THE ROYAL
SOCIETY

On the origin of species by means of assortative mating

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Assortative mating may split a population even in the absence of natural selection. Here, we study when this happens if mating depends on one or two quantitative traits. Not surprisingly, the modes of assortative mating that can cause sympatric speciation without selection are rather strict. However, some of them may occur in nature. Slow elimination of intermediate individuals caused by the gradual tightening of assortative mating, which evolves owing to relatively weak disruptive selection, provides the alternative scenario for sympatric speciation, in addition to fast elimination of intermediate individuals as a result of the direct action of strong disruptive selection under an invariant mode of assortative mating. Even when assortative mating alone cannot split an initially coherent population, it may be able to prevent the merging of species after their secondary contact.

Keywords: sympatric speciation; assortative mating; disruptive selection; multilocus traits

1. INTRODUCTION

Before a population can undergo sympatric speciation, at least two genotypes that are reproductively isolated from each other must appear within the range of its genetic variability. Thus, non-random mating is a prerequisite for sympatric speciation. Often, selection against the intermediate genotypes that carry alleles from both reproductively isolated genotypes is also necessary for its completion. However, under certain conditions, non-random mating can eliminate the intermediate genotypes even in the absence of selection.

This is always the case when differences at one locus in the diploid phase are enough for reproductive isolation, i.e. when the mating between the homozygotes 00 and 11 is prohibited (see Kondrashov & Mina 1986). If so, the frequency of heterozygotes 01 declines each generation by half of the frequency of the mating 01 × 01, slowly leading to the formation of the two species, 00 and 11. This happens because the prohibited mating 00 × 11 is the only one that increases the frequency of heterozygotes (from 0% in the parents to 100% in the offspring), whereas the mating 01 × 01 is the only one that decreases this frequency (from 100% in the parents to 50% in the offspring).

Analogously, two-locus reproductive isolation at the haploid phase also splits the population without selection. Assuming two unlinked diallelic loci each with alleles 0 and 1, it is easy to see that if the mating 00 × 11 is prohibited, the total frequency of intermediate individuals 01 and 10 declines each generation by half of the frequency of 01 × 10 mating. Single-locus reproductive isolation in haploids trivially constitutes speciation in itself because it immediately splits the population into two separate gene pools.

Although reproductive isolation due to differences at one diploid or two haploid loci is not impossible (see Kondrashov & Mina 1986; Orr 1991), it is certainly uncommon. Thus, we need to consider the impact of non-random mating under less restrictive assumptions. In this paper, we do this for the case of n unlinked loci, each with alleles 0 and 1. These loci determine the phenotype of an individual, consisting of either one or two quantitative traits. All the modes considered will be phenotypic, with no discrimination among genotypes constituting a given phenotype.

With one trait, its value in an individual is determined by the number of alleles 1 at all its n loci, i.e. the trait is the result of additive and equal contributions at each locus. With two traits, the n loci are subdivided into two non-overlapping sets of n_1 and n_2 loci ($n_1+n_2=n$), which determine additively, as in the case of one trait, the values of the first and the second trait of an individual, respectively.

For a single trait, we assume that it affects the mate choice of all organisms in the same way (similarity-based non-random mating). In contrast, in the case of two traits, only one trait will be expressed in a particular organism, with mating possible only between organisms expressing different traits (split-trait non-random mating). This describes mate choice depending on a mate preference trait, expressed in one sex, which is inherited independently of another phenotypic trait, expressed in the other sex, upon which the mate choice is based (Sved 1981*a*,*b*). Female preference–male trait systems are known, for example, in African cichlids (see Galis & Metz 1998) and *Drosophila* (Kelly & Noor 1997).

We will consider assortative mating only in the sense of Lewontin *et al.* (1966), i.e. we will assume that, despite

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Proc. R. Soc. Lond. B (1998) **265**, 2273–2278
Received 1 July 1998 *Accepted* 2 July 1998

mating being non-random, all genotypes are, on average, equally successful, so that there is no selective mating (sexual selection) and allele frequencies remain invariant over time.

2. MODES OF ASSORTATIVE MATING

Let us first consider one trait and describe a mode of assortative mating qualitatively, i.e. by which matings are permitted and which are not. To make speciation possible we must assume that individuals with the opposite extreme phenotypes cannot mate. We will also assume that individuals with identical phenotypes can mate. These assumptions are, of course, satisfied in the two three-phenotype cases considered above.

Where there are more than three possible phenotypes, many modes of assortative mating satisfy these assumptions. Let us consider two modes that are in a sense opposite extremes, namely, an interval-based mode and a threshold-based mode (figure 1). With the interval mode, mating between organisms with phenotypes i and j is impossible if $|i-j|>C$, so that the boundary between pairs of phenotypes that can and cannot mate is parallel to the diagonal of the first quadrant. In contrast, with the threshold mode, mating is impossible if $i<T_1$ and $j>T_2$, or if $i>T_2$ and $j<T_1$ ($T_1 \leqslant T_2$), so that this boundary consists of vertical and horizontal parts.

The interval mode constrains matings of an individual to a range of phenotypes specified by a maximal deviation C. In the extreme case of $C=0$, only individuals with identical phenotypes can mate. The threshold mode implies that two classes of individuals, $[0, T_1]$ and $[T_2, n]$, are prohibited from mating with one another, or, in other words, that mating can occur only within two classes $[0, T_2]$ and $[T_1, n]$. In the extreme case of non-overlapping classes $[0, T]$ and $[T, n]$ (where $T_1=T_2=T$), mating is restricted to individuals on the same side of a boundary T, which splits the population into two mating pools. This in itself is not true reproductive isolation, however, as long as matings within a pool can produce offspring that belong to the other pool.

The same modes are possible with the split-trait assortative mating. In this case the two axes in figure 1, as well as the values of i and j, and T_1 and T_2, describe phenotypes in the different traits.

3. RESULTS ON INTERVAL MODE

Let us first consider similarity-based assortative mating depending on one trait. In the most restrictive case of $C=0$, assortative mating leads to speciation, i.e. to the eventual disappearance of all genotypes except the two opposite extreme genotypes 00...0 and 11...1 (Wright 1921; Breese 1956), provided that the initial frequency of allele 1 is uniform across the loci. Otherwise, because allele 1 frequencies are conserved, some intermediates will necessarily persist (Ghai 1974), because if allele 1 has different frequencies at different loci, the population obviously cannot consist only of individuals 00...0 or 11...1.

With $C=1$ and uniform frequency of allele 1, assortative mating also leads to speciation. This follows from the fact that with $C \leqslant 1$, the phenotypic variance is a Lyapunov function, i.e. always grows with time, until the state with the maximal variance is reached. Indeed, the phenotypic variance in the offspring of two parents with either identical or adjacent phenotypes is always greater than this variance among the parents (because more extreme phenotypes appear in the offspring), unless all the parents breed true, which is the case only for extreme phenotypes (assuming equal allele frequencies). In contrast, the mean phenotype of the offspring remains the same as that of the parents, owing to additivity of the trait. These two facts guarantee the increase of the global variance. This conclusion holds for both haploid and diploid populations. Both one-locus diploid isolation and two-locus haploid isolation, considered above, satisfy the condition $C \leqslant 1$.

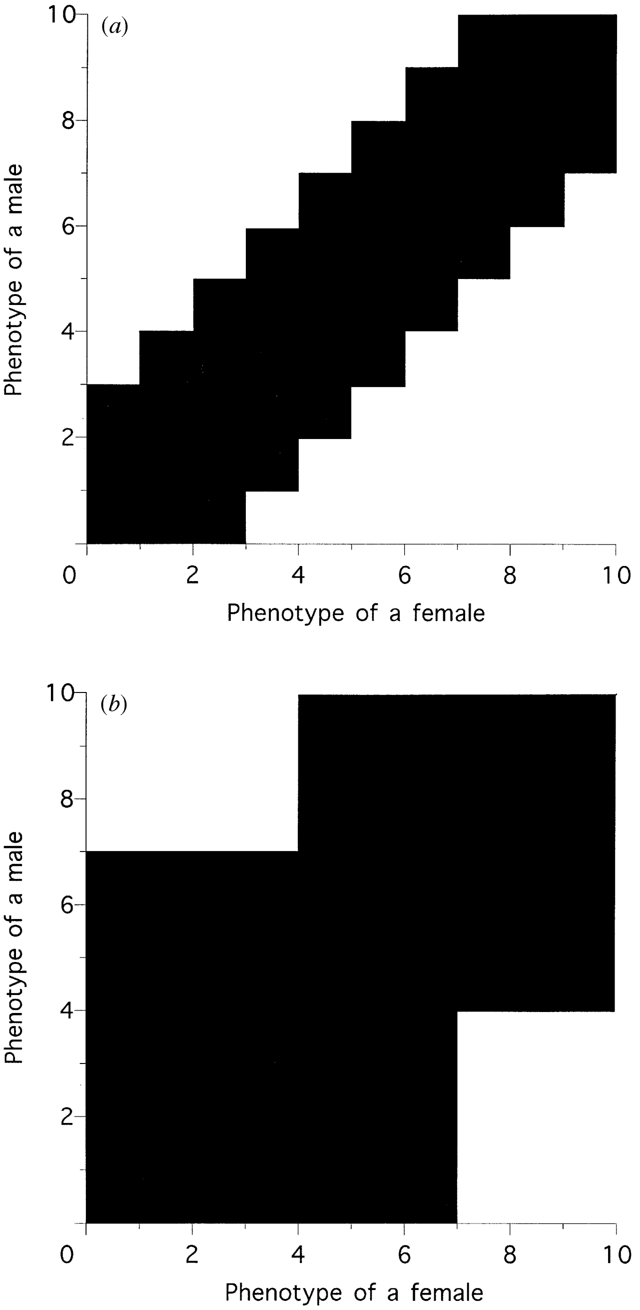

Figure 1. Possible (black) and impossible (white) matings under (a) interval assortative mating ($C=3$), and (b) threshold assortative mating ($T_1=4$, $T_2=7$).

With $C>1$, the phenotypic variance is no longer a Lyapunov function. For example, the variance among the offspring from the mating of 00…0 individuals with those carrying two alleles 1 at some of their n loci is smaller than among the parents, because some offspring with one allele 1 will be produced. So far, there is no mathematical treatment for this case. Instead, it was studied using individual-based computer simulations of a haploid population by Kulagina & Lyapunov (1966). In some runs with large n and $C>1$, speciation occurred. The authors erroneously attributed this outcome to the impact of random drift, instead of deterministic action of assortative mating. Later, Kamenshchikov (1972) obtained essentially the same results for diploids. However, because of random noise, individual-based models cannot provide precise information on the parameters required for speciation without selection.

We address this question using a deterministic exact hypergeometric phenotypic model (Barton 1992; Doebeli 1996; Shpak & Kondrashov 1998; THINK C programs are available on request), assuming that mating is random among the phenotypes that are permitted to mate. The hypergeometric model requires uniformity of allele 1 frequencies across all the loci (Shpak & Kondrashov 1998), which is also the necessary condition of speciation without selection (see above).

Table 1 presents equilibrium values of the phenotypic variance in a haploid population where the frequency of allele 1 is 0.5 at all the loci. When the distribution of phenotypes is binomial, which corresponds to independent distribution of all alleles, its variance is $n/4$. In the opposite case of speciation, where only the two extreme phenotypes are present, the variance is $n^2/4$.

The data presented in table 1 correspond to the initial distributions with low or moderate variance. Even in this case, speciation occurs when $C \leqslant C_{\text{crit}}$. We can see that C_{crit} increases with n as *ca.* $\sqrt{n}$. This is not surprising, as the standard deviation of the phenotype distribution in the offspring from a particular mating must be *ca.* $\sqrt{n}$, so that if the difference between the parent phenotypes is below $\sqrt{n}$, reproduction should generally increase the variance. However, we could not convert this heuristic reasoning into a proof. When C grows past C_{crit}, the equilibrium variance drops rapidly and soon becomes very close to $n/4$, whereas the equilibrium phenotype distribution becomes close to binomial.

Whereas with $C \leqslant C_{\text{crit}}$, speciation appears to be a globally stable equilibrium, with $C>C_{\text{crit}}$, the outcome may depend on the initial distribution. In such cases, marked by an asterisk in tables 1–4, the population speciates if the variance of the initial distribution is sufficiently high (usually more than 95–99% of the maximal possible value $n^2/4$), whereas with lower initial variances the value of the variance presented in a table is reached at equilibrium. This phenomenon only appears for $n>8$, after which the magnitude of C which leads to speciation from high initial variance seems to approach $n/2$ where n is large.

If $C>C_{\text{crit}}$, the convergence to speciation within the domain of its attraction is extremely slow. Some examples of the dynamics of the phenotypic distribution are presented in figure 2. All of these results apparently hold qualitatively if the frequency of allele 1 deviates from 0.5.

Table 1. *The equilibrium variance under interval assortative mating with one trait and haploidy*

(With $C>C_{\text{crit}}$, speciation may depend on the initial distribution. In such cases, marked by *, the population speciates if the variance of the initial distribution is sufficiently high, whereas with lower initial variances the value of the variance presented in a table is reached at equilibrium.)

	n						
C	1	2	4	8	16	32	64
0	0.25	1.0	4.0	16.0	64.0	256.0	1024.0
1	0.25	1.0	4.0	16.0	64.0	256.0	1024.0
2	—	0.5	1.7699	16.0	64.0	256.0	1024.0
3	—	—	1.0600	4.6425^*	64.0	256.0	1024.0
4	—	—	1.0	2.4193	64.0	256.0	1024.0
5	—	—	—	2.0765	7.1679^*	256.0	1024.0
6	—	—	—	2.0108	4.9143^*	256.0	1024.0
7	—	—	—	2.0009	4.2907	18.3483^*	1024.0
8	—	—	—	2.0	4.0893	11.7702^*	1024.0
9	—	—	—	—	4.0244	9.6260^*	1024.0
10	—	—	—	—	4.0055	8.7327^*	42.8128^*
11	—	—	—	—	4.0008	8.3296^*	27.6362^*
12	—	—	—	—	4.0000	8.1443^*	22.0559^*
13	—	—	—	—	4.0000	8.0605	19.3624^*
14	—	—	—	—	4.0000	8.0240	17.9149^*
15	—	—	—	—	4.0000	8.0089	17.0978^*
16	—	—	—	—	4.0000	8.0031	16.6266^*

The data on diploid populations (equation (8) from Shpak & Kondrashov (1998)) are presented in table 2. Obviously, the dynamics in a diploid population with some values of n and C are almost the same as in a haploid population with a twofold larger n and identical C.

Individual-based computer simulations, using the model described in Kondrashov (1986), confirm the basic conclusion about the values of C_{crit}. However, the initial-condition-dependent speciation under $C \geqslant C_{\text{crit}}$ cannot be studied by such simulations, because during the very slow approach to speciation, random drift destroys uniformity of allele frequencies across the loci, thus making the completion of speciation impossible.

Let us now consider split-trait interval-based assortative mating. Table 3 presents equilibrium covariances of the two traits for different n_1 (assuming $n_1 = n_2$) and C, as attained from uniform distributions. Obviously, in the case of speciation the covariance is maximal, $n_1 n_2/4$. Although covariance is always positive, speciation occurs only with $C=0$ and $n_1<8$, whereas in other cases the equilibrium covariance is not large. However, as with one trait, speciation occurred under much less restrictive conditions if the initial distribution was close to the maximal variance. As before, speciation was very slow in such cases.

4. RESULTS ON THRESHOLD MODE

The threshold mode of assortative mating is the most restrictive if $T_1 = T_2 = T$. This always leads to speciation. Let us consider the expression

$$D = (T - m_0)x_0 + (m_1 - T)x_1, \tag{1}$$

where x_0 and x_1 are the fractions of the population consisting of 'small' and 'large' individuals, i.e. of those

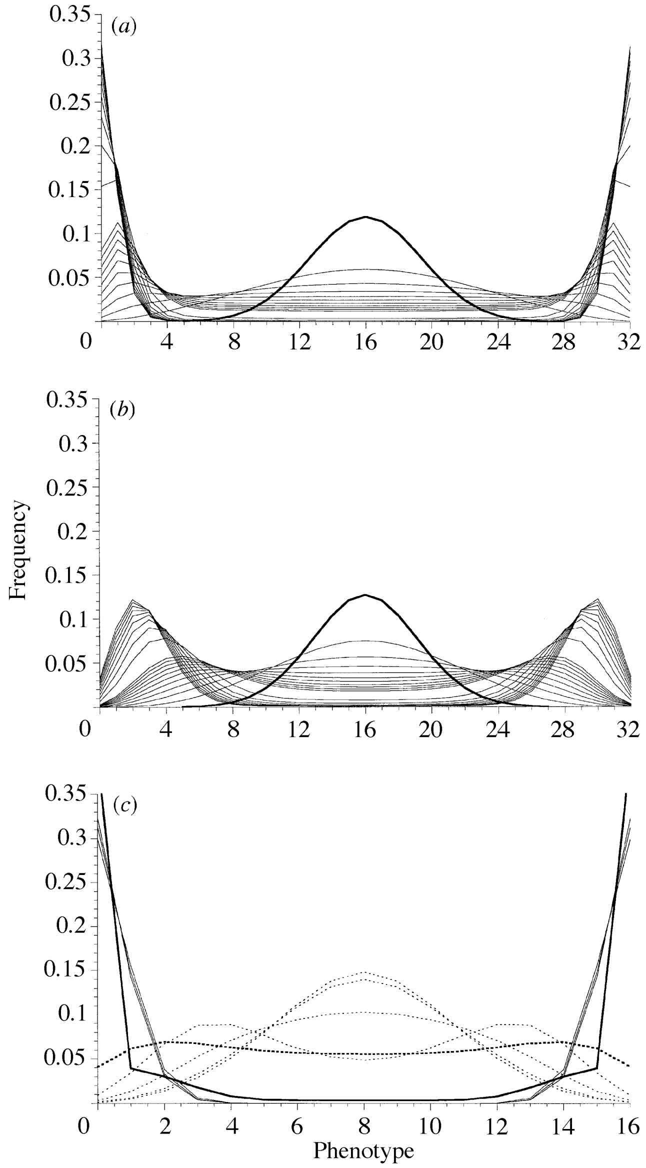

Figure 2. Dynamics of the phenotype distributions under similarity-based, interval assortative mating in the haploid population. Distributions after the first generation are set in bold font. (*a*) $n=32$, $C=3$; the distributions after generations 1, 11, ..., 101, 201, ..., 1001 are shown (the variance increases with time until speciation occurs). (*b*) The same, but with $C=5$. (*c*) $n=16$, $C=5$; the distributions after generations 1, 11, 31, 51 and 201 (essentially equilibrium) are shown as broken lines (the variance declines), and the distributions after generations 1, 10 001, 500 001 and 1 000 001 are shown as solid lines (the variance declines during the first few generations, after which it grows very slowly until speciation is reached).

with phenotypes below and above T (those with phenotype T can be included in either class), respectively, and m_0 and m_1 are the mean values of the trait within small and large individuals, respectively. In a sense, D is a weighted deviation of the two sides from the boundary T. We will show that D is a Lyapunov function (for a special case of $n=2$, this was carried out by Kondrashov & Molchanov (1980)).

Let us consider a particular (current) generation. Among all offspring, the fractions of small and large offspring of small individuals are p_{00} and p_{01}, whereas the fractions of small and large offspring of large individuals are p_{10} and p_{11} (there is no small × large interbreeding). The mean values of the trait within these four classes of offspring are a_{00}, a_{01}, a_{10}, and a_{11}, respectively. Without selection, $x_0=p_{00}+p_{01}$ and $x_1=p_{10}+p_{11}$, whereas $x_0'=p_{00}+p_{10}$ and $x_1'=p_{01}+p_{11}$ (prime denotes the next generation). Owing to the additivity of the trait, $m_0=(p_{00}a_{00}+p_{01}a_{01})/(p_{00}+p_{01})$ and $m_1=(p_{10}a_{10}+p_{11}a_{11})$, whereas $m_0'=(p_{00}a_{00}+p_{10}a_{10})/(p_{00}+p_{10})$ and $m_1'=(p_{01}a_{01}+p_{11}a_{11})/(p_{01}+p_{11})$. Because a_{00}, $a_{10}\leqslant T$ and a_{01}, $a_{11}\geqslant T$, $D'=(T-m_0')\,x_0'+(m_1'-T)\,x_1'\geqslant D$. Because mating is random within large fractions of the population, speciation proceeds slowly (data not reported), unlike the case of interval assortativity where speciation can be relatively fast.

Table 2. *The equilibrium variance under interval assortative mating with one trait and diploidy*

(*, see note to table 1.)

	n				
C	1	2	4	8	16
0	1.0	4.0	16.0	64.0	256.0
1	1.0	4.0	16.0	64.0	256.0
2	0.5	1.7813	16.0	64.0	256.0
3	—	1.0585	4.6591*	64.0	256.0
4	—	1.0	2.4161	64.0	256.0
5	—	—	2.0759	7.1668*	256.0
6	—	—	2.0107	4.9111*	256.0
7	—	—	2.0009	4.2895	18.3474*
8	—	—	2.0	4.0890	11.7657*

Table 3. *The equilibrium covariance under interval assortative mating with two traits and haploidy*

(*, see note to table 1.)

	n				
C	1	2	4	8	16
0	0.25	1.0	4.0	1.3748*	2.0096*
1	0.0	0.1006	0.4223*	1.2850*	2.6552*
2	—	0.0	0.1125	0.5379*	1.9106*
3	—	—	0.0179	0.2309*	1.0418*
4	—	—	0.0	0.0828	0.5917*
5	—	—	—	0.0214	0.3120*
6	—	—	—	0.0035	0.1567*
7	—	—	—	0.0003	0.0651
8	—	—	—	0.0	0.0243

As with interval assortativity, a Lyapunov function exists in the extreme case ($T_1=T_2$), but apparently does not exist if $T_1<T_2$. The data of numerical modelling show that threshold assortativity leads to speciation only with $T_1=T_2$, and when the difference between T_2 and T_1 increases the equilibrium variance rapidly approaches that of a binomial distribution. Table 4 presents the data for $T_1=n/2-\Delta$ and $T_2=n/2+\Delta$. Here the outcome does not depend on the initial distribution. With the split-trait assortative mating, speciation never occurred, even under $T_1=T_2$ (data not reported).

Table 4. *The equilibrium variance under threshold assortative mating with one trait and haploidy*

(*, see note to table 1.)

	n						
Δ	1	2	4	8	16	32	64
0	—	1.0	4.0	16.0	64.0	256.0	1024.0
1	—	0.5	1.0600	2.7500	9.1478	35.9398	148.5612
2	—	—	1.0	2.0472	4.7964	14.2324	52.3996
3	—	—	—	2.0009	4.1188	9.7215	29.0505
4	—	—	—	2.0	4.0119	8.4733	21.2203
5	—	—	—	—	4.0006	8.1144	18.1428
6	—	—	—	—	4.0000	8.0224	16.8559
7	—	—	—	—	4.0000	8.0034	16.3207
8	—	—	—	—	4.0000	8.0004	16.1098

5. DISCUSSION

Perhaps, the modes of assortative mating considered here are not the most favourable for speciation. Although we assumed that all permitted matings occur randomly, speciation may be facilitated if matings between similar individuals occur more often. Still, it seems that only rather stringent assortative mating can cause sympatric speciation without selection. In fact, only interval similarity-based assortative mating with $C\leqslant C_{\mathrm{crit}}\approx\sqrt{n}$ rapidly splits a population with initially unimodal phenotype distribution. In contrast, threshold similarity-based assortative mating or any mode of split-trait assortative mating splits such a population only very slowly, and only under extreme parameter values (tables 1–4 and figure 2).

How plausible is such strict assortativity in nature? Obviously, in the absence of selection the best strategy is to mate with the first partner. However, avoiding mating with dissimilar individuals is beneficial under disruptive selection (Wallace 1889, p. 179), whereas under stabilizing selection, avoiding mating with similar individuals is beneficial, at least for individuals having extreme phenotypes.

Qualitative analysis of the Wallace effect shows that moderate disruptive selection can lead to the fixation of a modifier that causes similarity-based assortative mating (Kondrashov 1984; Doebeli 1996) according to the trait under such selection. In contrast, split-trait assortative mating may evolve only under very strong disruptive selection, because this evolution requires establishment of linkage disequilibria between loci controlling different traits (A. S. Kondrashov and F. A. Kondrashov, unpublished data). If so, models of split-trait assortative mating without selection cannot describe sympatric speciation, although they still can be relevant to the event of a secondary contact between populations that diverged allopatrically.

Of course, assortative mating can also appear just as an unavoidable by-product of genetic variability, in particular, of variability concerned with time and/or place of mating. Interval assortative mating may occur, for example, when different individuals breed at different times, as is the case with many amphibians (Mayr 1963). Threshold assortativity may arise when mate choice depends on threshold traits. In this case, additive phenotypes considered above have the meaning of trait potential or liability (Roff *et al.* 1997), and the actual traits (e.g. the presence or absence of wings or a particular habitat choice) depend on them in a discontinuous manner. Thus, threshold habitat choice influenced only by genotypes, but not by the environment, leads to slow sympatric speciation without selection.

Three very different processes can cause the elimination of the intermediate phenotypes and thus complete sympatric speciation. The first, conventional option is strong selection against the intermediates (disruptive selection due to different available resources and competition (see Darwin 1859; Kondrashov & Mina 1986; Doebeli 1996); divergent selection in different habitats (see Bush 1994); or sexual selection (see Turner & Burrows 1995)), with invariant assortative mating. The second option is stringent, invariant (perhaps, interval similarity-based) assortative mating without selection. Finally, speciation may be completed as a result of evolution of more and more stringent similarity-based assortative mating driven by moderately strong disruptive selection. In the first two cases, the intermediate phenotypes are eliminated fast, if at all, whereas in the third case the elimination may be slow.

We regard the first and the third cases as more realistic. Under non-random mating, rare phenotypes are likely to suffer a disadvantage (i.e. non-random mating is likely to be selective, and not strictly assortative (Lewontin *et al.* 1966)). Thus, at least a weak frequency-dependent selection is required to keep a speciating population polymorphic, as well as to maintain coexistence of the newly formed species. In addition, at least a weak disruptive selection appears to be the only possible cause for uniformity of allele frequencies across all the loci affecting a particular trait (see Shpak & Kondrashov 1998), which is necessary for speciation.

Even when assortative mating alone cannot drive sympatric speciation, it may be enough to prevent merging of the two species produced allopatrically, after they came into secondary contact. This is the case both for similarity-based and for split-trait interval assortative mating (tables 1–3). This second possibility is important because reproductive isolation between species of apparently allopatric origin is often due to such assortative mating (Kelly & Noor 1997). Rapid, independent coevolution of female preference and male traits (Rice & Holland 1997) in different allopatric species can routinely create such situations.

Without selection, speciation, if only locally stable, is always a weak attractor with a small domain of stability. Thus, assortative mating alone can preserve species identity after secondary contact only if hybrids be rare. However, even weak selection against hybrids may be enough to keep them rare and preserve such species after their secondary contact. Such selection, which is necessary only to keep the population within the domain of attraction of speciation, can be much weaker than selection required by conventional scenarios of 'secondary reinforcement' (see Kelly & Noor 1997). However, without strong selection, merging of the species may be triggered by even a single mass production of hybrids (figure 2*c*).

This research was supported by the NSF (grant DEB-9417753) and was conducted using the resources of the Cornell Theory Center, which receives funding from Cornell University, New York State, the National Center for Research Resources at the National Institutes of Health (NIH), and members of the Center's Corporate Partnership Program. We thank two anonymous reviewers for useful comments.

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