Founder Effect Speciation: A Theoretical Reassessment

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FOUNDER EFFECT SPECIATION: A THEORETICAL REASSESSMENT

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Abstract.—We propose a series of simple models of founder effect speciation. In these models, the resulting reproductive isolation (as measured by the proportion of inviable hybrids or the strength of the barrier to gene exchange between populations) can be very high and can evolve with a high probability on the time scale of dozens or hundreds of generations. In developing our theoretical framework, we utilize Dobzhansky's idea that strong selection against hybrids between two genotypes can occur simultaneously with the existence of a chain of genotypes that connect those two and differ only weakly in fitness among themselves. The mathematical models that we have studied are closely related to the verbal schemes of Mayr's "genetic revolutions," Carson's founder-flush process, and Templeton's genetic transilience. For appropriate parameter values, our theoretical models demonstrate that founder effect speciation is plausible; its importance becomes an empirical question.

We discuss in this article how a population can evolve to a state that is reproductively isolated from its ancestor state. For those accepting the biological species concept (Mayr 1942), this is the central problem of speciation. Evolution of reproductive isolation is influenced (at least potentially) by many genetic, ecological, developmental, behavioral, environmental, and other factors in different ways. If one wants to make the discussion less speculative, one should necessarily concentrate on only some of them while neglecting others. Our analysis will be based on (and, hence, limited by) several simplifying assumptions. It is easier to list factors that we are going to consider than those that we are not. We will consider only postzygotic isolation manifested in (and defined as) reduced or zero fitness of hybrids and backcrosses. Following most previous theoretical discussions of the evolution of postzygotic isolation, we start by considering a randomly mating diploid population with discrete generations under constant viability selection. We assume that the population size is very large and externally regulated. Mutation and recombination rates are constant. We also assume that the loci are diallelic, that the population is dioecious, and that sexes are equivalent with

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respect to fitness. This set of assumptions is common in the population-genetics literature and can be called the standard population-genetics model.

The standard population-genetics model has been intensively analyzed (see reviews in Ewens 1979; Hastings 1989; Nagylaki 1992). The dynamic behavior of this model depends sensitively on selection (as described by genotype fitnesses) and recombination, but, nevertheless, two general observations can be made. Although examples of cyclic behavior are known (Akin 1979; Hastings 1981) and examples of evolution toward a line of equilibria can be easily constructed, typically the population evolves toward an equilibrium point (Hastings 1989). The second observation is that several such equilibria can be stable simultaneously (see, e.g., Franklin and Lewontin 1970; Feldman and Liberman 1979; Hastings 1985). Within the framework of the standard population-genetics model, different stable equilibria correspond to populations at different stable states. Genetic variability at these states is augmented or maintained by mutation. Two equilibria can be considered as describing two reproductively isolated populations if the corresponding hybrids have zero fitness. (Here by *hybrids* we mean all genotypes that can potentially be produced by a pair of individuals coming from populations at different equilibria.) The problem of the evolution of reproductive isolation is now the problem of how a population can move from one state to a different state reproductively isolated from the first one. Obviously, the evolution of reproductive isolation is not possible without relaxing some of the assumptions of the standard model, for otherwise the population stays at a given equilibrium forever.

Many assumptions can be relaxed, and many additional factors can be incorporated in the model. Among factors that can, potentially, contribute to the evolution of reproductive isolation, random genetic drift has attracted substantial attention. An obvious reason for this interest is that population sizes are never infinite, and, hence, stochastic factors are always present. With finite population sizes, random genetic drift can, presumably, move a population from the domain of attraction of one deterministic equilibrium to the domain of attraction of another deterministic equilibrium. This suggests that stochastic factors can cause evolution of reproductive isolation even when the overall selection regime does not change. Analytical approximations and numerical simulations (see, e.g., Lande 1979, 1985b, 1986; Walsh 1982; Barton and Charlesworth 1984; Barton and Rouhani 1987) show that the probability of stochastic transitions quickly diminishes with increasing population size. Unless selection is extremely weak, with population sizes of the order of thousands of individuals, stochastic transitions are practically impossible. The population sizes of most species are much larger (Nei and Graur 1984). However, two properties of natural populations may keep the probability of stochastic transitions nonnegligible: populations are typically subdivided, and the processes of extinction and colonization may be common. These properties can lead to a small effective population size (at a given location or during some time interval) and make stochastic transitions plausible.

Two theories utilizing these properties have been proposed: the shifting balance theory (Wright 1931, 1980) and the founder effect speciation theory (Mayr 1942, 1954). The theories have in common stochastic transitions initiated in a small subpopulation (partially or completely) isolated from the rest of the species, but

they differ in describing how the number of individuals with "new" genotypes becomes large enough to be considered a new species that can sustain itself.

The shifting balance theory considers a population subdivided into many groups connected by migration. In this scenario, a new adaptive combination of genes first becomes established by chance in a single subpopulation (or, in the continuous version of the theory, in a sufficiently large spatial area) and then takes over the whole population. Two stochastic and one deterministic mechanism of the latter stage (phase 3 in Wright's terminology) have been formally studied. Lande (1979, 1985a) has considered a situation in which a new combination of genes that has become established in a single subpopulation takes over the whole population as a result of stochastic extinction and colonization. In Barton and Rouhani's (1993) and Rouhani and Barton's (1993) models, the influx of migrants from demes carrying a new combination of genes makes it more likely that the deme will shift to this combination as a result of random fluctuations. Several articles considered the spread of a new combination of genes to be a deterministic process resulting from "competition" between different combinations of genes and excess population growth and excess emigration (see, e.g., Rouhani and Barton 1987; Gavrilets 1995). The general conclusion that can be drawn from all these analyses is that conditions for stochastic transitions are severe. Even under the most favorable conditions, stochastic peak shifts can occur rarely (at the time scale of tens of thousands generations) and can only result in weak reproductive isolation. To produce strong reproductive isolation, many subsequent peak shifts have to take place. Given these analyses, one can conjecture that the shifting balance process cannot be important if reproductive isolation is to evolve quickly.

A different scenario that can potentially result in a very rapid evolution of reproductive isolation is described by the theory of founder effect speciation. Several versions are known (Mayr 1942, 1954; Carson 1968; Kaneshiro 1980; Templeton 1980; Carson and Templeton 1984; see also Provine 1989, for a history of this theory). This theory has been the favored explanation for at least island speciation since 1954 (Provine 1989) and has been used to support the theory of punctuated equilibrium (see Somit and Peterson 1992). In the scenario envisioned in founder effect speciation, a few individuals found a new population that is geographically isolated from the ancestral species and that expands to fill a new area. In this theory, the stochastic shift happens during a short time interval when the size of the expanding population is still small. One of the inherent features of the shifting balance theory that makes the peak shift a slow and constrained process is the necessity to spread the new adaptive combination of genes from a local subpopulation to the rest of the population. During this stage new combinations of genes have to "compete" with the old ones that outnumber the former. (Haldane [1959] was one of the first to raise criticism of the shifting balance theory of this ground.) Founder effect speciation avoids this difficulty by simply removing the necessity for the new combination to take over: a local subpopulation grows to become a new species without interacting with the ancestor one.

The proponents of these theories proposed only verbal schemes without trying to formalize them. Later, formal analyses of founder effect speciation using analytical models and numerical simulation were undertaken in Charlesworth and

Smith (1982), Barton and Charlesworth (1984), Rouhani and Barton (1987), and Charlesworth and Rouhani (1988) and were summarized in Barton (1989). The general conclusion of these analyses is that a founder event cannot result in a sufficiently high degree of reproductive isolation with a sufficiently high probability to be a reasonable explanation for speciation. Barton (1989, p. 252) concludes his article by saying that "there are strong theoretical arguments that the particular genetic models of founder effect speciation put forward by Mayr, Carson and Templeton are unlikely to be effective." This view seems to have been accepted widely. For example, a review in *Nature* says with reference to Barton (1989) that "a major problem with founder-effect theories is that they do not seem to work when their verbal assumptions are transformed into mathematical models" (Coyne 1992, p. 514).

These conclusions are based on a biological interpretation of the results of analyses of some mathematical models. Any mathematical model of a complex biological process necessarily incorporates simplifying assumptions. The history of mathematical modeling (both in biology and other sciences) shows that relaxing or changing these assumptions can and often does result in dramatic changes in the predictions and conclusions based on the model. Within the framework of the standard population-genetics model, the most crucial assumption concerns relationships between genotype and fitness (i.e., the genetic basis of reproductive isolation and adaptation). Although numerous, the above cited articles with mathematical models for both the shifting balance process and founder effect speciation have considered primarily only two different fitness schemes. The first is selection on a single diallelic locus with heterozygotes having fitness smaller than both homozygotes. The second is disruptive (bimodal) selection on a single additive quantitative character. An inherent feature of these two models is that the fitness of hybrids is about the same as the fitness of the "worst" state a population has to pass through on its way from one equilibrium to another. Using the metaphor of adaptive landscapes, we might say that the depth of the adaptive valley that the population has to cross is approximately equal to the degree of reproductive isolation arising from the peak shift (see fig. 1A). Stochastic transitions across deep adaptive valleys are very unlikely; hence, the emergence of a highly reproductively isolated new species in a single step is unlikely as well.

Reproductive isolation has a complex, and largely unknown, genetic basis. Models analyzed in the articles cited above represent only a tiny proportion of possible models. An alternative scenario of evolution of reproductive isolation is based on the model proposed by T. H. Dobzhansky almost 60 yr ago (Dobzhansky 1937). His original model considers a two-locus, two-allele population initially monomorphic for a genotype, say *aaBB*. This population is broken up into two geographically isolated parts. In one part, mutation (and possibly selection) causes substitution of *a* for *A,* and a local race *AABB* is formed. In the other part, mutation (and possibly selection) causes substitution of *B* for *b,* which gives rise to a local race *aabb*. It is assumed that there is no reproductive isolation among genotypes *AABB, AaBB,* and *aaBB* and among genotypes *aaBB, aaBb,* and *aabb,* but genotypes *AABB* and *aabb* are considered to be reproductively isolated. In this scheme, strong selection against hybrids between races with the
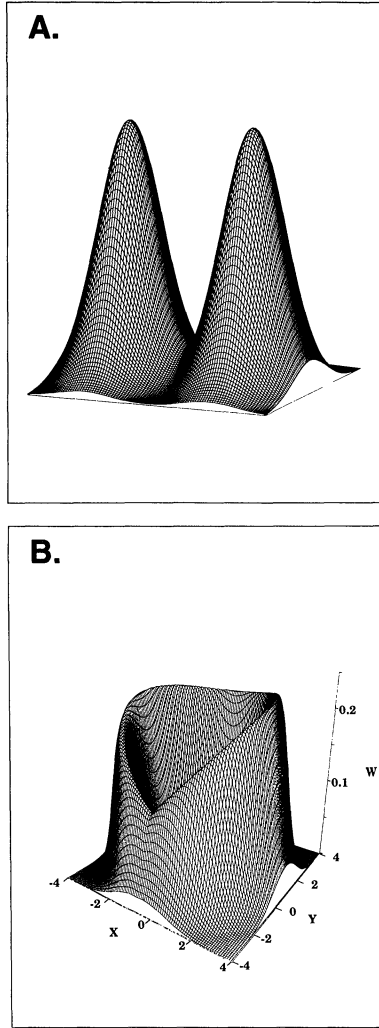
Fig. 1.—Fitness landscapes with two peaks, where X and Y are some genotypic character-istics inherited additively (i.e., X and Y values of a hybrid are half of the sum of the corre-sponding values of parents). A, Fitness landscape describing a situation when the fitness of F_1 hybrids is about the same as the fitness of the "worst" state that the population has to pass through on its way from one peak to another. B, Fitness landscape describing a situation when the fitness of F_1 hybrids is much less than the fitness of the "worst" state that the population has to pass through on its way from one peak to another.

genotypes *AABB* and *aabb* can be achieved, even though selection acting during the evolutionary divergence is weak. The scenario of evolution of reproductive isolation based on Dobzhansky's model assumes that the population moves from one adaptive peak to another without descending to the very bottom of the adaptive valley separating those peaks but following a rim connecting those peaks. This scenario utilizes the idea that when the population is characterized by more than one variable, the depth of the adaptive valley that the population has to cross can be completely unrelated to the degree of reproductive isolation arising from the peak shift (see fig. 1*B*). Different properties of models utilizing the same idea have been discussed and formally studied (see, e.g., Bengtsson and Christiansen 1983; Nei et al. 1983; Bengtsson 1985; Barton and Bengtsson 1986; Wagner et al. 1994). These models, however, were dismissed by Barton and Bengtsson (1986), who argued that the "Dobzhansky model, and similar schemes, would not in fact produce much reproductive isolation" (p. 370) because they do not result in a sufficiently strong barrier to gene exchange between the populations. This view was reiterated in subsequent publications (see, e.g., Barton and Rouhani 1987; Barton 1989), with a strong emphasis that this conclusion does not depend on genetic details.

The main purpose of this report is to propose simple Dobzhansky-type models of founder effect speciation. In these models, the resulting reproductive isolation (as measured by the proportion of inviable F_1 hybrids or the strength of the barrier to gene exchange between populations) can be very high and can evolve with a high probability. We will describe multilocus population-genetics models, quantitative genetics models, and models considering both major loci and quantitative traits simultaneously. The mathematical models that we will study are closely related to the verbal schemes of Mayr's (1954) "genetic revolutions," Carson's (1968) founder-flush process, and Templeton's (1981) genetic transilience. We conclude that in certain cases, founder effect speciation is plausible.

<div align="center">BASIC FRAMEWORK</div>

In the following sections, we will consider a series of models of evolution of reproductive isolation according to the scenario of founder effect speciation. These models will be constructed in such a way that their deterministic versions (corresponding to very large population sizes) have two (or more) simultaneously stable polymorphic equilibria. We will start by considering a very large population at one of these equilibria. We will assume that a new population is founded by a few individuals chosen randomly from this ancestral population. After the founding event, the population size rapidly approaches a very large value, at which all stochastic effects on allele frequencies effectively cease, and a deterministic description of the dynamics becomes appropriate again. During a brief period of relatively small population size, stochastic fluctuations may dramatically change the genetic structure of the population, which may result in a peak shift, that is, in the population settling down to an equilibrium different from the initial one. We will be interested in the ability of a single founder event to cause strong reproductive isolation. Strong reproductive isolation will be incorporated in the

models by positing that some of the hybrids between populations at different equilibria have zero fitness, that is, are inviable (see Nei et al. 1983). The degree of reproductive isolation between two populations will be characterized by the proportion of inviable (i.e., zero fitness) hybrids, I. Obviously, I lies between zero and one, with higher values corresponding to higher degrees of reproductive isolation. Other measures of reproductive isolation and their relationship to I will be discussed later.

Using a combination of simple analytical approximations and numerical simulations, we will study the probability of a single founder event to cause a peak shift, P; the degree of reproductive isolation corresponding to this shift, I; and the time that it takes for this isolation to evolve, T. In modeling the founder effect speciation process, we will follow previous work (Rouhani and Barton 1987; Charlesworth and Rouhani 1988), assuming that the process has two phases: stochastic and deterministic. The stochastic phase lasts during the time interval that it takes the population size to reach some specified value N_{max}. This value, N_{max}, is considered to be large enough that in populations with larger sizes, all stochastic effects on allele frequencies effectively cease on the time scale of, say, thousands of generations. The population size increases deterministically with a geometric rate $R : N_t = R^t N_0$, where t is the generation number and N_0 is the size of the founder population. When we use numerical simulations to compute the dynamics of allele frequencies during the stochastic phase, these simulations will be based on the discrete Fisher-Wright binomial scheme allowing for selfing (see Charlesworth and Rouhani 1988). To simplify comparison with previous results, we will consider the numerical values of N_0 (2, 4, and 8) and R (1.1, 1.3, 1.5, and 2) to be the same as used in Charlesworth and Rouhani (1988), N_{max} is 1,000 (intermediate between $N_{max} = 150$ used in Rouhani and Barton 1987, and $N_{max} = 10,000$ used in Charlesworth and Rouhani 1988).

GENETICS MODELS

In this section, we will present several two- and three-locus models of the evolution of strong reproductive isolation following a single founder event. An important feature of these models is that the fitness of individuals with more than one heterozygous locus is postulated to be zero. We will compare these models among themselves and with a simple one-locus model.

One-Locus Model

We begin by considering a simple one-locus, two-allele model in which homozygotes are equally fit, while heterozygotes have zero fitness (see fig. 2). We assume that forward and backward mutation rates are equal and very small. This model has two simultaneously stable equilibria, with genetic variability maintained by mutation. At these equilibria, the frequency of a rare genotype (AA or aa) is approximately μ^2, where μ is the mutation rate ($\mu \ll 1$). Let us imagine two large populations at different equilibria and consider the first-generation hybrids. Most of them will be heterozygotes and will not survive. The proportion of those that survive will be approximately 2μ. Thus, on the average, the degree
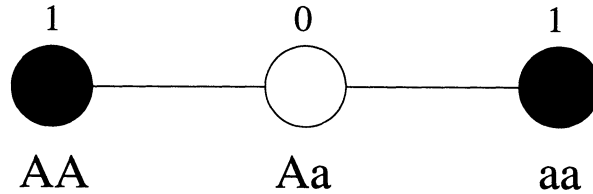
Fig. 2.—Fitnesses of three genotypes in the one-locus, two-allele model with inviable heterozygote and equally fit homozygotes. The genotypes common at two equilibria are shown with black circles.

of reproductive isolation as measured by the proportion of inviable hybrids, I, equals

$$I = 1 - 2\mu$$

and is very high. For example, with $\mu \gg 10^{-6}$, only one of a billion matings would produce viable progeny.

How probable is it for a single founder event to result in such a high degree of reproductive isolation? Let a new population be founded by N_0 individuals chosen randomly from the population, with allele A in common. With probability $N_0\mu^2$ it has a single individual with genotype aa, and one can disregard the chance that there is more than one such individual. At the end of the stochastic phase, the population may be fixed for the common genotype, may remain polymorphic, or may be fixed for the initially rare genotype. The first and last outcomes correspond to the return of the population to its initial equilibrium and to the peak shift, respectively. In the second case, the deterministic (i.e., very large) population returns to its initial state or moves to the new equilibrium depending on whether the frequency of genotype AA is greater or less than 0.5. The probability of a peak shift as a result of a single founder event is approximately

$$P = uN_0\mu^2,$$

where u is the probability that the frequency of genotype aa, which was present by a single copy in a founder population, is bigger than 0.5 at the end of the stochastic phase (including the probability that it is exactly one). This probability depends on the growth rate R and the size of the founder population N_0. If $N_0 = 2$, then from the symmetry considerations, it follows that u should be exactly 0.5. Table 1 illustrates how probable the peak shift is for some other parameter combinations. The values in this table were computed numerically using a procedure described in the previous section. With $N_0 = 4$, u becomes extremely small (see table 1); with $N_0 = 8$, the only observed outcome is fixation of allele A. Table 1 also reflects a well-known fact (see, e.g., Holgate 1966; Daley et al. 1982) that rapidly growing populations can preserve genetic variability. Both the proportion of viable hybrids and the probability of stochastic transition are very small. In this model, the evolution of strong reproductive isolation as a result of a founder event is extremely unlikely. However, if it happens, it only takes several generations.

TABLE 1

Simulated Frequencies of Different States of the One-Locus
Population at the End of the Stochastic Phase When the
Founder Population of Size N_0 Has a Single Genotype aa

R	$N_0 = 2$			$N_0 = 4$		
	A	a	Poly	A	a	Poly
1.1	25,235	24,765	0	49,704	296	0
1.3	24,956	25,043	1	49,875	125	0
1.5	24,808	25,186	9	49,962	38	0
2.0	24,062	24,290	1,648	49,994	2	4

Note.—In all cases, the number of runs is 50,000. A and a stand
for fixation of alleles A and a, respectively; *poly* denotes a situation
when the population remains polymorphic; $w_{AA} = w_{aa} = 1$; $w_{Aa} = 0$.

Two-Locus Models

Initial variability maintained by mutation.—Let us consider a two-locus, two-allele model in which the double heterozygote has zero fitness, two homozygotes have maximum fitness, and other genotypes have slightly reduced fitness (see fig. 3A, in which $0 < s_1, s_2 \ll 1$). We assume that forward and backward mutation rates in both loci are equal to μ and are much smaller than s_1, s_2. This model has two simultaneously stable equilibria, with genetic variability maintained by mutation. At each of these equilibria, one allele at each locus is common and another is rare, with the frequency μ/s_i. After selection, a homozygous genotype (*AABB* at one equilibrium or *aabb* at another equilibrium) is close to fixation, genotypes heterozygous at one locus have a low frequency $\mu/s_1 + \mu/s_2$, and all other genotypes have even lower frequencies. Linkage disequilibrium is very small (see, e.g., Hastings 1988). Let $s_1 = s_2 = s$. Let us imagine two large populations at different equilibria and consider the first-generation hybrids. Most of them will be double heterozygotes and will not survive. Among those that survive, the most common will be a product of matings between homozygotes common in one population and single-locus heterozygotes from another population whose frequency is approximately $4\mu/s$. Thus, the degree of reproductive isolation is

$$I = 1 - 4\mu/s.$$

For example, if $\mu = 10^{-6}$ and $s = 0.025$, then 99.984% of hybrids will be inviable.

How probable is it for a single founder effect to result in such a high degree of reproductive isolation? Let a new population be founded by N_0 individuals chosen randomly from a population with genotype *AABB* common. With the probability $2N_0\mu/s$, it has a single copy of a rare allele, say, a, and one can disregard the chance that there is more than one rare allele in the founder population. During the period of rapid growth, new mutation can be neglected and stochastic factors are the most important. At the end of this period, the population may be fixed for the initially common allele A, may remain polymorphic, or may be fixed for
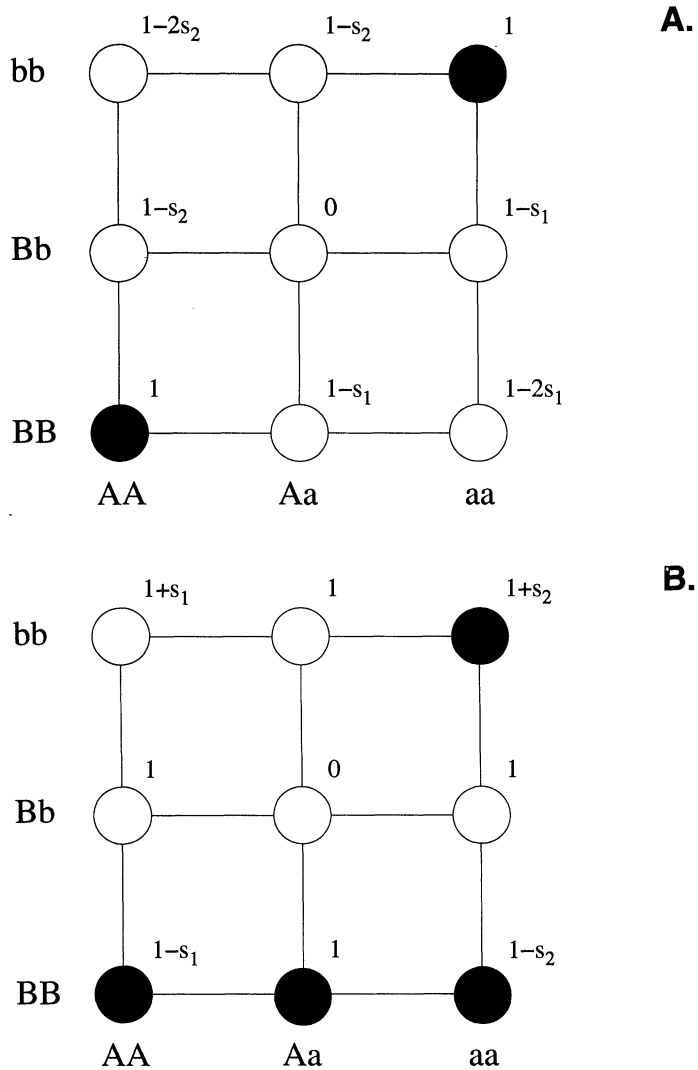
FIG. 3.—Fitnesses of genotypes in two-locus, two-allele models with inviable double heterozygotes. *A,* In this model there are two equilibria with genetic variability in both loci maintained by mutation. *B,* In this model, there is an equilibrium with genetic variability maintained by overdominance in locus A and by mutation in locus B and two equilibria with genetic variability maintained by mutation in both loci. The genotypes common at two equilibria are shown with black circles.

TABLE 2

Simulated Frequencies of Different States of the One-Locus Population at the End of the Stochastic Phase When the Founder Population of Size N_0 Has a Single Copy of Allele a

R	$N_0 = 2$			$N_0 = 4$			$N_0 = 8$		
	A	a	Poly	A	a	Poly	A	a	Poly
1.1	7,115	2,207	678	7,813	453	1,734	8,026	13	1,961
	7,457	1,864	679	8,222	291	1,487	8,379	8	1,613
	7,782	1,626	592	8,602	183	1,215	2,134	0	7,866
1.3	4,924	532	4,544	5,328	7	4,565	5,585	0	4,415
	5,260	397	4,343	5,666	4	4,330	5,935	0	4,065
	5,590	341	4,069	6,051	1	3,948	8,804	0	1,196
1.5	3,391	85	6,524	3,789	0	6,211	3,996	0	6,004
	3,636	69	6,295	4,042	0	5,958	4,218	0	5,782
	3,807	62	6,131	4,333	0	5,667	6,136	0	3,864
2.0	1,598	0	8,402	1,728	0	8,272	1,929	0	8,071
	1,686	2	8,312	1,910	0	8,090	1,970	0	8,030
	1,925	2	8,073	2,134	0	7,966	2,198	0	7,802

Note.—In all cases, the number of runs is 10,000. Here, A and a stand for fixation of alleles A and a, respectively, while poly denotes a situation when the population remains polymorphic. For each value of the population growth rate, R, the upper, medium, and lower lines correspond to $w_{AA} = w_{Aa} = w_{aa} = 1$ (no selection); $w_{AA} = 1$, $w_{Aa} = 0.975$, $w_{aa} = 0.95$; and $w_{AA} = 1$, $w_{Aa} = 0.95$, $w_{aa} = 0.9$, respectively.

the initially rare allele a. In the first two cases the deterministic (i.e., very large) population will return to its initial equilibrium. Let us consider the case when the population becomes fixed for the initially rare allele a. Now all individuals have genotype $aaBB$. When the population size is very large, random drift becomes unimportant but mutation begins to play its role. The state describing a population monomorphic for genotype $aaBB$ does not represent an equilibrium. With equal probabilities, one-half mutation will move the population back to its initial state (with genotype $AABB$ common) or to the new equilibrium (with genotype $aabb$ common). Note that introducing a small asymmetry into the model (e.g., by assuming that fitness of genotype aabb is $1 + \epsilon$, where ϵ is an extremely small number) can cause mutation to always move the population to the new equilibrium.

In this model, the probability of peak shift as a result of a single founder event can be represented as

$$P = uN_0\mu/s,$$

where u is now the probability of the fixation of an allele that was present by a single copy in a founder population of size N_0. This probability depends on the growth rate R. Note that in this model, the probability of peak shift is proportional to μ and thus is much higher than in the one-locus model in which the probability was proportional to μ^2.

Table 2 illustrates the plausibility of different events during the stochastic phase for some parameter combinations. The probability of the evolution of strong reproductive isolation via a single founder event is much higher than in the one-

locus model considered above, but its absolute value still is small. For example, if $N_0 = 2$, $R = 1.1$, $\mu = 10^{-6}$, and $s = 0.02$, then $P \approx 1.5 \times 10^{-5}$.

One can also estimate the time that it takes for strong reproductive isolation to evolve. The process has two steps: a stochastic one and a deterministic one. The latter corresponds to deterministic changes in the frequency of allele b caused by selection and mutation, and it is much longer than the former. The time that it takes for selection and mutation to change the allele frequency from 0% to 99% is approximately $T = 300$ generations when $s = 0.05$ and $T = 600$ generations when $s = 0.025$ (with $\mu = 10^{-6}$). These values of T were estimated numerically by iterating a single equation describing the dynamics of allele frequency in a single diallelic locus under selection (with fitnesses $1 - 2s : 1 - s : 1$) and mutation. Thus, in this two-locus model, a single founder event can initiate the evolution of strong reproductive isolation that will be completed on the time scale of several hundred generations. Increasing the strength of selection and/or mutation rate will result in increasing the rate of evolution.

Initial variability maintained by balancing selection.—In the model just considered, the probability of peak shift mostly depends on the amount of genetic variability present in the ancestor population. Genetic variability in this model was maintained by mutation, and, as a consequence, both the initial genetic variability and the probability of a peak shift were small. Balancing selection can maintain much higher levels of variability and can, presumably, make peak shifts more plausible. Let us consider a two-locus, two-allele model defined in figure 3B in which s_1, s_2 are small positive values. This model has two types of equilibria: an equilibrium in which genetic variability is maintained by overdominance in locus A and by mutation in locus B and two equilibria with rare alleles in both loci maintained by mutation. Let $s_1 = s_2$. At the equilibrium of the first type, common genotypes are *AABB, AaBB,* and *aaBB* (with the frequencies approximately in the proportions $1 : 2 : 1$). At two equilibria of the second type, common genotypes are *AAbb* or *aabb.* The proportion of viable hybrids resulting from matings between populations at equilibria of different types is approximately one-half. This value corresponds to the proportion of matings that result in offsprings homozygous in locus A and heterozygous in locus B. Thus, in this model

$$I \approx 0.5 .$$

Let a new population be founded by N_0 individuals chosen randomly from a population at an equilibrium of the first type. With a very high probability (equal approximately to $1 - \mu$), it is monomorphic for allele B. The system can be considered as a single-locus system (with three different genotypes—*AA, Aa,* and *aa*). During the period of rapid growth, new mutation can be neglected, and random drift is very important. At the end of this period, the population may be monomorphic or remain polymorphic. In the latter case, the deterministic (i.e., very large) population will return to its initial equilibrium. In contrast, a monomorphic population will be driven to a new equilibrium by mutation and selection.

Table 3 illustrates the plausibility of different events during the stochastic phase for some parameter combinations. If both selection and the growth rate are very small (i.e., if $s \approx 0$ and $R \approx 1$), the standard theory says that fixation occurs with

TABLE 3

Simulated Frequencies of Different States of the One-Locus
Population at the End of the Stochastic Phase When the
Founder Population of Size N_0 Is Drawn from an Infinite
Population with the Frequency of Allele A Equal to 0.5

R	$N_0 = 2$		$N_0 = 4$		$N_0 = 8$	
	Fix	Poly	Fix	Poly	Fix	Poly
1.1	9,033	967	6,050	3,950	2,273	7,727
	8,771	1,229	5,167	4,833	1,472	8,528
	8,490	1,510	4,509	5,491	986	9,014
1.3	4,021	5,979	1,012	8,988	72	9,928
	3,713	6,287	844	9,156	42	9,958
	3,384	6,616	665	9,335	22	9,978
1.5	1,710	8,290	191	9,809	2	9,998
	1,525	8,475	152	9,848	2	9,998
	1,346	8,654	118	9,882	3	9,997
2.0	249	9,751	4	9,996	0	10,000
	235	9,765	3	9,997	0	10,000
	230	9,770	0	10,000	0	10,000

Note.—In all cases, the number of runs is 10,000. *Fix* denotes a
situation when at the end of the stochastic phase the population is
monomorphic, while *poly* denotes a situation when the population
remains polymorphic. For each value of the population growth rate,
R, the upper, medium, and lower lines correspond to $w_{AA} = w_{Aa} = w_{aa} = 1$ (no selection); $w_{Aa} = 1$, $w_{AA} = w_{aa} = 0.95$; and $w_{Aa} = 1$, $w_{Aa} = w_{aa} = 0.9$, respectively.

a very high probability:

$$P \approx 1.$$

Table 3 also shows that rapidly growing populations can preserve genetic variability (cf. Holgate 1966; Daley et al. 1982). The time scale for the evolution of reproductive isolation in this model is the same as in the previous model, which is several hundred generations.

A Three-Locus Model

The first of the two-locus models that we described in the previous sections produces a high degree of reproductive isolation (with $I \approx 1 - \mu/s$) but with a low probability ($P \sim \mu/s$). In the second two-locus model, the probability of stochastic transition can be almost one, but the degree of reproductive isolation is far from complete (with $I \approx 0.5$). In this section, we describe a three-locus model that combines these two two-locus models, inheriting the high degree of reproductive isolation from the first and the high probability of stochastic transition from the second. We assume that individuals with two or three heterozygous loci are inviable. The fitnesses of genotypes that are important in our analyses are described in figure 4.

This model has two types of equilibria: an equilibrium in which genetic variability is maintained by overdominance in locus A and by mutation in loci B and C
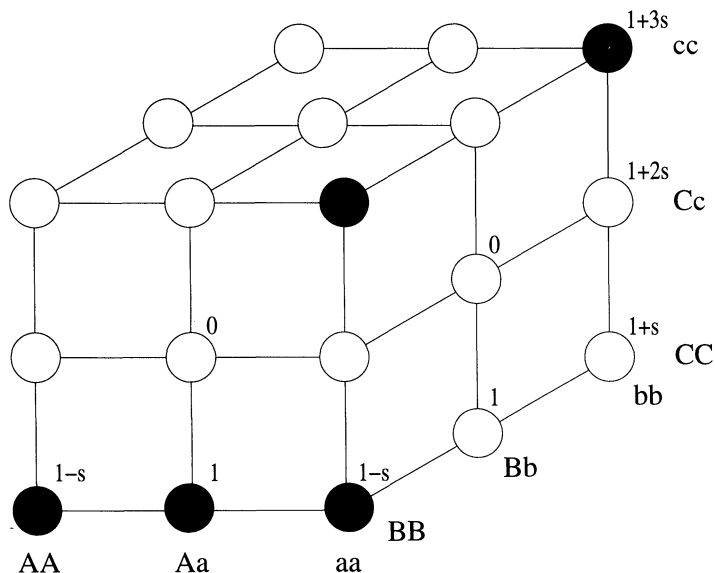
FIG. 4.—Fitnesses of some genotypes in a three-locus, two-allele model with inviable double and triple heterozygotes. The genotypes common at two equilibria are shown with black circles.

and an equilibrium with rare alleles in all three loci maintained by mutation. At the equilibrium of the first type, common genotypes are monomorphic in allele *B* and *C* and polymorphic at the first locus (with the frequencies of *AA, Aa,* and *aa* approximately in the proportions 1:2:1). At the equilibrium of the second type, common genotypes are *aabbcc*. Frequencies of rare genotypes in both populations will be order μ/s. Let us consider the first-generation hybrids between populations at equilibria of different types. Matings between genotypes that are common within their respective populations will result in individuals that are heterozygous in both B and C loci. These individuals are inviable. The most common viable offsprings will be a product of matings between a common genotype from one population and a rare genotype from another population. Thus, the proportion of viable hybrids resulting from matings between populations at equilibria of different types is roughly proportional to μ/s, and

$$I = 1 - O(\mu/s),$$

where $O(\mu/s)$ is a small value proportional to μ/s. Let a new population be founded by N_0 individuals chosen randomly from a population at an equilibrium of the first type. With a very high probability (equal approximately to $1 - \mu$), it is monomorphic for alleles *B* and *C*. The system can be considered as a single-locus system (with three different genotypes—*AA, Aa,* and *aa*). During the period of rapid growth, new mutation can be neglected, and random drift is very important. At the end of this period, the population may be monomorphic or remain polymorphic. In the latter case, the population will return to its initial equilibrium.

In contrast, a population monomorphic for allele a will be driven to the new equilibrium by mutation and selection. Table 3 can be used to illustrate the plausibility of different events during the stochastic phase for some parameter combinations. If both selection and the growth rate are small (i.e., if $s \approx 0$ and $R \approx 1$), the standard theory says that fixation occurs with a very high probability:

$$P \approx 1.$$

One can also estimate the time that it takes for strong reproductive isolation to evolve. As in the previous models, the process has two steps: a stochastic one and a deterministic one. The latter corresponds to deterministic changes in the frequencies of alleles b and c caused by selection and mutation and is much longer than the former. The time that it takes for selection and mutation to change these allele frequencies from 0% to 99% is approximately $T = 1,200$ generations for $s = 0.05$ and $T = 600$ generations for $s = 0.025$ (with $\mu = 10^{-6}$). These values of T were estimated numerically by iterating a standard system of equations describing the dynamics of gamete frequencies in a two-locus, two-allele system under selection and mutation. Thus, in this three-locus model, a single founder event may result in strong reproductive isolation on a time scale of several hundred generations. Increasing the strength of selection and/or mutation rate will result in increasing the rate of evolution.

In the two- and three-locus models considered in this section, genetic drift accompanying the founding event can result in a complete loss of genetic variability in one locus that in turn would completely change selection pressure on another major locus (or loci), which would cause the population to evolve to a new state. Without providing the details, we easily may see how to extend this argument to more loci. These models can be considered as describing Mayr's (1954) genetic revolutions.

<center>QUANTITATIVE GENETICS MODELS</center>

Barton and Charlesworth (1984), Rouhani and Barton (1987), Charlesworth and Rouhani (1988), and Barton (1989) have studied peak shifts in founder populations using models of disruptive selection on a single quantitative character. They assume a specific form of fitness function, which results in two adaptive peaks, and analyze how the probability of peak shift and the resulting degree of reproductive isolation depend on different parameters. One of their main results is that in this model the probability of a peak shift that induces a significant degree of reproductive isolation is very small. These authors consider this to be a major objection to the founder effect speciation theory. In this section, using a heuristic argument, we show that analyses given by these authors can be used to argue that a single founder event may result in strong reproductive isolation with a high probability. The basic idea is to introduce an additional quantitative trait (or traits) and construct a Dobzhansky-type model similar to those presented in the previous section. Let us consider the model studied by Charlesworth and Rouhani (1988). These authors model a single additive trait, z, controlled by a large number of unlinked loci with individually small effects. The distribution of z in the popula-

tion is assumed to be normal. The relationship between fitness w_1 of an individual and its phenotypic value z is described using a sum of two Gaussian functions:

$$w_1(z) = 0.5 \exp\left(-\frac{(z + 1)^2}{2\omega^2}\right) + 0.5 \exp\left(-\frac{(z - 1)^2}{2\omega^2}\right).$$

This fitness function has two maxima located at z trait values of -1 and 1, with the maxima separated by a valley with a depth proportional to ω^{-1}.

Let a new population be founded by N_0 individuals chosen randomly from a large population at one of these peaks. At the end of the period of rapid growth, the population may remain in the domain of attraction of the initial peak or may be in the domain of attraction of the new peak. Charlesworth and Rouhani (1988) have shown (e.g., see their fig. 3) that following a founder event, stochastic shifts between two peaks have a high probability (of order of tens of percentages) provided $\omega \geq 0.9$. Let us introduce an additional quantitative trait, y, uncorrelated with z, that is under Gaussian stabilizing selection with optimum zero and strength γ:

$$w_2(y) = \exp\left(-\frac{y^2}{2\gamma^2}\right).$$

Let the fitness of individuals with trait values z and y be $w(z, y) = w_1(z)w_2(y)$. The resulting fitness function still has two maxima located at $(-1, 0)$ and $(1, 0)$ on the (z, y) plane (see fig. 5A). The existence of an additional trait should not strongly influence the probability of peak shift, and numerical results of Charlesworth and Rouhani should be approximately true in this case too. Let us make the fitness function more complex by introducing epistatic interactions between the traits in determining fitness, as shown in figure 5B. This fitness scheme assumes that the selection on a trait changes from stabilizing to disruptive depending on the other trait value. Such changes and even more complex selection regimes should be common when the fitness function has multiple peaks. In figure 5B the fitness function has two new peaks at $(-1, -1)$ and $(-1, 1)$, and the point $(-1, 0)$, which was a peak in figure 5A, has become a saddle. Provided $\gamma \ll \omega$, the new peaks are separated by a deep valley from the old peak at $(1, 0)$. This means that in this model with a probability equal approximately to the corresponding numerical values in Charlesworth and Rouhani (1988), the population starting at the peak at $(1,0)$ will end up on a new adaptive peak separated from the initial one by a very deep adaptive valley. The hybrids between initial and final populations will have extremely low fitness, and two populations will be strongly reproductively isolated. For example, if $\omega = 0.9$ and $\gamma = 0.01$, the fitness of hybrids between individuals most common at their respective populations lying at different axes is approximately 7×10^{-6}. If $\omega \geq 0.9$, the probability of such a peak shift is on the order of one in 10 or greater.

Charlesworth and Rouhani (1988) do not present numerical values for the time that it takes to approach a new equilibrium after crossing the adaptive valley. However, presumably it should be much shorter (on the time scale of dozens of generations) than in the multilocus models that we considered in the previous
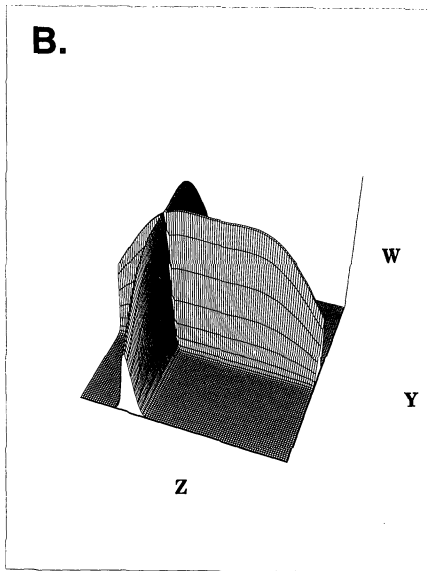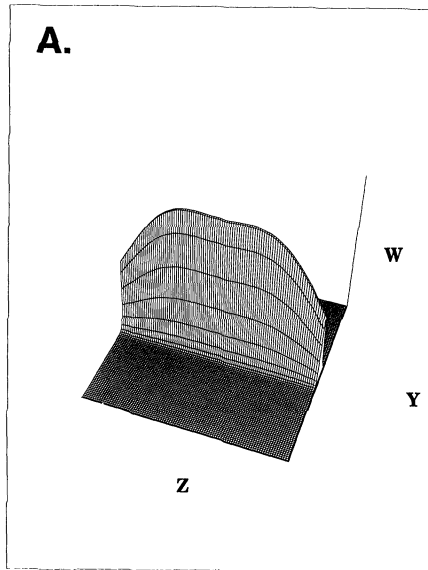
Fig. 5.—Fitness landscape describing selection on two additive traits. *A*, Two peaks separated by a shallow valley. *B*, Three peaks, two of which are separated by deep valleys from the third peak.
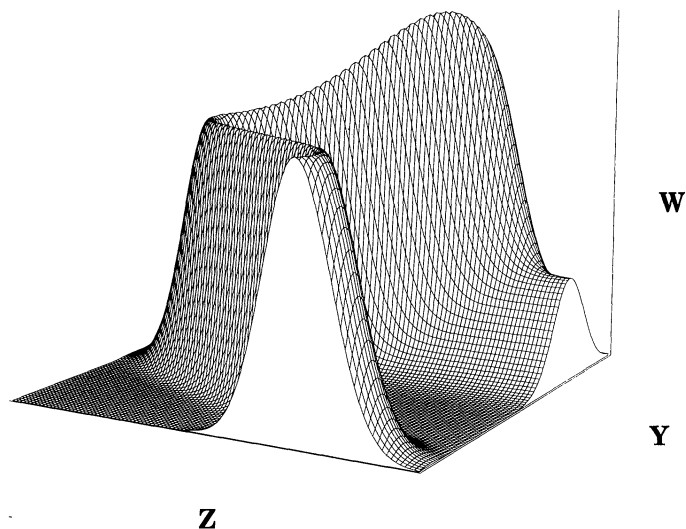
FIG. 6.—Fitness landscape describing "directional" selection $w_{het}(x, y)$ on two quantitative traits. In this model, the movement toward an adaptive peak will follow a "rim" that goes around a deep "adaptive valley."

section in which new variability was supplied by mutation. We conclude that in this and similar models, strong reproductive isolation can rapidly evolve with a high probability. In quantitative genetic models that consider many loci with minor effects on fitness, genetic drift becomes more important than selection in a rapidly growing population and is able to move the population to the domain of attraction of a new state. This process requires that during the stochastic phase, the level of genetic variability remains large enough. This class of models can be considered as related to Carson's (1968) founder-flush model.

MAJOR AND MODIFIER LOCI

The models that we described in the two previous sections can be combined to produce models incorporating both major loci and quantitative traits simultaneously in a way similar to that used in Petry (1982) and Lande (1983). As an example, let us take the three-locus model analyzed above and modify it in the following way. Assume that individuals are different with respect to a major diallelic locus (with alleles A and a) and two quantitative traits z and y (which take the place of the loci B and C in the three-locus model). Let heterozygous individuals Aa have fitness $w_{het}(z, y,)$ while homozygous individuals AA and aa have fitness $(1 - s)w_{hom}(z, y)$. Assume that $w_{het}(z, y)$ describes stabilizing selection on z and y, with both optima at zero. Let $w_{hom}(z, y)$ define directional selection of the form described in figure 6.

Provided s is not very small and stabilizing selection acting on heterozygotes is sufficiently strong relative to directional selection acting on homozygotes, this

model has a stable equilibrium with the frequency of A equal to 0.5 and the mean values of z and y slightly displaced from zero. If a population at this state undergoes a bottleneck, with a high probability (see table 3), all variability in the major locus will be lost, which will result in a complete change in selection pressure on quantitative traits z and y. As a consequence, the population will evolve along the rim described in figure 6 to a new state that will be highly reproductively isolated from its initial state. The time scale of this evolution will be about the same as in the quantitative genetics models discussed in the previous section (i.e., of order of dozens of generations). In this model considering both major and minor loci simultaneously, genetic drift can result in a complete loss of genetic variability in a major locus, which in turn will result in a complete change in selection pressure on the minor loci and will cause the population to evolve to a new state. This class of models is related to Templeton's (1981) genetic transilience model.

DISCUSSION

Any genetic model of the evolution of reproductive isolation includes two basic components: one describing the genetic basis of reproductive isolation and a second specifying a mechanism that causes emergence of a new population reproductively isolated from its ancestor. Important characteristics of such a model are the degree of resulting reproductive isolation, overall plausibility of emergence of isolation, and the time that it takes for a given level of reproductive isolation to evolve.

Modeling the Genetic Basis of Reproductive Isolation

The genetic basis of reproductive isolation and differences among closely related species is complex and largely unknown. We do know that both major and minor loci can be involved, and epistasis in fitness is present (see discussions and references in Barton 1989; Orr and Coyne 1992; Wagner et al. 1994). Our analysis of the evolution of postzygotic reproductive isolation has been limited by the assumptions of the standard population-genetics model listed at the beginning of this article. Within the framework of this model, the genetic basis of reproductive isolation is specified by the relationship between genotype and fitness. Previous mathematical models of the evolution of reproductive isolation (cited above) have primarily considered two different fitness schemes: selection on a single diallelic locus with underdominance and disruptive selection on a single additive quantitative character. An inherent feature of these two models is that the fitness of hybrids is about the same as the fitness of the "worst" state a population has to pass through on its way from one equilibrium to another. As a consequence, in these models the depth of the adaptive valley that the population has to cross is approximately equal to the degree of reproductive isolation arising from the peak shift.

In this article, we have considered different models utilizing Dobzhansky's (1937) idea that strong selection against hybrids between two genotypes can occur simultaneously with the existence of a chain of genotypes that connect those two

and differ only weakly in fitness among themselves. Using the metaphor of adaptive landscapes, we find that in Dobzhansky-type models, a rim connecting two adaptive peaks goes around a deep adaptive valley (see figs. 1B, 5B, 6). Other properties of models utilizing the same idea have been discussed and formally studied (see, e.g., Bengtsson and Christiansen 1983; Nei et al. 1983; Bengtsson 1985; Barton and Bengtsson 1986; Wagner et al. 1994).

In this article, we considered three different classes of Dobzhansky-type models: a few loci with major effects on fitness, many loci with small effects on fitness, and both major and minor loci simultaneously. In all cases, there was epistasis in fitness, and the viability of some genotype was extremely small or zero. The latter assumption represents a major difference from most previous models of the evolution of reproductive isolation considering mainly weak selection (but see Nei et al. 1983). Strong selection seems to be quite common in natural populations (Endler 1986). Strong selection should be certainly incorporated in any model attempting to describe the evolution of strong postzygotic isolation when some hybrids are inviable. Assuming strong selection instead of weak selection in population-genetics models can result in drastic changes in conclusions (for examples, see Gavrilets 1993; Gavrilets and Hastings 1993, 1994a, 1994b).

Measuring the Strength of Reproductive Isolation

In this article, the strength of reproductive isolation between two populations has been measured using a simple and intuitively clear measure—the proportion of inviable F_1 hybrids, I. The I value is related to the mean fitness of F_1 hybrids, $\overline{w}_{F_1}$, with the obvious relation $\overline{w}_{F_1} \leq 1 - I$. The models considered above assume that the fitness of some individuals is zero or very close to zero. In these models only an extremely small proportion of matings between different populations result in viable F_1 hybrids, and the initial reproductive isolation is very high. One can argue, however, that when two populations initially at different "adaptive peaks" meet and exchange individuals over an extended period of time, even a small amount of gene flow between them is sufficient to re-create all genotypes along the rim connecting two peaks and, thus, significantly and rapidly reduce the degree of reproductive isolation (Barton and Bengtsson 1986; Barton and Rouhani 1987).

In discussing consequences of prolonged hybridization on reproductive isolation, one should first define an appropriate measure. A standard measure is to consider how quickly two populations are losing differentiation in a neutral locus (see, e.g., Nagylaki 1976; Barton 1979, 1986; Spirito et al. 1983; Bengtsson 1985; Barton and Bengtsson 1986). Barton and Bengtsson (1986; see also Bengtsson 1985; Barton 1986) discuss a measure, b, of the strength of the barrier to genetic exchange between hybridizing populations characterizing the ease with which a neutral allele that initially is present in only one of the populations can "flow" across a stable hybrid zone into the population in which it was initially absent. With a migration rate m between two populations, a neutral allele will be delayed for $\approx b/m$ generations (Barton and Bengtsson 1986). Barton and Bengtsson (1986) consider a Dobzhansky-type model in which fitness depends exponentially on the

TABLE 4

NUMBER OF GENERATIONS THAT IT TAKES TO REDUCE THE DIFFERENCE IN THE NEUTRAL ALLELE
FREQUENCIES TO HALF OF ITS INITIAL VALUE

RECOMBINATION RATE		MODEL 1		MODEL 2	
r	R	$m = .003$	$m = .006$	$m = .030$	$m = .060$
.50	.50	126	62	284	104
.05	.50	157	73	301	109
.50	.05	125	62	284	104
.05	.05	184	83	301	109
Neutral case		115	57	11	5

NOTE.—The fitnesses are as specified in fig. 4, with $s_1 = 0.025$ and $s_2 = 0.05$. In model 1, $w_{AaBb} = 0.95$; in model 2, $w_{AaBb} = 0$.

number of heterozygous loci. They find that in this model the strength of the barrier to genetic exchange between hybridizing populations as measured by b is weak in spite of the fact that the mean fitness of F_1 hybrids is small. This finding has been used to argue that the barrier to gene flow across a hybrid zone should depend primarily on the depth of the "adaptive valley" that the population has to cross on its way from one equilibrium to another (Barton and Rouhani 1987) and that the "Dobzhansky model, and similar schemes, would not in fact produce much reproductive isolation" (Barton and Bengtsson 1986, p. 370).

Let us imagine two large populations initially at two different equilibria controlled by a balance between mutation and selection acting on two loci A and B. Consider a third "neutral" locus C. We take the special order of loci to be ABC. Let R be the recombination rate between the loci under selection A and B and r be the recombination rate between B and C, and further assume that recombination occurs independently between the first, second, and third positions. Let one neutral allele be fixed in one population but absent in the other. After individuals begin to migrate between the populations, the difference in the frequency of the neutral allele is expected to decay gradually. The rate of decay should depend on the recombination rates, the migration rate m, and fitnesses. We are going to compare two models. In the first model, the fitnesses are as defined in figure 3A. The second model differs from the first one only in that the fitness of the double heterozygote equals that of a low-fitness double homozygote AAbb (i.e., $w_{AaBb} = 1 - 2s_1$). These two models have the same depth of the "adaptive valley" that the population has to cross on its way from one equilibrium to another, but they result in different fitnesses of F_1 hybrids. The strength of the barrier to genetic exchange between hybridizing populations, b, is meant as a measure related to the rate of decay of the difference in the frequencies of the neutral allele. In table 4 we compare the time that it takes to reduce the difference between the frequencies of the neutral allele in two populations to half of its initial value in these two models for some parameter values. Also given are the values corresponding to a neutral model—that is, to a model with no selection on A and B loci. (These values and data presented in table 4 were found using numerical iteration of

corresponding dynamic systems.) In model 2, for $m = 0.003$ and $m = 0.006$, after a short transient period, no changes in the neutral allele frequency were observed during at least 200,000 generations. In model 1, for $m = 0.03$ and $m = 0.06$, the cline in the frequencies of alleles in loci A and B is not stable, and the whole system moves to one or another equilibrium state. This and table 4 show that strong selection against double heterozygotes significantly reduces or even completely prevents the gene flow of neutral alleles between populations. As expected, the amount of recombination between the loci under selection does not influence the outcome if a double heterozygote is inviable, and increasing the linkage between the neutral and selected loci increases the strength of the barrier to the gene flow.

The measure b for the strength of reproductive isolation was defined for situations when two populations remain differentiated in spite of the gene flow between them. If the migration rate increases above some critical value, m_c, this differentiated state in general can become unstable, and the whole system moves to one or another equilibrium state (i.e., the genetic barrier between two populations collapses). The critical value m_c can be used as an alternative measure of the degree of reproductive isolation between two populations that characterizes the ability of two populations to remain differentiated in spite of the gene flow between them. If m_c is small, negligible gene flow is sufficient to destroy genetic differentiation, while if $m_c \gg 0.5$, two populations can remain differentiated even in sympatry. The value of m_c is expected to be small, which reflects the power of migration over selection (Barton 1992; Gavrilets 1994). Let us consider a two-locus model with fitnesses as in figure 3, with $s_1 = 0.025$ and $s_2 = 0.03$. Numerical simulations show that if $w_{AaBb} = 0.95$, then m_c is approximately 6.7×10^{-3}, while if the double heterozygote is inviable, m_c is approximately 1.2×10^{-2}. Although this difference is not very impressive, nonetheless it shows that Dobzhansky-type models can have higher values of m_c as well.

Properties of genetic barriers in Dobzhansky-type models can be influenced by many factors, including the spatial arrangement of populations, and should be studied in more detail. Our preliminary study, however, allows us to conclude that Barton and Bengtsson's finding is not general and that Dobzhansky-type models can produce strong reproductive isolation as measured by the proportion of inviable F_1 hybrids or the strength of the barrier to the gene flow.

Genetic Revolution, Founder Flush, and Genetic Transilience

In this article, the dynamics of a series of Dobzhansky-type models have been analyzed under the scenario of the theory of founder effect speciation (Mayr 1942, 1954; Carson 1968; Kaneshiro 1980; Templeton 1980). That is, we considered a growing population founded by a few individuals, and we were interested in the ability of a single founder event to result in strong reproductive isolation. The models that we considered were different with respect to genetic details.

In models with several major loci, genetic drift accompanying the founder event can result in complete loss of genetic variability in one locus, which in turn would completely change the selection pressure on another major locus (or loci) and cause the population to evolve to a new state. These models can be considered

as describing Mayr's (1954) genetic revolutions. In the quantitative genetic models that consider many loci with minor effects on fitness, genetic drift can become more important than selection in a rapidly growing population and move the population to the domain of attraction of a new state. A necessary condition of this transition is that during the stochastic phase, the level of genetic variability remains large enough. This class of models can be considered as related to Carson's (1968) founder-flush model. In the models considering both major and minor loci simultaneously, genetic drift can result in a complete loss of genetic variability in a major locus, which in turn would result in complete change in selection pressure on the minor loci and cause the population to evolve to a new state. This class of models is related to Templeton's (1981) genetic transilience model. The time scale for the evolution of strong reproductive isolation in these models depends on the genetic details and can be as small as several hundred or even several dozen generations. We have shown that in all these models, very strong reproductive isolation can evolve with a high probability.

Relation to Other Models

The classic view is that reproductive isolation evolves as a side effect of genetic changes. Genetic changes can be induced by many factors and their combinations. In comparing the theory of founder effect speciation with alternative theories, two somewhat trivial points should be kept in mind. Obviously, it is quite plausible that the founder population is exposed to a different physical or biotic environment and, as a consequence, experiences a selection pressure different from that one acting on the ancestor population. The first point is that the scenario underlying this theory (as well as the shifting balance theory) allows for reproductive isolation to evolve even when the overall selection pressure does not change. The second point is that after a founder event, strong reproductive isolation can evolve very rapidly, on the time scale of dozens or hundreds of generations, with a high probability. This is in contrast to stochastic models of stable populations in which even in Dobzhansky-type models, strong reproductive isolation evolves very slowly (e.g., Nei et al. 1983; Wagner et al. 1994). The theory of founder effect speciation is not supposed to explain all or most speciation events, but the mechanism underlying this theory should be accepted as one of many mechanisms acting in natural populations that can lead to speciation.

Experimental Evidence for Founder Effect Speciation

Experimental studies attempting to duplicate the founder effect process have been recently reviewed by Rice and Hostert (1993) and A. R. Templeton (unpublished manuscript), with diametrically opposite conclusions. Rice and Hostert (1993) conclude that there is "little or no support" for this theory of speciation. This conclusion is challenged by A. R. Templeton (unpublished manuscript), who argues that it is flawed because in Rice and Hostert's article the most relevant experimental evidence was not considered, inconsistent criteria for evaluation were used, and predictions of the theory were inaccurately portrayed. A. R. Templeton (unpublished manuscript) concludes that "strong and extensive" ex-

perimental evidence exists for at least some of the versions of the founder effect speciation theory. The original articles should be consulted for more details.

CONCLUSIONS

In certain cases the mechanisms underlying the founder effect speciation theory can definitely work. In particular, a high degree of reproductive isolation can be achieved in Dobzhansky-type models. It seems that the appeal expressed in the last sentence of Barton and Hewitt (1981, p. xx) still remains praiseworthy: "Perhaps the way forward is to analyze in detail the differences between diverging taxa, and to recognize that the various theories of speciation are not necessarily mutually exclusive."

ACKNOWLEDGMENTS

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