

A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL OF REINFORCEMENT IN HYBRID ZONES

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Abstract.—An individual-based model consisting of two dioecious populations in a two-dimensional environmental grid was constructed. Each population began with, and never exceeded, 1000 individuals; extinction was allowed. Genomes consisting of 30 biallelic loci for male sexual advertisement call, female mate preference, and population origin were constructed, and lineages of each individual in the starting populations were followed for 2000 generations. Type and level of hybrid disadvantage, initial population distribution, patchiness of environmental resources, and level of mate choice were varied. Persistence of bimodal hybrid zones was nonexistent at low levels of hybrid disadvantage and universal at high levels of hybrid disadvantage, with a narrow threshold in which persistence was unpredictable. Persistence occurred at lower levels of hybrid disadvantage when populations were initially parapatric rather than sympatric, and environments were patchy rather than homogeneous. Increased divergence in mating systems occurred when hybrid disadvantage was high, hybrids were infertile, populations were initially parapatric, and increased female choice was allowed. Mating system divergence was much higher in interacting populations compared with noninteracting populations, indicating that reinforcement caused most of the observed divergence. When hybrids were infertile, reinforcement contributed to speciation, because under hybrid infertility the probability of persistence at low levels of hybrid disadvantage was positively related to mate choice. The results agree with previous one-dimensional spatial models in finding that population persistence is more likely in parapatric and patchy population distributions. In addition, the results show that hybrid infertility may facilitate the process of reinforcement and speciation.

Key words.—Agent-based model, assortative mating, homogamy, reproductive character displacement, speciation.

Received December 31, 2001. Accepted December 16, 2002.

In the process of geographic speciation, an important stage is reached when contact is established between members of the two derived genetic systems following expansion of one or both of their geographic ranges (Littlejohn 1993). If the genomes of individuals within each of the two systems have not diverged too far from those in the other, then cross-mating and the production of viable and fertile hybrids may occur. If the fitness of the resulting hybrids is lower than that of the progeny of pure parental crosses, then natural selection may act to improve the specificity and efficiency of attraction and choice of mates by parental individuals. This process is termed “reinforcement” (sensu Blair 1955) and leads to the evolution and maintenance of positive assortative mating (i.e., homogamy). A pattern of geographic variation in which differences in systems of mate attraction and choice are greater in sympatry than in allopatry and that may have resulted from the action of reinforcement is termed “reproductive character displacement.” Littlejohn (1999) has reviewed this terminology and provided references.

The significance of reinforcement in speciation has been a topic of considerable controversy (see reviews by Butlin 1987; Hewitt 1988; Howard 1993; Rice and Hostert 1993; Liou and Price 1994; Noor 1999; Marshall et al. 2002). In efforts to model the reinforcement process mathematically, several authors concluded that stringent conditions are required for reinforcement to occur (Paterson 1978; Moore 1979; Spencer et al. 1986; Sanderson 1989; Kirkpatrick 2000). Results of several recent studies of natural systems and outcomes of recent models, however, are consistent with divergence through reinforcement (e.g., Rundle and Schluter 1998; Cain et al. 1999; Kirkpatrick and Servedio 1999; Bar-

ton 2000; Hendry et al. 2000; Higgie et al. 2000; Servedio 2000).

Two forms of hybrid disadvantage can be distinguished: (1) hybrid inviability occurs when hybrids are less likely to survive to reproductive age than are parental types; and (2) hybrid infertility occurs when hybrids are likely to produce fewer viable offspring than do parental types. Where hybrid infertility is complete, hybrids produce no viable offspring. Partial hybrid infertility implies that hybrids and their descendants are less likely to produce viable offspring than are parental types. Partial and complete hybrid infertility are common in nature (see Barton and Hewitt 1989; Kelly and Noor 1996; Noor 1999) and may evolve faster than hybrid inviability (Coyne and Orr 1997). Most models of reinforcement treat infertility and inviability as identical, while removing hybrids in a process equivalent to inviability (e.g., Sawyer and Hartl 1981; Sved 1981; Spencer et al. 1986). Spencer et al. (1986) argued that the selection pressure for reproductive character displacement is weak. Substituting hybrid infertility for inviability results in increased numbers of living hybrids, and therefore increased mating encounters between hybrid and parental-type individuals. This demographic aspect and associated costs in reproduction may result in increased selection pressure for reinforcement. Gavrilets and Cruzan (1998) found that hybrid infertility produced greater reductions in gene flow than did hybrid inviability, which could facilitate reinforcement. Alternatively, if production of parental-type individuals is increased under hybrid inviability, as suggested by Liou and Price (1994), then extinction may be reduced and reinforcement more likely when hybrids are inviable rather than infertile. We developed an individual-based, spatially explicit model to di-

rectly compare the likelihood of population coexistence and reinforcement under different levels of hybrid infertility and inviability.

Spatial distribution can influence the predictions of evolutionary models in complex ways (e.g., Day 2000; Durrett et al. 2000; Ranta et al. 2000). In geographic models with limited migration, one effect is that individuals are more likely to encounter other individuals with similar genotypes; consequently, gene flow is reduced. Reduced gene flow decreases the loss of genetic diversity over time. Durrett et al. (2000) found that in a spatial model of a hybrid zone, genetic diversity persisted much longer than was predicted by previous nonspatial models.

A hybrid zone, or a zone of overlap with hybridization, is usually thought to form when members of two derived genetic systems migrate into contact after a period of geographic separation. Thus, the initial state of hybridizing populations is usually expected to be parapatry rather than sympatry (Barton and Hewitt 1989; for an overview of sympatric speciation see Doebili and Deickmann 2000). In an initially sympatric distribution, encounters between individuals are random with respect to population origin; thus, there is a high rate of genetic introgression in the absence of reproductive barriers. Initial parapatry reduces the rate of introgression because individuals are most likely to encounter individuals originating from the same population; they will only contact individuals of dissimilar origin along a linear interface or narrow zone of overlap. So initially parapatric populations may be less likely to merge or become extinct than are initially sympatric ones; this state could increase the probability of reinforcement. Additionally, parapatry may reduce the degree of reinforcement because homogamy is favored only within the zone of overlap, and therefore the overall selection pressure is small relative to opposing forces (Liou and Price 1994).

Recently, several authors have approached the problem of limiting gene flow through island models (Servedio and Kirkpatrick 1997; Cain et al. 1999; Kirkpatrick and Servedio 1999; Servedio 2000). Rather than explicitly modeling a spatial environment, these models allowed for limited one-way and two-way migration between partially differentiated populations. Servedio and Kirkpatrick (1997) investigated the effects of limiting gene flow on reinforcement in a four-locus simulation model. Migrants were selected against, and hybrids were disadvantaged. They found that reinforcement was more likely when migration was low and symmetrical between populations. In the current model, we simulated individuals at discrete locations on a two-dimensional grid. This allowed a more explicit view of gene flow within spatially distributed populations than that provided by island models. We compared population coexistence and levels of reproductive character displacement in initially parapatric and initially sympatric populations.

According to the mosaic hybrid zone model (Harrison and Rand 1989), species are distributed among a number of geographic patches that correspond to their ecological needs, with interactions between two species occurring only when their patches contact. Cain et al. (1999) developed a one-dimensional, two-locus model of reinforcement within mosaic hybrid zones. They concluded that an allele for assortative

mating is likely to be favored under a wide range of conditions in mosaic hybrid zones. The mosaic model of Cain et al. (1999) incorporated two factors that may influence reinforcement. First, hybridizing taxa are to some extent geographically isolated by continual environmental selection against one taxon or the other within each habitat patch. In addition, the very fact of localization within patches (i.e., the distribution of populations among a number of local areas such that individual interactions occur mainly within areas and rarely between areas) reduces gene flow. Within patches, natural selection can operate. Migration between patches allows for recolonization after local extinction. Patchiness may thus act as a buffer against extinction of hybridizing species, which has been considered a major barrier to reinforcement (Spencer et al. 1986). A factor hypothesized to prevent reinforcement is the swamping of cumulative change by gene flow from outside the hybrid zone (Liou and Price 1994); low rates of gene flow between hybridizing and nonhybridizing patches may reduce this effect.

In this paper, we look at the impact of patchiness in the absence of isolation through environmental selection. Populations are distributed in patches, but all patches are equally suitable habitat for all individuals. This permits a useful contrast with the traditional mosaic model of Cain et al. (1999), allowing us to isolate the effects of population distribution per se (patchiness) from the effects of environmental selection combined with patchiness (mosaicism).

Our model differs from that of Cain et al. (1999) in several other respects. In our model, individuals are localized within a two-dimensional spatial environment, potentially a more realistic technique than one-dimensional stepping-stone models. We modeled 30 biallelic loci, in contrast to the biallelic two-locus model of Cain et al. (1999). When hybridity is determined by a single biallelic locus, matings among hybrids have a minimum 50% chance of producing individuals indistinguishable from parentals. As the number of differentiated loci increases, this chance declines. The probability of reinforcement appears to be crucially affected by the rate of production of parental types. Hence, polygenic models may predict very different evolutionary outcomes.

Following the terminology of Servedio (2000), ours is a preference model, in that mate choice is determined by separate display and preference traits. In contrast, Cain et al. (1999) used an assortative mating model, in which mating display and preference traits are identical. Servedio (2000) found that when populations were subject to two-way gene flow, reinforcement occurred most easily under an assortative mating model. Doebili and Deickmann (2000) described a broad range of conditions under which reinforcement can lead to sympatric speciation within assortative mating models. The conditions under which reinforcement can contribute to speciation in preference models are less clear.

Negative heterosis, that is, the evolutionary loss of alternative alleles caused by heterozygote disadvantage (Paterson 1978), could lead to divergence between mating systems by reducing mating system variation within each population. There is no reason to expect loss of variation due to negative heterosis to be increased by interactions between populations; loss of variation may be decreased when gene flow occurs between populations. In contrast, loss of variation due to

reinforcement can only occur when cross-mating is occurring between individuals of the two populations. Thus, comparing the rate of loss of mating system variation in interacting and noninteracting populations provides a conservative estimate of the proportion of divergence that is accounted for by reinforcement.

Differences in the likelihood of hybrid zone persistence may occur because of factors other than reinforcement. If reinforcement is a cause of bimodal hybrid zone persistence, persistence should occur more frequently when high levels of mate choice are permitted. Factors other than reinforcement that influence persistence should be unrelated to mate choice. We compared the likelihood of persistence and degree of mating system divergence when females chose between different numbers of males.

This paper examines the effects of the following four factors on the evolution of reproductive character displacement and population coexistence within a hybrid zone: (1) form and degree of hybrid disadvantage; (2) initial population distribution; (3) patchiness of reproductive resources; and (4) number of potential mates encountered by females. Although the model is based on the hybrid zone among frogs of the *Geocrinia laevis* complex in which the resources of reproduction are sites for calling by males and for oviposition (see Littlejohn 1988), it is designed to be of general application.

METHODS

The model was written in C++ on an 800-MHz computer using the freeware C/C++ compiler DJGPP (Delorie Software, Deerfield, NH) and Allegro graphics library. Initially a two-dimensional lattice grid was created. Areas of the grid were designated as sites of a resource necessary for reproduction (e.g., calling and oviposition sites). Diploid individuals were created, consisting of a 30-locus genome at a location on the grid. Each locus had two possible alleles, coded as 1 or 0. The genome coded for three traits of 10 loci each: male advertisement call, female preferred advertisement call, and a type trait used to distinguish the two populations and measure hybridity. Each individual possessed all 30 loci, but expressed either male signal or female preference, depending on its sex. Initially all traits except type were randomly allocated. Sex was randomly allocated; no attempt was made to model sex allocation genetically, as preliminary runs showed that this has no effect on the outcome of the simulation. Advertisement call, the particular advertisement call preferred by a female, and type, were each scored between 0 and 20 by summing the alleles at appropriate loci. Initially, 2000 individuals were created. Half were given only 1 allele at the type loci, and half were given only 0 alleles at these loci. An individual with more than 90% 1 alleles at the type loci was called "type 1"; an individual with less than 10% 1 alleles at these loci was called "type 2"; all other individuals were called "hybrids." This value was chosen to reflect the minimum degree of hybridity thought likely to be detected in field populations. Visual inspection of the data suggests that on completion of the simulation almost all individuals assigned to parental types had no hybrid alleles.

The simulation ran as a series of breeding seasons separated by nonbreeding periods. A cycle of nine nonbreeding

season updates, followed by one breeding update was used. During nonbreeding updates, individuals moved at random, one grid square per round. During breeding season updates, all individuals moved in a random walk until they arrived at a breeding site. Each female registered the genetically encoded advertisements of a limited number of males at her location and at randomly selected adjacent grid locations. Provided she had encountered a male, each female would mate with the male she had encountered whose advertisement was closest to her genetically encoded preferred advertisement. There were several potentially unrealistic aspects to this procedure. A female would always mate if she had encountered a male during the previous season, no matter how distant his advertisement from her preferences. Advertisements and preferences were entirely genetically determined without environmental influence. Males could mate with unlimited females. Females mated at most once per season and produced no more than one offspring per season that survived to reproductive age; hence females, on average, survived two to three seasons to sustain population levels.

For offspring, one allele for each locus was selected randomly from each parent, simulating complete recombination or zero linkage. Production of surviving offspring was affected by the alleles of parents and offspring at the type loci. If hybrid infertility were present, then individuals with intermediate type scores were less likely to produce offspring than were highly homozygous individuals. If hybrid inviability were present, then offspring with intermediate type scores were less likely to survive to the next breeding season. Surviving offspring were positioned within one grid square of the female parent. Probabilities of an individual being infertile or inviable, $Pr(i)$, were calculated as:

$$Pr(i) = d[tL - abs(tS - tL)]/tL \quad (1)$$

where tS is the individual's type score, tL is the total number of type loci, and d is the level of hybrid infertility or inviability.

For example, an individual with type locus alleles 0-1 1-0 1-0 1-1 1-1 1-1 1-1 0-1 1-1 1-1 would have 16 type 1 alleles of 20 (80%), and would be classified as a hybrid. If hybrid inviability were 75%, then the probability that this individual would not reach maturity would be $0.75[10 - (16 - 10)]/10$, or 30%. If hybrid infertility were 90%, then the probability that, upon mating, this individual would produce inviable offspring would be $0.90(0.4)$, or 36%. Type loci were allocated separately from mating system loci to allow a measure of hybridity that was independent of mating system evolution.

Between breeding seasons, individuals would disperse at random to an adjacent grid square along the x and y planes. At the start of the next breeding season, all individuals would move randomly, one square at a time, until they arrived at reproductive resource sites. If there were more than 1000 type 1 or type 2 individuals, or more than 2000 individuals in total, then populations would be culled at random to fit these carrying capacities.

Experiments

In each condition, 40 replications were completed, each running for 2000 generations. Sympatric and parapatric initial

population distributions were compared. In the parapatric condition, type 1 individuals were inserted at random locations on the right (x -maximum) half of the grid; type 2 individuals were inserted at random locations on the left (x -minimum) half of the grid. This meant that populations were initially separate but would meet by migration in the center of the grid, forming a zone of overlap with hybridization. In the sympatric condition, both types were inserted at random locations throughout the grid.

We limited and varied the maximum number of male signals each female could process in a single breeding season (mate choice levels) to assess the extent to which availability of mate choice influenced population persistence. Mate choice levels were 1 (no mate choice), 2, 4, 8, and 16 signals per season.

Patchy and homogeneous reproductive resource distributions were compared. In the patchy distribution, the grid was of 100×100 squares with 9% coverage (900/10,000 grid squares) in randomly placed reproductive resource sites, which were 5×5 grid squares in area. In the homogeneous condition, the grid was of 30×30 squares, with 100% coverage (900/900 grid squares) in reproductive resource sites.

Type of hybrid disadvantage was varied between hybrid inviability and hybrid infertility. For each of these conditions, levels of hybrid disadvantage were tested at 5% increments between 0% and 100%, giving 21 categories.

A persistent bimodal hybrid zone was considered to have occurred if more than 20 individuals of each parental type persisted after 2000 generations, corresponding to 20 times the expected frequency of parental genotypes in an introgressed population. In practice, the distinction was always clear-cut, with either large populations of each type or a single hybrid swarm after 2000 generations. The number of persistent bimodal hybrid zones formed, the difference between the types in average female preference where bimodal hybrid zones occurred, and the average number of male signals analyzed by each female were recorded after 2000 generations for each condition described above. Female preference was the sum of alleles (scored as 1 or 0 as described above) at the 10 mating preference loci for each individual. The difference between the two types in average female preference was used as a measure of mating system divergence. Divergence in signal traits of males was not analyzed. Because males could fertilize unlimited numbers of females without cost, female preference was the selective force driving male signal evolution; male signal evolution followed, but did not cause, evolution in female preference.

Divergence in mating systems could be a consequence of negative heterosis (Paterson 1978) rather than reinforcement. To test this possibility, we measured divergence of female mating preference after 2000 generations between noninteracting populations. Noninteracting populations occupied the same space, but individuals of one population did not interact with individuals of the other population; females did not consider males from the other population as potential mates. This test was replicated 40 times each for patchy and homogeneous resource distributions at each mate choice level.

RESULTS

Number of Signals Processed by Females

The average number of signals processed per female per season was close to the maximum for each mate choice level (MCL), apart from MCL = 16 (MCL = 1, mean = 0.989; MCL = 2, mean = 1.96; MCL = 4, mean = 3.81; MCL = 8, mean = 6.61; MCL = 16, mean = 8.24). Average signals processed per season was higher in homogeneous environments than in patchy environments ($F_{1,7416} = 1378.29$, $P < 0.001$) at high mate choice levels, but was indistinguishable for different forms of hybrid disadvantage ($F_{1,7416} = 1.53$, $P = 0.216$) and for different population distributions ($F_{1,7416} = 0.09$, $P = 0.763$).

Occurrence of Bimodal Hybrid Zones

Figure 1 shows the proportion of experimental runs in which persistent bimodal hybrid zones occurred, grouped according to mate choice level and graphed against level of hybrid disadvantage.

In all conditions, the likelihood of persistence increased with hybrid disadvantage. This relationship showed a strong threshold effect, with a rapid change from an extremely low probability of persistence to an extremely high probability of persistence within a narrow band of hybrid disadvantage levels. The value of the threshold hybrid disadvantage level for persistence varied with the experimental conditions. Around the threshold, the relationship was approximately linear.

A general linear model analysis of variance for hybrid disadvantage level, initial population distribution, environment type, form of hybrid disadvantage, and mate choice level was used to assess differences in the mean proportion of persistent zones. The persistence threshold was much lower in initially parapatric distributions (40–70% hybrid disadvantage; Fig. 1E–H) than in initially sympatric distributions (55–85% hybrid disadvantage; Fig. 1A–D; $F_{1,519} = 270.23$, $P < 0.001$). Visual inspection suggests that persistence was slightly higher at high levels of mate choice in parapatric populations. The gradient of change in probability of persistence with hybrid disadvantage appears to have been steeper in homogeneous environments (Fig. 1C, D, G, H) than in patchy ones (Fig. 1A, B, E, F); in patchy environments, persistent hybrid zones occurred at lower levels of hybrid disadvantage ($F_{1,519} = 36.37$, $P < 0.001$). This difference was larger in parapatric (Fig. 1A–D) compared with sympatric distributions (Fig. 1E–H).

Analysis of variance failed to confirm any difference in the mean likelihood of divergence between hybrid disadvantage types ($F_{1,512} = 0.48$, $P = 0.491$) or between levels of mate choice ($F_{4,512} = 0.65$, $P = 0.629$). However, visual inspection of the data suggested that under hybrid infertility (Fig. 1B, D, F, H) the persistence threshold was lower when greater mate choice was allowed.

Degree of Mating System Divergence

Figure 2 shows the relationship between average mating system divergence (as measured by the average difference between parental populations in mean female preference) and

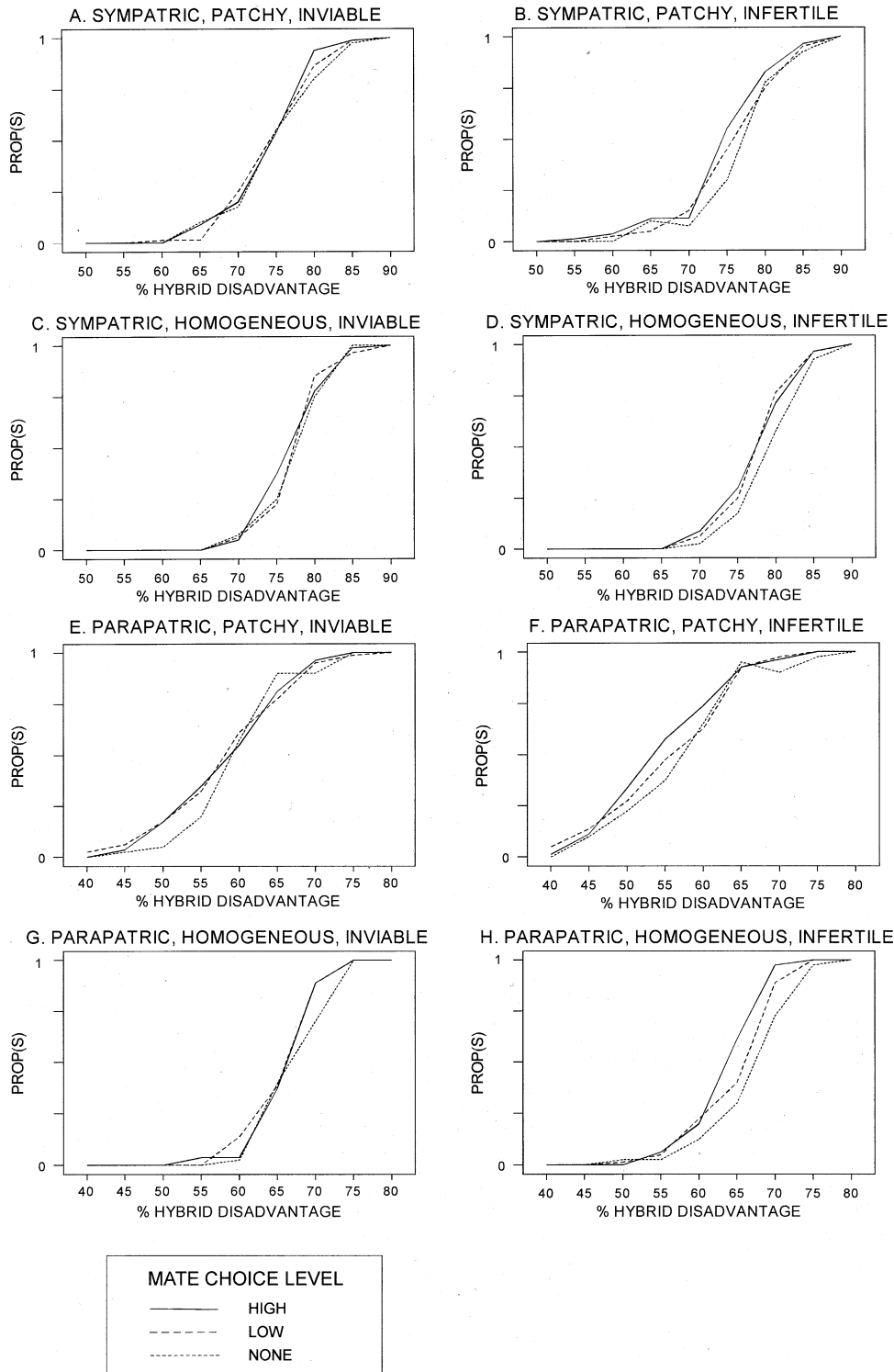


FIG. 1. Proportion of systems, Prop(S), in which persistent bimodal hybrid zones existed plotted against level of hybrid disadvantage (%) and grouped according to mate choice level (MCL). For visual simplicity MCLs are grouped into no mate choice (MCL = 1), low mate choice (MCL = 2, 4), and high mate choice (MCL = 8, 16). Separate graphs are shown for each condition of initial population distribution (parapatric/sympatric), environment (patchy/homogeneous), and type of hybrid disadvantage (infertile/inviable).

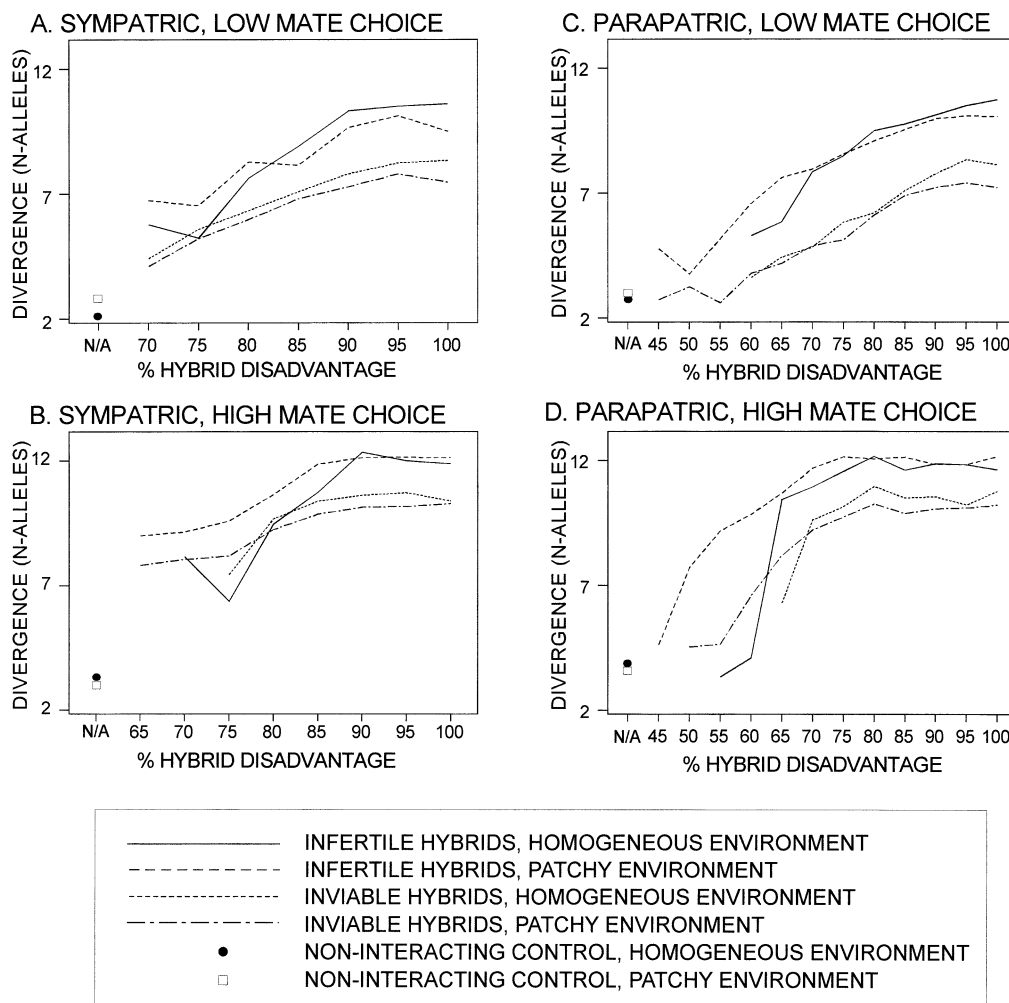


FIG. 2. Average amount of divergence in mating system (as the mean difference between populations in average sum of alleles at mate preference loci) plotted against level of hybrid disadvantage. Results are for persistent bimodal hybrid zones only; nine datapoints based on fewer than five observations were excluded to avoid small-sample distortion. Mate choice levels are binned as for Figure 1, excluding the no-choice condition. Data are grouped by type of hybrid disadvantage and initial population distribution, with separate graphs for each condition of environment type (patchy/homogeneous) and mate choice level (high/low). Mean divergence in mating system among noninteracting (i.e., allopatric) control populations is also shown.

hybrid disadvantage level. Graphs of the no-choice condition are not shown, because in the no-choice condition divergence was very low and unaffected by other factors (mean divergence = 0.97; standard deviation = 0.88; range 0.00–5.20; $n = 1042$).

Mean divergence in interacting populations is generally much higher than in the noninteracting controls ($t_{518} = 39.79$, $P < 0.001$), except at low levels of hybrid disadvantage in the initial parapatry condition. The increased divergence in interacting populations when compared with noninteracting populations confirms that reinforcement, rather than negative heterosis, caused most of the divergence observed.

A multivariate analysis of variance was used to assess differences in mean divergence among levels of hybrid disadvantage, type of hybrid disadvantage, initial population distribution, and environmental patchiness; mate choice level was excluded from this analysis because of unequal sample variance. Divergence was positively correlated with hybrid

disadvantage level in all conditions ($F_{12,375} = 6.01$, $P < 0.001$; $r_{\text{adj}}^2 = 38.5\%$, $P < 0.001$). The relationship appears to have been nonlinear, with smaller increases in divergence at higher levels of hybrid disadvantage; in the high mate choice condition, divergence was uncorrelated with hybrid disadvantage in the range of 85% to 100% hybrid disadvantage ($r_{\text{adj}}^2 = 0.5\%$, $P = 0.256$). Divergence was positively related to mate choice level ($r_{\text{adj}}^2 = 16.8\%$, $P < 0.001$). Differences between mate choice conditions declined as mate choice level increased (MCL = 2, mean = 5.9360; MCL = 4, mean = 9.5351; MCL = 8, mean = 10.413; MCL = 16, mean = 10.628). Divergence was also greater when hybrids are infertile rather than inviable ($F_{1,375} = 17.33$, $P < 0.001$). This relationship was strong at high levels of hybrid disadvantage and remained present, but less consistent, at lower levels of hybrid disadvantage. Divergence seems to have been greater in parapatric rather than in sympatric distributions at low levels of hybrid disadvantage; this relationship disap-

peared at high levels of hybrid disadvantage and was not confirmed in the statistical test ($F_{1,375} = 2.19$, $P = 0.139$).

The effects of environment type are unclear. At high levels of hybrid disadvantage, in the low mate choice condition, divergence appears to have been greater when the environment is homogeneous. In the high mate choice condition, this difference is not apparent. At low levels of hybrid disadvantage divergence appears to have been greater in patchy rather than homogeneous environments. This trend is not apparent in the low mate choice condition under hybrid inviability. Analysis of variance did not confirm any consistent difference in divergence between environment types ($F_{1,375} = 0.69$, $P = 0.406$).

DISCUSSION

Mating preferences were reinforced under most of the experimental conditions studied where persistent bimodal hybrid zones occurred, except when hybrid disadvantage was very low and populations were initially parapatric. At levels of hybrid disadvantage where population persistence was uncertain, the degree of reinforcement was strongly correlated with the level of hybrid disadvantage; this correlation weakened at higher levels of hybrid disadvantage. Reinforcement was increased when females chose between many males and when hybrids were infertile rather than inviable. At moderate levels of hybrid disadvantage, reinforcement was greater in initially parapatric rather than initially sympatric populations.

The probability of persistence of bimodal hybrid zones was not strongly related to the degree of reinforcement, because only slight differences were seen between conditions with and without mate choice. Persistence had a strong threshold relationship to the level of hybrid disadvantage, with rapid change in persistence probability from zero to one across a small range of hybrid disadvantage levels. Within this narrow threshold range of hybrid disadvantage levels, initial parapatry (as opposed to initial sympatry, which could only occur through sympatric speciation) and population patchiness (as opposed to homogeneous distribution), each decreased the probability of populations merging through genetic introgression. When hybrids were infertile rather than inviable, and possibly when populations were initially parapatric, the threshold appears to have been lower at higher levels of mate choice, suggesting that high levels of reinforcement caused by hybrid infertility and initial parapatry could play a small role in increasing the probability of speciation.

The finding that patchy, parapatric populations are more likely to persist and undergo reinforcement agrees with a number of previous studies that have considered populations with limited gene flow (Servedio and Kirkpatrick 1997; Cain et al. 1999; Kirkpatrick and Servedio 1999; Servedio 2000). But past studies have not considered individuals moving in a spatially explicit, two-dimensional environment; rather, they have modeled populations occurring at a very small number of locations along a single dimension. Conditions for coexistence in narrow zones of overlap have been modeled by Key (1968, 1981), Bull (1991), and Bull and Possingham (1995). In populations with a narrow zone of overlap, encounters between individuals of similar genetic origin are always more frequent than are encounters between individ-

uals of different genetic origin. Thus, in narrow zones of overlap there are reduced pressures from ecological competition, introgression, and reinforcing selection that result from interactions between individuals of the two populations. Several studies have examined the implications of this condition for reinforcement using island or stepping-stone models (e.g., Servedio and Kirkpatrick 1997; Cain et al. 1999; Kirkpatrick and Servedio 1999; Servedio 2000). Like previous models that have considered spatial aspects of hybrid zones, our model provides support for reinforcement under a relatively broad range of conditions. Unlike previous models, it emphasizes spatial distribution in the absence of ecological differences between hybridizing taxa. Because the two models differ on a number of other parameters, a direct comparison with the mosaic model of Cain et al. (1999) is not possible. It is clear, however, that population patchiness (independent of ecological differences between taxa) can account for some of the enhanced likelihood of persistence in mosaic hybrid zones (and, thereby, increased likelihood of reinforcement).

Competition between individuals appears to play a fundamental role in population coexistence and reinforcement. As was found in previous studies (e.g., Crosby 1970; Sawyer and Hartl 1981; Spencer et al. 1986; Liou and Price 1994), bimodal hybrid zones existed only where the carrying capacities for each system were separately determined. In effect, the members of each system did not compete with members of the other system for any limiting resource. Although competition for a limiting resource is not necessarily prevalent in hybrid zones, some form of competition between the closely related parental forms (and their hybrids) could be expected, leading to selective pressure for ecological differentiation if not extinction of one population (Schluter and McPhail 1993).

We observed a consistent increase in both the likelihood of population coexistence and the degree of reproductive character displacement under hybrid infertility compared with hybrid inviability when mate choice was allowed. This result contrasts with the findings of Liou and Price (1994), who argued that hybrid inviability increases the likelihood of reinforcement because it reduces the probability of extinction of parental populations by increasing production of parental-type juveniles. However, this outcome seems specific to the model of Liou and Price (1994), where the entire population was replaced after each breeding event, and hence nonproduction of inviable hybrids directly resulted in the production of extra parental-type individuals. The model could be applicable to sympatric K-regulated populations, provided competition between hybrids and nonhybrids limits the parental population size. It is difficult to see how this degree of competition could occur in a zone of overlap with hybridization, since the majority of parental individuals are uninfluenced by hybrids in such zones.

In our model, there was little competition between hybrids and parentals. Survival of infertile hybrids only reduced survival of parental individuals when the carrying capacity of 2000 individuals of either type (plus hybrids) was exceeded. When the carrying capacity was exceeded, randomly chosen individuals (of the type exceeding the carrying capacity, or hybrids) were culled. Under normal circumstances, only par-

entals who mated with heterospecifics or hybrids suffered a reduction in fitness, and this reduction in fitness was identical to that occurring under hybrid inviability. However, in a hybrid infertility model, hybrids were produced in much larger numbers. Individuals were therefore likely to encounter hybrids as mates more often. As a result, the cumulative selective pressure upon individuals to avoid hybridization was greater under hybrid infertility than under hybrid inviability. A more realistic approach would incorporate spatially localized ecological competition between individuals, creating the possibility of ecological divergence between populations. Such divergence could have an interactive effect upon hybrid disadvantage. We are currently developing a simulation to address this question.

Negative heterosis can cause loss of mating system variation through selection against heterozygotes, and thus result in mating system divergence between populations (Paterson 1978; Moore 1979). This divergence is independent of interactions between the two populations. In contrast, divergence caused by reinforcement occurs only in interacting populations. In the current data, mating system divergence occurred in noninteracting populations as well as in interacting ones. This supports Paterson's argument that negative heterosis may reduce mating system variation. However, the extent of mating system divergence was much smaller and more variable in noninteracting populations than in interacting populations. Hence most of the mating system divergence that we observed in interacting populations can be attributed to reinforcement, rather than negative heterosis.

Previous models that incorporate a one-dimensional spatial distribution of populations have concluded that reinforcement is facilitated by spatial distribution (Servedio and Kirkpatrick 1997; Cain et al. 1999; Kirkpatrick and Servedio 1999). Spatial separation reduces gene flow and therefore enhances population persistence in the face of introgression. The current findings support this conclusion in the context of a two-dimensional spatial distribution of individuals. As concluded from earlier models, our data imply that patchiness and parapatry are favorable conditions for the persistence of hybridizing populations. Both spatial and nonspatial models have, in general, considered hybrid inviability rather than hybrid infertility as the cause of hybrid disadvantage. We found that hybrid infertility may increase the likelihood of population persistence through increased reinforcement.

ACKNOWLEDGMENTS

We thank R. Sadedin for invaluable programming assistance. M. Scroggie provided several key references and his critical discussion of this project is greatly appreciated. K. Hamza's detailed comments on statistical analysis were most helpful. Last, but in no sense least, we thank M. Noor for his insightful editorial commentary. The University of Melbourne and Monash University supported this study.

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