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On the Evolution of Premating Isolation after a Founder Event

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ABSTRACT: We present a new simple model for the evolution of premating reproductive isolation. Using this model we first analyze the level of genetic variability maintained by mutation in a large stable population. Then we consider the plausibility of the evolution of strong premating reproductive isolation after a founder event. We demonstrate that after a founder event a new adaptive combination of genes may rise to high frequencies in the presence of an old combination of genes. We compare the probabilities of speciation after a founder event with those in a stable population and with those when reproductive isolation is due to viability selection against hybrids. We argue that premating reproductive isolation is more efficient than postmating reproductive isolation in maintaining the integrity of sympatric species. This might have contributed to the pattern of stronger premating isolation than postmating isolation between closely related pairs of sympatric species.

Keywords: speciation, premating isolation, mathematical models, reproductive isolation.

Founder effect speciation is proposed to result from a population bottleneck followed by a rapid increase in population size (Mayr 1942, 1954; Templeton 1980; Barton and Charlesworth 1984; Carson and Templeton 1984). In this scenario new adaptive combinations of genes arise and become established in a new population via a combined action of random drift, selection, and other factors. If a new adaptive combination of genes is sufficiently different from the one common in the source population, speciation may have occurred.

The hypothesis that speciation could be facilitated by a population bottleneck was largely stimulated by studies of the Hawaiian *Drosophila* (Carson and Templeton 1984). In the Hawaiian archipelago, most species of *Drosophila* are endemic to a single island (Carson 1982). The evidence from geology, chromosomal inversion patterns, and prevailing winds suggests that the majority of speciation events occurred after colonization of a new island that had recently become habitable (Carson and Clague 1995; DeSalle 1995). The relationship between islands and endemism in Hawaii inspired verbal models that propose that a single migrant female can found a new species (Carson and Templeton 1984). Whether bottlenecks and population flushes can result in exceptionally rapid species formation is the subject of a debate that has recently intensified. The argument concerns the theoretical foundations of this scenario (Barton 1996; Gavrilets and Hastings 1996; Slatkin 1996; Charlesworth 1997) as well as interpretation of empirical and experimental data (Rice and Hostert 1993; Templeton 1996).

Most previous theoretical studies of founder effect speciation have mainly concentrated on postmating isolation in the form of viability selection against hybrids and recombinants (see Orr 1991 for a notable exception). With this form of reproductive isolation, founder effect speciation can occur if there is a specific genetic architecture. Speciation is highly probable if the old and the new adaptive combinations of genes are connected by a ridge of high-fitness genotypes (Gavrilets and Hastings 1996). It has been argued that such ridges should be common in multilocus systems—the idea reflected in a new metaphor of "holey adaptive landscapes" (Gavrilets 1997*a;* Gavrilets and Gravner 1997; Gavrilets et al. 1998).

Possibilities for the evolution of premating reproductive isolation after a founder event have been studied much less frequently. Prezygotic behavioral isolation is widespread and may play a major role in speciation in some taxa (Giddings et al. 1989). In *Drosophila,* prezygotic isolation is significantly stronger than postzygotic isolation for sympatric species (Coyne and Orr 1989, 1997). Speciation in birds proceeds with the evolution of behavioral barriers to interbreeding; postmating isolation evolves much later (Grant and Grant 1996, 1997). The incipient stages of speciation of a pair of *Heliconius* butterflies appear to have been catalyzed by the association

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Table 1: Percent mating in no-choice tests

	Male		
Female	Drosophila silvestris	*F_1 hybrid*	Drosophila heteroneura
D. silvestris	80	76	58
F_1 hybrid	48	78	86
D. heteroneura	0	56	75

of strong mating preferences with divergence in warning coloration and ecology (McMillan et al. 1997).

Behavioral premating isolation is measured with tests that provide no opportunity for alternative partners (no-choice tests), ones that provide just one sex with options (female-choice and male-choice tests), and tests that provide several potential mates to each sex (multiple-choice tests). It is generally measured between two species, but examination of behavioral isolation of hybrids from the parental species can also be very useful (e.g., David et al. 1974; Lachoise et al. 1986; Coyne and Orr 1989; Krebs and Markow 1989; Price and Boake 1995; Wu et al. 1995; Davies et al. 1997; McMillan et al. 1997).

Table 1 presents an example of data arising in studies of premating isolation (data from Price and Boake 1995; C. R. B. Boake, unpublished data). We show percent matings in no-choice tests involving *Drosophila silvestris, Drosophila heteroneura,* and their F_1 hybrids. These species are endemic to the island of Hawaii. It appears that *D. silvestris* evolved from an ancestor that arrived from Maui and that *D. heteroneura* resulted from a split from *D. silvestris* (DeSalle and Giddings 1986). On Hawaii they are sympatric and ecologically extremely similar (Kaneshiro and Boake 1987). Their courtship behavior is also very similar, consisting of nearly identical action patterns but somewhat different time budgets (Hoikkala and Welbergen 1995). In the wild, males defend territories that are visited by females. It is unknown how many males are visited by a female before she mates. Females very rarely mate more than once (Craddock and Johnson 1978). Hybrids have been occasionally found in the wild, all of which are progeny of the cross between a female *D. silvestris* and a male *D. heteroneura* (Carson et al. 1989). The failure to find reciprocal hybrids reflects asymmetries in the probability of mating rather than postzygotic isolation (see table 1): mating between female *D. heteroneura* and male *D. silvestris* is very unlikely, but when such matings do take place, all hybrids are viable and fertile (Craddock 1974; Ahearn and Templeton 1989; Price and Boake 1995).

Here we present a new simple model for the evolution of premating reproductive isolation, which might be useful in relating experimental data such as those in table 1 to evolutionary theories. This model was motivated by a desire to evaluate the plausibility of founder effect speciation driven by behavioral differences and to get insights into evolutionary implications of the differences between postmating and premating reproductive isolation.

A Model for Premating Reproductive Isolation

Let us consider a single diploid population with nonoverlapping generations. We will concentrate on a single locus with two alleles A and a. For instance, some of the factors involved in premating isolation in birds (plumage, morphology, and behavior) appear to be under single-gene control (Grant and Grant 1996, 1997). In other cases, the single-locus model is obviously an oversimplification. For example, Coyne (1996) has identified several loci on different chromosomes underlying premating isolation. We, however, believe that introducing additional loci in the model described below will actually only enhance the effects we are interested in here (Higgs and Derrida 1992; S. Gavrilets, unpublished manuscript).

Indices $i = 1, 2, 3$ will correspond to genotypes **AA**, **Aa**, and **aa**, whose frequencies will be x, y, and z, respectively. Note that genotype frequencies among females and males become equal after one generation. We assume that females and males encounter each other randomly. We assume that females mate only once whereas males may participate in many matings. Let the probabilities that an encounter between a female with genotype i and a male with genotype j results in mating be given by table 2, where all entries (mating probabilities) are nonnegative. If a female does not mate with a given male, she may mate with a male she encounters later. If a female does not mate after the nth encounter, she does not produce any offspring. The latter assumption reflects the idea that the time interval during which females can mate is limited. This model is appropriate for species with a threshold female preference function (Janetos 1980; Lande 1981), in which a female has limited time for choosing a mate and samples males until she encounters one that meets her criteria. Threshold preferences

Table 2: Mating probabilities

Female genotype	*Male genotype*		
	AA	***Aa***	***aa***
AA	α_1	β_1	γ_1
Aa	β'_1	δ	β'_2
aa	γ_2	β_2	α_2

have been inferred in studies of cockroaches (*Nauphoeta cinerea;* Moore and Moore 1988) and jungle fowl (*Gallus gallus;* Zuk et al. 1990). The model introduced above belongs to a general class of models of positive assortative mating (O'Donald 1980).

Let us consider a female **AA**. With probabilities x, y, and z she encounters a male with genotype **AA**, **Aa**, or **aa**, and mates with him with probabilities $\alpha_1 x$, $\beta_1 y$, and $\gamma_1 z$, respectively. With probability $r_{AA} = 1 - \alpha_1 x - \beta_1 y - \gamma_1 z$ the encounter does not result in mating. Thus, the overall probability $P(\mathbf{AA} \times \mathbf{AA})$ that this female mates with male **AA** is $\alpha_1 x + r_{AA}\,\alpha_1 x + r_{AA}^2 \alpha_1 x + \cdots + r_{AA}^{n-1}\,\alpha_1 x$, which can be represented as $\alpha_1 x f(r_{AA})$, with $f(t) \equiv (1 - t_n)/(1 - t)$. The overall frequency of $\mathbf{AA} \times \mathbf{AA}$ matings in the population is $xP(\mathbf{AA} \times \mathbf{AA}) = \alpha_1 x^2 f(r_{AA})$. This frequency reduces to $\alpha_1 x^2$ if $n = 1$, and to $\alpha_1 x^2/(\alpha_1 x + \beta_1 y + \gamma_1 z)$ if n is very large (cf. O'Donald 1980). Increasing n makes it easier for a rare genotype to find an appropriate mate. In a similar way, one can determine overall frequencies of all other possible matings. For instance, the overall frequency of **aa** times **aa** matings in the population is $\alpha_2 z^2 f(r_{aa})$, where $r_{aa} = 1 - \gamma_2 x - \beta_2 y - \alpha_2 z$.

Mating probabilities can be estimated using experimental data such as those presented in table 1. If $n = 1$, then the parameters of the model are estimated by the corresponding values of table 1. That is $\alpha_1 = 0.80$, $\beta_1' = 0.48$, and so on. If $n > 1$, then to estimate parameters one should use the probabilities of no mating. For instance, the probability that a female **AA** does not mate with a male **AA** in a no-choice test is $(1 - \alpha_1)^n$. According to table 1, this probability for *Drosophila silvestris* times *Drosophila silvestris* pairs is 0.2. Thus, $\alpha_1 = 1 - 0.2^{1/n} \approx 0.275$ if $n = 5$, and $\alpha_1 \approx 0.149$ if $n = 10$. The corresponding estimates for β_1' are 0.12 and 0.06 for $n = 5$ and $n = 10$, respectively. Note that if $n > 1$, the differences in the probabilities of different matings are actually higher than it appears from the data in table 1. For instance, if $n = 10$, the ratio $\alpha_1/\beta_1' \approx 2.48$, whereas the ratio of the corresponding elements in table 1 is $80/52 \approx 1.54$. We do not have direct estimates of n in the experiments reported in table 1. Indirect evidence suggests that n was not bigger than 2 or 3. In lekking species, females can sample many males before copulating, and in such species n can be at least on the order of 10 (see, e.g., Andersson 1994).

Let us turn to the predictions of the model regarding evolutionary dynamics. The probabilities of different matings can be used to find the frequencies of different genotypes of offspring (see table 3), which in turn allow one to find the genotype frequencies in the next generation. For example, to find the frequency of genotype **AA** one has to add the frequencies of all matings (i.e., matings $\mathbf{AA} \times \mathbf{AA}$, $\mathbf{AA} \times \mathbf{Aa}$, $\mathbf{Aa} \times \mathbf{AA}$, and $\mathbf{Aa} \times \mathbf{Aa}$) times the proportion of **AA** offspring resulting from these matings (that is 1, 1/2, 1/2, and 1/4, respectively). The genotype frequencies in the next generation become:

Table 3: Mating types and offspring

Mating types	*Frequency of mating*	*Offspring*		
		AA	***Aa***	***aa***
Female: **AA**:				
Male:				
AA	$\alpha_1 x^2 f(r_{AA})$	1	0	0
Aa	$\beta_1 xyf(r_{AA})$	1/2	1/2	0
aa	$\gamma_1 xzf(r_{AA})$	0	1	0
Female: **Aa**:				
Male:				
AA	$\beta_1' xyf(r_{Aa})$	1/2	1/2	0
Aa	$\delta y^2 f(r_{Aa})$	1/4	1/2	1/4
aa	$\beta_2' yzf(r_{Aa})$	0	1/2	1/2
Female: **aa**:				
Male:				
AA	$\gamma_2 xzf(r_{aa})$	0	1	0
Aa	$\beta_2 yzf(r_{aa})$	0	1/2	1/2
aa	$\alpha_2 z^2 f(r_{aa})$	0	0	1

$$\phi x' = \left(\alpha_1 x^2 + \frac{1}{2}\beta_1 xy\right) f(r_{AA}) + \left(\frac{1}{2}\beta_1' xy + \frac{1}{4}\delta y^2\right) f(r_{Aa}), \tag{1a}$$

$$\phi y' = \left(\frac{1}{2}\beta_1 xy + \gamma_1 xz\right) f(r_{AA}) + \left(\frac{1}{2}\beta_2 zy + \gamma_2 xz\right) f(r_{aa}) + \left(\frac{1}{2}\beta_1' xy + \frac{1}{2}\beta_2' zy + \frac{1}{2}\delta y^2\right) f(r_{Aa}), \tag{1b}$$

and

$$\phi z' = \left(\alpha_2 z^2 + \frac{1}{2}\beta_2 zy\right) f(r_{aa}) + \left(\frac{1}{2}\beta_2' zy + \frac{1}{4}\delta y^2\right) f(r_{Aa}). \tag{1c}$$

Here ϕ is a normalizing factor such that $x' + y' + z' = 1$, and r_{AA}, r_{Aa}, and r_{aa} are the probabilities that an encounter between a male and a female **AA**, **Aa**, and **aa**, respectively, does not result in mating. The expressions for r_{AA} and r_{aa} have been given above, whereas $r_{Aa} = 1 - \beta_1' x - \delta y - \beta_2' z$.

If $n = 1$, the model is equivalent to the general model of fertility selection (see Bodmer 1965; Hadeler and Liberman 1975) and a model of parental selection (Gavrilets 1998). This model has been used in the context of hybrid zones for predicting the form of single-locus clines (Gavrilets 1997*b*) and the strength of the genetic barrier to neutral gene flow (Gavrilets and Cruzan 1998). Thus, with $n = 1$ the model can be interpreted as describing both postmating and premating reproductive isolation, whereas the case of $n > 1$ is for premating reproductive isolation only.

Dynamic system (1) always has two monomorphic equilibria corresponding to fixation of alleles **A** and **a**. The conditions for local stability of these equilibria can be found using standard methods. If $n = 1$, the equilibrium with allele **A** fixed is stable if

$$\alpha_1 > \frac{(\beta_1 + \beta_1')}{2}. \tag{2a}$$

If $n \to \infty$, this equilibrium is stable if

$$\alpha_1 > \beta_1. \tag{2b}$$

The conditions for stability of the equilibrium with allele **a** fixed have the same form, with index 2 taking the place of index 1. (A general formula for arbitrary n is given in the appendix.) Summarizing, with $n = 1$, a rare allele will decline in frequency if the probability of matings between common homozygotes is higher than the average of the probabilities of matings involving a common homozygote and a heterozygote. With $n \to \infty$, the probability of matings between common homozygotes should be higher than the probability of matings between a common homozygous female and a heterozygous male. When both monomorphic equilibria are stable, no other equilibria appear to be stable. In general, the dynamics of (1) can be rather complicated. For instance, if $n = 1$, the possibilities include simultaneous stability of several polymorphic equilibria, simultaneous stability of both polymorphic and monomorphic equilibria, and even cycling (Bodmer 1965; Hadeler and Liberman 1975; Gavrilets 1998). We have not attempted to explore these possibilities.

Using data on *D. silvestris* and *D. heteroneura* given in table 1 and assuming that $n = 1$, we find that both monomorphic equilibria are stable. The general formula given in the appendix can be used to show that given table 1 the monomorphic equilibria are actually stable for any n.

Mutation-Selection Balance

With no other factors, a rare allele will eventually disappear from the population if the conditions from the previous paragraph are satisfied. However mutation, which is a ubiquitous source of genetic variability, will maintain rare alleles in the population. We assume that the locus under consideration is subject to mutation with rate μ (equal for forward and backward mutations) where μ is small. Standard regular perturbation methods can be used to estimate the level of genetic variability maintained by mutation-selection balance.

Let us consider the mutation-selection balance equilibrium with allele **a** close to fixation. Then if $n = 1$, the equilibrium frequency of heterozygotes is

$$y^* = \mu \frac{\alpha_2}{\alpha_2 - (\beta_2 + \beta_2')/2}, \tag{3a}$$

whereas if $n \to \infty$,

$$y^* = \mu \frac{2\alpha_2}{\alpha_2 - \beta_2}. \tag{3b}$$

(A general formula for arbitrary n is given in the appendix.) The equilibrium frequency of rare homozygotes, x^*, is second order in μ (and is negligible), and the equilibrium frequency of common homozygotes is $z^* = 1 - x^* - y^*$. Note that changing n can only result in a small increase in the equilibrium frequency of heterozygotes (maximum by a factor of 2 if $\beta_2 = \beta_2'$).

Assume now that $\alpha_2 = \beta_2 = \beta_2'$—that is, homozygotes **AA** do not distinguish hybrids **Aa** from their own type and the reciprocal matings are equally likely. (This situation seems to be the case for two butterfly species studied by Davies et al. [1997].) If $n = 1$, the equilibrium frequency of heterozygotes is

$$y^* = \sqrt{\frac{2\mu\alpha_2^2}{2\alpha_2^2 - \delta(\gamma_1 + \gamma_2)/2}}, \tag{4a}$$

whereas if $n = \infty$,

$$y^* = \sqrt{\frac{4\mu\alpha_2^2}{2\alpha_2^2 - \delta(\alpha_2 + \gamma_2)/2}}. \tag{4b}$$

One can see that the heterozygote has a much higher frequency than in the previous case. The equilibrium frequency of rare homozygotes $x^* = \delta(y^*)^2/(4\alpha_2)$ and is order μ. Note that as n increases from $n = 1$ to $n = \infty$, y^* increases by a factor of $\sqrt{2}$. Thus, the equilibrium frequency of the "foreign" allele **A** does not change significantly with changes in n. In the model we consider, mating behavior as characterized by parameter n is not very important in large populations. We will see below

Table 4: The number of fixations of a rare allele in a viability selection model out of 10^6 runs

	Population size N					
v_{Aa}	*25*	*50*	*100*	*200*	*400*	*800*
.99	16,967	7,160	2,529	501	35	0
.90	3,150	192	1	0	0	0
.50	0	0	0	0	0	0
.10	0	0	0	0	0	0

that in small populations parameter n plays a much more profound role.

Using the data from table 1 and assuming that $n = 1$, we find that the frequencies of heterozygotes at the two mutation-selection balance equilibria will be 4.4μ and 18.8μ.

Stochastic Transitions between Different Equilibria

The dynamic model presented in the previous section has two stable equilibria. Assume that there are two subpopulations with genotype frequencies close to those at these two different equilibria. Because matings between individuals from different subpopulations will have reduced probability, one can say that these subpopulations are reproductively isolated to some degree by premating isolating factors. Systems with two equilibria are common in theoretical studies of speciation. Of specific interest is the probability of stochastic transitions between two equilibria caused by random genetic drift (e.g., Lande 1979, 1985*a,* 1985*b;* Walsh 1982; Wu 1985; Barton and Rouhani 1987; Rouhani and Barton 1987; Gavrilets and Hastings 1996; Michalakis and Slatkin 1996). This probability can be interpreted as the probability of evolution of reproductive isolation. Below we present numerical results concerning stochastic transitions in the model we have introduced. As a reference point we will use the standard one-locus two-allele viability selection model. The probability of stochastic transitions in this model has been studied extensively (Lande 1979; Hedrick 1981; Walsh 1982).

One-Locus Two-Allele Viability Selection Model

Table 4 reports the number of fixations of an initially rare allele **a** in a stable population of size N observed in numerical simulations. Initially, the population had a single heterozygote **Aa** (which could have arisen by mutation) and $N - 1$ homozygotes **AA.** The viability selection model used assumed equal fitnesses of homozygotes ($v_{\mathrm{AA}} = v_{\mathrm{aa}} = 1$) and different (reduced) viabilities of heterozygote v_{Aa}. The number of runs was 1,000,000 for each parameter configuration. In the neutral case, that is, when $v_{\mathrm{Aa}} = 1$, the probability of fixation is $1/(2N)$. Table 4 shows that even with only 25 individuals no peak shifts are observed for $v_{\mathrm{Aa}} \leq 0.5$. This illustrates the well-known fact (e.g., Lande 1979; Walsh 1982; Hedrick 1991) that in this model the probability of a stochastic transition across even moderately deep adaptive valleys (say, with $v_{\mathrm{Aa}} \leq 0.5$) is extremely low.

Table 5: Mating probabilities used in simulations

Female genotype	*Male genotype*		
	AA	***Aa***	***aa***
AA	1	.95	0
Aa	.95	.95	.95
aa	0	.95	1

Peak Shift in a Stable Population

Next we consider the plausibility of stochastic transitions in our model of premating isolation. Here we used mating probabilities defined in table 5.

This model assumes complete reproductive isolation between different homozygotes whereas heterozygotes have slightly reduced probabilities of mating (cf. McMillan et al. 1997, where in mate choice experiments, matings between *Heliconius erato* and *Heliconius himera* were a tenth as likely as matings within a species, whereas F_1 hybrids of both sexes mated frequently with both pure forms). The matrix of mating probabilities above defines a "holey" adaptive landscapes for pairs of individuals (cf. Gavrilets 1997*a;* Gavrilets and Gravner 1997). The initial conditions and the number of runs were the same as in the viability selection model. In addition to different population sizes we also considered different n values (see table 6).

Table 6: The number of fixations of a rare allele in the model of premating isolation out of 10^6 runs

	Population size N					
n	*25*	*50*	*100*	*200*	*400*	*800*
1	530	2	0	0	0	0
2	1,209	14	0	0	0	0
4	3,006	132	0	0	0	0
8	5,828	603	6	0	0	0
16	8,399	1,146	35	0	0	0
32	9,880	1,555	36	0	0	0
64	10,818	1,916	80	0	0	0

Evolution of strong premating isolation as a result of stochastic transitions is much more plausible than evolution of strong postmating reproductive isolation (cf. tables 4 and 6 and different rows in table 6 with the first row). Table 6 shows that for small N and large n the probability of fixation of a rare allele **a** can be on the order of one-tenth of a percent and higher. Thus, with premating reproductive isolation, stochastic transitions to a completely isolated state are plausible in small populations. This observation suggests that founder events after which populations necessarily pass through a stage with very small size might be associated with an increased probability of speciation. One can also see that increasing n results in a significant increase in the probability of speciation.

Stochastic Transitions after a Founder Event

Let us consider what happens after a few individuals from a large population with genetic variability that is maintained by mutation found a new population. In modeling the founder effect speciation process we follow previous work (Rouhani and Barton 1987; Charlesworth and Rouhani 1988; Gavrilets and Hastings 1996) 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 timescale of, say, thousands of generations. The population size increases deterministically with a geometric rate R: $Nt = R_t N_1$, where t is the generation number and N_1 is the size of the population in the first generation. Our numerical simulations are based on the discrete Fisher-Wright sampling scheme allowing for selfing (cf. Charlesworth and Rouhani 1988; Gavrilets and Hastings 1996). A major difference from previous work is that instead of a binomial scheme we used a multinomial scheme, sampling genotypes rather than gametes. This is necessary since no Hardy-Weinberg proportions are expected in the model. To simplify comparison with previous results, the numerical values of N_0 (2, 4, and 8), R (1.1, 1.3, 1.5, and 2), and $N_{\max}$ (1,000) will be the same as used in an earlier study (Gavrilets and Hastings 1996).

Numerical Simulations

We assume that a single fertilized female founds a new population with initial size N_1. The most plausible scenario to have both alleles present in the founding populations is to assume that this migrant is a heterozygous female fertilized by a common homozygous male or a common homozygous female fertilized by a heterozygous male. In either case, the offspring frequencies will be in the proportions **AA**:**Aa**:**aa** = 1/2:1/2:0 and the initial frequency of the (rare) allele **a** is 1/4. The overall probability of such a founder event is approximately equal to the frequency of heterozygotes in the large ancestral population that was estimated in the previous section for the case of mutation-selection balance. We will be interested in a possibility of the evolution of very strong premating reproductive isolation after a founder event. We will use the same matrix of mating probabilities as defined above.

In general there are several possible outcomes of the stochastic phase. First, the rare allele **a** may be lost and the new population will be similar in its genotypic structure to the old one. This outcome has the highest probability. Second, the initially rare allele **a** may become fixed. The individuals from the new populations, which have genotype **aa**, will not mate with individuals from the old population, which have genotypes **AA**. In this case, the outcome of the founder event is (allopatric) speciation. Third, it is possible that heterozygote **Aa** is lost from the new population, while both homozygotes **AA** and **aa** are present. There will be no mating between different homozygotes, and, thus, the outcome of the founder event is sympatric speciation. Finally, at the end of the stochastic phase the population may have all genotypes present. This case does not allow for simple interpretation because the deterministic dynamics will depend on the frequencies of all genotypes.

Table 7 reports some outcomes of the stochastic phase for different initial population sizes N_0, population growth rates R, and parameter n. The initial conditions were the same as before. The number of runs was 10,000. The columns under "**a** fixed" give the percentage of runs that ended up with the initially rare allele fixed. This percentage represents an underestimate of the probability of speciation after the founder event specified above. (This is an underestimate because a significant proportion of runs, especially those for $R = 1.5$ and $R = 2.0$, end up with polymorphic populations, some of which will eventually evolve toward fixation of **a**.) The columns under "**Aa** lost" give the percentage of runs that ended up with heterozygotes lost and both alternative homozygotes present at frequencies larger than 5%. This value can be interpreted as the probability of sympatric speciation.

With low rates of growth, the probability of fixation of an allele is close to its initial frequency (as in the neutral case). The data given in table 7 show that increasing the growth rate and the size of the initial population decreases the probability of allopatric speciation. This is in accord with what is expected from biological considerations and has been observed in simulations (e.g., Gavrilets and Hastings 1996). One can also see that increasing

Table 7: The probabilities (%) of different outcomes of the stochastic phase after a founder event (10,000 runs)

	$N_0 = 2$		$N_0 = 4$		$N_0 = 8$	
R	***a*** *fixed*	***Aa*** *lost*	***a*** *fixed*	***Aa*** *lost*	***a*** *fixed*	***Aa*** *lost*
1.1:						
n:						
1	22.9	0	18.4	0	8.3	0
8	22.7	0	20.6	.2	8.8	.3
16	23.1	.3	19.8	2.1	7.7	2.9
32	21.9	.5	18.2	4.4	7.3	5.4
1.5:						
n:						
1	5.1	.7	0	0	0	0
8	4.4	2.8	.3	1.5	0	.1
16	3.3	5.3	.2	3.1	0	.3
32	3.1	6.9	.1	4.9	0	.7
2.0:						
n:						
1	.5	0	0	0	0	0
8	.2	3.1	0	.4	0	0
16	.2	4.9	0	1.0	0	0
32	.1	5.7	0	1.6	0	0

n dramatically increases the probability of sympatric speciation and that there appears to be an optimum population growth rate for sympatric speciation.

Discussion

This model shows the plausibility of two processes of speciation after a bottleneck. The first is standard allopatric speciation when strong premating isolation from an ancestral species rapidly evolves after founding a new population (table 7). Small populations can be found on volcanic islands, where tiny patches of habitat could be isolated by lava flows, as happened repeatedly in the Hawaiian chain (Carson 1982); similarly, in a highly dissected landscape, nearby populations can be isolated genetically. The probability of a peak shift is far more sensitive to the growth rate of the population and to the population size than it is to the process of mate choice characterized by parameter *n*. The second more intriguing process is sympatric speciation when both the old and the new adaptive combinations of genes that are strongly reproductively isolated reach high densities simultaneously. Here speciation is a consequence of the elimination of "intermediate" gene combinations (i.e., hybrids). The probability of sympatric speciation increases with an increasing number of males sampled. Similar behavior has been previously observed in much more complex models with many loci and alleles (Nei et al. 1983; Wu 1985; Higgs and Derrida 1992; Turner and Burrows 1995). Even though the overall probability of founder effect speciation is low, the model does show that such a process is plausible and gives concrete probabilities in some simple cases.

In general, strong premating reproductive isolation evolves much more easily than does strong postmating reproductive isolation (cf. table 4 with tables 6 and 7). An example of two Hawaiian species, *Drosophila silvestris* and *Drosophila heteroneura,* is illuminating in this respect. They show very strong though asymmetric premating reproductive isolation but no postmating reproductive isolation (Craddock 1974; Ahearn and Templeton 1989). Both species share the same polymorphism for a particular chromosome III sequence, which is absent from their *Drosophila planitibia* ancestor (Carson 1982). This strongly suggests that both were derived from a single founder population, which was polymorphic for this inversion, rather than from two separate founder populations.

Besides founder effect speciation and sympatric speciation, our model can be used for addressing some other important evolutionary problems. Let us compare the efficiency of postmating and premating reproductive isolation in preventing the fusion or extinction of sympatric species. To simplify the argument and presentation, we consider an extreme case of complete reproductive isolation. Let x and z be the proportions of individuals in an isolated location that belong to species A and species B, respectively. We start with the case of postmating reproductive isolation. We assume that individuals mate randomly with no respect to the species affiliation. Offspring of $A \times A$ and $B \times B$ matings are perfectly viable and fertile, but all hybrids are completely inviable and/or sterile. The frequency of $A \times A$ matings is x^2, and these matings result in A offspring. The frequency of $B \times B$ matings is z^2, and these matings result in B offspring. Thus, in the next generation the ratio of the proportions of A and B individuals is

$$\frac{x_{t+1}}{z_{t+1}} = \frac{x_t^2}{z_t^2} \qquad (5)$$

where subscripts specify the generation number. After t generations $(x_t/z_t) = (x_0/z_0)^{2t}$, where x_0 and z_0 are initial proportions. For example, if initially species B is twice as abundant as species A (i.e., $x_0/z_0 = 1/2$), just after 5 generations it will be $2^{10} \approx 1{,}000$ times more abundant than species A (which will be practically extinct). Thus, extremely strong or even complete postmating reproductive isolation is not able to maintain two sympatric species. Any initial differences in species abundances become immediately augmented here, and the more abundant species has a strong advantage.

Let us turn now to the case of premating isolation. As-

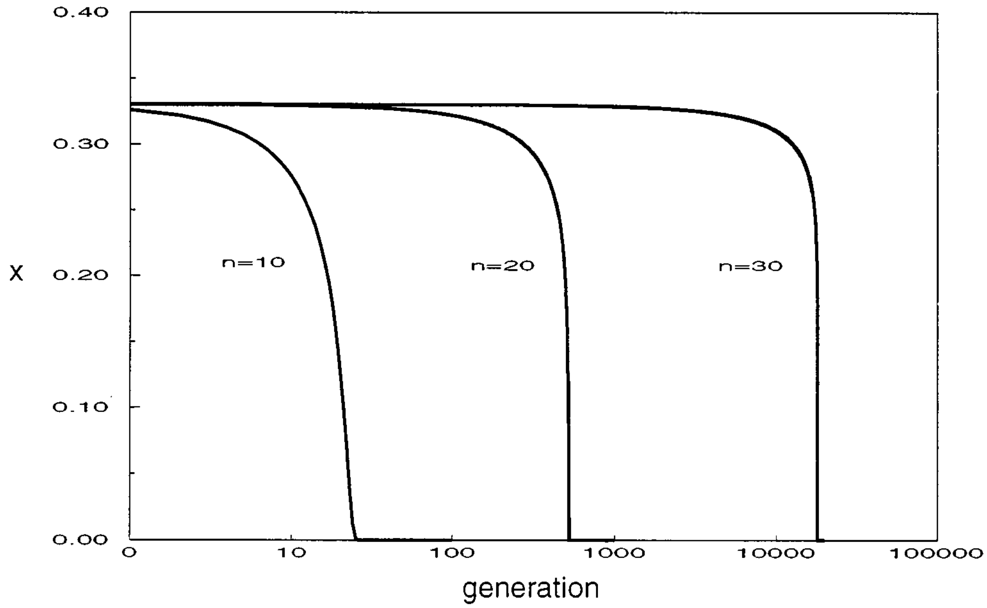

Figure 1: The dynamics of the frequency x of an initially rare genotype **AA** for different n values. At generation 0, $x = 0.33$ meaning genotype **BB** is twice as abundant as genotype **AA**.

sume that $\gamma_1 = \gamma_2 = 0$ whereas all other elements of the matrix of mating probabilities equal 1. Given there are no hybrids initially, the ratio of the proportions of individuals belonging to species *A* and *B* in the next generation can be found by dividing (1a) by (1c) and is

$$\frac{x_{t+1}}{z_{t+1}} = \frac{x_t}{z_t}\frac{1 - (1 - x_t)^n}{1 - (1 - z_t)^n}. \qquad (6)$$

If $n = 1$ (mating is a once in a lifetime opportunity) the right-hand side of (6) reduces to x^2/z^2, which is identical to (5). Increasing *n,* however, greatly increases the time until the extinction of one of the species (see fig. 1; cf. Higgs and Derrida 1992, p. 460). In the extreme case of $n = \infty$ (i.e., if females can afford waiting for a very long time for a "right guy"), $x_{t+1}/z_{t+1} = x_t/z_t$. This means the relative proportions remain the same, and, thus, premating reproductive isolation will maintain genetic differentiation of two sympatric species forever. Extending the duration of coexistence increases the plausibility of further genetic and ecological divergence, which can complete speciation. In natural populations *n* (i.e., the number of possible encounters between a female and males) should be high. Thus, strong premating isolation can be very effective in maintaining distinct sympatric populations. At the same time, even extremely strong postmating isolation cannot prevent extinction of the less abundant species.

The simple argument just described has implications for the problem of how to use the biological species concept with allopatric taxa. One protocol is based on the following reasoning (Coyne and Orr 1989). The strength of isolation between sympatric species is presumably sufficient for them to be distinct. One can conclude that allopatric taxa with total reproductive isolation as strong as that between sympatric species would maintain their integrity on secondary contact and, thus, could be regarded as distinct species. To measure the total isolation, Coyne and Orr (1989) suggested an index that includes both premating and postmating isolation components. If postmating isolation is not effective in maintaining the integrity of species, as our simple model seems to indicate, only premating isolation should be considered in developing protocols similar to that in Coyne and Orr (1989).

Coyne and Orr (1989, 1997) describe what seems to be a general empirical pattern of speciation in *Drosophila:* in young sympatric species, premating isolating factors are much stronger than postmating isolating factors. In contrast, for young allopatric species, both premating and postmating factors appear to be equally strong. A similar pattern has been seen in other taxa as well (Hostert 1997). The explanation for this pattern that Coyne and Orr (1989, 1997) find the most plausible is reinforcement: the enhancement of postmating isolation by natural selection acting against the production of unfit hybrids (Dobzhansky 1940). Both theoretical and experimental work has shown that a necessary condition for reinforcement to be effective is the preexistence of strong postmating isolation between taxa (e.g., Hostert 1997). Among 25 closely related sympatric pairs of taxa with strong premating isolation reviewed by Coyne and Orr, a significant proportion of pairs do not show strong (any?) postmating isolation (e.g., Yoon and Aquadro 1994; see also Hollocher et al. 1997). This suggests that in addition to reinforcement other factors might have contributed to the pattern deduced by Coyne and Orr (1989).

The fact that only populations separated by very strong premating isolation persist in sympatry might have contributed to the pattern. A similar "fusion/extinction hypothesis" attributed by Coyne and Orr (1989) to Templeton (1981) was discussed by them in some detail and rejected. For one reason, they believed that this hypothesis predicts that both pre- and postmating isolation will be stronger in sympatry. However, the argument above shows that premating isolation is far more important than postmating isolation. Second, they argued that if strong premating isolation had evolved before the two populations became sympatric, then one should expect to see at least some cases of strong premating isolation between recently diverged allopatric species, but they reported no such cases. However, many experiments have demonstrated that premating reproductive isolation can evolve rapidly as a by-product of random genetic drift or artificial selection (e.g., Rice and Hostert 1993; Templeton 1996). Rapid evolution of strong premating isolation should occur in natural populations as well, but likely with a much lower probability than in experiments. This might explain the absence of strong premating isolation between 10 young allopatric pairs of species in Coyne and Orr's (1997, fig. 3*a*) data. Larger sample sizes are needed to detect rare events. (For example, if a specific event, say a rapid origin of premating isolation between a pair of allopatric populations, has a 3% probability, then the probabilities that no such events will be observed in 10 trials and in 20 trials are 74% and 54%, respectively.)

Our model suggests several lines of empirical research. First, analyses such as those in table 1 are rare, and usually come from *Drosophila* (but see Wells and Henry 1992; Davies et al. 1997). Our knowledge of hybrid viability and fertility is far more extensive than our knowledge of hybrid mating success; more studies would help to assess how commonly applicable the model might be. Second, n, the number of males visited by a female, has a strong influence on the probability of speciation (tables 6 and 7); knowing its exact value is not as important as getting an idea of its size. This variable may be measured through the daunting task of following females in natural populations, but it may be estimated if one knows the likelihood that a courting male is unsuccessful and the proportion of each type of male in the population. Third, the models show that speciation can occur despite very high hybrid mating success (95% of conspecific success), but most studies of hybrid mating success have not used sufficiently large sample sizes to accurately estimate this variable. Empirical studies will need to be conducted on species that are in the process of diverging. Young habitats such as those found on islands, the great lakes of Africa, or the lakes of southern Alaska and western Canada might house a variety of emerging species.

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APPENDIX

Equations for the Case of Arbitrary n

The condition for stability of monomorphic equilibria (arbitrary n) is

$$\frac{\beta_2}{\alpha_2} + \frac{1 - (1 - \beta_2')^n}{1 - (1 - \alpha_2)^n} < 2.$$

The equilibrium frequency of heterozygotes at the mutation-selection balance with allele A close to fixation (arbitrary n) is

$$y^* = \mu \frac{2\alpha_2[1 - (1 - \alpha_2)^n]}{\alpha_2 - \beta_2 + \beta_2(1 - \alpha_2)^n + \alpha_2(1 - \beta_2')^n - 2\alpha_2(1 - \alpha_2)^n}.$$

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