

Divergent Outcomes of Reinforcement Speciation: The Relative Importance of Assortative Mating and Migration Modification

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ABSTRACT: Most studies of reinforcement speciation focus on the evolution of assortative mating, but R. A. Fisher argued that migration modification is likely to be a common alternative mechanism. Despite previous models showing that assortative mating and migration modification may both be involved in reinforcement, no one has determined their relative evolutionary importance. This is surprising because understanding the biological conditions favoring these mechanisms may explain why certain pairs of species exhibit abutting, nonoverlapping geographical ranges with habitat fidelity while other pairs coexist in sympatry with sexual isolation. In this article, we explicitly model the evolution of both mechanisms simultaneously. First, we explore how these mechanisms differ in their evolutionary dynamics. Second, we ask how they affect each other's evolution and whether the interaction alters their relative importance in reinforcement. Our results reveal that assortative mating may evolve faster and under a broader range of biological conditions than migration modification. However, direct evolutionary interactions favor migration modification when populations experience strong divergent selection. Depending on the nature of postmating isolation, these mechanisms may either interfere with each other's evolution or coevolve in the same system. These results illustrate the importance of studying multiple mechanisms of speciation simultaneously in future speciation models.

Keywords: dispersal behavior, hybrid zones, secondary contact, sexual isolation, ecological selection, geographical ranges.

Reinforcement speciation is a process by which natural selection is thought to favor the evolution of premating

isolation mechanisms when populations meet during secondary contact and experience partial postmating isolation. Reinforcement has had a controversial history but has recently gained both theoretical and empirical support (Servedio and Noor 2003; Coyne and Orr 2004). Theoreticians are now turning their attention to the conditions that are expected to favor the evolution of reinforcement (Servedio and Noor 2003). Within this context, there is a need to explore the relative importance of different mechanisms of reinforcement speciation because there are many ways by which species achieve premating isolation, including temporal, mechanical, habitat, and ethological mechanisms (Fisher 1930; Dobzhansky 1937; Mayr 1963; Coyne and Orr 2004).

In particular, Fisher (1930) argued that secondary contact between partially reproductively isolated populations may lead to natural selection favoring genotypes that either cease to migrate into other populations or discriminate in mating against individuals that migrate from other populations (pp. 127–128, 130–131). Since Fisher's verbal arguments, reinforcement models have largely focused on the evolution of mating preferences (e.g., Felsenstein 1981; Spencer et al. 1986; Liou and Price 1994; Kelly and Noor 1996; Servedio and Kirkpatrick 1997; Servedio 2000, 2004). Only two studies have investigated whether a migration modification behavior, reducing migration into another population, may serve as a reinforcement speciation mechanism (Balkau and Feldman 1973; Karlin and McGregor 1974). Despite the general conclusion that both mechanisms may evolve when introduced at low frequencies, there is still a lack of understanding of their relative evolutionary importance in reinforcement speciation. This is because no study has investigated the evolution of these behaviors simultaneously in a single theoretical model. The focus of this article is to directly address this question.

The migration modification behavior is an example of a "one-allele" mechanism (Felsenstein 1981) because the fixation of the same sedentary allele in both populations will result in speciation (Balkau and Feldman 1973; Karlin and McGregor 1974; but see "Discussion"). On the other hand, the evolution of mating preference may take the

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form of a “one-allele” or a “two-allele” mechanism (see Felsenstein 1981; Servedio 2000). A one-allele mechanism would be an allele that makes individuals assortatively mate with other individuals that match their phenotype at a particular marker trait such as body size (see Servedio 2000). This requires that the marker trait originally exhibit some divergence between populations. The mechanism has recently gained theoretical attention (e.g., Kelly and Noor 1996; Dieckmann and Doebeli 1999; Servedio 2000, 2004) in light of accumulating empirical evidence suggesting its plausibility in nature. For instance, size-assortative mating is found in threespine sticklebacks (McKinnon and Rundle 2002), sea horses (Jones et al. 2003), and *Drosophila* (Hegde and Krishna 1997), while assortative mating in Darwin’s finches is based on beak morphology and song (Podos 2001; see Servedio 2004 for other examples). The first unambiguous genetic evidence for a one-allele assortative mating mechanism has been illustrated in *Drosophila pseudoobscura* and *Drosophila persimilis* (Ortiz-Barrientos and Noor 2005).

A two-allele mating preference mechanism would involve each allele conferring a preference for a specific phenotypic marker, regardless of the phenotype of the individual exercising the preference (Servedio 2000). Felsenstein (1981), Liou and Price (1994), and Servedio (2000) demonstrated that a two-allele mating preference mechanism is generally less likely to evolve than a one-allele assortative mating mechanism because in the two-allele case, recombination can create mismatching, maladaptive preference-fitness genotypes that limit the evolution of preference (see also Spencer et al. 1986; Servedio and Kirkpatrick 1997). No one has extended these results to compare the relative likelihood of the evolution of a migration versus that of a mating behavior, even though these distinct mechanisms might exhibit strikingly different biogeographical signatures of reinforcement speciation.

In particular, if populations evolve to avoid migrating into each other’s geographical range, this would lead to the reinforcement of geographical allopatry. The result would be a species pair with abutting, nonoverlapping geographical ranges, even if physical barriers to migration no longer exist (Balkau and Feldman 1973; Karlin and McGregor 1974). On the other hand, if populations evolve divergent mating preferences, their geographical ranges could be largely overlapping, resulting in a species pair coexisting in sympatry (Servedio and Kirkpatrick 1997; Coyne and Orr 2004). These outcomes may contribute to explaining why certain species pairs exhibit nonoverlapping ranges that lack physical barriers (e.g., Vaughan 1967; White 1978; Bowers and Brown 1982; Patton et al. 1984; Sullivan et al. 1986; Lee et al. 1996) and why others show

largely overlapping ranges (Marshall et al. 2002; Coyne and Orr 2004).

In order to understand the relative importance of these strikingly different outcomes of reinforcement speciation, one would like to understand how migration modification differs from mating preference evolution in relative ability to reinforce postmating isolation. This needs to be done without confounding the effect of a one-allele versus a two-allele genetic architecture (Felsenstein 1981; Servedio 2000). Thus, it would be optimal to hold the genetic architecture constant when comparing the evolution of a migration behavior with that of a mating behavior. Naturally, we would like to first understand how one-allele migration modification and assortative mating systems differ and then extend the results to more complex two-allele models in the future.

Migration modification and assortative mating evolution differ in characteristics that may potentially lead to different evolutionary dynamics during reinforcement. For instance, assortative mating typically requires a marker trait upon which mate choice is exercised, whereas an allele that simply reduces migration does not require such a trait. This might make it easier for the migration modification mechanism to evolve in response to selection. On the other hand, alleles reducing the migration rate may be less likely to spread into the other population and may be less able to avoid hybridization with migrants. It is very difficult to predict how these differences will influence the evolutionary dynamics of these mechanisms in terms of their relative speed and probability of evolution.

Direct evolutionary interactions between assortative mating and migration modification may also affect their relative importance in reinforcement. This is because the evolution of one mechanism could erode the selective advantages of the other during secondary contact, since both rely on the presence of hybrids for their evolution. Thus, these mechanisms might be evolutionarily “competitive” during speciation. At present, we do not know to what extent each mechanism will curtail the other’s evolutionary potential and especially whether this interaction will change their evolutionary importance relative to cases when each segregates alone. Here we have developed a population-genetic model to explicitly answer these questions. Empirical studies can then begin to shed light on which mechanism has played a more important role in reinforcement, in specific cases and generally.

Model

Following Felsenstein (1981), Kelly and Noor (1996), Servedio and Kirkpatrick (1997), and Servedio (2000, 2004), we consider a two-island model. Each island contains a single finite population with discrete generations. We assume that these two populations have historically diverged

in allopatry (i.e., because of a vicariance event) and are now back in secondary contact (i.e., because of the diminished physical barrier). To be able to explore a wide range of parameters and test the robustness of our results, we study a model consisting of three diallelic loci with haploid individuals that undergo a transient diploid stage during reproduction.

The first locus describes a fitness trait/phenotypic marker that has diverged in allopatry to fixation of alternative alleles (B_1 vs. B_2) in each population by drift and/or selection (see below for a two-locus Dobzhansky-Muller epistatic fitness model). To see the effect of recombination, we also explore a scenario where one locus represents a fitness trait (with alleles B_1 and B_2) and another locus represents a marker trait (with alleles T_1 and T_2). Again, we assume that the above alleles diverged in allopatry and therefore exhibit linkage disequilibrium before secondary contact. We then study varying degrees of recombination between fitness and marker loci. In this case, the marker locus T is selectively neutral. In general, these initial conditions represent relatively high divergence of fitness and/or marker traits, making it more conducive to speciation (e.g., Kirkpatrick and Ravigné 2002). This condition facilitates comparing the evolution of alternative isolating mechanisms when reinforcement is actually likely to occur.

We assume that selection at the fitness locus is against unfit mating pairs during the diploid reproductive stage because of reduced fertility or partial offspring inviability (i.e., fecundity selection or “prezygotic postmating isolation”; see Marshall et al. 2002; Servedio and Noor 2003; Coyne and Orr 2004). First, we explore an “intrinsic postmating isolation” model, where only heterotypic matings (B_1 haplotypes with B_2 haplotypes) experience reduction in fitness. This is an example of fitness underdominance at a single locus and is modeled by assuming a fitness of 1 for the homotypic matings and a fitness of $1 - s$ for the heterotypic matings in each island, where s is the selection coefficient (fig. 1A). This model gave results qualitatively similar to those of a two-locus Dobzhansky-Muller epistatic fitness model, where B and D loci interact to produce two parental haplotypes B_1D_1 and B_2D_2 and hybrid haplotype matings B_1D_2 and B_2D_1 , with hybrid haplotypes having a fitness of $1 - s$, where s is fecundity selection (see apps. A and B in the online edition of the *American Naturalist*).

We also explore a “niche-based postmating isolation” model, where in addition to overall fitness underdominance of heterotypic matings (as above), the homotypic matings experience divergent niche selection across the two islands. We model this scenario by assuming that in each island, the fitness of the favored homotypic mating (resident) is equal to 1, while the fitness of the heterotypic mating and the unfavored homotypic mating (immigrant)

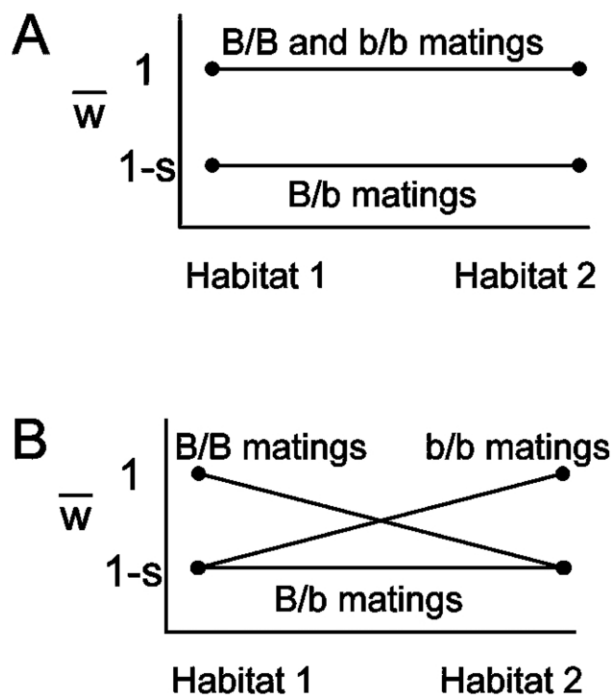


Figure 1: Mean fitness of homotypic matings (BB and bb) and heterotypic matings (Bb) at the fitness locus B in each habitat. *A*, Intrinsic postmating isolation model, where heterotypic matings experience fitness underdominance ($1 - s$) relative to homotypic matings of fitness 1, independent of habitat. *B*, Niche-based postmating isolation model, where both heterotypic matings and immigrant homotypic matings have lower fitness of $1 - s$ in each habitat relative to resident homotypic matings of fitness 1. In this case, local ecological selection creates both hybrid underdominance averaged across both habitats and divergent selection against immigrant genotypes.

is equal to $1 - s$ (niche selection is symmetrical; fig. 1B). Niche-based postmating isolation occurs because the fitness of hybrids falls in between the two niches of the parental haplotypes, and it has been recently observed in a variety of systems (e.g., Ratcliffe and Grant 1983; Nagel and Schluter 1998; Nosil et al. 2002, 2003).

The second locus describes the mating behavior of female individuals, which may have either a random mating allele (A_1) or a positive assortative mating allele (A_2), the latter causing assortative mating with males matching that female at the marker/fitness locus B (see Ortiz-Barrientos and Noor 2005). Single-locus determination is involved in mating discrimination in mole rats (Beiles et al. 1984), controls courtship song and timing of mating behavior in *Drosophila* (Doi et al. 2001; Tauber et al. 2003), and has been demonstrated to contribute to reinforcement between *Drosophila pseudoobscura* and *Drosophila persimilis* (Ortiz-Barrientos and Noor 2005). Genes of major effect are also known to cause sexual isolation in many other

groups (Ritchie and Phillips 1998). When fitness and marker traits are each encoded by a different locus, B and T, respectively, the assortatively mating female haplotypes A_2 choose to mate with like males at the selectively neutral marker locus T. Because males of most species are often indiscriminate in their mating behavior (see Andersson 1994), males mate randomly, regardless of their haplotype.

Before secondary contact occurs, 99% of individuals in both populations carry the random mating allele, A_1 , and only 1% of individuals carry the assortative mating allele, A_2 . Introducing allele A_2 at a low frequency (0.01) at the A locus before secondary contact represents the process of recurrent mutation while keeping the A locus initially in linkage equilibrium with all other loci. We first assume that the strength of mating preference is 100% and then explore a 50% genetic penetrance scenario (Falconer 1981), where the individual female carrying an assortative mating allele still has a 50% chance of mating randomly. "Speciation" is defined as the point at which the assortative mating allele fixes in both populations (i.e., the allele conferring random mating disappears).

The third locus in our model describes migratory/dispersal behavior, which, following analytical models of Balkau and Feldman (1973) and Karlin and McGregor (1974), is defined in reference to the other population. This locus may have either an allele M_1 with a tendency to migrate into the other population or an allele M_2 with a tendency to remain relatively sedentary because of either behavioral (e.g., philopatry) or morphological (e.g., reduction in wings) attributes. Some traits involved in migratory/dispersal behavior and ability are known to have single-locus determination in organisms where this could be investigated, such as *Drosophila* (Osborne et al. 1997) and other insects (Roff 1986, 1994). Before secondary contact, 99% of the individuals in both populations have a genetic tendency to migrate (allele M_1), and 1% of individuals have a genetic tendency to remain sedentary (allele M_2). Both alleles are initially in linkage equilibrium with all other loci.

The actual probability of migration for genetically migratory haplotypes, M_1 , is determined by the extent to which the previous physical barrier has broken down (see Darlington 1943; MacArthur and Wilson 1967). This probability of migration describes the "initial migration rate" between the two populations. For instance, if the barrier has eroded to a point where the probability of migration for genetically migratory individuals becomes 0.10, the initial migration rate between the two populations will then also be around 0.10 (see X-axis in fig. 2). We first explore a scenario where the probability of migration of a relatively sedentary haplotype M_2 is 0.0 (100% genetic penetrance). We then study a 50% genetic penetrance scenario where the genetically sedentary individual still has a 50% chance of behaving like a genetically migratory

individual (see above). Speciation occurs when the sedentary behavior allele evolves to fixation in both populations (i.e., the migration tendency allele disappears).

The Approach

The model has three loci, each with two alleles in each population that are interacting via migration. Because the allelic frequencies in each population must be explicitly considered (e.g., Karlin and McGregor 1974), this yields a total of 16 different haplotypes (eight in each population). To approach the problem analytically, 16 simultaneous equations would have to be derived. As in studies by Balkau and Feldman (1973) and Servedio and Kirkpatrick (1997), both the number and the complexity of these equations prevented us from deriving analytical solutions and linear stability analyses. A weak selection approximation method of Barton and Turelli (1991) was also recently shown to be inadequate for describing reinforcement speciation (Gavrilets 2004, p. 367; Servedio 2004). Thus, following previous models of reinforcement (e.g., Felsenstein 1981; Spencer et al. 1986; Liou and Price 1994; Kelly and Noor 1996; Servedio and Kirkpatrick 1997; Servedio 2000, 2004), we studied the question using numerical simulations. Simulations also allowed us to explicitly consider stochastic processes in reinforcement speciation. Particularly, the loss of genetic variation at the fitness marker or reinforcement loci due to genetic drift was explicitly explored in our model (see below). A deterministic analytical model would ignore this important feature of biological populations.

A Monte Carlo simulation was performed in BASIC (code available upon request). Here, we briefly describe the order of events as specified by the simulation program. First, 1,000 starting females and males are sampled from the initial haplotype frequencies in each population (asymmetrical population sizes were also studied). Second, each female chooses a male, depending on her mating behavior locus and her phenotype at the marker locus. There are no costs to being choosy (i.e., every female mates; but see "Discussion" for relaxation of this assumption). This creates 1,000 mating pairs in each population (a model with 5,000 mating pairs in each population gave qualitatively similar results; see app. A). Third, each pair produces progeny with a maximum clutch size (fecundity) of 10 offspring with a fitness of 1. The production of progeny haplotypes depends on the haplotypes of both parents and the recombination rates between different loci. Selection acts on less fit matings by decreasing the fecundity of those matings by a certain fraction, as determined by s (fig. 1). We then update the progeny count in each population and determine whether each offspring will migrate to the other island or remain within the parental island, depending on

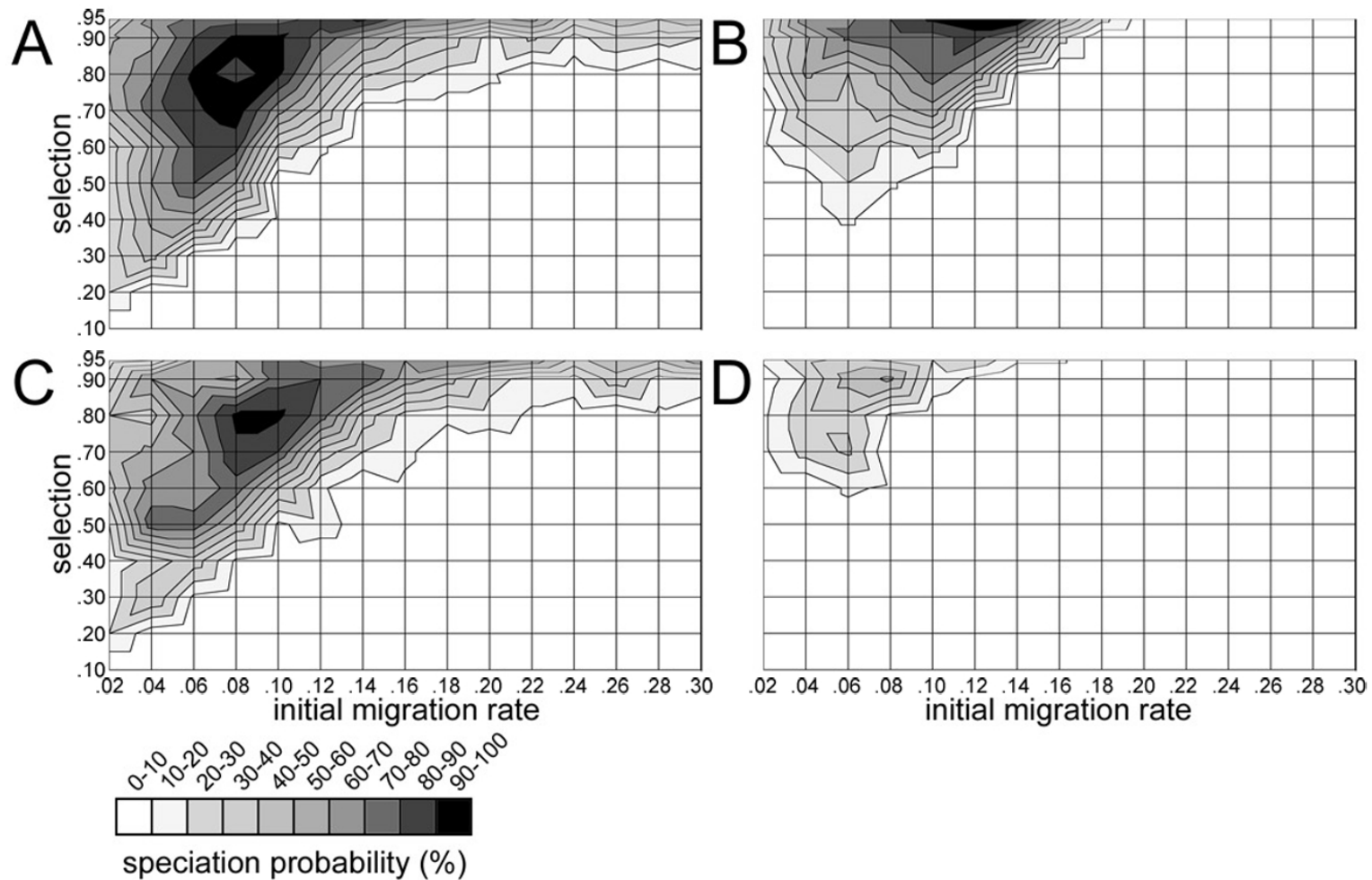


Figure 2: Probability of evolution of assortative mating (A, C) and migration modification (B, D) isolation mechanisms under varying strength of initial secondary contact between the two populations (X-axis: initial migration rate) and intrinsic postmating isolation (Y-axis: selection against heterotypic matings; see fig. 1A). The probability of evolution is defined as the proportion of 25 runs resulting in the fixation of the allele of interest in both populations for each combination of migration and selection. Each run was started with a different random number seed, the distribution of which was sampled from <http://www.random.org>, which generates true random numbers from atmospheric radio noise (see Foley and Wilson 2001). The combination of selection and migration parameters actually simulated is shown by the intersection of values marked along the axes. The rest of the graph is an interpolation of these points. A, Probability of fixation of the assortative mating allele when it initially segregates at 1% in each population in the absence of the migration modification allele. B, Probability of fixation of the migration modification allele when it initially segregates at 1% in each population in the absence of the assortative mating allele. C, Probability of fixation of the assortative mating allele when it and the migration modification allele both initially segregate at 1% in each population. D, Probability of fixation of the migration modification allele when it and the assortative mating allele both initially segregate at 1% in each population.

Table 1: Average number of generations to speciation via fixation of assortative mating and migration modification (sedentary behavior) alleles in the intrinsic postzygotic isolation model

Selection	Initial migration rate														
	.02	.04	.06	.08	.1	.12	.14	.16	.18	.2	.22	.24	.26	.28	.3
Assortative mating allele:															
.95	412	228	152	108	104	90	113	105	91	110	95	97	119	107	93
.9	400	204	134	116	83	116	136	180	134	134	84	86	131	217	167
.8	346	203	124	99	98	105	104	124	118						
.7	379	174	114	104	129	72									
.6	305	166	115	98	86										
.5	314	166	134	114											
.4	264	176	146	141											
.3	299	206													
.2	339														
.1															
Migration modification allele:															
.95	445	279	197	146	121	100	86	77	69						
.9	541	302	206	157	130	109	88	83							
.8		327	235	175	140	123									
.7		384	254	215	171										
.6		439	305	242	194										
.5			352	288											
.4			400												
.3															
.2															
.1															

Note: Sample size per average varies across the table from a minimum of 5 to a maximum of 25. Blanks indicate no event.

its migration locus and the probability of migration. Finally, the postselection, postmigration haplotype frequencies are updated in both populations, and the program loops back to the beginning of the reproductive cycle to initiate the next generation.

We end each run when variation is lost at any of the above loci. Possible outcomes include, first, a single allele at the marker/fitness locus is fixed in both populations, second, the assortative mating allele is lost in both populations, third, the migration modification allele is lost in both populations, fourth, assortative mating is fixed in both populations (speciation), and finally, migration modification (sedentary behavior) is fixed in both populations (speciation). We end each run if none of the above outcomes result after 1,000 generations; however, this situation is rare. Complete tables of the frequencies of all outcomes are available upon request.

Intrinsic Postmating Isolation Model

Independent Evolution

We begin with a historical scenario in which populations have diverged in their fitness and marker loci in allopatry and experience partial hybrid fitness reduction at the fitness locus (fig. 1A). We first studied the evolution of each

mechanism independently by assuming that the two populations segregate for either assortative mating or migration modification alleles at 0.01, but not both.

First, assortative mating and migration modification generally evolved at intermediate migration levels (i.e., when secondary contact is intermediate) and at high selection against hybrids (i.e., at later stages of postmating isolation; fig. 2A, 2B). This result is consistent with previous models of reinforcement speciation (see Servedio and Noor 2003). However, despite this similarity, there were several important differences between the evolution of these two mechanisms. First, the relative position and size of the probability peaks (optimal conditions) of these mechanisms differed (designated by black surfaces in fig. 2A, 2B). Migration modification evolution was most likely to occur at higher migration rates and with stronger selection against hybrids than assortative mating evolution and exhibited a smaller probability peak (fig. 2A, 2B).

Second, migration modification evolved under much more restrictive conditions than assortative mating (compare fig. 2A with fig. 2B). Only assortative mating was able to evolve when high migration rates were combined with high selection (top-right corner of fig. 2A) and when low migration rates were combined with low selection (bottom-left corner of fig. 2A). This result was consistent with the observation that migration modification almost

Table 2: Average number of generations to genetic extinction in intrinsic postzygotic isolation model when assortative mating or migration modification (sedentary behavior) evolves

Selection	Initial migration rate														
	.02	.04	.06	.08	.1	.12	.14	.16	.18	.2	.22	.24	.26	.28	.3
Assortative mating model:															
.95					76	51	38	38	59	41	33	48	38	33	51
.9					142	115	97	72	59	94	93	67	79	60	78
.8					114	161	66	49	39	39	34	53	54	37	40
.7					116	86	37	48	32	33	28	35	29	30	35
.6				133	89	57	41	35	29	40	31	30	34	32	30
.5			195	101	62	42	61	34	34	34	34	33	30	30	31
.4			154	55	53	45	43	40	44	38	38	37	40	40	37
.3			77	54	53	51	50	51	54	51	46	44	48	47	49
.2		130	79	76	68	74	69	66	66	69	72	69	69	65	63
.1	244	140	132	145	118	132	124	120	133	115	120	116	124	119	127
Migration modification model:															
.95								29	23	18	16	14	13	13	13
.9						108	38	26	21	19	16	15	15	13	14
.8						69	34	26	20	19	18	17	16	16	17
.7					103	43	31	26	21	21	20	19	20	18	18
.6				362	58	35	29	27	24	23	23	22	23	21	22
.5				101	48	35	30	28	27	27	26	28	26	27	27
.4			171	50	41	37	36	35	34	35	35	31	33	32	32
.3			83	50	50	50	46	46	44	44	44	43	43	44	44
.2		124	72	68	64	61	63	63	62	68	61	65	65	62	63
.1	305	132	109	119	110	112	116	113	109	113	101	121	142	111	131

Note: Sample size per average varies across the table from a minimum of 5 to a maximum of 25. Blanks indicate no event.

always evolved more slowly than assortative mating (table 1). This result is somewhat robust to relaxing various assumptions of the model (see app. A). It applies to situations when population sizes are not too asymmetrical (e.g., less than 20% different), genetic penetrance of the assortative mating allele is rather high (e.g., higher than 50%), and recombination between fitness and marker loci is rather low (e.g., $r < 0.1$). It was also observed when we explored a two-locus Dobzhansky-Muller epistatic model (app. A). Relaxing the above assumptions generally led to a reduction in the probability of assortative mating evolution, approximating that of migration modification evolution. Nevertheless, the above results clearly indicate that assortative mating has the potential to evolve faster and under a broader range of conditions than migration modification.

As expected, both mechanisms were often lost by drift at low selection and low migration rates (fig. 2A, 2B). However, as selection and migration rates increased, the greatest impediment to speciation became the loss of genetic variation at the fitness/marker loci in both populations (henceforth referred to as “genetic extinction” of one of the populations; see Karlin and McGregor 1974; Coyne and Orr 2004, p. 370). We found that at higher selection-migration conditions, the loss of genetic variation at the fitness/marker loci occurred faster when migration mod-

ification was evolving than when assortative mating was evolving (table 2). Since migration modification evolved more slowly than assortative mating (see above), it was less able to forestall genetic extinction at the fitness/marker loci, which led to its lower probability of evolution.

In total, the above results answer our question of whether these two behavioral isolating mechanisms exhibit different evolutionary dynamics despite both having a “one-allele” genetic architecture. Our results show that their relative conditions and speed of speciation differ substantially and generally favor the evolution of assortative mating over that of migration modification.

Simultaneous Evolution

When both assortative mating and migration modification alleles segregated simultaneously, we found that the two mechanisms exhibited evolutionary interference. Whenever one mechanism initially evolved to fixation in these populations, the allele conferring the other mechanism did one of three things: increased to only a very low frequency (“polymorphism”), increased in one population but not the other (“asymmetry”), or was completely lost in both (“loss”; fig. 3A). For instance, when the assortative mating allele evolved to fixation first, the migration modification allele was lost over 75% of the

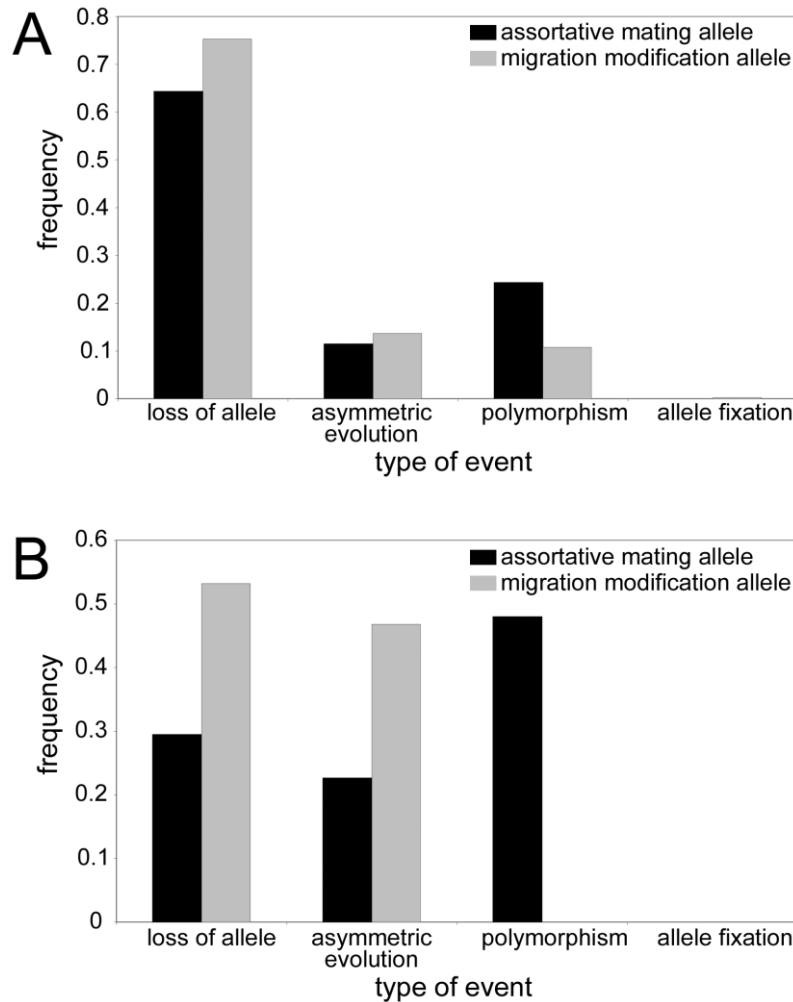


Figure 3: Frequency of evolutionary events of the assortative mating allele (*black bars*) and the migration modification allele (*gray bars*) when the other allele became fixed in both populations. Both alleles initially segregate at 1% in both populations. “Polymorphism” is defined as any frequency of the allele above 10% in both populations. “Asymmetrical evolution” is when the allelic frequency is above 10% in one population and below 10% in the other population. “Loss” is defined as any allelic frequency below 10% in both populations, but in most cases (ranging from 50% to 100% of all “loss” events), the alleles were 0% in both populations. *A*, Intrinsic postmating isolation model; *B*, niche-based postmating isolation model.

time. Similarly, when the migration modification allele evolved to fixation first, the assortative mating allele was lost over 64% of the time. Even when the allele remained polymorphic in both populations (fig. 4A), only about 4% of the time did it reach a frequency of 40% or more in both islands (30 out of 790 runs for assortative mating and 7 out of 123 runs for migration modification). Our results also show that when one mechanism is first allowed to fix in both populations, it either prevents the other mechanism from increasing toward fixation (in the 100%-penetrance case) or allows it to fix only at a very low rate and under the strongest selection-migration conditions (in the 50%-penetrance case; data not shown).

These results suggest that these mechanisms generally interfere with each other’s evolution, since each mechanism reduces gene flow that could have fueled the other’s evolution (see also Moore 1957; Spencer et al. 1986).

This effect may be illustrated by showing how migration modification and assortative mating alleles reduced each other’s probability of evolution and split the selection-migration parameter space when both evolved simultaneously from 1% frequency (compare fig. 2A, 2B with fig. 2C, 2D). This result held well when we increased the population sizes by a factor of five (app. A). In general, assortative mating once again evolved under a broader range

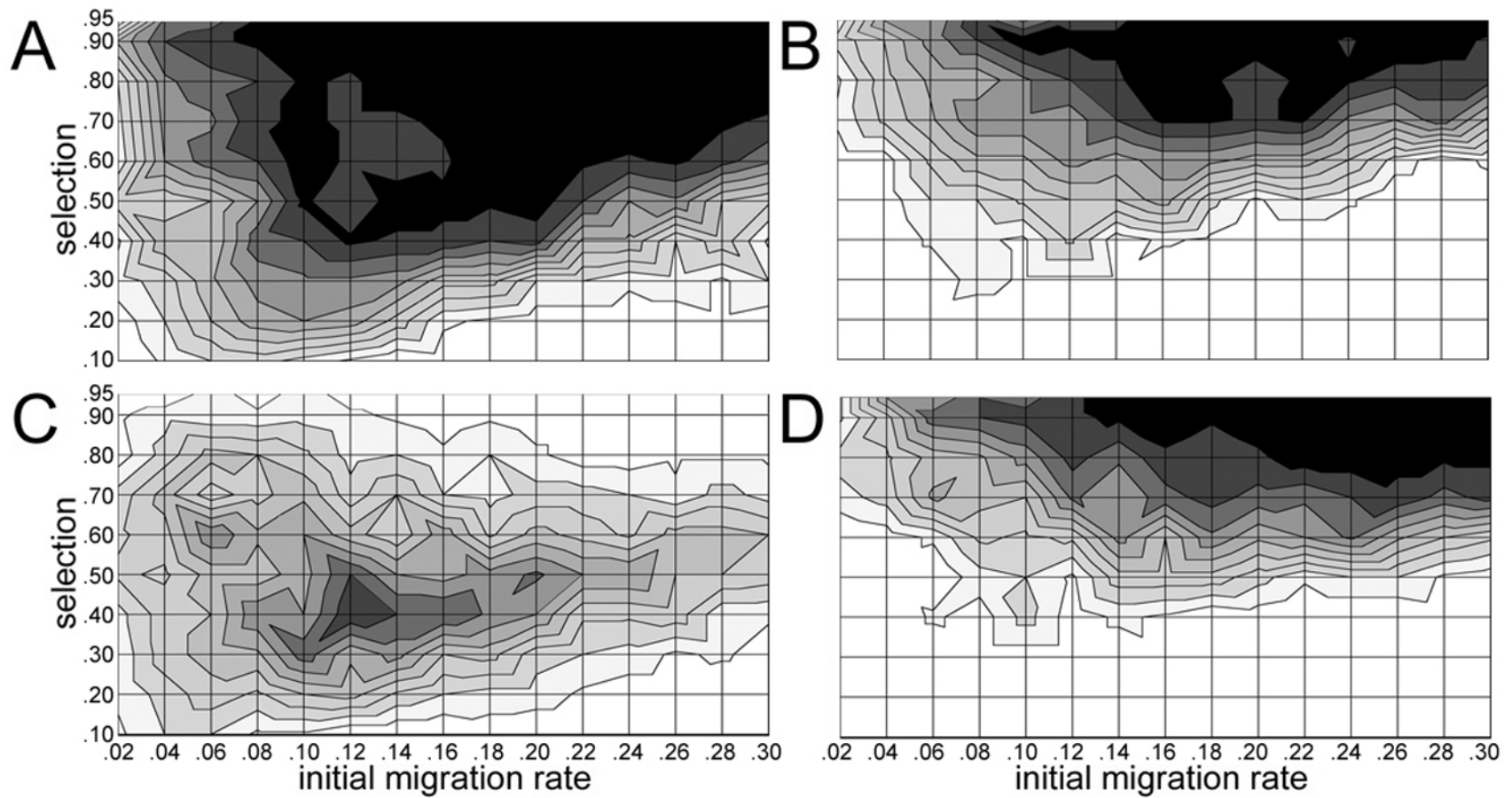


Figure 4: Probability of evolution of assortative mating (*A, C*) and migration modification (*B, D*) isolation mechanisms under the niche-based postmating isolation model, where the Y-axis is selection against heterotypic and homotypic immigrant matings (see fig. 1*B*). All other parameters are the same as in figure 2. *A*, Probability of fixation of the assortative mating allele when it initially segregates at 1% in each population in the absence of the migration modification allele. *B*, Probability of fixation of the migration modification allele when it initially segregates at 1% in each population in the absence of the assortative mating allele. *C*, Probability of fixation of the assortative mating allele when it and the migration modification allele both initially segregate at 1% in each population. *D*, Probability of fixation of the migration modification allele when it and the assortative mating allele both initially segregate at 1% in each population.

Table 3: Average number of generations to speciation via fixation of assortative mating and migration modification (sedentary behavior) alleles in the niche-based postmating isolation model

Selection	Initial migration rate														
	.02	.04	.06	.08	.1	.12	.14	.16	.18	.2	.22	.24	.26	.28	.3
Assortative mating allele:															
.95		588	337	291	227	181	153	130	119	105	92	85	80	71	64
.9	987	538	363	281	216	189	153	131	119	102	93	89	80	72	66
.8	924	557	347	278	208	177	155	132	120	104	103	89	84	80	78
.7		517	337	270	210	184	150	135	125	118	102	98	90	94	91
.6		520	365	260	234	188	170	148	143	119	120	111	110	109	107
.5	798	466	339	266	224	192	176	163	152	150	143	130	131	119	130
.4		468	370	270	239	216	201	182	178	185	165	166	153	180	
.3	916	472	374	316	265	271	243	232	227	234	219	198	220		239
.2		604	434	406	366	336	366								
.1	696	779	614	693	808		843		980	888	538				
Migration modification allele:															
.95		257	189	140	123	101	85	76	67	58	53	47	45	41	38
.9	591	302	201	154	122	104	88	77	68	63	56	53	48	46	41
.8	590	326	234	177	134	115	101	89	80	71	67	63	57	55	49
.7	701	348	260	191	160	136	116	102	95	86	82	77	69	67	61
.6			273	222	188	160	138	128	117	112	98	96	87	78	84
.5			343	262	241	202	180	165	151	138	141	126			
.4			482	334	333	272	254	235							
.3				496	414	470	387								
.2															
.1															

Note: Sample size per average varies across the table from a minimum of 5 to a maximum of 25. Blanks indicate no event.

of conditions than migration modification. Therefore, we conclude that these evolutionary interactions do not alter the relative importance of these mechanisms compared to when both evolve independently.

Niche-Based Postmating Isolation Model

Independent Evolution

Here we examine whether the above conclusions hold for niche-based postmating isolation. Here, the two parental haplotypes experience divergent selection at the fitness/marker trait, and hybrids suffer fitness underdominance with respect to this ecological trait (see fig. 1B). The ecological trait locus is the object of female preference, as determined by the assortative mating locus (see Ratcliffe and Grant 1983; Nagel and Schluter 1998; Nosil et al. 2002, 2003).

The first result showed that niche-based isolation increased the probability of reinforcement speciation under a much broader range of conditions, especially at higher, near-sympatric migration rates (compare fig. 4A, 4B with fig. 2A, 2B). This result is consistent with recent empirical findings of Nosil (2004) and suggests that high migration need not be a constraint on reinforcement, as was previously thought (e.g., Liou and Price 1994; Servedio 2000;

Servedio and Noor 2003). This result held for the evolution of both assortative mating and migration modification. However, surprisingly, the speed of evolution for both mechanisms was not faster with niche-based isolation (table 3; compare with table 1). Indeed, at low migration rates, the time to speciation was typically twice as long for assortative mating evolution in this model. Thus, the speed of speciation is inconsistent with, and therefore cannot explain, the higher probability of speciation. To explain this paradoxical result, we point out that genetic extinction evolved much more slowly under the niche-based isolation model than under the intrinsic isolation model (table 4; compare with table 2). This allowed the two populations to coexist for a longer period of time, explaining why both mechanisms were able to fix more frequently even though they themselves did not fix more rapidly.

Comparing the probability of evolution of both mechanisms, we found that migration modification once again evolved under a more restrictive set of selection-migration conditions than assortative mating (fig. 4A, 4B). First, migration modification again failed to evolve when selection was low (fig. 4B). Second, migration modification evolution again displayed a smaller probability peak compared to assortative mating (compare fig. 4B with fig. 4A). These results are consistent with the observation that migration modification evolved more slowly than assortative mating

Table 4: Average number of generations to genetic extinction in niche-based postmating isolation model when assortative mating or migration modification (sedentary behavior) evolves

Selection	Initial migration rate														
	.02	.04	.06	.08	.1	.12	.14	.16	.18	.2	.22	.24	.26	.28	.3
Assortative mating model:															
.95															
.9															
.8															
.7														36	32
.6												62	40	50	48
.5										58	55	61	51	54	
.4								88	82	85	64	69	64	67	
.3						100	119	95	97	95	97	89	84	80	
.2				189	220	144	148	139	137	138	121	128	116	123	
.1			283	379	257	252	247	227	231	208	247	205	278	237	
Migration modification model:															
.95															
.9															
.8															
.7														34	38
.6										73	64	55	50	47	41
.5									102	79	76	58	51	53	47
.4								118	97	83	69	66	60	58	57
.3				425	273	160	105	96	91	79	77	77	76	75	
.2			862	209	250	146	136	129	132	117	113	115	111	115	115
.1		803	303	184	245	234	223	190	203	203	192	210	178		

Note: Sample size per average varies across the table from a minimum of 5 to a maximum of 25. Blanks indicate no event.

at lower selection regimes (see $s = 0.3, 0.4$ in table 3; fig. 5). Further, at intermediate selection regimes of $s \approx 0.4$ – 0.6 , the relative fixation speeds were similar (table 3; fig. 5), but the migration modification allele was still about 14% less likely to become fixed under these conditions (compare fig. 4B with fig. 4A). This reflects the relative inability of the migration modification allele to spread between populations and rescue itself from being lost by genetic drift (data not shown).

As selection increased, migration modification eventually caught up with assortative mating and became equally probable at the highest selection pressures (fig. 4A, 4B). This result is consistent with the observation that at higher selection regimes, the relative speeds of these mechanisms intersected in such a way that migration modification became the faster-evolving mechanism (see $s \geq 0.6$ in table 3; fig. 5). In general, these results are rather robust to various assumptions of the model. They especially apply when population sizes are not too asymmetrical (e.g., less than 20% different) and when the genetic penetrance of reinforcement alleles is not too low (e.g., higher than 50%; see app. B). They were also observed when we explored a two-locus Dobzhansky-Muller epistatic model with divergent selection (app. B). In total, the results for the niche-based postmating isolation model support our earlier conclusion that assortative mating has a greater potential to

evolve than migration modification when these mechanisms evolve independently. We next asked whether this result holds if these mechanisms segregate simultaneously.

Simultaneous Evolution

When the two mechanisms evolved simultaneously, their relative evolutionary importance was substantially altered under the most favorable selection-migration conditions. Even though conditions for the evolution of migration modification were more restrictive than those for assortative mating during their independent evolution (see above), it was migration modification that outcompeted the evolution of assortative mating, not vice versa (fig. 4C, 4D). Strikingly, the evolution of assortative mating was substantially curtailed under the strongest selective conditions (fig. 4C). Recall that some of these conditions allowed assortative mating to evolve 90%–100% of the time when it evolved alone (fig. 4A). On the other hand, assortative mating had no noticeable effect on the evolution of migration modification (compare fig. 4B with fig. 4D). Thus, our results suggest that the evolutionary interactions between these two isolating mechanisms under the niche-based isolation model alter their relative importance in favor of migration modification under the most favorable

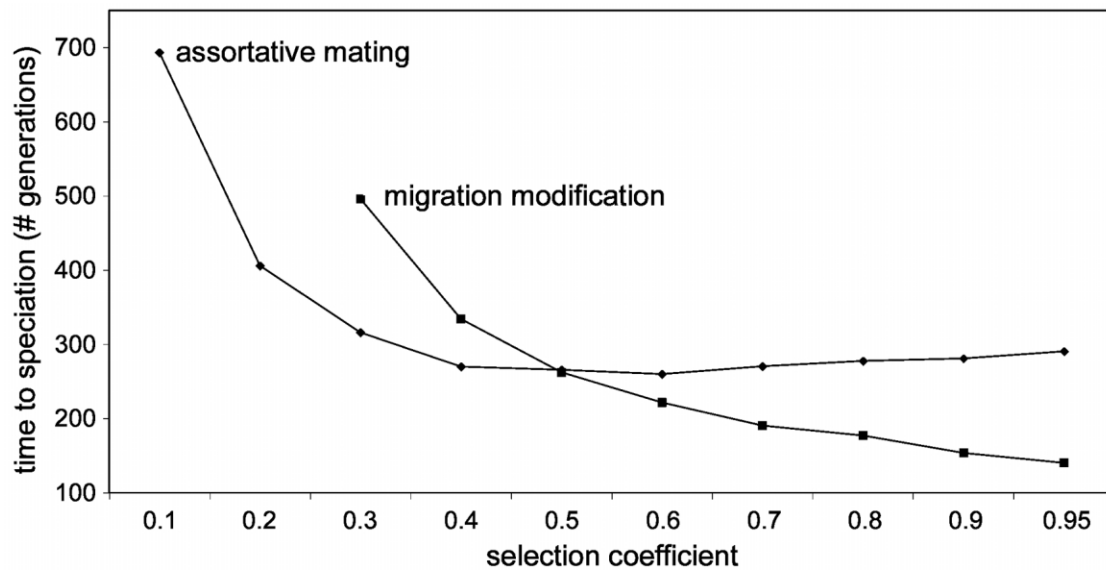


Figure 5: Example of the time to fixation of the assortative mating and migration modification alleles as a function of selection coefficient under the niche-based postmating isolation model in figure 4A, 4B. The initial migration rate is 8%. The relationship is similar for all other migration rates in figure 4A, 4B (data not shown).

evolutionary conditions. This result held well when population sizes were 20% asymmetrical and when the genetic penetrance of both alleles was reduced to 50% (see app. B). This robustness suggests that this result is likely to be general.

The observation that migration modification evolved faster than assortative mating under the higher selection regimes ($s \geq 0.6$ in table 3; fig. 5) is likely to explain why it outcompeted the latter when both evolved together. However, the consequence of this difference in relative speed on the probability of evolution was not detected when these mechanisms evolved independently (see above). Recall that migration modification evolved under more restrictive conditions than did assortative mating. Only when these mechanisms evolved simultaneously were we able to detect the evolutionary effect of migration modification on assortative mating.

These results suggest that these mechanisms generally split the parameter space when both evolve simultaneously during secondary contact. The evolution of migration modification interferes with that of assortative mating by preventing this allele from fixing under conditions where it had previously fixed. Nevertheless, we did find that when migration modification did evolve to fixation, about 50% of the time assortative mating also evolved to be polymorphic in both populations (fig. 3B). We explored this phenomenon in an additional way, by looking at the probability of evolution of assortative mating when migration modification was first allowed to fix in both populations.

When both alleles had 100% genetic penetrance, the assortative mating allele was unable to fix above the neutral fixation rate of 1% for any conditions (data not shown). The results were also found when both alleles had 50% genetic penetrance (data not shown). However, in this case, the fixation of the migration modification allele allowed the subsequent invasion of the assortative mating allele, especially at the highest selection and migration rates (data not shown). Therefore, the evolution of migration modification can prevent the assortative mating allele from fixing (invading) across the two populations, although the assortative mating locus may still remain polymorphic in the system.

On the other hand, when the assortative mating allele was first allowed to fix, migration modification had no difficulty fixing (invading) in both populations (fig. 6). Indeed, the probability of migration modification was much higher when populations were initially assortatively mating than when populations were initially randomly mating (compare fig. 6 with fig. 4B). This intriguing result suggests that after populations speciate via assortative mating, they are likely to subsequently become geographically allopatric during the last stages of speciation. This result supports the general importance of migration modification evolution when populations experience niche-based isolation. These results suggest that under niche-based isolation, these mechanisms are unlikely to evolve separately unless a migration modification allele of major effect

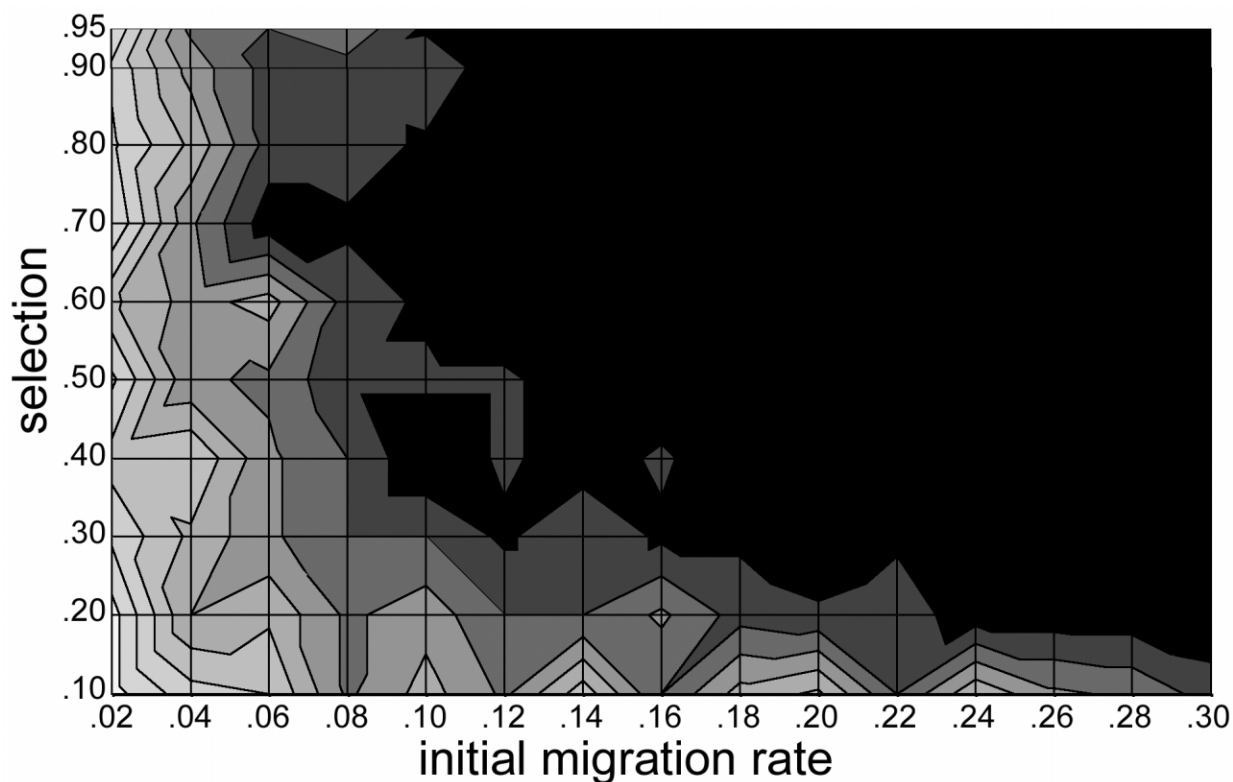


Figure 6: Probability of fixation of the migration modification allele when it initially segregated at 1% in each population while the assortative mating allele was initially fixed in both populations (all individuals mate assortatively) under the niche-based postmating isolation model as in figure 4. Genetic penetrance of both alleles was 100%. Compare this model with that in figure 4B to see how assortative mating facilitates the evolution of the migration modification mechanism.

evolves first, reinforcing geographical allopatry and preventing the fixation of assortative mating.

Discussion

The goal of this study was to determine the relative evolutionary importance of assortative mating and migration modification in reinforcement speciation. To answer this question, we wanted to understand the major differences in their evolutionary dynamics in terms of their relative speed and probability of evolution. We also wanted to understand to what extent these isolating mechanisms would affect each other's evolution during speciation and whether this interaction would change their relative importance in reinforcement.

Our findings indicate that these isolating mechanisms differ in their evolutionary dynamics despite both being "one-allele" models. We showed that assortative mating has the potential to be more evolutionarily important than migration modification when these mechanisms evolve independently during secondary contact. Our results showed

that assortative mating might evolve faster and under a broader range of conditions under both intrinsic and niche-based postmating isolation models. These results suggest that assortative mating is a more effective strategy in avoiding hybridization because females are able to cue in on the marker traits of the males when deciding with whom to mate. On the other hand, individuals that remained sedentary seemed less able to avoid hybridization because they could not prevent individuals from the other population from immigrating and mating with the residents. This led to the faster stochastic loss of genetic variation at the fitness/marker loci ("genetic extinction") and prevented migration modification from evolving under a broader range of conditions.

Despite these results for independent evolution, we also showed how direct evolutionary interactions play an essential role in determining the relative evolution of these isolating mechanisms. First, these mechanisms showed evolutionary interference when both evolved simultaneously in the intrinsic isolation model. These results suggest that assortative mating and migration modification

mechanisms are likely to evolve separately under these conditions. In the niche-based isolation model, we found that evolutionary interactions dramatically altered the relative importance of these mechanisms in favor of migration modification when populations experienced strong divergent selection. This striking result was observed only when these mechanisms evolved simultaneously because migration modification was then able to outcompete assortative mating and curtail the latter's evolution. In this case, after migration modification evolves across the system, it prevents the subsequent fixation of assortative mating, although the latter mechanism may remain polymorphic across the populations. On the other hand, if assortative mating evolves first, migration modification may readily invade this system, forcing the already sexually isolated populations to become geographically allopatric. Therefore, in the niche-based isolation model, both mechanisms may coexist in the same system. These results suggest that divergent selection generally favors the evolution of migration modification over that of assortative mating. The latter genotypes were unable to avoid immigrating into the habitat to which their ecological trait is maladaptive. Upon immigrating, these individuals mated assortatively with other maladapted immigrants and thus experienced local ecological costs that sedentary individuals typically avoided. This result illustrates the importance of studying multiple mechanisms of speciation simultaneously in future speciation models.

Some Model Assumptions

Before we discuss the implications and predictions of our results, we note some limitations of our model. First, our model assumes single loci of major phenotypic effects governing the traits of interest. This assumption allowed us to explore a wide range of parameters and to test the robustness of our results. Although complex traits such as behaviors are often polygenic, genetic data on assortative mating and migratory traits in a range of organisms indicate that simple genetic architectures are not uncommon (Beiles et al. 1984; Roff 1986, 1994; Osborne et al. 1997; Ritchie and Phillips 1998; Doi et al. 2001; Tauber et al. 2003; Ortiz-Barrientos and Noor 2005). As in previous models of reinforcement speciation, increasing the number of loci is likely to decrease the overall probability of speciation for both mechanisms (Barton and Hewitt 1981; Kirkpatrick and Servedio 1999). Further, we compared only "one-allele" mechanisms to understand how a migration modification behavior differs from that of assortative mating. Future work should test whether our conclusions also extend to "two-allele" mating and migration mechanisms. This should be done by comparing a two-allele "mating preference" behavior (Servedio 2000) with

a two-allele "habitat preference" behavior, often modeled in the context of sympatric speciation under different historical conditions (see Diehl and Bush 1989; Johnson et al. 1996; Fry 2003).

Our model assumed no direct costs of being choosy (mating assortatively). However, when this cost of assortative mating was added to the model (i.e., if a female does not find her preferred type, she does not mate), we found that the probability of assortative mating evolution decreased only slightly (data not shown). The model also assumed no direct costs of being sedentary (Hamilton and May 1977; Bengtsson 1978; Levin et al. 1984; Doebeli and Ruxton 1997) or physically migrating to the other population (Rousset and Gandon 2002; Yukilevich 2005). However, it is likely that costs associated with maladaptive hybridization or dispersing into a habitat to which individuals are maladapted, which were modeled here, are likely to dominate the evolutionary dynamics upon secondary contact (Balkau and Feldman 1973; Karlin and McGregor 1974; Asmussen 1983; Mesz ena et al. 1997; Kisdi 2002).

Finally, we explored only one example of niche-based postmating isolation, where selection against the hybrid matings and the immigrant homotypic matings was identical at $1 - s$ in each island. We modified this assumption by reducing selection against homotypic relative to heterotypic matings (e.g. Hatfield and Schluter 1999, where $w_{\text{homo}} = 1 - s/2$ and $w_{\text{hetero}} = 1 - s$ in each habitat), and the results were more similar to the intrinsic isolation model results (data not shown). This is because the intrinsic isolation model assumes no homotypic immigrant selection at all. In contrast, if immigrant homotypic matings experience even stronger selection than heterotypic matings, as was recently illustrated by Nosil (2004), then conditions for reinforcement should increase even further, and migration modification should become an even more important mechanism relative to assortative mating.

Biogeographical and Evolutionary Predictions

Assuming genetic variation among natural populations for both assortative mating and migration modification mechanisms, we predict that assortative mating is generally more likely to evolve than migration modification when populations experience intrinsic isolation. On the other hand, we expect migration modification to dominate or both mechanisms to be found together when populations experience niche-based isolation. Because most attention in empirical studies of reinforcement is given to the evolution of mating preferences, there is currently a lack of sufficient empirical data to address these claims. Studies of dispersal within secondary-contact zones are rare and generally do not ask how dispersal evolves within this con-

text (but see Schilthuizen and Lombaerts 1995; Erlandsson et al. 1998).

Because we found that migration modification directly competed with assortative mating as a reinforcement mechanism, it would be particularly interesting to revisit previous studies of reinforcement that, despite exhibiting partial postmating isolation, failed to show an increase in sexual isolation in sympatric zones relative to allopatric zones (see Marshall et al. 2002; Coyne and Orr 2004 for numerous examples). Could many of these cases be explained by the evolution of migration modification behaviors, eroding the selective advantage of assortative mating?

Ranges of sibling and sister species are often geographically adjacent (abutting) but largely or completely non-overlapping, despite the apparent absence of any physical barriers to dispersal (e.g., Vaughan 1967; White 1978; Bowers and Brown 1982; Patton et al. 1984; Sullivan et al. 1986; Lee et al. 1996). It is possible that these systems are examples of a migration modification mechanism having evolved to completion after a secondary-contact event some time in the past. Testing this hypothesis would require historical evidence of past physical barriers, combined with molecular evidence for subsequent secondary contact (e.g., Barton and Hewitt 1985; Hewitt 1989) and present-day evidence for strong philopatry and/or dispersal directionality away from the other species (e.g., Erlandsson et al. 1998).

Note that this mechanism is not in conflict with the traditional "competitive exclusion" explanation for abutting species ranges because divergent ecological selection may also take the form of competition (see Brown and Lomolino 1998; Case and Taper 2000). However, in our model, abutting species ranges result because populations in secondary contact evolve migration modification when faced with divergent ecological selection. Indeed, we found that additive divergent selection is sufficient for the evolution of migration modification, although evolution is less likely with additive divergent selection alone than if hybrid fitness reduction is also present (data not shown). Comparing the fitness of hybrids and parentals can test additive versus underdominant divergent selection. Even though our results agree with the "competitive exclusion" hypothesis in explaining abutting species ranges, we stress that competition is not necessary to explain this phenomenon. Our results clearly show that purely genetic incompatibilities (i.e., intrinsic postmating isolation) could lead to abutting species ranges. The results predict that for this scenario to be likely, incompatibilities should be strong.

In conclusion, this study represents one of the first examples of how the evolution of multiple competing speciation mechanisms can be explored in a theoretical context. It is also probably the first clear illustration of why

future studies of speciation should consider direct evolutionary interactions between competing isolating mechanisms. Our findings suggest that understanding the relative importance of different speciation mechanisms may be inadequate until they are studied simultaneously. Within the field of reinforcement, we emphasize that this approach can help us understand the diversity of outcomes of secondary contact phenomena, including cases where sister species either show large geographical overlap or display abutting, nonoverlapping ranges without physical barriers to dispersal.

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