and MCGREGOR (1972). Insofar as migration modification is concerned in these models, the results are the same as for the haploid case above. If the populations are in a stable migration-selection balance and if b is a selectively neutral mutation at the B locus, which causes Bb individuals to migrate at the rate m^*, then b will increase in frequency if and only if $m^* < m$. One of the key differences between the diploid and haploid models of modification lies in the effect of m^{**}. Thus if $m^{**} > m^* < m$, it is conceivable that a polymorphism be established for the neutral modifying locus B/b. This has been discussed in detail for the recombination case by FELDMAN and BALKAU (1973a).

DISCUSSION

Remark I: The model analyzed above is clearly a very simple one. The qualitative results, however, extend to more general selection models but the algebra then becomes so messy that numerical analysis is more profitable. It is our conjecture that the qualitative findings will hold true when both the selected characters and the propensity to migrate are polygenic in nature.

Remark II: For the type of selection regimes discussed above, the qualitative result is that there is selection to reduce the frequency of immigration into an environment in which most of the immigrants will be at a disadvantage relative to their original environment. Such data as have been reported by EHRLICH (1961, 1965) on the low frequency of dispersal from colonies of the butterfly *Euphydrias editha* could be explained in this way. Our analysis also makes precise some of the discussions by MAYNARD SMITH (1964) and VAN VALEN (1971) concerning the evolution of dispersal, and group selection (see Remark III in the latter context). Clearly, selection for reduced migration is tantamount to selection for geographic isolation. Our results could then also be interpreted as providing a possible framework in which to set ideas on speciation (MAYR 1970).

Remark III: The way in which the model was set up above, that is the order of recombination, selection and migration, may not be the most natural. KARLIN and MCGREGOR (1973) have examined a different migration modification model but with essentially the same results—namely, that migration reduction is favored. In their models, selection happens after migration with the result that the mean fitnesses in populations I and II are functions of the migration parameters. Noting that the overall equilibrium mean fitness is a decreasing function of the migration rate, they then use their powerful mean fitness principle to prove that migration reduction occurs.

Remark IV: KARLIN and MCGREGOR (1973) have pointed out that as the original migration rate m becomes small the rate of increase of the modifying allele b also decreases. Thus it becomes increasingly difficult to stop further migration by selection. The same is true of recombination reduction.

Remark V: Clearly other linear evolutionary pressures, such as mutation, will obey the above laws; i.e., mutation will be reduced in a population under mutation-selection balance.

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