Heredity (1978), **40** (3), 371-384

EVOLUTION IN CLOSELY ADJACENT PLANT POPULATIONS

IX. EVOLUTION OF REPRODUCTIVE ISOLATION IN CLINAL POPULATIONS

MICHELLE CAISSE* and JANIS ANTONOVICS
Department of Botany, Duke University, Durham, North Carolina 27706, U.S.A.

Received 1.ix.77

SUMMARY

The evolution of reproductive isolation along a cline was investigated using a computer simulation of 10 linearly arranged populations connected by gene flow and subjected to selection which varied either linearly or in a stepwise manner. For nearly all combinations of parameter values a monotonic cline was rapidly established in frequency of alleles at the selected locus. Only at high levels of selection ($> 0{\cdot}1$) and high levels of assortative mating ($> 0{\cdot}4$) was there divergence in frequency of the gene determining reproductive isolation. Under these conditions divergence was slow and the cline for the isolating gene was often inverse for many generations, although at equilibrium the cline was always monotonic. Linkage between the selected gene and the isolating gene promoted divergence. Both genetic divergence and reproductive isolation may therefore occur between populations connected by gene flow. Conditions leading to isolation are more stringent than those permitting genetic divergence suggesting that the " cohesion of the biological species " is neither maintained by gene flow nor by the uniformity of selection but by the weakness of forces leading to selection for reproductive isolation. The existence of inverse clines in isolating mechanisms strongly suggests the evolution of isolation in sympatry (following divergence either in sympatry or allopatry,) but it is invalid to conclude that a monotonic cline for reproductive isolation gives *a priori* evidence of its evolution in allopatry.

1. INTRODUCTION

IT was formerly asserted that speciation could not occur within a group of populations which are connected to one another by migration, since it was believed that the effect of gene flow would be to erase any influence that divergent selection would impose (Mayr, 1970). However, many now accept that adjacent populations may diverge genetically if subjected to appropriate selection pressures. In evidence of this, there is a large literature on clinal and microgeographic variation for genetically determined characters in natural plant and animal populations (for papers in this series see: Aston and Bradshaw, 1966; Jain and Bradshaw, 1966; McNeilly, 1967; McNeilly and Antonovics, 1968; Antonovics, 1968*a*; Watson, 1969; Antonovics and Bradshaw, 1970; for other examples see Kettlewell and Berry, 1961, 1969; Endler, 1973; Karlin and Richter-Dyn, 1976).

There have also been a number of theoretical investigations which have clarified the relationship between gene flow and selection in producing a

* Present address: Department of Linguistics, University of California, Berkeley, California, U.S.A.

cline (Jain and Bradshaw, 1966; Endler, 1973; Slatkin, 1973; Karlin and Richter-Dyn, 1976). These studies have shown that in general, the degree of genetic divergence in response to divergent selection pressures depends on the balance between selection and migration. The slope of the cline of allele frequency varies directly with selection intensity and inversely with gene flow and is affected by the shape of the selection and migration functions. The range of values of selection and migration which permits some divergence is quite broad.

If one considers that the first step in speciation is the evolution of clinal or ecotypic variation, then the consummatory step must be the evolution of reproductive isolating barriers between these types. The work being presented here investigates the nature of the cline in allele frequency for a gene which determines reproductive isolation, given that there is clinal selection for alleles at another locus. An important impetus for making the study is that the form of such a cline may differ depending on the conditions under which speciation takes place. " Speciation ", as it is used here, is taken to include both genetic divergence, usually manifest as morphological dissimilarity, and reproductive isolation. (Both of these may exist to varying degrees between two populations of organisms; the problem of the extent to which divergence is necessary in order that species be taxonomically recognised is not addressed here.) Speciation may be sympatric, allopatric, or a combination of both. Populations may diverge morphologically during allopatry, and may at the same time lose partially or wholly the ability to interbreed. They may become morphologically divergent during allopatry without loss of the ability to interbreed and if they again come into contact may evolve reproductive isolation. A third possibility is that both morphological and sexual divergence ensue sympatrically. A distinction is sometimes made between populations which hold adjacent habitats (" parapatric ") and those which are interspersed together throughout an area, perhaps holding different ecological niches (" sympatric "). Here any populations which are either adjacent or interspersed and thereby connected by gene flow, are referred to as being sympatric.

It has been proposed that if reproductive isolation evolves during sympatry, then prezygotic isolating mechanisms would be restricted to regions of overlap of the two species, because only there would there be selective advantage to isolation. This pattern is sometimes referred to as " reproductive character displacement " or the " Wallace effect " after A. R. Wallace who first suggested that the overlap of two divergent forms which produce hybrids with reduced fitness would give an impetus for the evolution of sexual isolation. Examples of the Wallace effect and their relation to speciation have been recently reviewed by Levin (1970), Murray (1972), Scudder (1974), and Bush (1975).

Extending this concept slightly, one might expect that populations which are most closely adjacent would be most isolated from one another, while those further apart ought to be less genetically isolated. This sort of distribution of frequencies may be referred to as an " inverse cline ". While there are reasons for believing that reproductive isolation evolved under sympatry may yield an inverse cline for reproductive isolation, this is not the only possibility. Firstly, the contention that there may be divergence in an isolating gene in the face of gene flow is subject to the same counter-

arguments as are levelled against first-order sympatric divergence. In fact, the arguments are more telling here, because, as Crosby (1970) points out, selection against hybridisation is second order and is therefore likely to be relatively less effective. Nevertheless, several workers have shown theoretically that the evolution of reproductive isolation can occur under such a situation (Maynard Smith, 1966; Antonovics, 1968*b*; Dickinson and Antonovics, 1973). Secondly, we may expect that gene flow from populations near the boundary to those far from it will tend to disperse isolating genes throughout the range of the diverging forms. The extent and stability of an inverse cline are therefore not clear.

Thus it is the aim here to ascertain whether sympatric evolution of isolation yields an inverse cline, to investigate whether the cline differs for primary sympatry versus secondary re-establishment of sympatry after a period of allopatric divergence, and to study the general dynamics of evolutionary changes in isolating genes at the boundary between divergent populations.

2. Methods

The model presented here simulated a situation in which there were 10 populations occupying 10 habitats arranged linearly. There were two dimorphic loci, one affected by selection (*A*,*a* locus) and the other not directly selected, but determining reproductive isolation (*B*,*b* locus). Gene flow between the populations was in the form of male gamete (pollen) migration (*M*) only. Migration took place either between adjacent populations only (stepping stone) or was distributed according to a negative exponential function. For the latter, the amount of pollen entering population I from population J was equal to $e^{-M|I-J|}$, (fig. 1), and for the former it was equal to M. Populations were numbered sequentially, such that $|I-J|$ represented the distance between two populations.

Each habitat was characterised by certain selection coefficients (S) for the three genotypes at the A locus. There was no dominance at this locus. Selection was of two sorts: varying linearly from habitat 1 through habitat 10, or changing abruptly in a stepwise manner between populations 5 and 6 and having a slope of zero on either size of that boundary (the null point). Selection was symmetrical about the null point. Where selection coefficients are given in the text, they are for the *AA* genotype.

A second locus, *B*, determined prezygotic reproductive isolation; its action simulated flowering time differences in plant populations. *BB* and *Bb* individuals mated *inter se* and *bb* individuals mated *inter se* with frequency T; mating was random with frequency $1-T$. Values of T ranged from zero (panmixis) through one (complete assortative mating). Recombination (R) between A and B was varied between 0 (complete linkage) and 0·5 (no linkage).

In a standard run, the initial values for A and a were 0·5; the initial values for B in populations 1 through 5 were 0·4, and 0·6 in populations 6 through 10. Had the initial frequencies of B been identical in all populations, there would have been no divergence at all (Maynard Smith, 1966; Dickinson and Antonovics, 1973). Initial genotype frequencies were in linkage equilibrium. Each generation was begun with pollen migration, followed by mating, then selection. Runs were for 400 generations, unless

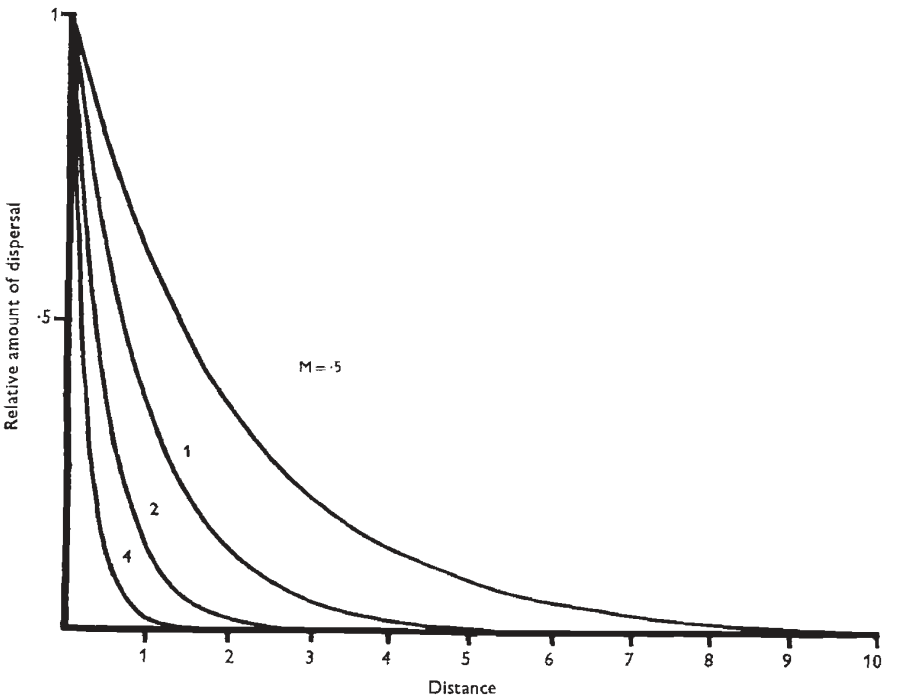

FIG. 1.—Negative exponential pollen distribution curves for various values of M. Relative abundance $= e^{-M\,(\text{distance})}$

equilibrium was reached sooner. It was considered that equilibrium existed if the sum of the absolute changes in frequency in all 10 populations for both A and B was less than 0·0005 over 20 generations. For each run, the following data were obtained for each population every 20th generation: frequency of allele A, frequency of allele B, and linkage disequilibrium (D). At equilibrium or termination of the run the frequency of each of the 10 possible genotypes was also printed out.

For many of the runs, divergence and inverseness in the frequency of the isolating allele (B) were calculated. " Divergence " was calculated as the difference between the maximum and minimum frequencies of B, regardless of where they occurred along the cline and " inverseness " was calculated as the divergence minus the difference between the frequencies of allele B in populations 1 and 10.

3. RESULTS

The results presented are those for the 400th generation of each run, unless equilibrium by the criteria stated above was achieved. Whether a true equilibrium was reached is discussed in section (v). In all cases where the run ended before the 400th generation, there was no inverseness of the cline for gene B. Initially (sections (i) and (ii)) the discussion assumes no linkage and $T = 0{\cdot}9$. In section (iii) the effects of varying linkage and T are considered.

(i) *Step clinal selection*

Divergence in allele frequency at the *B* locus as well as inverseness of the cline regularly increases as the strength of selection on gene *A* is increased (table 1). In general, selection of less than 5 per cent is insufficient to produce divergence in *B* but 10 per cent selection is sufficient for most values of migration. In the starting population divergence is 20 per cent and inverseness is 0, so that anything greater than this represents an increase over the original. Degree of divergence, given that it occurs at all, is not strongly dependent on migration. Inverseness of the cline depends strongly

TABLE 1

Effect of migration and step clinal selection on divergence and inverseness of the cline for genes A *and* B. *Recombination* R = 0·5 *and degree of assortative mating,* T = 0·9. *The* AA *genotype has the given selection coefficients,* S, *in populations* 1-5 *and* S = 0 *in populations* 6-10

			Migration							
			Negative exponential					Stepping stone		
Selection			0·5	1	2	2·5	4	0·5	0·1	0·05
0·75	Divergence	*A*	98	100	100	100	100	100	100	100
	Divergence	*B*	92	96	97	95	96	86	92	94
	Inverseness	*B*	0	0	19	44	76	10	54	68
0·50	Divergence	*A*	96	99	100	100	100	100	100	100
	Divergence	*B*	90	95	95	94	95	84	90	93
	Inverseness	*B*	0	0	20	44	75	5	53	67
0·10	Divergence	*A*	21	72	95	99	100	81	98	100
	Divergence	*B*	3	75	64	65	78	61	57	71
	Inverseness	*B*	0	0	22	36	59	0	30	49
0·05	Divergence	*A*	11	32	82	93	100	52	92	98
	Divergence	*B*	0	5	21	21	26	13	20	22
	Inverseness	*B*	0	0	0	0	0	0	0	2
0·01	Divergence	*A*	2	7	31	48	74	12	48	62
	Divergence	*B*	0	1	13	17	20	4	17	20
	Inverseness	*B*	0	0	0	0	0	0	0	0

on migration and goes up as migration rate goes down. Large amounts of migration favour a monotonic cline for several reasons. The region in which selection for divergence occurs is made broader, encompassing more populations on either side of the null point. Greater migration across the null point reduces the contrast between populations 5 and 6, and high migration rate enhances the spread of alleles from central to distal populations. Fig. 2 shows allele frequencies of *B* as a function of population number for several magnitudes of selection to illustrate some specific clinal patterns. The graphs are not completely symmetrical about the boundary because of dominance at the *B* locus. At low levels of selection there may be considerable divergence at the selected locus, *A*, but no divergence at the assortative mating, *B*, locus.

(ii) *Linear selection*

Linear selection bears a similar relationship to inverseness and divergence as does step clinal selection (table 2). An increase in selection yields an

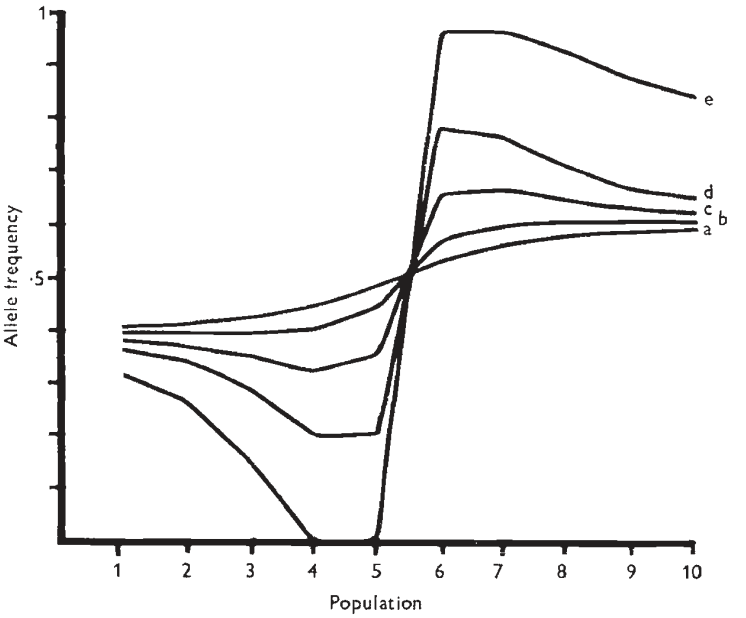

FIG. 2.—Frequency of allele *B* plotted against population number for different strengths of step selection. $M = 2{\cdot}5$, negative exponential; $R = 0{\cdot}25$; $T = 0{\cdot}9$. Selection against the *AA* genotype in populations 1-5 is (a) 0·02, (b) 0·04, (c) 0·06, (d) 0·08, (e) 0·9.

TABLE 2

Effect of migration and linear selection on divergence and inverseness of the cline for genes A *and* B. *Recombination,* R = 0·5 *and degree of assortative mating,* T = 0·9. *The* AA *genotype has the given selection coefficient in population* I

			Migration							
			Negative exponential					Stepping stone		
Selection			0·5	1	2	2·5	4	0·5	0·1	0·05
0·75 – (0·75) I	Divergence	*A*	95	99	100	100	100	100	100	100
	Divergence	*B*	88	94	91	88	84	88	78	77
	Inverseness	*B*	0	0	21	47	63	0	43	54
0·05 – (0·05) I	Divergence	*A*	89	97	100	100	100	100	100	100
	Divergence	*B*	86	93	82	68	40	88	60	43
	Inverseness	*B*	0	0	23	46	20	0	31	21
0·25 – (0·025) I	Divergence	*A*	60	87	97	99	100	92	100	100
	Divergence	*B*	69	86	40	28	21	81	26	23
	Inverseness	*B*	0	0	5	4	1	0	3	3
0·1 – (0·01) I	Divergence	*A*	15	41	87	96	100	60	94	98
	Divergence	*B*	0	0	21	20	20	17	20	20
	Inverseness	*B*	0	0	0	0	0	0	0	0
0·05 – (0·005) I	Divergence	*A*	8	22	70	85	99	38	84	94
	Divergence	*B*	0	2	16	18	20	6	18	20
	Inverseness	*B*	0	0	0	0	0	0	0	0

increase in both inverseness of the cline and in divergence. For most levels of negative exponential migration, a selection differential of 0·225 between the end populations will produce divergence. With negative exponential

migration a very low level of migration will reduce the degree of divergence but increase somewhat the degree of inverseness. With stepping-stone migration, reduced migration also reduces divergence but increases inverseness. Fig 3 shows allele frequencies as a function of population number for several magnitudes of linear selection.

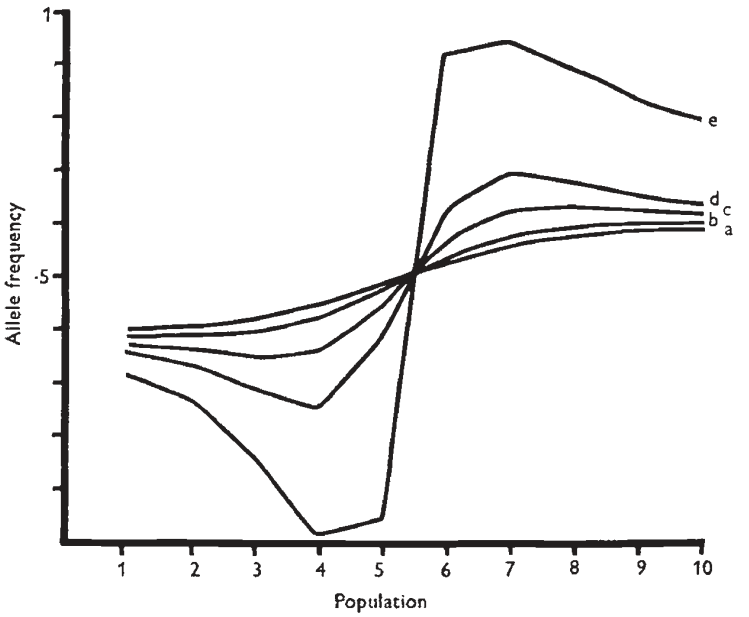

FIG. 3.—Frequency of allele *B* plotted against population number for different strengths of linear selection. $M = 2{\cdot}5$, negative exponential; $R = 0{\cdot}25$; $T = 0{\cdot}9$. Selection against the *AA* genotype in population 1 is (a) 0·045, (b) 0·081, (c) 0·135, (d) 0·225, (e) 0·675.

(iii) *Recombination and degree of assortative mating*

The degree of linkage between genes *A* and *B* may profoundly influence the outcome of selection for assortative mating (table 3). Complete linkage favours divergence more strongly than no linkage. This result is especially marked where selection is low: with no linkage there may be no divergence in the assortative mating gene but with linkage divergence may be very great. Correspondingly levels of linkage disequilibrium between the two genes are greatest at low levels of selection (table 3).

As the degree of assortative mating determined by gene *B* increases, so do divergence and inverseness (table 4). Low selection coefficients demand large values of *T*, if isolation is to occur.

(iv) *The* A *locus and its interaction with the* B *locus*

The cline for the selected gene *A* is always monotonic. Divergence at the *A* locus increases with increasing selection and with decreasing migration (tables 1 and 2). It is reasonable to suppose that where there is much divergence at gene *B*, this will encourage divergence in gene *A* by diminishing

TABLE 3

Effect of migration and step clinal selection on linkage disequilibrium (expressed as percentage of maximum possible disequilibrium). Recombination, R = 0·1 *and degree of assortative mating,* T = 0·9. *The* AA *genotype has the given selection coefficient* S, *in populations* 1-5 *and* S = 0 *in populations* 6-10

		Migration						
		Negative exponential				Stepping stone		
Selection		0·5	1	2	4	0·5	0·1	0·05
0·75	% *D*	3	2	1	0	4	1	0
	△ Freq. *B*	6	4	1	1	12	2	2
0·50	% *D*	5	3	2	0	5	2	1
	△ Freq. *B*	7	5	3	2	15	3	2
0·10	% *D*	36	29	13	2	42	11	6
	△ Freq. *B*	77	20	33	14	37	31	16
0·05	% *D*	58	59	36	6	26	24	13
	△ Freq. *B*	55	82	72	59	81	62	57
0·01	% *D*	2	9	18	13	14	17	15
	△ Freq. *B*	0	4	9	2	7	7	2

% *D* = percentage linkage disequilibrium, △ Freq. *B* = absolute increase in frequency of assortative mating gene as a result of complete linkage (*R* = 0) with the selected gene.

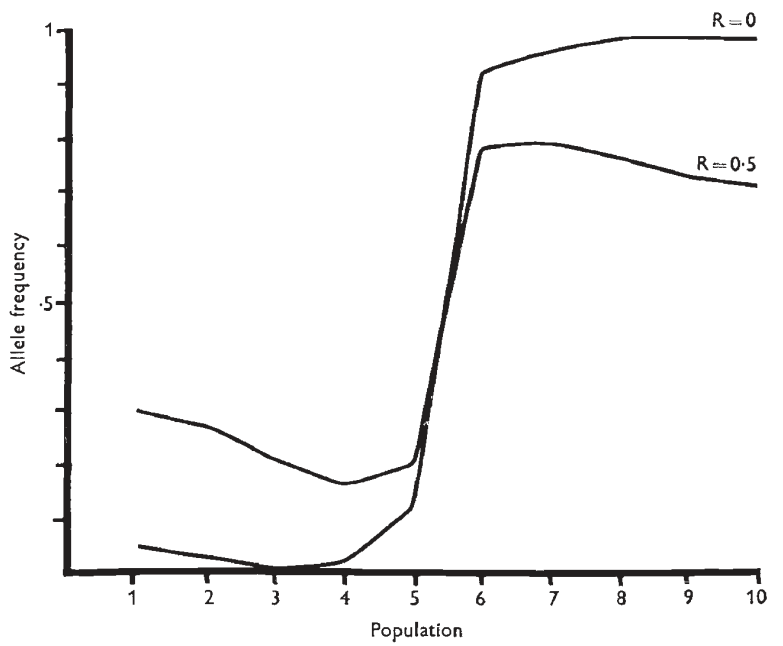

FIG. 4.—Frequency of allele *B* plotted against population number, for complete linkage (*R* = 0) and no linkage (*R* = 0·5). *M* = 2, negative exponential; *T* = 0·9. Step selection against the *AA* genotype in populations 1-5 is 0·1.

successful matings between individuals from divergent populations. Table 5 shows that *B* often has the largest effect on *A* where migration and selection are only just strong enough to result in divergence at the *B* locus. Here,

TABLE 4

Effect of varying degrees of assortative mating and step clinal selection on divergence and inverseness. Recombination, R = 0·1; *migration was negative exponential,* M = 2. *The* AA *genotype has the given selection coefficient,* S *in populations* 1-5 *and* S = 0 *in populations* 6-10

		T					
Selection		0	0·2	0·4	0·6	0·8	1
0·75	Div.	6	31	86	94	97	100
	Inv.	0	2	4	3	8	75
0·5	Div.	2	12	64	90	96	100
	Inv.	0	0	7	4	8	73
0·1	Div.	1	2	5	11	49	100
	Inv.	0	0	0	0	6	52
0·05	Div.	1	2	3	6	18	100
	Inv.	0	0	0	0	0	35
0·01	Div.	1	1	2	4	8	48
	Inv.	0	0	0	0	0	11

TABLE 5

Divergence at the A *locus when assortative mating,* T = 0. △ *Div. represents the difference in divergence at the* A *locus when* T = 0·9 *and* T = 0. *Recombination,* R = 0·5. *The* AA *genotype has the given selection coefficients,* S *in populations* 1-5 *and* S = 0 *in populations* 6-10

		Migration (*M*)				
Selection		0·5	1	2	2·5	4
0·75	Div.	85	98	100	100	100
	△ Div.	13	2	0	0	0
0·5	Div.	74	95	100	100	100
	△ Div.	22	4	0	0	0
0·1	Div.	21	55	94	98	100
	△ Div.	0	17	1	1	0
0·05	Div.	11	32	82	93	100
	△ Div.	0	0	0	0	0
0·01	Div.	1	6	31	47	74
	△ Div.	1	1	0	1	0

selection on *A* is moderate and subject to the influence of gene *B* in reducing the effect of gene flow. Where selection is high and/or migration low divergence in *B* has negligible effect.

(v) *Initial gene frequencies and time*

When initial values of gene *A* frequency were other than 0·5, the equilibrium values were unaffected. This was also true in the particular case where the populations on either side of the null point were fixed for alternative alleles, this representing evolution at the *A* locus during allopatry prior to the present period of secondary sympatry between the two types of populations.

In many cases, early in a run the cline of allele frequency at the *B* locus was strongly inverse and tended toward a monotone curve with succeeding generations, thus raising the question whether inverseness was an ephemeral

or a stable condition. Some runs were carried through over 800 generations and these still did not become monotonic; one even increased in inverseness over the value at the 400th generation. In order to ascertain the true equilibrium form of the cline, (generations = ∞) runs were performed with the initial frequency of allele *B* equal to 0 in populations 1 through 5 and equal to 1 in populations 6 through 10 (figs. 5 and 6). In these trials, which were run for 400 generations, the cline did not move toward inverseness but merely lost its sharpness at the centre due to migration across the boundary. This repre-

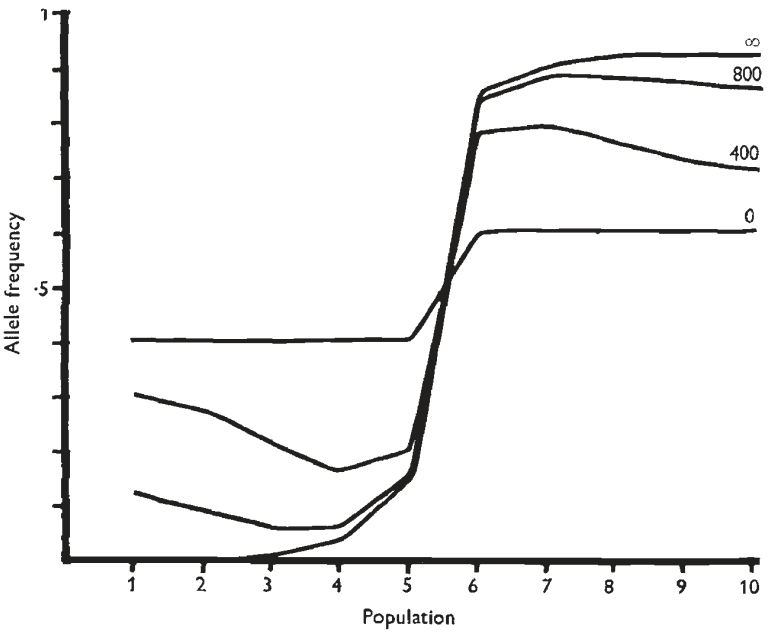

FIG. 5.—Frequency of allele *B* plotted against population number at successive generations during a run. $M = 2$, negative exponential; $R = 0{\cdot}5$; $T = 0{\cdot}9$. Step selection against the *AA* genotype in populations 1-5 is 0·1.

sents sympatry following evolution of isolation in allopatry; under these circumstances no inverse cline is established. Thus, theoretically, at equilibrium the cline will be monotonic. However, the time necessary to achieve equilibrium may at least in some cases be very long (fig. 6). Therefore while divergence increases steadily with time, inverseness reaches a peak and then steadily declines.

In all cases except those where there was a strong interaction between the *A* and *B* locus, equilibrium for the selected gene was approached far more rapidly (often within 50 generations) for the selected *A* locus than for the assortative mating *B* locus.

4. Discussion

Lewontin (1967) has said that elucidating the mechanisms of speciation remains the greatest unsolved problem for population geneticists. The

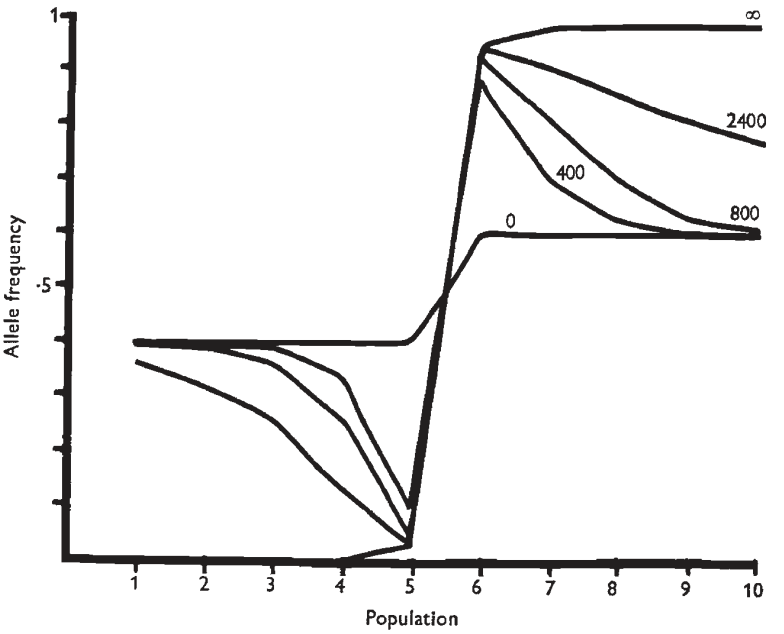

FIG. 6.—Frequency of allele *B* plotted against population number at successive generations during a run. $M = 4$, negative exponential; $R = 0{\cdot}5$; $T = 0{\cdot}9$. Step selection against the *AA* genotype in populations 1-5 is 0·1.

available theory of mechanisms of speciation is unsatisfying because there is no clear accordance with empirical observations; the pressures which lead to speciation, as distinct from infraspecific variation, are not obvious from the geographical or ecological distributions of species and there is a dearth of theoretical models which explore the speciation process.

This simulation study has shown that theoretically both genetic divergence and reproductive isolation may occur between populations connected by gene flow. It has also been shown that the theoretical equilibrium state for the distribution of allele frequencies of a gene determining reproductive isolation is monotonic. However, there is often a non-equilibrium state during which an inverse cline exists; the time required to reach equilibrium may be very great so that inverseness is apparently stable. The inverseness is shown to exist either where the initial genetic divergence took place in sympatry or allopatry, as long as reproductive isolation evolves in sympatry through the Wallace effect. Where reproductive isolation evolves in allopatry, no inverse cline is seen. The duration and perhaps degree of inverseness must depend on the number of populations under observation, that is the distance from the null point, so that had more than 10 populations been involved the duration of the inverse stage would have been longer.

The present study therefore shows that the evolution of isolation will occur if selection pressures and migration rates are appropriate and this evolution is independent of initial extent of divergence for other traits. Thus there is no theoretical reason for believing that divergence must be allopatric. However, it has generally been assumed that the cases in which the Wallace effect is known to have acted involve secondary contact of the two species

(Blair, 1964; Smith, 1965). It is often quite difficult to determine *post facto* whether divergence has occurred in allopatry or sympatry. In at least one case it is quite clear that isolation has evolved in sympatry, that of grasses growing on a metal mine (McNeilly and Antonovics, 1968); in others it seems quite likely (e.g., Dobzhansky and Koller, 1938). It is to be expected that further research will reveal more situations in which both divergence and isolation have been unambiguously sympatric.

In spite of the vast literature on the problem of what constitutes a species, there are still no well-accepted criteria for delimiting species: the biological species concept has not been incorporated into taxonomic practice. Maybe it cannot be (Sokal and Crovello, 1970). The question which is frequently posed is, why don't all geographic races become isolated species? Erlich and Raven (1969) exemplify this feeling when they cite the historically held view that species maintain their identity and cohesiveness because they represent a common gene pool, i.e., are bound by gene flow; and they dispute this view because empirically determined rates of gene flow are quite low. They conclude that since species cannot be unitary because of gene flow (see also Levin and Kerster, 1974), they must be so because of selection. However, the traditional view has existed precisely because it is untenable to believe that selection pressures are sufficiently constant to maintain the observed similarities within species over extremely large geographical ranges. Natural species themselves give evidence of this: many species do hold small ranges, and there are frequently geographic races. The unifying force must by default be gene flow. Mayr (1970), in order to escape this dilemma, appeals to the unknown when he says, ". . . in addition to gene flow—the cohesion of species is due to the fact that all of its populations share the same homeostatic systems and that this species-wide system of canalisation provides great stability ".

The data presented here show that the conditions which lead to reproductive isolation (i.e. speciation) are very different from those which lead to infraspecific variation. Virtually any at least approximately realistic regime of selection (of the two-range type) and migration will result in some differentiation for the selected gene, though the slope of the cline may be very slight (Slatkin, 1973; Endler, 1973). Even though there may be genes present which determine a high degree of assortative mating, if selection is too low or migration either too low or high, then no isolation whatsoever will evolve. Thus, the conditions leading to isolation are far more stringent than those permitting genetic divergence.

Factors other than the difference in the particular parameter values investigated here are probably important for the processes of divergence and isolation. It may be that the genetic resources from which to select for isolation are lacking. It has been shown that evolution of isolation is much more likely to occur if the gene available confers a high degree of isolation. If the population contains only genes which confer low amounts of assortative mating, selection will have to be very strong to result in divergence in their frequency. It might also be the case that there exist ecological pressures operating in the reverse direction on an isolating gene. For example, selection for divergence in flowering time might be balanced by stabilising selection on flowering time. McNeilly and Antonovics (1968) found that while differences in flowering time between two sites was probably best explained as a response to gene flow between two areas under different

selection regimes, the difference in at least one case was in the direction expected on purely ecological grounds. Littlejohn (1965) suggests that because of the essential invariance in pulse repetition rate in *Hyla ewingi* mating calls, except in the region of sympatry, there must be strong stabilising selection on this call component. This may reflect that " only the intense selection pressure for the maintenance of reproductive efficiency in sympatry is sufficient to lead to any marked change in this component". Crosby (1970) emphasises the weakness of the " second-order selection pressures " for isolation and simulated a situation which demonstrated it. He allowed variation in both time of flowering and duration of flowering, where reproductive output was independent of both of these factors. Under these circumstances divergence for flowering time evolved between two species which produced hybrids less fit than themselves. If those individuals which flowered longer had only a slight reproductive advantage (4·1 per cent for each week over 2, with a maximum of 6 weeks' flowering), then the duration of flowering of each species increased so that only very little divergence for flowering time was possible. Thus in this example, appealing because it is so easily envisioned as occurring in nature, a moderately small direct selective advantage reverses the effect of rather strong indirect effects (hybrids could have as little as 25 per cent fertility). More generally we can envisage that depending on the degree of selection against the isolating gene, either isolation will not occur, may be less than expected, or inverseness will be the stable equilibrium state. The " cohesion " of a species and our feelings that there is reality in the biological species concept may therefore be neither because of gene flow nor because of the uniformity of selection, but instead may simply be due to the weakness of the forces leading to selection for isolating mechanisms and the serendipitous ease with which a wide range of factors may counteract such forces.

This study has further shown that the interpretation of clinal patterns as evidence of particular past evolutionary events may be quite complex. For example, it is not valid to conclude that a monotonic cline for reproductive isolating mechanisms gives evidence of their evolution during allopatry. Under certain sets of conditions, no inverseness is to be expected at any time from the Wallace effect. Indeed, in all cases a monotonic cline is the equilibrium situation. One can state with more assurance that if an inverse cline does exist it is likely to signify the operation of the Wallace effect. The latter statement, however, assumes that there are no direct ecological pressures on the genes for reproductive isolation, producing an inverse cline coincidentally.

With this computer model we have attempted to explore some problems pertinent to the process of speciation. This initial simulation could profitably be extended with studies of greater genetic and ecological complexity; for example polygenic models which include gene interactions, models which explore zygotic migration and assymetrical migration patterns may yield interesting results. But apart from theoretical studies it is of the utmost importance, if we are to retrace with some degree of fidelity the nature of past processes that have led to present-day patterns of divergence, that we gather precise empirical data on gene flow, selection, and heritability of isolating traits in specific clinal situations. To date, speciation has been studied predominantly from a taxonomic perspective; far too rarely has it been viewed in an analytical population genetic context.

5. References

ANTONOVICS, J. 1968*a*. Evolution in closely adjacent plant populations. V. Evolution of self-fertility. *Heredity, 23*, 219-238.

ANTONOVICS, J. 1968*b*. Evolution in closely adjacent plant populations. VI. Manifold effects of gene flow. *Heredity, 23*, 507-524.

ANTONOVICS, J., AND BRADSHAW, A. D. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity, 25*, 349-362.

ASTON, J. L., AND BRADSHAW, A. D. 1966. Evolution in closely adjacent plant populations. II. *Agrostis stolonifera* in maritime habitats. *Heredity, 21*, 649-664.

BLAIR, W. F. 1964. Isolating mechanisms and interspecies interactions in anuran amphibians. *Q. Rev. Biol., 39*, 334-344.

BUSH, G. 1975. Modes of animal speciation. *Annual Rev. Ecol. Syst., 6*, 339-364.

CROSBY, J. L. 1970. The evolution of genetic discontinuity: computer models of the selection of barriers to interbreeding between subspecies. *Heredity, 25*, 253-297.

DICKINSON, H., AND ANTONOVICS, J. 1973. Theoretical considerations of sympatric divergence. *Amer. Nat., 107*, 256-274.

DOBZHANSKY, TH., AND KOLLER, P. C. 1938. An experimental study of sexual isolation in *Drosophila*. *Biol. Zent., 58*, 589-607.

ENDLER, J. 1973. Gene flow and population differentiation. *Science, 179*, 243-250.

ERLICH, P., AND RAVEN, P. 1969. Differentiation of populations. *Science, 165*, 1228-1232.

JAIN, S. K., AND BRADSHAW, A. D. 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity, 21*, 407-411.

KARLIN, S., AND RITCHER-DYN, N. 1976. Some theoretical analyses of migration selection interaction in a cline: a generalized two range environment. In S. Karlin and E. Nevo. *Population Genetics and Ecology: Proceedings.*

KETTLEWELL, H. B. D., AND BERRY, R. J. 1961. The study of a cline. *Amathes glareosa* Esp. and its melanic *f. edda* Staud. (Lep.) in Shetland. *Heredity, 16*, 403-414.

KETTLEWELL, H. B. D., AND BERRY, R. J. 1969. Gene flow in a cline. *Amathes glareosa* Esp. and its melanic *f. edda* Staud. (Lep.) in Shetland. *Heredity, 24*, 1-14.

LEVIN, D. A. 1970. Reinforcement of reproductive isolation: plants versus animals. *Amer. Nat., 104*, 571-581.

LEVIN, D. A., AND KERSTER, H. W. 1974. Gene flow in seed plants. In Th. Dobzhansky, M. K. Hecht, and W. C. Steere. *Evolutionary Biology*, 7. Plenum Press, New York.

LEWONTIN, R. 1967. Population genetics. *Ann. Rev. Genet., 1*, 37-70.

LITTLEJOHN, M. J. 1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution, 19*, 234-243.

MAYNARD SMITH, J. 1966. Sympatric speciation. *Amer. Nat., 100*, 637-650.

MAYR, E. 1970. *Populations, Species and Evolution.* Belknap, Cambridge, Mass.

MCNEILLY, T. 1967. Evolution in closely adjacent plant populations. III. *Agrostis tenuis* on a small copper mine. *Heredity, 23*, 99-108.

MCNEILLY, T., AND ANTONOVICS, J. 1968. Evolution in closely adjacent plant populations. IV. Barriers to gene flow. *Heredity, 23*, 205-218.

MURRAY, J. 1972. *Genetic Diversity and Natural Selection.* Harper, N.Y.

SCUDDER, G. G. E. 1974. Species concepts and speciation. *Can. J. Zool. 52*, 1121-1134.

SLATKIN, M. 1973. Gene flow and selection in a cline. *Genetics, 75*, 733-756.

SMITH, M. H. 1965. Behavioral discrimination shown by allopatric and sympatric males of *Peromyscus eremicus* and *P. californicus* between females of the same two species. *Evolution, 19*, 430-435.

SOKAL, R. R., AND CROVELLO, T. J. 1970. The biological species concept: a critical evaluation. *Amer. Nat., 104*, 127-153.

WATSON, P. J. 1969. Evolution in closely adjacent plant populations. VI. An entomophilous species *Potentilla erecta* in two contrasting habitats. *Heredity, 24*, 407-422.