GENETIC POLYMORPHISM IN A SUBDIVIDED POPULATION*

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Previous analyses of polymorphism in a subdivided population (Levene 1953; Deakin 1966) have made assumptions about the mode of migration from one niche to another. These are generally of a highly artificial character. We here adopt a more plausible approach based on the use of stochastic matrices. This yields not only a sufficient condition for genetic polymorphism [in the sense defined by the author (Deakin 1966)], but also a necessary one.

We suppose a population to be subdivided among n distinct niches, the ith of which supports a proportion c_i of the total. As in both previous analyses, we here take the quantities c_i to be constants. Two alleles A, a are assumed to be present in the ith niche in the proportions p_i, q_i ($=1-p_i$), respectively. The fitnesses of the genotypes AA, Aa, aa are taken to be W_i, 1, V_i, respectively.

Suppose the probability of an allelic migration (i.e. either through an actual migration or by interbreeding) from the ith niche to the jth is k_{ij}. Then $\mathbf{K}$, the $n\times n$ matrix whose elements are the k_{ij}, is a stochastic matrix (see Gantmacher 1959). In particular

$$\sum_{j=1}^{n} k_{ij} = 1 \tag{1}$$

for all i. The effect of this migration is to change p_i to P_i where

$$P_i = \sum_{j=1}^{n} k_{ji}c_j p_j\,. \tag{2}$$

This equation takes the place of equation (1) in Deakin's (1966) paper.

The effects of selection may be analysed as in that paper, to yield as the final result

$$\Delta p_i = \frac{P_i Q_i}{2\bar{w}_i}\frac{\partial \bar{w}_i}{\partial P_i} + P_i - p_i\,, \tag{3}$$

where

$$Q_i = 1 - P_i\,,$$

and

$$\bar{w}_i = P_i^2 W_i + 2P_iQ_i + Q_i^2 V_i\,.$$

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If Δp_i in equation (3) is put equal to zero, the equilibrium situations are found. Obviously

$$p_1 = p_2 = \ldots = p_n = 0 \tag{4}$$

is an equilibrium, and by symmetry

$$p_1 = p_2 = \ldots = p_n = 1 \tag{5}$$

is another.

These two equilibria will be termed trivial. All others are polymorphic in the sense of Deakin (1966). If both equilibria (4) and (5) are unstable, the situation will necessarily be polymorphic. We shall speak of this polymorphism as exhibiting total stability. Obviously total stability implies the existence of a polymorphic situation; if polymorphic equilibria exist and are stable, we may observe polymorphism even in the absence of total stability.

However, such equilibria will not necessarily be stable to large disturbances. The criterion for stability is one of stability to infinitesimal disturbances. If a trivial solution is stable, then a sufficiently large finite disturbance can cause the extinction of either A or a. By assumption, this new situation will then be stable. We thus examine conditions for total stability.

We now examine the stability of (4). For a small disturbance from (4)

$$\Delta p_i = (P_i/V_i) - p_i \tag{6}$$

(see Deakin 1966). Equation (6) may be written

$$\Delta p_i = \sum_{j=1}^{n} \left(\frac{k_{ji} c_j}{V_i} - \delta_{ij} \right) p_j, \tag{7}$$

where δ_{ij} is the Kronecker delta. Set now

$$\begin{aligned} q_i &= p_i (V_i c_i)^{\frac{1}{2}}, \\ l_{ij} &= \left(\frac{c_i}{V_i} \frac{c_j}{V_j} \right)^{\frac{1}{2}} k_{ji}, \end{aligned} \tag{8}$$

so that equation (7) becomes

$$\Delta q_i = \sum_{j=1}^{n} (l_{ij} - \delta_{ij}) q_j. \tag{9}$$

Equation (9) has the same stability properties as equation (7). It may be written in matrix notation as

$$\Delta \mathbf{q} = (\mathbf{L} - \mathbf{I}) \mathbf{q}, \tag{10}$$

where $\mathbf{q}$ is the column vector with elements q_i, $\mathbf{L}$ is an $n \times n$ matrix with elements l_{ij}, and $\mathbf{I}$ is the unit matrix of this dimension.

For the trivial solution to be stable, $\mathbf{L} - \mathbf{I}$ must exhibit the property that the real part of every eigenvalue is negative. In other words every eigenvalue of $\mathbf{L}$ must have a real part less than unity. Thus if (4) is to be unstable, $\mathbf{L}$ must possess at least one eigenvalue with a real part larger than unity. This condition is both necessary and sufficient.

All l_{ij} satisfy $l_{ij} \geqslant 0$, and thus $\mathbf{L}$ is a non-negative matrix in the sense of Gantmacher (1959). We may also assume it to be irreducible in that author's terminology.

We now take the absolute value of each eigenvalue of $\mathbf{L}$ in turn and let r be the largest quantity so formed. Then

$$r \leqslant \max_{1 \leqslant i \leqslant n} \sum_{j=1}^{n} l_{ji}$$

(see Gantmacher 1959). A sufficient condition for (4) to be stable is:

$$r < 1\,,$$

and this will hold if, for all i,

$$\left(\frac{c_i}{V_i}\right)^{\frac{1}{2}} \sum_{j=1}^{n} \left(\frac{c_j}{V_j}\right)^{\frac{1}{2}} k_{ij} < 1\,, \tag{11}$$

where use has been made of equation (8).

The inequality (11) will certainly be true if, for all i,

$$c_i < V_i\,, \tag{12}$$

because of the relation (1).

Condition (12) is thus sufficient to ensure the stability of (4). Conversely, if (4) is to be unstable, it is necessary that, for some i,

$$V_i < c_i\,. \tag{13}$$

A sufficient condition that (4) be unstable is that, for some i, $l_{ii} > 1$, i.e.

$$V_i < c_i k_{ii}\,. \tag{14}$$

This may be proved either by the argument of Deakin (1966) or by observing that if the condition (14) is violated for all i, the trace of the matrix $\mathbf{L}-\mathbf{I}$ is positive and hence not all the eigenvalues can be negative.

We note that condition (14) implies the inequality (13) as required for consistency. The only case not covered by the two conditions is that in which for no i does (14) hold, but (13) is satisfied for one or more of the niches. More precise analysis of the matrices involved is then required. Such exceptional cases become more likely as the k_{ii} decrease, i.e. as migration increases.

Equilibrium (5) may be similarly analysed. The final result is that a necessary condition for total stability is that, for some i, j,

$$V_i < c_i, \quad W_j < c_j\,, \tag{15}$$

while a sufficient condition is that, for some i, j,

$$V_i < c_i k_{ii}, \quad W_j < c_j k_{jj}\,. \tag{16}$$

It should be noted that condition (15) here obtained as a necessary condition is identical in form to that obtained by Deakin (1966) as a sufficient condition extending Levene's (1953) result. The difference lies in the assumptions made on the pattern of migration. The pattern considered here is presented as more plausible than those patterns envisaged in the earlier analyses.

It should also be noted that in the above analysis none of the quantities V_i may become zero. It may, however, be shown that the results still hold in such a case, and the same naturally applies to the quantities W_j.

References

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