THEORETICAL CONSIDERATIONS OF SYMPATRIC DIVERGENCE*  

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It has been argued that sympatric divergence may be initiated by disruptive selection giving rise to a stable polymorphism; this may then be followed by the evolution of reproductive isolation and speciation. Mather (1955) discussed the implications of disruptive selection, and theoretical work has adequately demonstrated that such a mechanism can maintain polymorphism. Levene (1953) gave conditions, extended by Prout (1968) and generalized by Deakin (1968), for a stable polymorphism in a multiple-niche situation. Particular aspects of the fate of a gene in a two-niche situation have been considered by Parsons (1963), Hanson (1966), Jain and Bradshaw (1966), Levins and MacArthur (1966), Antonovics (1968a, 1968b), Bryant (1969), and Maynard Smith (1970), while James (1970) investigated chromosome polymorphism in a similar environmental situation. The most detailed examination of sympatric speciation is that of Maynard Smith (1966), who deduced conditions for polymorphism of a dominant gene in a two-niche situation both with and without habitat selection, and also discussed possible isolating mechanisms.  

Here we consider, in greater detail than previous workers, the establishment of a polymorphism in a two-niche situation and the effects of this on the genetic structure of a population. We then delineate certain conditions under which reproductive isolation may occur. Details of the derivation of the equations describing the models may be obtained from the authors.  

SINGLE-GENE CHARACTER  

The model was of two niches, X and Y, with interbreeding populations consisting of the genotypes AA, Aa, and aa. The size of the population in each niche was assumed constant, being controlled by factors other than the selection process considered. Generations were assumed to be separate. Genotype fitnesses are shown in table 1. There was gene flow between the two niches, and it remained at the same level in successive generations. Only males migrated, and mating occurred after migration. Offspring were subjected to selection in the environment where they were produced. Hence the  

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TABLE 1
FITNESS OF GENOTYPES IN NICHE X AND Y, IN THE SINGLE-GENE CASE
WITH AND WITHOUT DOMINANCE

<table>
<thead>
<tr>
<th>Genotype</th>
<th>No Dominance</th>
<th>Dominance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AA</td>
<td>Aa</td>
</tr>
<tr>
<td>Niche X</td>
<td>1</td>
<td>1 - (\frac{1}{2}S_x)</td>
</tr>
<tr>
<td>Niche Y</td>
<td>1 - (S_y)</td>
<td>1 - (\frac{1}{2}S_y)</td>
</tr>
</tbody>
</table>

Note.—\(S_x\) = selection coefficient against \(aa\) in niche \(X\); \(S_y\) = selection coefficient against \(AA\) in niche \(Y\).

The model was designed primarily to reflect plant situations, where there is pollen transfer between sessile organisms and seed flow may be considered negligible.

The level of gene flow from niche \(X\) to niche \(Y\) was defined as the number of male gametes produced in niche \(X\) and uniting with female gametes in niche \(Y\) as a fraction of the total number of male gametes which unite with female gametes in niche \(Y\); gene flow from niche \(Y\) to niche \(X\) was defined similarly. Hence gene flow could range from 0.0 to 1.0, and random mating of the two subpopulations was represented by gene flow of 0.5 in both directions.

In order to estimate the phenotypic divergence between the two populations, each population was given a "phenotypic score," \([AA] + \frac{1}{2}[Aa]\) when there was no dominance, and \([AA] + [Aa]\) when there was dominance, where \([AA]\) and \([Aa]\) were the frequencies of the genotypes \(AA\) and \(Aa\), respectively. A difference of 0.2 in the phenotypic scores of the two populations was arbitrarily chosen as a criterion for "phenotypic divergence," as this would probably be readily observable in an experimental or field situation. Maximum phenotypic divergence would be characterized by scores of one in niche \(X\) and zero in niche \(Y\). The genetic load was estimated from the proportion of the population eliminated by selection in each generation.

Initially, both alleles were at a frequency of 0.5. Equilibrium was assumed to have occurred if the gene frequency in both niches changed by less than .0001 between generations. If equilibrium had not been reached after 400 generations, the simulation was stopped.

Results

The results have been presented as "phase diagrams" (fig. 1), showing, for different selection pressures and varying amounts of gene flow: (1) conditions for maintenance of polymorphism over the two niches (both alleles present in an overall frequency greater than .025), indicated by both the shaded and striped areas; and (2) conditions for "phenotypic divergence"
Fig. 1.—Phase diagrams showing, for a single gene character, conditions for polymorphism and phenotypic divergence between two niches under varying levels of gene flow, symmetric and asymmetric selection pressures, with and without dominance. Vertical axis of each phase diagram represents gene flow from niche Y to niche X, and the horizontal axis, gene flow from niche X to niche Y. $S_x$ = selection coefficient against $aa$ in niche $X$; $S_y$ = selection coefficient against $AA$ in niche $Y$. (See text.)

between the two niches (a difference of more than 0.2 in the phenotypic scores), indicated by shaded areas.

Each phase diagram refers to a particular combination of selection pressures in niche $X$ and niche $Y$, as indicated by the values of $S_x$ and $S_y$ along the top. The horizontal axis of each diagram defines the gene flow from niche $X$ to niche $Y$, which ranges from 0.0 to 1.0; similarly, the vertical axis defines the gene flow from niche $Y$ to niche $X$. High levels of gene flow are unlikely to occur in natural situations; hence the sections of the phase diagrams below the diagonals are the more important. Figure 1a shows the results without dominance; figure 1b, when there is dominance. At equilibrium, the genetic load on the population, averaged over the two niches, was lower if there was dominance. Equilibrium was reached rapidly, especially when selection pressures were high and there was no dominance. For example, with selection pressures of 0.2 in each niche and gene flow of 0.2 in both directions, equilibrium was reached in 24 generations when there was no dominance and 88 generations with dominance.

The variance in each subpopulation decreased from generation to generation. At equilibrium, the variance in the phenotypic score of each subpopulation was lower if selection pressures were high and, in general, if gene flow was low.

The level of heterozygosity in the subpopulations is shown in figure 2, using a format similar to figure 1. If the favored gene was dominant or intermediate in a particular niche (fig. 2a, b), the proportion of heterozygotes in that niche was always equal to, or greater than, the Hardy-Weinberg expectation; this excess reached an appreciable level (e.g., over 30%) if the
Fig. 2.—Phase diagrams showing, for a single gene character, the percentage excess or deficit of heterozygotes in each subpopulation under varying levels of gene flow, symmetric and asymmetric selection pressures, and in the following instances: (a) no dominance, excess heterozygosity in niche Y; (b) $A$ dominant, excess heterozygosity in niche $X$; (c) $A$ again dominant, deficit heterozygosity in niche $Y$. Vertical axis of each phase diagram represents gene flow from niche $Y$ to niche $X$, and the horizontal axis, gene flow from niche $X$ to niche $Y$. $S_a = \text{selection coefficient against } aa \text{ in niche } X$, $S_A = \text{selection coefficient against } AA \text{ in niche } Y$. (See text.)

Selection pressure in that niche was high, if the gene flow into the niche was high, and if the gene flow out of the niche was low. If the favored gene in a particular niche was recessive (fig. 2c), there was a slight deficit of heterozygotes in that niche.

TWO-GENE AND THREE-GENE CHARACTERISTICS

In many natural situations, characters are determined by more than one gene. An elementary "polygenic" system was therefore investigated: the single-gene model was extended by including either one or two more genes. The genes were unlinked, they had the same degree of dominance, and they contributed equally to the same character. Gene flow occurred as before. Since the aim of this model was to compare a character determined by one gene with a character determined by several genes, selection pressures were chosen such that the complete homozygotes had the same values as the homozygotes in the one-gene case; that is, the average effect of each gene was correspondingly reduced.

The phenotypic score for the polygenic cases was defined in a similar way to the phenotypic score for the one-gene case. For example, for two genes and no dominance the phenotypic score was
\[ [AABB] + \frac{3}{4} ([AaBB] + [AABb]) + \frac{1}{2} ([aaBB] + [AAbb] + [AaBb]) + \frac{1}{4} ([Aabb] + [aaBb]). \]

**Results**

Results for the polygenic cases were similar to those for the one-gene case, given the same amounts of gene flow and equivalent selection pressures (table 1). In particular, a polymorphism was maintained under almost exactly the same conditions. As more genes contributed to the character undergoing selection, there was less phenotypic divergence between the niches, genetic load increased, and the heterozygosity at a particular locus decreased. While inclusion of a second gene produced a marked change in population structure, the addition of a third gene had less effect.

The zygotes, AA, Aa, and aa, did not assort at random with BB, Bb, and bb or CC, Cc, and cc. For example, in the two-gene case, selection favored an excess of AABB in niche X and aabb in niche Y, and gene flow interacted with this to produce an excess of double heterozygotes AaBb in both niches. This "zygotic association" (Allard, Jain, and Workman 1968) also occurred in the three-gene case where there was a similar excess of complete homozygotes and complete heterozygotes.

**Evolution of Dominance**

Gene B was considered to be the dominance modifier of gene A and unlinked to A so that, if BB or Bb genotypes were present, the dominance relations of A and a were changed as shown in table 2. It was assumed that initially A showed no dominance and the presence of B was allowed to (1) cause A to have dominant effects in both niches; (2) cause the favored gene to be dominant in both niches so that there was, overall, heterozygous advantage; and (3) cause heterozygous advantage in each niche separately. Gene B was introduced at a frequency of .1 in a heterozygous state. Equilibrium was assumed to have been reached if the genotype frequencies in both niches changed by less than .0001 between generations.

**Results**

The conditions under which the modifiers spread and the rate at which they spread are shown by figure 3, using, as before, the general format of figure 1. The shaded areas show where modifier genes reached fixation (allele B present in an overall frequency greater than .9); the different types of shading show the number of generations required for this to occur. Under the converse conditions, either allele A or allele a swamped both niches before modifiers spread appreciably. Effects of dominance modification on
TABLE 2

<table>
<thead>
<tr>
<th>Fitness</th>
<th>Genotype</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AA</td>
<td>Aa</td>
</tr>
<tr>
<td>Before modification:*</td>
<td></td>
<td>1</td>
<td>1 - 1S_y</td>
</tr>
<tr>
<td>Niche X</td>
<td></td>
<td>1</td>
<td>1 - 1S_y</td>
</tr>
<tr>
<td>Niche Y</td>
<td></td>
<td>1 - S_y</td>
<td>1 - S_y</td>
</tr>
<tr>
<td>After modification:†</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Case 1:</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Niche X</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Niche Y</td>
<td></td>
<td>1 - S_y</td>
<td>1 - S_y</td>
</tr>
<tr>
<td>Case 2:</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Niche X</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Niche Y</td>
<td></td>
<td>1 - S_y</td>
<td>1 - S_y</td>
</tr>
<tr>
<td>Case 3:</td>
<td></td>
<td>1</td>
<td>1 + 0.18_y</td>
</tr>
<tr>
<td>Niche X</td>
<td></td>
<td>1</td>
<td>1 + 0.18_y</td>
</tr>
<tr>
<td>Niche Y</td>
<td></td>
<td>1 - S_y</td>
<td>1 + 0.18_y</td>
</tr>
</tbody>
</table>

Note.—Case 1, A dominant in both niches; case 2, favored gene in each niche dominant in that niche, giving overall heterozygous advantage; case 3, heterozygous advantage in both niches. S_x and S_y represent selection coefficients in niches X and Y, respectively, as in table 1.

* No dominance.
† Differing types of dominance.

The equilibrium results can be inferred from figure 1 by comparing the model where A is dominant with the model without dominance.

EVOLUTION OF LINKAGE

A three-gene model was investigated, in which a dominant gene C controlled the linkage between genes A and B. If zygotes CC or Cc were present, A and B were linked in the coupling phase; if cc was present, A and B were completely unlinked. This modifier gene, C, affected only the meiotic products of AaBb, as in table 3.

Selection pressures were not affected by the genotypes CC, Cc, or cc and remained as for the two-gene case (see table 1). Initially C was present in a frequency of .1.

Results

In this model and in all subsequent ones, results for symmetric cases only are shown (i.e., the selection pressures in niche X and niche Y were equal.

TABLE 3

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>Gametes</th>
</tr>
</thead>
<tbody>
<tr>
<td>AaBbCc (linkage)</td>
<td>ABC, abc</td>
</tr>
<tr>
<td>AaBbCc (linkage)</td>
<td>ABC, ABC, abc</td>
</tr>
<tr>
<td>AaBbCc (no linkage)</td>
<td>ABC, abc, ABC, abc</td>
</tr>
</tbody>
</table>
and opposite \([S_x = S_y = S]\), and gene flow from niche \(X\) equaled gene flow from niche \(X\) to niche \(Y\). Further, only gene flow up to 0.5 (representing random mating) was considered. The spread of linkage modifiers after 1,000 generations is shown in figure 4. In this and subsequent figures the horizontal axis represents the level of gene flow between the niches, and the vertical axis represents the selection pressure in each niche. The different shading patterns show the conditions under which the overall gene frequency of the linkage modifiers had reached \(0.3, 0.5, \text{ and } 0.7\). When linkage modifiers were introduced into the population, they either remained at the same low frequency or spread very slowly (e.g., under the comparatively favorable conditions of selection pressures given by \(S = 0.8\) and gene flow 0.3 in both directions, it required over 1,900 generations for the linkage modifier, gene \(C\), to reach a frequency of 0.9). The spread of linkage was facilitated by high selection pressures and by a certain low level of gene flow, but if the level of gene flow became very high, linkage again spread very slowly. The spread of the linkage modifiers was virtually unaffected by the degree of dominance of genes \(A\) and \(B\).
ASSORTATIVE MATING

In this model we assumed that gene $A$ controlled a character undergoing disruptive selection as described for a single gene character; a second, dominant gene $B$ caused assortative mating. Gene $B$ caused a constant proportion, $\alpha$, of the $BB/Bb$ females to mate with $BB/Bb$ males and the same proportion, $\alpha$, of $bb$ females to mate with $bb$ males while the remainder mated at random (see table 4). This is only one of many possible assortative mating schemes (Seudo and Karlin 1969; Karlin and Seudo 1969), and it was chosen partly because it includes the case discussed by Maynard Smith (1966) and partly because the models described here are designed to reflect plant populations and this assortative mating scheme represents the situation where there are flowering-time differences between two populations.

Our primary interest was the situation where the selection pressures were not affected by the assortative mating gene, so that disruptive selection acted

\begin{table}[h]
\centering
\begin{tabular}{l c c c}
\hline
\textbf{FREQUENCY} & \textbf{FREQUENCY OF MALE GENOTYPES AFTER MIGRATION} \\
\textbf{OF FEMALE} & \textbf{BB}  & \textbf{Bb}  & \textbf{bb}  \\
\textbf{GENOTYPES} & $x^1$ & $y^1$ & $z^1$ \\
\hline
$BB \ x \ \ldots \ldots \ \frac{\alpha x^1}{x^1 + y^1} + (1-\alpha) xz^1$ & $\frac{\alpha y^1}{x^1 + y^1} + (1-\alpha) xy^1$ & $(1-\alpha) xz^1$ \\
\hline
$Bb \ y \ \ldots \ldots \ \frac{\alpha y^1}{x^1 + y^1} + (1-\alpha) yz^1$ & $\frac{\alpha y^1}{x^1 + y^1} + (1-\alpha) yy^1$ & $(1-\alpha) yz^1$ \\
\hline
$bb \ z \ \ldots \ldots \ (1-\alpha) xz^1$ & $(1-\alpha) yz^1$ & $\alpha z + (1-\alpha) xz^1$ \\
\hline
\end{tabular}
\caption{Frequency of Matings When a Dominant Gene $B$ Causes Assortative Mating of Degree $\alpha$}
\end{table}

Note.—$x^1$, $y^1$, $z^1$ and $x$, $y$, $z$ represent frequency of male and female genotypes, respectively, after migration.
TABLE 5  
FITNESS OF GENOTYPES FOR THE ASSORTATIVE-MATING MODEL WHEN THE SELECTED GENE, A₁, SHOWS NO DOMINANCE

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Niche X</th>
<th>Niche Y</th>
<th>Niche X</th>
<th>Niche Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>AABB</td>
<td>1</td>
<td>1 - $S$</td>
<td>1</td>
<td>(1 - $S$)(1 - $\Sigma$)</td>
</tr>
<tr>
<td>AAbb</td>
<td>1</td>
<td>1 - $S$</td>
<td>1 - $\Sigma$</td>
<td>1 - $S$</td>
</tr>
<tr>
<td>AaBB</td>
<td>1 - $\frac{1}{2}$S</td>
<td>1 - $\frac{1}{2}$S</td>
<td>1 - $\frac{1}{2}$S</td>
<td>(1 - $\frac{1}{2}$S)(1 - $\Sigma$)</td>
</tr>
<tr>
<td>AaBb</td>
<td>1 - $\frac{1}{2}$S</td>
<td>1 - $\frac{1}{2}$S</td>
<td>1 - $\frac{1}{2}$S</td>
<td>(1 - $\frac{1}{2}$S)(1 - $\Sigma$)</td>
</tr>
<tr>
<td>Aabb</td>
<td>1 - $\frac{1}{2}$S</td>
<td>1 - $\frac{1}{2}$S</td>
<td>(1 - $\frac{1}{2}$S)(1 - $\Sigma$)</td>
<td>1 - $\frac{1}{2}$S</td>
</tr>
<tr>
<td>aaBB</td>
<td>1 - $S$</td>
<td>1</td>
<td>1 - $S$</td>
<td>1 - $\Sigma$</td>
</tr>
<tr>
<td>aaBb</td>
<td>1 - $S$</td>
<td>1</td>
<td>1 - $S$</td>
<td>1 - $\Sigma$</td>
</tr>
<tr>
<td>aabb</td>
<td>1 - $S$</td>
<td>1</td>
<td>(1 - $S$)(1 - $\Sigma$)</td>
<td>1</td>
</tr>
</tbody>
</table>

Note.—In case 1 there is no direct selection acting on the assortative-mating gene; selection acts only on A₁. In case 2 selection acts also on the assortative-mating gene, B₁, which is assumed dominant. $S$ = selection coefficient on aa in niche X and AA in niche Y. $\Sigma$ = selection coefficient on bb in niche X and on BB in niche Y.

directly only on the genotypes AA, Aa, and aa. The level of this selection was, as usual, denoted by $S$ (table 5, case 1). However, in some situations ecological factors may be such that disruptive selection acts independently on the character causing assortative mating (e.g., McNeilly and Antonovics 1965). So we investigated the situation where there was also a level of disruptive selection, $\Sigma$, acting directly on the assortative mating genotypes, BB, Bb, and bb. The selection pressures which occur in the latter situation are shown by table 5, case 2.

Initial frequencies of B were slightly different in the two niches (e.g., 0.4 and 0.6), since otherwise no change whatsoever occurred in the frequencies of the assortative mating genes.

Results

The outcome was independent of the initial frequencies of the assortative mating genes, although the gene frequencies changed very slowly at first if the initial difference in frequency of B between the niches was small. Further, it made no difference to the final outcome whether A and a were initially present in frequencies of .5 or in their equilibrium frequencies as obtained from the one-gene model.

Introduction of assortative mating genes into the two-niche system produced two alternative results: (1) the assortative mating gene B returned to the same frequency in both niches, so that the populations did not become isolated in any way and the frequencies of A were unchanged; or (2)
allele $B$ increased in one niche and allele $b$ in the other, so that there was some reproductive isolation between the two populations, and consequently the frequencies of the selectively favored allele, $A$ or $a$, increased in the appropriate population.

Figure 5 shows the results when $A$ is not dominant. The separate 'cells' in the figures correspond to different values of $\alpha$, the degree of assortative mating, and to different values of $\Sigma$, the level of disruptive selection acting directly on the assortative mating genotypes. Each 'cell' shows the extent of the reproductive isolation evolved after 400 generations. As in the previous figure, the horizontal axis of each cell indicates the level of gene flow, while the vertical axis of each cell indicates the level of disruptive selection.

![Figure 5](image)

**Fig 5.**—Phase diagrams showing degree of difference in frequency of genes determining assortative mating (isolation) under a range of levels of assortative mating and under different low levels of symmetric disruptive selection acting on the assortative-mating gene, $B$, itself. $\Sigma =$ selection coefficient against assortative-mating gene in each niche; $\alpha =$ degree of assortative mating. Each phase diagram, or 'cell,' shows the level of symmetrical selection acting on the selected gene, $A$ (vertical axis), and the level of symmetric gene flow (horizontal axis). Initial divergence in frequency of assortative mating genes $= \frac{1}{2}$, selected gene no dominance; values show extent of isolation after 400 generations. (See text.)
(S) acting on genotypes AA, Aa, and aa. The darker shading corresponds to a difference of more than .8 in the frequency of gene B in niches X and Y (i.e., almost complete reproductive isolation); the lighter shading, to a difference of more than .4 in the frequency of gene B in the two niches (i.e., partial reproductive isolation); in the blank areas reproductive isolation did not evolve appreciably.

Isolation could arise rapidly. For example, when the selection pressure, S, on genotypes AA, Aa, and aa was 0.8 and the level of gene flow was 0.3, partial isolation arose in 31 or eight generations if the degree of assortative mating, α, was 0.6 or 0.9, respectively, and almost complete isolation evolved in 18 generations if α was 0.9.

Reproductive isolation was, as expected, facilitated by a high degree, α, of assortative mating and by an increasing level of disruptive selection acting directly on the assortative mating genotypes. It occurred more readily if there was also a high level, S, of disruptive selection acting on AA, Aa, and aa, and a low level of gene flow. Any tendency toward isolation could be swamped if the level of gene flow increased. However, when Σ = 0.0, isolation did not evolve when the gene flow between the niches was very close to zero (e.g., for α = 0.5, selection pressures given by S_x = S_y = 0.8, and no dominance, reproductive isolation did not evolve for gene flow of less than 0.005 or more than 0.3 in both directions), but it did evolve for levels of gene flow between 0.01 and 0.25. On the other hand, when disruptive selection acted directly on the genotypes BB, Bb, and bb (i.e., Σ = 0.05, 0.10), isolation could be maintained at much higher levels of gene flow between niches.

When gene A was dominant, isolation evolved under similar conditions and to much the same extent. The only notable differences were that isolation was less likely to occur if there was a low degree of assortative mating and isolation was accompanied by an association of the dominant genes (i.e., the genotypes AABB and aabb were formed in niches X and Y, respectively, in preference to AAbb and aaBB).

SELFING

We assumed that gene A controlled a character undergoing disruptive selection, as before, and a second, dominant gene, B, caused selfing. If B was present, a constant proportion, α, of the females produced offspring without the involvement of males, while the remainder outcrossed at random (see table 6).

Previous work (Crosby 1949; Antonovics 1968a) has shown that a selfing gene spreads through a population if no viability effects oppose it. However, in natural populations selfing genes do not always spread, presumably because of the effects of inbreeding depression. So in this two-niche model, the automatic spread of the selfing gene was prevented by imposing selection, Σ, against it (see table 7). This selection against the selfing genotypes acted completely independently of the disruptive selection, S, on genotypes AA,
TABLE 6
Frequency of Matings When a Dominant Gene B Causes Selfing of Degree α

<table>
<thead>
<tr>
<th>Frequency of Female Genotypes</th>
<th>Frequency of Male Genotypes after Migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB x</td>
<td>( ax + (1 - α)xz^1 )</td>
</tr>
<tr>
<td>Bb y</td>
<td>( (1 - α)xy^1 )</td>
</tr>
<tr>
<td>bb z</td>
<td>( (1 - α)xz^1 )</td>
</tr>
<tr>
<td></td>
<td>( (1 - α)yz^1 )</td>
</tr>
<tr>
<td></td>
<td>( (1 - α)xz^1 )</td>
</tr>
</tbody>
</table>

Note.—\( x^1, y^1, z^1 \) and \( x, y, z \) represent frequency of male and female genotypes, respectively, after migration.

TABLE 7
Fitness of Genotypes for the Selfing Model, When the Selected Gene Shows No Dominance and the Selfing Gene, B, Shows Dominance with Respect to Fitness

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Niche X</th>
<th>Niche Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>AABB</td>
<td>( 1 - Σ )</td>
<td>( (1 - S)(1 - Σ) )</td>
</tr>
<tr>
<td>AAbb</td>
<td>( 1 - Σ )</td>
<td>( (1 - S)(1 - Σ) )</td>
</tr>
<tr>
<td>Abb</td>
<td>( 1 )</td>
<td>( 1 - S )</td>
</tr>
<tr>
<td>AaBB</td>
<td>( (1 - \frac{1}{2}S)(1 - Σ) )</td>
<td>( (1 - \frac{1}{2}S)(1 - Σ) )</td>
</tr>
<tr>
<td>AaBb</td>
<td>( (1 - \frac{1}{2}S)(1 - Σ) )</td>
<td>( (1 - \frac{1}{2}S)(1 - Σ) )</td>
</tr>
<tr>
<td>Aabb</td>
<td>( (1 - \frac{1}{2}S) )</td>
<td>( (1 - \frac{1}{2}S) )</td>
</tr>
<tr>
<td>aABB</td>
<td>( (1 - S)(1 - Σ) )</td>
<td>( 1 - Σ )</td>
</tr>
<tr>
<td>aAbb</td>
<td>( (1 - S)(1 - Σ) )</td>
<td>( 1 - Σ )</td>
</tr>
<tr>
<td>aabb</td>
<td>( 1 - S )</td>
<td>( 1 )</td>
</tr>
</tbody>
</table>

Note.—\( S \) = selection coefficient on \( aa \) in niche \( X \) and \( AA \) in niche \( Y \). \( Σ \) = selection coefficient on \( bb \) in niche \( X \) and \( BB \) in niche \( Y \).

Aa, and aa. Allele B was introduced at a low frequency, \( 01 \), in a heterozygous state.

Results

Figure 6 shows the results when \( A \) is not dominant. As before, the separate "cells" in the figures correspond to different values of \( α \), the degree of selfing, and to different values of \( Σ \), the level of inbreeding depression. In each "cell" the shaded areas show the conditions of gene flow and disruptive selection under which the selfing genes reached fixation. The different shading patterns indicate the number of generations required for this to occur.

In the two-niche situation, selfing spread despite inbreeding depression (given by \( Σ = 0.34 \) for \( α = 1 \) and \( Σ = 0.20 \) for \( α = 0.5 \)) chosen so as to be just sufficient to eliminate a gene for self-fertility from a single isolated population. However, a slight increase in the selection against selfing again prevented its spread. The selfing gene spread more readily when there was a high degree of selfing, intense selection on \( A \), and high gene flow between
FIG. 6.—Phase diagrams showing spread of genes for selfing (isolation) under two levels of selfing, and different degrees of selection against the gene, B, for self-fertility. $\Sigma =$ selection coefficient against selfing gene (inbreeding depression); value in the left-hand cell is that just sufficient to prevent spread of the selfing gene of its own accord (without gene flow and selection), while right-hand cells show somewhat greater values, $\alpha =$ degree of self-fertility. Each phase diagram, or "cell," shows the level of symmetrical selection acting on the selected gene, A (vertical axis), and the level of symmetric gene flow (horizontal axis). Initial frequency of selfing gene = .01, selected gene no dominance, selfing gene dominant. (See text.)

the populations. The degree of dominance of the gene, A, undergoing disruptive selection did not appreciably affect either the conditions for the spread of selfing or the rate at which it spread. When the selection pressures against the selfing gene were the same in both niches, as was assumed for the results presented here, the selfing gene either spread and went to fixation or was completely eliminated from both populations. When the selection pressures against the selfing gene were different in the two niches, the selfing gene, when it spread, could reach different intermediate frequencies in the two populations.

DISCUSSION

Selection in heterogeneous environments with migration between sub-habitats can occur in several qualitatively different ways ("migration-selection cycles"). Each cycle can be considered to consist of the following series of alternatives:

A. 1. Diploids migrate or
2. Haploids migrate;
B. 1. No differential migration of genotypes or
2. Differential migration (migrational selection);
C. 1. Migrants mate with residents only or
2. Migrants mate with themselves and residents;
D. 1. Mating after selection or
   2. Mating before selection;
E. 1. Zygotic selection or
   2. Gametic selection.

Migration may occur at diploid or haploid stages of the life cycle, or in different ways (juveniles and adults) within each stage. If mating occurs before selection, it is immaterial whether diploids or haploids migrate unless the level of migration is itself under genetic control ("migrational selection" [Fisher 1930; Parsons 1963]), and there can by definition be no gametic selection.

In our study only migration selection cycles of the type \((A1 \text{ or } A2-B1-C1-D2-E1)\) were considered; this closely mimics the pattern of pollen flow and selection in higher plant populations, although clearly additional types of gene flow and selection may be operating in such populations. The most obvious additional process is seed transport between populations \((A1-B1-C2-D2-E1)\), but under high selection pressures seed flow has less influence on population structure than pollen flow (Antonovics 1968b). Gametic selection may also be operating, since competition on the style between different types of pollen is well known (Darlington and Mather 1949, p. 253; Muleahy 1971).

The underlying assumptions in the one-gene model were identical with those of Maynard Smith (1966). His model with habitat selection by females corresponds to our migration-selection cycle \((B1-C1-D2-E1)\), and his model with no habitat selection corresponds to cycle \((B1-C2-D2-E1)\). As expected, our numerical results confirmed those of Maynard Smith over the restricted range of conditions for which our simulation overlapped his.

Both Maynard Smith’s model and ours assumed that the size of the population was controlled independently of the selection process under consideration. This is likely in many plant populations, where populations are spatially separated (parapatric) and where population size in each subhabitat is controlled by density-dependent factors acting independently in each subhabitat. Another assumption was that the size of the populations and the gene flow remained the same through successive generations. These two factors are intrinsically linked: if, as assumed in these models, populations are sufficiently large for random fluctuations to be ignored, a change in the size of one population manifests itself only as a change in the magnitude of the gene flow between populations. The assumption of constant population sizes would not be true in a colonizing situation. This colonizing period will have profound effects on the initial strategy of the population but will not affect the final equilibrium (Antonovics 1968a, 1968b). Gene flow of more than 0.5 in one direction may result from a highly polarized wind direction, from differences in population density, or from flowering-time differences; but in all these cases gene flow in the opposite direction is correspondingly reduced. Hence it is unlikely that the sum of the values of gene flow in both directions would be greater than 1.0 (i.e., the sections of
figs. 1, 2, and 3 above the diagonal represent levels of gene flow which rarely occur in natural situations).

Results for the one-gene character show that comparison of observed genotype frequencies with Hardy-Weinberg expectations discloses very little about the forces acting on a population. An excess of heterozygotes does not necessarily indicate heterosis (see Ford 1964); it may be due to migration and selection (see fig. 2). However, a polymorphism showing close agreement with Hardy-Weinberg frequencies is possible despite gene flow and selection (e.g., for $S < 0.4$ and any gene flow). Furthermore lack of spatial genetic heterogeneity in a population does not imply lack of selective heterogeneity (see Antonovics and Bradshaw 1970); as shown by figure 1, there is a wide range of conditions for which morph frequencies may be approximately the same in both niches.

Results for disruptive selection on two and three genes are in qualitative agreement with the theoretical results for one gene. The maintenance of populations with distinct polygenic characters despite gene flow is in harmony with studies of natural populations (e.g., the transition from "southern English" to "east Cornish" types of Maniola jurtina in Cornwall [Ford 1964] and plant populations at the border of metal-contaminated and uncontaminated soil [Jain and Bradshaw 1966; Urquhart 1971]).

Polygenic control of a character produces a range of phenotypes, whereas it may be argued that a population consisting of two distinct phenotypes would be better adapted to a two-niche environment in which the selection pressures remain constant from year to year (Lewis and John 1964, p. 170). If there is no dominance, linkage of the genes contributing to a character would reduce the range of phenotypes to three; evolution of dominance would further restrict the population to two possible phenotypes, and so might be expected to play an important part in the strategy of a population in a two-niche situation (Sheppard 1958). The proportion of genotypes in the "wrong" niche may be further reduced by evolution of reproductive isolation.

The possibility that linkage might evolve was indicated by the lower genetic load for a one-gene character than for a polygenic character under equivalent conditions. The zygotic association, which developed under high selection pressures and low gene flow in the model of the two-gene character, is the first step toward linkage, as it implies an excess of the genotypes $AABB$, $aabb$, and $AaBb$, all of which may be formed by the fusion of $AB$ and $ab$ gametes. Most models of the evolution of linkage assume epistatic interaction between the genes involved (Kimura 1956; Ford 1964, p. 91; Turner 1967; O'Donald 1968), whereas our model shows that linkage may also evolve between noninteracting genes. In the two-niche situation, linkage evolved very slowly compared with either the original establishment of the polymorphism or the rate of evolution of other adaptations such as dominance and reproductive isolation (see figs. 3, 6). This suggests that linkage would not be caused by disruptive selection unless the selective pressures remained at a constant high level over a long period of time. Few models of
the evolution of linkage have discussed the rate of such evolution. The computer simulation of O'Donald (1968) is an exception, and his results suggest that, with epistasis, linkage would evolve much more rapidly.

The advantages of dominance modification are suggested by the results of the one-gene model, which show that for the same level of gene flow, the genetic load is lower if there is dominance. Dominance modifiers, by definition, act on the heterozygote and so spread more rapidly when there are many heterozygotes. Under disruptive selection, a high level of heterozygosity was maintained by gene flow. An increase in the degree of dominance of the gene raised the level of heterozygosity in the niche where that gene was favored (see fig. 2a, b) and further helped the spread of the modifiers. Overdominance modifiers spread more rapidly, since they gave a selective advantage to the heterozygote. This shows that, under disruptive selection, overdominance and heterosis could evolve rapidly. If there were low selection pressures in one niche and high selection pressures in the other, the allele which became dominant was that favored in the niche where intense selection was operating (e.g., in the mine/pasture situation tolerance would be expected to become dominant [Antonovics 1968b; Urquhart 1971]). There is evidence for the evolution of dominance and overdominance in certain populations which are undergoing disruptive selection but which are not strictly analogous to the present model (e.g., modifiers for tail length in Papilio dardanus [Clarke and Sheppard 1960], the evolution of inversion heterosis in Drosophila [Dobzhansky 1950; Dobzhansky and Levene 1951], and the differing degrees of dominance and differing selection pressures on the melanistic form of Amathes glaciosa in Shetland [Kettlewell et al. 1969]). Our results are in harmony with those of O’Donald (1968), who used computer models to show that dominance could evolve in certain cases of disruptive and frequency-dependent selection.

We have considered two mechanisms which could lead to reproductive isolation: (1) assortative mating due, in particular, to flowering time differences, and (2) self-fertility. These characters are known to be to some extent under genetic control; moreover, there is ample variability in natural populations on which selection could act (e.g., flowering-time differences in different ecotypes [summarized by McNeilly and Antonovics 1968], genetic variation in flowering time within populations [Lawrence 1963; Hayward 1970], and genetic variation in the degree of self-fertility [summarized by Antonovics 1968a; Jain and Marshall 1968]).

The results of the assortative-mating model showed that reproductive isolation readily evolved in response to interpopulation gene flow. Effects of the degree of dominance of gene A emphasize the complex interplay of factors operating in a natural situation. If gene A shows dominance, the populations are already better adapted to the two-niche environment than when A shows no dominance; hence there is less advantage to the populations in establishing isolation. If reproductive isolation is to evolve in the absence of ecological factors which directly affect the assortative-mating genotypes, it must be initiated by random fluctuations causing small differences in the frequencies
of the assortative-mating genes in the two populations. In many natural situations the mechanism which causes assortative mating may itself be subject to selection (e.g., beak size in finches [Lack 1961]; warmer, drier soil favoring earlier flowering on a mine [McNeilly and Antonovics 1968]). This would greatly facilitate the initiation of reproductive isolation and, as shown by figure 5, it would ensure that isolation was maintained under a wider range of conditions (see also Maynard Smith [1966] for discussion). Rapid evolution of reproductive isolation in response to artificial selection has been obtained by Thoday and Gibson (1962) using Drosophila and Paterniani (1969) using maize.

The model of self-fertility showed that reproductive isolation between the two niches could also evolve through selfing. The predicted spread of self-fertility despite inbreeding depression which would eliminate it from a single isolated population suggests that self-fertility may readily be established if a new niche becomes available for colonization. In contrast with assortative mating, self-fertility was more likely to spread if there was a high level of gene flow. There is evidence, from natural populations on mines and the adjacent pastures, that self-fertility can evolve in response to the deleterious effects of gene flow (Antonovics 1968a). More selfing occurs in the population on the mine than on the pasture, but the selfing gene does not reach fixation on the mine. Our model suggests that this could only arise if there was less inbreeding depression on the mine than on the pasture. This has already been postulated, on different grounds, by Antonovics (1968a).

Our model has shown that in a two-niche situation it is possible to establish a polymorphism, both for a single-gene and for a polygenic character, over a wide range of conditions. In such a polymorphic population linkage may evolve slowly, while dominance or overdominance modifiers can spread much more rapidly. Isolating mechanisms can arise in response to the deleterious effects of gene flow, selfing being more probable when there is a high level of gene flow and assortative mating when there is a low level of gene flow. There has been much circumstantial evidence that sympatric speciation may be possible (Thoday and Gibson 1962; Maynard Smith 1966; McNeilly and Antonovics 1968; Antonovics 1968a); this model provides an unequivocal demonstration that it is feasible. The model also emphasizes the point made by Thoday and Gibson (1970) that the heterogeneity of the environment can have far-reaching effects on the genetic architecture of the population.

SUMMARY

A deterministic computer simulation was made of a population occupying two niches. The size of the population in each niche was assumed constant, and there was gene flow between niches. The gene flow represented pollen transfer among plant populations. The basic model described one gene with two alleles, different alleles being selectively favored in different niches,
This model was extended to investigate, in turn, situations where the character undergoing selection was polygenic, where there were modifiers causing linkage of the polygenes, where there were modifiers causing changes in the dominance relations of the alleles, and where genes determined assortative mating and self-fertility. Results showed that a polymorphism could be maintained particularly with high levels of selection and/or low levels of gene flow, both in single-gene and polygenic cases. Linkage modifiers spread slowly in the population, but evolution of dominance or overdominance occurred rapidly, particularly under high levels of selection and gene flow. Isolation between populations in each of the two niches could arise through assortative mating or through self-fertility. The conditions under which each of these evolutionary steps occurred were clearly defined. Selection in heterogeneous environments with migration between subhabitats was shown to occur in several qualitatively different ways ("migration-selection cycles"). The assumptions of the model and the results were discussed in relation to studies on natural and experimental populations.

LITERATURE CITED


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