

THE ROLE OF REINFORCEMENT IN SPECIATION: Theory and Data

Maria R. Servedio¹ and Mohamed A.F. Noor²

¹*Department of Biology, CB# 3280, Coker Hall, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599; email: servedio@email.unc.edu*

²*Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803; email: mnoor@lsu.edu*

Key Words pre mating isolation, postmating isolation, sympatric speciation, incompatibilities, divergent selection

■ **Abstract** To assess the frequency and importance of reinforcement in nature we must begin by looking for its signature in the most likely places. Theoretical studies can pinpoint conditions that favor and inhibit reinforcement, and empirical studies can identify both how often these conditions occur and whether reinforcement results. We examine how well these tools have addressed these questions by searching for gaps and mismatches in theoretical and empirical studies of reinforcement. We concentrate on five areas: (a) a broad assessment of selection against interspecific mating, (b) the mode and genetic basis of nonrandom mating, (c) the geography of speciation, (d) divergent selection on mating cues, (e) and the genetics of reproductive isolation. We conclude that reinforcement has probably not been looked for where it is most likely to occur. We pinpoint however, many further areas of study that may ultimately provide a strong assessment of the importance of reinforcement in speciation.

“The grossest blunder in sexual preference, which we can conceive of an animal making, would be to mate with a species different from its own and with which the hybrids are either infertile or, through the mixture of instincts and other attributes appropriate to different courses of life, at so serious a disadvantage as to leave no descendants.”

—Fisher, 1930 pp. 130

OVERVIEW

Until recently, the primary questions concerning speciation by reinforcement have been whether it can occur and whether any cases can be documented. In the past decade, these questions have been answered. Theoretical studies have shown reinforcement to be feasible under various conditions, and several compelling cases of species that have diverged via reinforcement have been identified (Noor 1999).

In this review, we suggest changing the emphasis of future studies; reinforcement can occur, but what is its frequency and importance in speciation?

Most studies have traditionally required identifying selection against hybrids as a prerequisite for reinforcement (Butlin 1987, Howard 1993). The response to this selection would result in an increase, and possibly eventual completion of, premating isolation between taxa. We refer to selection against hybrids as a “classic” criterion of reinforcement. Butlin (1987) further restricts this definition to cases where hybrids have nonzero fitness. These definitions ignore many processes that are virtually identical to classic reinforcement. To assess how often this whole set of processes occurs in nature, we must think beyond these classic concepts to form a broader definition. Reinforcement in the “broad sense” is an increase in prezygotic isolation between hybridizing populations in response to any type of selection against interspecific matings, regardless of whether hybrids themselves are unfit. In contrast to the apparent division within the literature, we also consider reinforcement to be virtually identical to the latter stage of sympatric speciation, where hybrids are ultimately selected against because of phenotypic differences from diverging parental populations (Kirkpatrick & Ravigné 2002). We therefore consider many models of sympatric speciation to apply to reinforcement. Let us emphasize that we do not suggest that all prezygotic isolation between any two species pairs is a result of reinforcement. We use the term “speciation by reinforcement” as a shorthand to indicate that reinforcement has contributed to prezygotic isolation.

Previous attempts to determine the importance of reinforcement in speciation have concentrated on reviews or reanalyses of empirical studies, using the classic definition of reinforcement as a criterion for inclusion (e.g., Howard 1993, Noor 1997b). We instead attempt to elucidate the role that reinforcement may play in speciation by combining theoretical and empirical approaches, focusing on the broad-sense definition of reinforcement. In this review, we identify conditions theory has predicted may be favorable for reinforcement and evaluate the fit of empirical studies to the assumptions and conclusions of these models. Have researchers even looked for evidence of reinforcement in the most promising systems? We address this question by examining individual components of reinforcement, not in a comprehensive manner (e.g., Kirkpatrick & Ravigné 2002), but with the intention of interpreting the data that are available and identifying gaps in the theoretical and empirical literature.

INCOMPATIBILITIES

The definitions of reinforcement above include some form of selection against interspecific matings. Traditionally this just encompassed low hybrid viability or fertility resulting from intrinsic genetic incompatibilities or interactions with the environment. A number of other mechanisms, however, can promote the evolution of premating isolation in broad-sense reinforcement. If these alternative

incompatibilities are common, this would suggest that the frequency of reinforcement may have been underestimated in the past.

Costs Associated with Forming Unfit Hybrids—Intrinsic Versus Extrinsic Postzygotic Incompatibilities

As the classic driving force behind reinforcement, postzygotic incompatibilities have dominated the theoretical and empirical reinforcement literature. Much of this work concentrates on “intrinsic” genetic incompatibilities: hybrids are unfit regardless of their ecological surroundings. Intrinsic incompatibilities can include hybrid inviability, hybrid sterility, or behavioral dysfunctions that prevent hybrids from mating. There are innumerable examples of intrinsic incompatibilities in hybrids across plants, animals, and fungi.

Theoretical studies of reinforcement have incorporated intrinsic incompatibilities in several ways. One of the most basic is to consider a single locus that is underdominant for a character affecting fitness (Balkau & Feldman 1973 in their “disruptive selection” model; Cain et al. 1999; Sanderson 1989). This type of incompatibility is observed, for example, when hybrid dysfunctions result from chromosomal arrangement differences between species (e.g., King 1993, White 1969), which appears to be an uncommon mode of speciation (e.g., Coyne et al. 1993, Navarro & Barton 2003).

Intrinsic incompatibilities commonly arise from sets of loci that interact epistatically to produce low hybrid fitness, as first described by Dobzhansky (1937) and Muller (1942). Many empirical studies have found evidence for these epistatic incompatibilities (e.g., Fishman & Willis 2001, Lammissou et al. 1996, Orr & Irving 2001, Rawson & Burton 2002) and several theoretical studies have examined the patterns and consequences of the accumulation of these incompatibilities in populations (e.g., Orr 1995, Turelli & Orr 2000). Dobzhansky-Muller incompatibilities have been shown to drive reinforcement in theoretical studies, even when selection against hybrids is relatively weak (Kelly & Noor 1996, Kirkpatrick & Servedio 1999, Servedio 2000, Servedio & Kirkpatrick 1997).

Few theoretical studies of reinforcement consider intrinsic incompatibilities that lead to hybrid sterility, not inviability (Kelly & Noor 1996, Liou & Price 1994). In general, hybrid sterility appears to evolve slightly earlier in evolutionary divergence than hybrid inviability (Presgraves 2002, Price & Bouvier 2002, Sasa et al. 1998, Wu & Davis 1993), so the former is potentially a more common agent of selection for reinforcement. Liou & Price (1994) directly compared the effect on reinforcement of hybrid sterility and hybrid inviability. Reinforcement was found more often with hybrid inviability than sterility, owing largely to an increased probability of extinction when viable but infertile hybrids consume resources. They modeled reduced fertility by removing a fraction of hybrid adults from the mating pool; this is the same as assuming that these individuals chose not to mate, so can also be considered as a model of an intrinsic hybrid mating dysfunction (which has not been explicitly modeled elsewhere).

Whereas such intrinsic incompatibilities appear very common, until recently, few studies showed that hybrids may bear “extrinsic” genetic incompatibilities: lower fitness associated with a specific set of ecological conditions (Coyne & Orr 1998). As such, the frequency of hybrid incompatibilities that could drive reinforcement may be greater than previously perceived. Ecologically dependent isolation may occur when hybrids intermediate to the parental species in phenotype cannot efficiently exploit the available environments used by its parents. This can be tested using reciprocal transplants (Rundle & Whitlock 2001). An example of these incompatibilities has been described elegantly in the literature on benthic and limnetic morphs of the three-spine stickleback (fish) *Gasterosteus aculeatus* (Hatfield & Schluter 1999, Rundle 2002). When raised in the laboratory, hybrids between these morphs, which display intermediate morphology, are fully viable and fertile (Hatfield & Schluter 1999; McPhail 1984, 1992). However, a transplant experiment in the wild revealed that F₁ hybrids grew at lower rates than benthics in the littoral zone and limnetics in the open water (Hatfield & Schluter 1999), despite showing no growth reduction in the laboratory. Similar data have been obtained in birds (see Grant & Grant 1998; Price 2003).

The most comprehensive model of reinforcement that includes extrinsic incompatibilities is Kirkpatrick’s (2001) multilocus model. Kirkpatrick considers two traits; one is involved in premating isolation and the other is an ecologically relevant trait under both stabilizing and directional selection. He identifies three major conditions favorable to reinforcement when hybrids are intermediate to parental species in their ecological niche: (a) larger differences between the parental mean phenotypes, (b) stronger stabilizing natural selection around a local ecological optimum, and (c) many loci contributing to the ecological adaptation. Notably, as the parental mean phenotypes diverge, the effect of selection against hybrids on reinforcement increase rapidly, proportional to the square of the difference in parental mean phenotypes. However, this model assumes weak selection, which may not be representative of many speciation events. It would be useful to evaluate the robustness of the results to higher selection intensities.

A gray area in the dichotomy between intrinsic and extrinsic incompatibilities exists when hybrids are unable or unwilling to secure mates through behavioral hybrid dysfunction or have an intermediate phenotype that is not attractive to the choosing sex. Behavioral hybrid dysfunction has been documented in hybrids of a variety of taxa including Lepidoptera (Davies et al. 1997, Pashley & Martin 1987), *Drosophila* (e.g., Noor 1997a), birds (Buckley 1969), and frogs (Hobel & Gerhardt 2003), but is surely far more widespread. This behavioral anomaly may be intrinsic if the hybrids have a deficiency that prohibits courting or mating, but may be extrinsic if they are selecting mates based on cues that are rare or absent in their population. As pointed out above, the infertility version of the reinforcement model of Liou & Price (1994) can be interpreted as using this type of incompatibility.

In contrast to the situation where the hybrids are behaviorally dysfunctional, they may merely be unattractive to either of the purebred parental populations when the populations are divergent in sexual ornaments (e.g., in *Heliconius*,

Jiggins et al. 2001, Naisbit et al. 2001). Vamosi & Schluter (1999) demonstrated an example of sexual selection against male hybrids between benthic and limnetic threespine sticklebacks. Although there is no sexual selection against hybrids in the lab, male hybrids have difficulty competing in the wild, where the male's choice of microhabitat for nesting among limnetics is crucial to their mating success. Although no reinforcement models have specifically examined "unsexy" hybrids, all models of sympatric speciation by sexual selection (e.g., Higashi et al. 1999, Kawata & Yoshimura 2000) can be considered reinforcement models based on low hybrid attractiveness, if they are examined with the appropriate initial conditions.

Costs to Interspecific Matings—Postmating, Prezygotic Incompatibilities

Selection against hybrids is not the only mechanism that can drive the evolution of premating isolation. The exact patterns of preference divergence that result from classic reinforcement can evolve owing to postmating, prezygotic incompatibilities. Servedio (2001) used a multilocus model to obtain an expression for the expected strength of selection that these incompatibilities would place on mating preferences. She showed that incompatibilities from postmating, prezygotic interactions are expected to be comparable if not greater in strength to those from low hybrid viability, when both types of incompatibilities are caused by pairs of interacting loci.

Postmating, prezygotic incompatibilities can take the form of (a) mechanisms that increase female mortality between mating and offspring production or (b) mechanisms that reduce female fertility. In the first category, direct injury may result from morphological or behavioral differences during courtship and copulation, as illustrated in the carabid beetles *Carabus (Ohmopterus) maiyasnus* and *C. (O.) iwawakianus*. Using dissections, Sota & Kubota (1998) found that females of these species involved in heterospecific matings often die owing to rupture of their vaginal membranes, while males of one of the species often had broken genital parts. A similar type of incompatibility may result when costs do not take effect immediately but imperil a female's future reproduction. For example, interspecific hybridization may pose a threat because of the transmission of parasites or diseases to which only one of the taxa has evolved some resistance.

There is much evidence for the second category of postmating, prezygotic incompatibilities, those that reduce female fertility (reviewed by Markow 1997, Howard 1999). Females of the green lacewing species *Crysopa quadripunctata*, for example, showed low fertility when crossed with *C. slossonae* owing to low rates of sperm transfer from the bursa copulatrix to the spermatheca (Albuquerque et al. 1996). This is only one of many specific mechanisms that can lower fertility in an interspecific cross (see Servedio 2001).

Postmating, prezygotic incompatibilities may often evolve alongside postzygotic incompatibilities, although the former is generally not looked for once the

latter is discovered. Postmating, prezygotic incompatibilities may also drive broad sense reinforcement when postzygotic isolation is absent or weak.

What is Needed Now?

When biologists try to demonstrate reinforcement they often look only for hybrid inviability or reduced fertility as a driving force. We strongly discourage this practice. Taken together, theoretical and empirical studies have demonstrated that other kinds of postmating isolation exist that can lead to broad sense reinforcement. We hope that this discussion will convince researchers to look more broadly for sources of incompatibilities in future work, expanding our understanding of when reinforcement may occur.

We initially hoped to review the relative frequencies of extrinsic versus intrinsic incompatibilities in various taxa. However, we have concluded that there has been a strong bias in the types of incompatibilities that researchers have investigated: *Drosophila* researchers have disproportionately sought hybrid sterility/inviability, whereas vertebrate ecologists have disproportionately studied ecological or behavioral differences. Investigators need to look more uniformly at the relative contributions of these different barriers to gene exchange in diverse taxa.

NONRANDOM MATING AND FERTILIZATION

Fundamental issues affecting the probability of reinforcement are the mode and genetic basis of nonrandom mating and fertilization. Theory predicts that certain conditions are particularly favorable to reinforcement. We briefly discuss these below, concentrating on mechanisms at a single locus (nonrandom mating controlled by many loci is discussed further in the section on Genetics of Reproductive Isolation). There is, unfortunately, scant empirical work examining some of the important distinctions that emerge from theory. We point out promising systems in which future studies may find this evidence. Although our examples focus on nonrandom mating, the generalities drawn should apply to nonrandom fertilization as well.

Nonrandom Mating in Reinforcement

In a landmark paper, Felsenstein (1981) presented one of our most valuable insights into the genetics of speciation. He pointed out that assortative mating during speciation can occur by either a one-allele or a two-allele mechanism. In a one-allele process, the substitution of a single allele across both of two diverging populations can reduce interpopulational mating (e.g., an allele that uniformly depresses migration rates). In contrast, in a two-allele system, assortative mating is caused by the substitution of alternate alleles, contributing a distinct preference or fertilization affinity, into each diverging population. Reinforcement is easier to achieve with a one-allele than a two-allele mechanism. Felsenstein noted that, in a

two-allele model, recombination can break up beneficial genetic associations (linkage disequilibrium) between the nonrandom mating alleles and the locally adapted allelic combinations in each population; this can not occur in a one-allele model where specific linkage between the mating locus and locally adapted loci is not necessary for speciation. Using Felsenstein's basic two-allele model, Trickett & Butlin (1994) confirmed that a suppressor of recombination would be favored, and consequently speciation would be easier to achieve.

Felsenstein's distinction has been thoroughly discussed in many papers and reviews (e.g., Kirkpatrick & Ravigné 2002). Felsenstein (1981) himself reviewed the major speciation models published to date in the context of his categories. Since then, further one-allele models (reinforcement: Cain et al. 1999, Kelly & Noor 1996, Sanderson 1989; sympatric speciation: Kawecki 1996, 1997) have generally found reinforcement to be less restrictive than have two-allele models (Kirkpatrick 2000, 2001; Payne & Krakauer 1997; Servedio & Kirkpatrick 1997; with multiple loci: Liou & Price 1994; sympatric speciation models: Dieckmann & Doebeli 1999; Higashi et al. 1999; Kawecki 1996, 1997; Kondrashov & Kondrashov 1999). The one-allele/two-allele distinction does not apply with all forms of population structure however (e.g., one-allele mechanisms do not ease conditions for reinforcement in a peripheral isolate; Servedio 2000).

In a paper comparing a one-allele assortative mating model and a two-allele preference model, Servedio (2000) identified an additional factor that may facilitate speciation in many one-allele models. A single allele that causes assortative mating (for example, by inducing females to prefer males that share their body size) may automatically form genetic associations that lead to it being favored by indirect natural and sexual selection in all parts of its range. This occurs because such an allele may naturally form genetic associations with the high fitness trait alleles in each population (because these traits occur at a high frequency). In one-allele systems that face such unopposed selection, reinforcement will always occur. In contrast, in a two-allele model opposing forces of indirect selection will always be acting on the alleles to maintain a polymorphism in the mating system across both populations. Conditions for the maintenance of such a polymorphism will naturally be more restricted.

A detail often ignored in the literature is that many purported one-allele systems must involve an underlying two-allele mechanism to produce two species; the order in which these mechanisms are established may influence the way in which we categorize the system. Take, for example, a hypothetical case where a single allele causes females to prefer males that share their body size. If size had already diverged in two populations, and we were examining the spread of the allele causing assortative mating, we would consider this to be a one-allele system. If, on the other hand, females initially aggregated and mated with males of similar size, and we were examining the spread of an allele for large size in a population with small size, we would view this as a two-allele system. It may sometimes be impossible to determine post facto whether a one-allele or two-allele mechanism was ultimately responsible for the commencement of isolation.

There is very little firm evidence regarding the relative frequency of one-allele versus two-allele reinforcement mechanisms during natural speciation events. However, some candidate systems may be promising places to distinguish these mechanisms. Two-allele systems may be much easier to demonstrate than one-allele ones, and may be common in cases where preferences are for traits not shared by the female herself. For example, different male song features are associated with mating success in *Drosophila pseudoobscura* and *Drosophila persimilis*: interpulse interval is important to females of the former whereas intrapulse frequency is important to those of the latter (Williams et al. 2001). It is hard to imagine this system arising through the fixation of a single allele.

Other general patterns or types of isolation may also be more likely from two-allele systems than one-allele systems, unless asymmetrical effects of genetic backgrounds are imposed on a one-allele system. Divergence in flowering time and allochronic isolation (e.g., Cox & Carlton 1991, Lloyd et al. 1983), for example, would be likely to fit a two-allele system if these characters have a heritable basis. A two-allele system may also be indicated when there are asymmetrical mate preferences: one taxon may exhibit a strong preference for conspecifics while the other taxon displays little or no preference (e.g., Bordenstein et al. 2000, Helbig et al. 2001, Michalak et al. 1997). This suggests that alleles causing a preference have arisen only in the discriminating taxon. This hypothesis can be directly evaluated by genetic manipulations.

The best examples of one-allele systems may be alleles that cause a reduction in migration rate (Balkau & Feldman 1973, Fisher 1930) and alleles that lead to self-pollination. Fishman & Wyatt (1999) showed that selection against crossing with the heterospecific *Arenaria glabra* promoted the evolution of selfing in *Arenaria uniflora* in areas of sympatry; *A. uniflora* is an outcrosser in areas of allopatry. Although in this specific system *A. glabra* only outcrosses, if alleles for selfing were to spread in two incipient species, this would be an example of speciation by a one-allele mechanism.

Another possible example of a one-allele mechanism may be the spread of alleles causing individuals to sexually imprint on parental phenotypes (Irwin & Price 1999, Lorenz 1952, Slabbekoorn & Smith 2002, Vos 1995). If, however, imprinting is an ancestral factor in mate choice and isolation is caused by song divergence (Grant & Grant 1997a,b), then the mechanism is still fundamentally two-allele (different alleles for song must be predominant in each population). This of course assumes that song divergence has a genetic as well as a learned component, although the evidence may be stronger for the latter (e.g., Lynch & Baker 1994, Mundinger 1982). A similar phenomenon occurs when an allele causes individuals to preferentially mate on the host from which they emerged, as is true for many phytophagous insects (e.g., Feder et al. 1994). Although this is a one-allele mechanism, if mating on the host is ancestral and host choice is the divergent trait, then the system is two-allele. Via & Hawthorne (2002), for example, find different quantitative trait loci (QTL) with positive effects for acceptance of alfalfa and of

clover, indicating this possible case of host-race divergence can best be explained as a two-allele system.

Direct Selection for Assortative Mating

Although not the scenario considered in reinforcement, premating isolation may also evolve if selection acts on nonrandom mating alleles directly. Such direct selection can act in either one-allele or two-allele systems. Kirkpatrick & Ravigné (2002) point out that direct selection should be the most efficient source of premating isolation, and describe several scenarios in which it may have acted. Even in the context of reinforcement, any direct selection acting on preferences can often overwhelm indirect selection caused by low hybrid fitness to be the primary force driving the evolution of premating isolation (Kirkpatrick & Barton 1997, Servedio 2001). Ecological character displacement and sensory bias can also cause direct selection on mating preferences to produce a pattern identical to reproductive character displacement, and may therefore be confused with reinforcement (Noor 1999, Servedio 2001). Despite the ease with which direct selection is expected to lead to speciation, there are very few empirical examples, partly owing to the difficulty of measuring selection on mating preferences in most systems. It is therefore very difficult to assess how commonly this mechanism occurs.

What is Needed Now?

Whereas theoretical studies have consistently demonstrated the advantages of one-allele over two-allele systems in leading to reinforcement in two populations, empirical studies have not yet begun to evaluate the relative frequency of these mechanisms. Although this will be a challenging task, as discussed above, this information is necessary to determine the ease with which reinforcement can occur in natural systems.

THE GEOGRAPHY OF SPECIATION

The geographic orientation of incipient species can affect both the likelihood of reinforcement and the chance that it will be detected. The most critical aspect of geography is its influence on rates and patterns of gene flow, which are crucial to determining whether reinforcement will occur. Second, the patterns of physical overlap of species can be important in determining whether researchers will search for reinforcement in the species pair.

Gene Flow

One generalization that may be made about divergence and speciation is that they tend to be inhibited by gene flow. No one argues about whether allopatric speciation is a likely scenario. It is helpful to view the geographical settings considered for

speciation and reinforcement with this generalization in mind. We can see that, although increasing gene flow tends to inhibit speciation, patterns of gene flow and structure of populations can be crucial as well.

Fairly low gene flow may occur when two populations with non-overlapping ranges exchange long-distance migrants. Several numerical studies have found that, in this case, lowering migration rates increases the chance of reinforcement (Felsenstein 1981, Kelly & Noor 1996, Servedio & Kirkpatrick 1997); less migration decreases the chance that the populations will homogenize.

As gene flow in these two-island models becomes increasingly asymmetric, pre-mating isolation occurs less often (Servedio & Kirkpatrick 1997). At the extreme, when migration is one-way, as in a peripheral isolate receiving migrants from a large parental population, pre-mating isolation may evolve rarely (Servedio & Kirkpatrick 1997). Migration from the "continent" will effectively swamp pre-mating isolation evolution on the "island." The flycatchers *Ficedula albicollis* and *Ficedula hypoleuca*, which show reinforcement in a continental cline (Sætre et al. 1997), demonstrate much less pronounced isolation on recently colonized islands that receive strongly asymmetric migration (Sætre et al. 1999). Although there may be other explanations for this pattern in flycatchers, it is consistent with the theoretical expectations described above. Nosil et al. (2003), using the walking-sticks *Timema cristinae*, examined the effects of migration asymmetries between host races more closely, by determining the amount of female discrimination present in study populations that evolved under different migration regimes. Their results suggest that reinforcement does have the strongest effect when the size of the two populations involved is the most similar; the effect declines as migration becomes very asymmetric.

Kirkpatrick (2000) elegantly demonstrates that migration in a speciation model has dual effects. He considers a population that can be interpreted as an island receiving continental migrants with rate m . He shows that an equation for the change in the mean of a trait used as a cue for assortative mating in the island population, \bar{T} , has two terms that contain migration, $m(\bar{T}' - \bar{T})$ and $-m(\bar{T}' - \bar{T})I$, where \bar{T}' is the mean of the assortative mating trait in the foreign population and I is a measure of the intensity of selection against immigrants and hybrids. The first term in this decomposition represents the homogenizing effect of migration, changing the mean of the focal population toward the mean of the migrants. The second term, however, demonstrates that migration can also cause evolution away from the mean of the foreign population; it provides opportunities for selection against hybrids and immigrants, which are important driving forces for divergence. The consistent homogenizing effect of migration found by the other models discussed above indicates that the former effect may generally outweigh the latter. Nosil et al.'s (2003) study of walking-sticks, however, suggests that with low migration rates (and in finite populations), the latter effect may be sometimes more important. If low migration rates can hinder reinforcement due to a lack of selection against hybrids, an intermediate migration rate would therefore be optimal for reinforcement.

Because migration tends to prevent the evolution of premating isolation, sympatry should be a particularly unfriendly environment for speciation. Despite the fact that sympatric conditions have been the most difficult for reinforcement in numerical studies that have made the comparison (when $m = 0.5$, Felsenstein 1981, Kirkpatrick & Ravigné 2002, Liou & Price 1994, Servedio & Kirkpatrick 1997), models of sympatric speciation often imply that it can occur easily (Felsenstein 1981). There is also increasing empirical evidence for sympatric speciation in many natural systems, such as phytophagous insects (reviewed in Berlocher & Feder 2002). As Kirkpatrick & Ravigné (2002) point out, evolution of premating isolation in the last stages of sympatric speciation is conceptually identical to reinforcement; reinforcement may even be easier because it may be driven by forms of intrinsic postmating isolation that cases of sympatric speciation may not possess.

Reinforcement faces several challenges when secondary contact occurs in a hybrid zone (see Howard 1993). Selection against hybrids driving reinforcement, for example, only occurs in the zone (Moore 1957), and premating adaptations that evolve in the zone are likely to be swamped out by migration from the parental populations outside of the zone (Bigelow 1965). Because hybrid zones generally occur on the edge of a species range, migration may also tend toward unidirectionality into the zone originating mainly from the center of the range, biasing against reinforcement. Liou & Price (1994) found, however, that reinforcement occurred more easily in a three-neighborhood stepping-stone model than within a single population. In contrast to a similar model by Sanderson (1989) that reached the opposite conclusion owing to a direct cost of divergence, the pattern Liou & Price (1994) observed was likely determined by lower effective migration in the hybrid zone model than in sympatry. Cain et al. (1999) suggest reinforcement may also occur more easily when hybrid zones exist in a mosaic structure; with a patchy distribution of each species; than in a tension zone where alleles representative of each species change in a monotonic cline (but see Turelli et al. 2001). This could occur if the formation of hybrids over a broader region in a mosaic zone resulted in stronger selection for premating isolation; however, the increased opportunities for introgression in a mosaic zone may also have the tendency to homogenize the population.

In hybrid zones and areas of geographic overlap fitting a stepping-stone model, patterns of premating isolation are often consistent with reinforcement. Although there are several alternative explanations for these patterns (e.g., ecological character displacement), there are many apparent cases of reproductive character displacement, defined as the divergence of mating characters in sympatry but not in allopatry (e.g., Butlin 1987, Howard 1993, Noor 1999). Displacement along clinal hybrid zones has yielded convincing evidence of reinforcement in flycatchers (Sætre et al. 1997), but still remains to be explored further in other taxa (e.g., snails, Schilthuizen & Lombaerts 1995). Comparisons of areas of sympatry and allopatry have yielded evidence of reproductive character displacement and/or reinforcement across many taxa, including snails (e.g., Wullschleger et al.

2002), *Drosophila* (e.g., Coyne & Orr 1989, 1997; Noor 1995, 1997b), copepods (Holynska 2000), sticklebacks (Rundle & Schluter 1998), and frogs (e.g., Gerhardt 1994, Loftus-Hills & Littlejohn 1992).

Signature of Reinforcement

One noteworthy fact from the section above is that reinforcement per se has only been convincingly demonstrated in a few geographical situations (e.g., sympatry versus allopatry, tension zones). Reinforcement has not been found, for example, where theory has predicted it may occur the most easily: in two populations exchanging long distance migrants (i.e., when migration occurs at a low rate). The simple explanation for this pattern is that reinforcement is commonly looked for only where it can leave the signature of reproductive character displacement (Howard 1993). To identify reinforcement by this signature, species must have both allopatric and sympatric populations or regions. Reinforcement may occur, however, in cases that do not fit this description, for example in two populations exchanging migrants or in populations whose ranges overlap completely.

Even when species do maintain allopatric and sympatric populations, the signature of reinforcement may be easily erased by the spread of premating isolation mechanisms into areas of allopatry (Walker 1974). This may eventually occur whenever there is gene flow maintaining the integrity of each incipient species. It would be especially likely, however, when premating isolation alleles are selectively neutral in allopatry; this is also the most favorable case for reinforcement. Once again we may be missing reinforcement when it is most likely because we generally look for evidence of a signature.

A signature is not necessary to demonstrate reinforcement, however. An alternative, when feasible, would be to collect temporal data. Pfennig (K.S. Pfennig, unpublished manuscript), for example, demonstrated a decreasing frequency of hybridization between *Spea bombifrons* and *S. multiplicata* over 27 years in an area of syntopy. She ruled out several alternative explanations, including a decline of opportunity for hybridization and changes in habitat affecting hybrid production. This type of convincing demonstration is an informative alternative strategy when reinforcement does not leave a signature.

Extinction

Sympatry of incipient species may affect the likelihood of extinction (e.g., van Doorn et al. 1998). Extinction has been found in several reinforcement models. Liou & Price (1994), using an individual-based model, reached the conclusion that extinction was likely particularly when one species greatly outnumbered the other, such that the rarer species frequently produced maladapted hybrids. Deterministic reinforcement models can obtain results that may also be interpreted as extinction, for example the loss of variation of one population's alleles (e.g., Servedio & Kirkpatrick 1997) or population fusion (Kelly & Noor 1996). There are many

studies in the ecological literature examining conditions for the coexistence of sympatric species (e.g., Connell 1983, Schoener 1983, Volterra 1926, Yoshimura & Clark 1994); these may be relevant to studies of reinforcement, and should be examined further in this context.

What is Needed Now?

As discussed above, most empirical studies only look for reinforcement where it leaves the signature of reproductive character displacement; creative approaches such as temporal studies have the potential to greatly broaden the situations in which reinforcement is found. Another obvious omission in both theory and empirical work is further consideration of when incipient species can coexist in sympatry. Finally, further empirical studies should be undertaken to confirm and quantify the effects of migration rates and asymmetries on reinforcement.

SELECTION ON MATING CUES

Although ostensibly driven by selection against interspecific matings, reinforcement may include mating cues that are under natural selection, or sexual selection already present at the time of secondary contact. This selection itself can drive premating divergence. It can be a powerful force, capable of eclipsing selection against hybrids (M.R. Servedio, unpublished manuscript). If this type of selection is common, then the number of putative empirical cases of reinforcement may be overestimated. Here we examine how selection on mating cues promotes premating isolation in theoretical studies, and review evidence for this selection in natural systems. This selection can create the appearance of reinforcement, thereby confounding our attempts to determine reinforcement's frequency in nature.

Two Components to Nonrandom Mating

Many models of speciation and reinforcement consider a system of nonrandom mating with two components. The first is a locus or set of loci that causes mate choice (e.g., a mating preference). The second is the cue upon which the first component acts (e.g., a male trait). Because both components are involved in nonrandom mating, linkage disequilibrium builds between them. Any outside source of selection, such as natural or sexual selection, on the cue will therefore cause both components to evolve. An analogous association could evolve between loci conferring habitat preference and performance in that habitat. In reinforcement models, loci that cause selection against hybrids or against interspecific matings also form genetic associations with the loci involved in mate choice. It is difficult to determine whether selection on the mating cue or selection against hybrids is the primary determinant of nonrandom mating evolution in models where both occur. Selection against hybrids may sometimes contribute little to the evolution of premating divergence in the system (Kirkpatrick & Servedio 1999) even though

the traditional signature of reproductive character displacement is present. This occurs even in haploid models arranged so that extrinsic selection on hybrids at the mating cue is absent (M.R. Servedio, unpublished manuscript).

Several reinforcement models include natural selection driving the divergence of a mating cue (Cain et al. 1999, Kirkpatrick & Servedio 1999, Servedio 2000, Servedio & Kirkpatrick 1997). This selection alone is capable of driving speciation; selection against hybrids merely adds to this force (Kirkpatrick & Servedio 1999). This can be illustrated by considering sympatric speciation models, where selection against hybrids is initially absent (see Turelli et al. 2001). Dieckmann & Doebeli (1999), for example, find sympatric speciation occurring when the cue for assortment, an ecological trait determining resource use, is under divergent selection owing to competition.

Like natural selection, sexual selection can also favor mating cues during reinforcement (Kirkpatrick & Ravigné 2002, Kirkpatrick & Servedio 1999). Several studies of reinforcement assume some initial sexual selection is already causing a small amount of divergence at the time of secondary contact (Liou & Price 1994, Kelly & Noor 1996). They then examine the spread of alleles that strengthen this nonrandom mating. This evolution will occur in concert with any selection against hybrids also present, thereby amplifying the perceived importance of reinforcement.

These assumptions about natural and sexual selection on mating cues are well met in threespine sticklebacks, where reinforcement may be involved in some of the divergence of benthic and limnetic forms in postglacial lakes (Rundle & Schluter 1998). Limnetic sticklebacks are generally small and narrow bodied, whereas benthics are large and deep bodied. Not only is body size under divergent natural selection in these lakes, but it is an important component of mate choice, and thus may help drive premating divergence (Nagel & Schluter 1998). Divergent sexual selection also operates on male color in sticklebacks, and may play a similar role in the development of premating isolation (Boughman 2001). Selection against hybrids may have only a minor effect on divergence when compared to these other selective forces, and therefore the importance of reinforcement may be minimal in this system.

Divergent natural selection has also been shown to act on mating cues in *Heliconius* butterflies and in Darwin's finches. *Heliconius melpomene* and *Heliconius cydno* undergo disruptive selection on their color patterns because they each mimic a different model species (Mallet 1999). Males of each species also preferentially court females of their own mimetic pattern (Jiggins et al. 2001). Reinforcement may also be acting in this species pair, which produces hybrids that are not efficient mimics of either model. Podos (2001) similarly demonstrated in Darwin's finches that divergent selection on bill morphology and body size can shape song performance, which may be used in species recognition. While song performance per se may not act as a mating cue, beak shape and size may themselves function in conspecific mate choice (Grant 1986).

A first step to identifying natural selection on mating cues, and therefore assessing the frequency of this force that may amplify the appearance of

reinforcement, may be to search for evidence of natural and sexual selection operating in the same direction on a trait in general. Large song repertoire size in birds, for example, may be selectively favored initially through a physiological benefit to varying the syringial muscles used in song production (the anti-exhaustion hypothesis; Lambrechts & Dhondt 1988). If this selection pressure exists it would reinforce the evolution of female preferences for large repertoires, present in a variety of species (Gil & Gahr 2002, Searcy & Yasukawa 1996), until a constraint is reached. Body size may also sometimes be under divergent natural and sexual selection (see Servedio 2000). There may be few known examples of natural and sexual selection acting in the same direction because of a research bias; many studies instead look for evidence of honesty and handicaps in sexually selected traits (Gil & Gahr 2002, Grafen 1990).

One Component to Nonrandom Mating

In other speciation models there is only a single component to mate choice or habitat selection (e.g., Kondrashov 1983, Rice 1987, Drossel & McKane 2000). Selection on this single component would comprise direct selection for divergence, and would thus greatly facilitate speciation (e.g., Kirkpatrick 2000, Kirkpatrick & Ravigné 2002). The clearest examples of this phenomenon are in the habitat choice of phytophagous insects, which may be selected to colonize new hosts, or to specialize from a generalist ancestor (e.g., Berlocher & Feder 2002).

Several models that include a single component to nonrandom mating find speciation without direct selection on mate or habitat choice (reinforcement: Balkau & Feldman 1973, Felsenstein 1981; sympatric speciation: Kawecki 1996, 1997; Kondrashov & Shpak 1998; two-character model of Kondrashov & Kondrashov 1999). In reinforcement and the latter stages of sympatric speciation, selection against hybridization is likely to be the driving force for this divergence.

What is Needed Now?

Divergent selection on mating cues may be a primary driving force during both reinforcement and sympatric speciation, and may greatly enhance ecological speciation mechanisms (e.g., Schluter 2001). Reinforcement, even in its broad sense, may play a small role in speciation if divergent selection on mating cues is also present. It is therefore crucial that more empirical studies search for evidence of this pattern of divergent selection. One place to start this search may be in potential examples of natural and sexual selection acting in the same direction on traits. Evidence of natural selection on cues in single component systems may also provide much needed evidence of speciation by direct selection.

In most taxa, it may not be possible to demonstrate that divergent sexual selection has preceded secondary contact and thus has served as a driving force for initial divergence. This mechanism may be common, however, and warrants both further empirical and theoretical study.

GENETICS OF REPRODUCTIVE ISOLATION

One may envision coexisting species as sets of alleles in linkage disequilibrium (e.g., Dobzhansky 1937, Mallet 1995, Ortíz-Barrientos et al. 2002). Geneticists can conceive of reinforcement as a way to increase the linkage disequilibrium between genes causing premating and postmating isolation (Felsenstein 1981). Recombination among such loci in a two-allele system therefore opposes reinforcement and leads to fusion. Hence, the genetic basis of reproductive isolation can easily impact the probability or speed of attaining reinforcement. Various theoretical models have examined how the genetics of reproductive isolation (both premating and postmating) can impact reinforcement.

Most empirical studies of the genetics of reproductive isolation have been descriptive and focused on specific issues: the number and relative distribution (especially X versus autosome) of reproductive isolation genes, the interactions causing the preferential sterility of the heterogametic sex (Haldane's Rule) and whether the same genes control male and female components of sexual isolation. This abundant data can be applied to evaluate predictions of theoretical models of the reinforcement process.

Numbers and Distribution of Genes

Results of theoretical models are inconsistent in their predictions of how robust the probability of reinforcement may be to the differences in numbers of genes controlling premating isolation. Models where each mating character is expressed by a single locus (Felsenstein 1981, Kelly & Noor 1996, Servedio & Kirkpatrick 1997) and by multiple loci (e.g., Liou & Price 1994) both find reinforcement under certain conditions. Some models obtain results robust to control by any number of loci as long as selection and migration rates are low (Kirkpatrick 2000, 2001; Kirkpatrick & Servedio 1999), but these assumptions may often not be met in nature. In contrast, several studies that varied the numbers of loci controlling mating traits found speciation to be more difficult (or take longer) with increasing numbers of loci controlling mating (Dieckmann & Doebeli 1999, Kondrashov & Kondrashov 1999). Reflecting the inconsistency of the theoretical models, high-resolution empirical studies have estimated dramatically different numbers of loci affecting facets of premating isolation (e.g., Doi et al. 2001, Ting et al. 2001).

Kirkpatrick & Servedio (1999) varied the number of loci interacting to produce hybrid incompatibilities during reinforcement. They found that although having more loci per interaction leads to more preference evolution, this effect might not be very large (Kirkpatrick & Servedio 1999). A similar effect can result from increasing the number of loci involved in ecological selection during sympatric speciation (but see Dieckmann & Doebeli 1999, Kirkpatrick 2001, Kondrashov & Kondrashov 1999). The chromosomal distribution of genes contributing to reproductive isolation may affect the probability of reinforcement more profoundly than the number of loci, however. For example, the placement of genes on sex

chromosomes versus autosomes changes the likelihood of reinforcement. Kelly & Noor's (1996) study, based on the biology of *Drosophila*, is unique in considering both the effects of sex linkage and sex-limited expression. They find that a combination of male limited fertility reduction and X-autosome epistasis (but not one or the other characteristic) is favorable to reinforcement. Both of these conditions hold in *Drosophila*, and evidence of reinforcement has been found in *Drosophila* in several studies (Coyne & Orr 1989, 1997; Noor 1997b).

High-resolution genetic studies of hybrid dysfunctions have shown that they result from deleterious interactions between genes on the X-chromosome and autosomes (Noor et al. 2001a, Orr & Irving 2001; see also Turelli & Orr 1995), genes on the Y-chromosome and autosomes (Lamnissou et al. 1996, Pantazidis et al. 1993), nuclear and cytoplasmic genes (Rawson & Burton 2002, Willett & Burton 2001), and genes on the X- and Y-chromosomes (Orr 1987). However, finer-scale studies have illustrated that seemingly simple interactions causing sterility may actually involve three or more loci (e.g., Carvajal et al. 1996, Palopoli & Wu 1994), even in taxa that diverged less than 200,000 years ago (Orr & Irving 2001). This observation is consistent with mathematical models of the accumulation of incompatibilities causing hybrid sterility. Certain paths to the evolution of hybrid sterility are barred because they require intermediate genotypes that are also sterile. However, the proportion of paths that face this impediment decreases with the complexity of the genetic basis of sterility (Orr 1995). Thus, three-gene interactions causing hybrid sterility can evolve more easily than two-gene interactions, and so on.

These empirical observations are consistent with what appear to be "best-case" scenarios for reinforcement based on the models of Kelly & Noor (1996) and Kirkpatrick & Servedio (1999). To some extent, the models' predictions of greater reinforcement may stem from the fraction of F_2 or backcross hybrids that would be sterile or inviable, both increasing with the conditions outlined. As more hybrids are sterile, the selection intensity for reinforcement will necessarily be stronger. Further theoretical analyses are needed to supplement these initial theoretical studies. For example, the Kirkpatrick & Servedio (1999) model assumes that all hybrid mixtures of alleles at sterility-conferring loci produce equivalent hybrid sterility, though empirical data suggest incompatibilities tend to be complex with only certain combinations causing sterility.

Linkage Between Premating Isolation and Postmating Isolation

As discussed extensively above, many theoretical studies have suggested that linkage between premating and postmating isolation can enhance the probability of reinforcement, particularly in "two-allele" models (Felsenstein 1981, Servedio 2000, Trickett & Butlin 1994; see review in Ortíz-Barrientos et al. 2002). Servedio & Sætre (2003) point out that sex linkage will exaggerate this effect, because, in the heterogametic sex, recombination is absent and recessive alleles involved in

postmating isolation are expressed immediately. Tighter linkage and sex linkage both not only facilitate the evolution of premating divergence, but can strengthen amounts of intrinsic postzygotic isolation as well (Servedio & Sætne 2003).

Linkage between genes affecting premating and postmating isolation has been identified in some taxa (e.g., Noor et al. 2001b, Sætne et al. 2003). In the case of *D. pseudoobscura* and *D. persimilis*, all forms of reproductive isolation map to three regions that are inverted between the two species (Noor et al. 2001b). Noor et al. (2001b) suggested that chromosomal rearrangements prevent fusion of hybridizing species and facilitate reinforcement through creating this linkage. Similarly, Sætne et al. (2003) find sex linkage on the Z chromosome for both sexual trait and postmating isolation alleles in *Ficedula* flycatchers. In hybridizations of *D. mojavensis* and *D. arizonae*, the largest effects on both hybrid sterility and hybrid male sexual isolation map to the fourth chromosome (Pantazidis et al. 1993, Zouros 1981, Zouros et al. 1988). Interestingly, all of these species pairs are proposed to have diverged in part via reinforcement (Noor 1995, Sætne et al. 1997, Wasserman & Koepfer 1977). Such linkage is not universal, however, such that sexual isolation and hybrid sterility are not linked in various allopatric species (e.g., Coyne 1992, 1996).

Nonetheless, simple genetic mapping studies of female species preferences and male hybrid sterility are not necessarily comparable. Alleles causing hybrid male sterility often bear recessive effects (Turelli & Orr 1995), making X-chromosomal sterility alleles easier to identify than autosomal ones. Backcross hybrids can be used to compare hemizygous X-chromosomes from one species with those from the other in any possible autosomal background. In contrast, F₁ male sterility precludes forming hybrid females that are homozygous for X-chromosomes from one species and homozygous for autosomes from the other (as could be formed from an F₂ cross), so recessive interaction effects are more difficult to detect. More appropriate comparisons may be hybrid male sterility with preferred male characters or male preferences.

Linkage Between Male and Female Components of Premating Isolation

In classic theoretical studies, Lande (1981) and Kirkpatrick (1982) showed that female preferences could evolve as a correlated response to selection on males, occurring even with free recombination. Decreased recombination between male trait and female preference loci has been shown, however, to increase the likelihood of speciation (Servedio 2000, Trickett & Butlin 1994), hence possibly facilitating reinforcement. While male and female components of sexual isolation are linked in *D. pseudoobscura* and *D. persimilis* (Noor et al. 2001b), this linkage is not observed in *D. simulans* and *D. mauritana* (Coyne 1996), between the races of *D. melanogaster* (Ting et al. 2001), or between the pheromone races of moth *Ostrinia nubilalis* (Lofstedt et al. 1989).

A different form of “preference” and “preferred traits” observed between species is in the selective binding of conspecific sperm or pollen to eggs (see

review in Howard 1999). Interestingly, unlike the cases noted above, in some fungi, plants, and sea urchins, cases have been documented where genes that encode sperm bindin are either the same as or linked to genes that encode its egg-surface receptor (reviewed in Swanson & Vacquier 2002).

What is Needed Now?

Both theory and data are often lacking with regard to the genetic basis of species mating preferences, hybrid dysfunctions, and their effects on the probability or progress of reinforcement. Much available data are exclusive to a small number of *Drosophila* species, so information from unrelated taxa may be especially interesting. More data on the genetic basis of these traits in taxa with female heterogamety may be particularly enlightening. Sætre et al.'s (2003) observation of disproportionate effects of the Z-chromosome is consistent with extensive empirical evidence of sex linkage of species differences in Lepidoptera (Iyengar et al. 2002; see reviews in Sperling 1994, Prowell 1998). Unfortunately, similar genetic studies in birds are rare and often very low in resolution, particularly with regard to hybrid dysfunctions (see review in Grant & Grant 1997).

CONCLUSIONS

The questions of whether reinforcement can or does happen no longer apply—theoretical studies have demonstrated a range of general conditions under which reinforcement may be expected, and empirical studies have yielded numerous examples that it does occur. As in the classic neutralist-selectionist debate, we now face the more daunting challenge of determining the frequency and importance of reinforcement relative to other means of speciation. We may now return to the question posed in the introduction: whether, according to theoretical predictions, we have looked for reinforcement in the most promising systems.

In short, no. There are several areas where reinforcement should be investigated that have not received much attention. First, most empirical studies have focused on intrinsic genetic incompatibilities as being the driving force for reinforcing selection and considered reinforcement to be impossible without overt evidence of hybrid sterility or inviability. We outlined several alternative factors preventing the full success of interspecies matings; these can also drive reinforcement in the broad sense. Potentially harder to deal with is that reinforcement is only studied in systems where it can leave a signature. Because such systems do not necessarily possess the conditions most conducive to reinforcement, we may be missing many cases by this practice.

Beyond this, confounding factors that may reduce the frequency or importance of reinforcement have not been adequately investigated. For example, divergent selection between populations on mating cues can lead to the appearance of reinforcement despite a relative lack of selection against interspecies matings. Direct selection on nonrandom mating genes can have a similar effect. Unfortunately,

very little empirical data exists on the frequency of either of these types of selection. Finally, though not discussed above, hybrids may sometimes be more fit than one or more parental types under certain ecological conditions (Levitan 2002, Pfennig & Simovich 2002; see review by Arnold & Hodges 1995).

We note several other considerations that might help to assess the potential for reinforcement to be common. For example, identifying a high frequency of one-allele systems of nonrandom mating would suggest that reinforcement could occur easily in a wide range of taxa. Gaining a better understanding of the genetic architecture of speciation would also help to determine whether conditions favorable to reinforcement, such as sex linkage of postmating and premating isolating factors, are prevalent. However to identify specific cases of reinforcement, or assess its frequency, we must do more than determine when conditions for it are favorable. We must look at a subset of these cases in more detail with selection, temporal and/or biogeographic studies, to identify whether reinforcement has occurred.

Synthesizing theoretical predictions with empirical data is the means of addressing broad questions about the frequency of any evolutionary process. Intrinsic barriers exist between theory and empirical investigations: no model can capture all the complexities of a natural system without making itself so specific as to be uninformative for any other system. Compromises must be made in theoretical studies to capture generalities observed in numerous systems. Similar allowances must be made in the interpretation of empirical studies—investigators must consider the likelihood of the observed outcome in their particular system and use caution in making generalizations from their results. With these considerations in mind, further integrations of future theoretical and empirical work are necessary for understanding the frequency and importance of reinforcement in speciation.

ACKNOWLEDGMENTS

We thank Jerry Coyne, Mark Kirkpatrick, Lindy McBride, Trevor Price, Brad Shaffer, Michael Turelli, and John Wiens for comments on the manuscript. MRS is supported by NSF grant DEB 0234849. MAFN is supported by NSF grants DEB 9980797 and 0211007.

**The *Annual Review of Ecology, Evolution, and Systematics* is online at
<http://ecolsys.annualreviews.org>**

LITERATURE CITED

- Albuquerque GS, Tauber CA, Tauber MJ. 1996. Postmating reproductive isolation between *Chrysopa quadripunctata* and *Chrysopa slossonae*: Mechanisms and geographic variation. *Evolution* 50:1598–606
- Arnold ML, Hodges SA. 1995. Are natural hybrids fit or unfit relative to their parents. *Trends Ecol. Evol.* 10:67–71
- Balkau BJ, Feldman MW. 1973. Selection for migration modification. *Genetics* 74:171–74
- Berlocher SH, Feder JL. 2002. Sympatric speciation in phytophagous insects: Moving

- beyond controversy? *Annu. Rev. Entomol.* 47:773–815
- Bigelow RS. 1965. Hybrid zones and reproductive isolation. *Evolution* 19:449–58
- Bordenstein SR, Drapeau MD, Werren JH. 2000. Intraspecific variation in sexual isolation in the jewel wasp *Nasonia*. *Evolution* 54:567–73
- Boughman JW. 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature* 411:944–48
- Buckley PA. 1969. Disruption of species-typical behavior patterns in F1 hybrid *Agapornis* parrots. *Zeit. Tierpsychologie* 26:737–47
- Butlin R. 1987. Speciation by reinforcement. *Trends Ecol. Evol.* 2:8–13
- Cain ML, Andreasen V, Howard D. 1999. Reinforcing selection is effective under a relatively broad set of conditions in a mosaic hybrid zone. *Evolution* 53:1343–53
- Carvajal AR, Gandarela MR, Naveira HF. 1996. A three-locus system of interspecific incompatibility underlies male inviability in hybrids between *Drosophila buzzatii* and *D. koepferae*. *Genetica* 98:1–19
- Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661–96
- Cox RT, Carlton CE. 1991. Evidence of genetic dominance of the 13-year life-cycle in periodical cicadas (Homoptera, Cicadidae, *Magicicada* Spp). *Am. Midl. Nat.* 125:63–74
- Coyne JA. 1992. Genetics of sexual isolation in females of the *Drosophila simulans* species complex. *Genet. Res. Camb.* 60:25–31
- Coyne JA. 1996. Genetics of sexual isolation in male hybrids of *Drosophila simulans* and *D. mauritiana*. *Genet. Res. Camb.* 68:211–20
- Coyne JA, Meyers W, Crittenden AP, Sniegowski P. 1993. The fertility effects of pericentric inversions in *Drosophila melanogaster*. *Genetics* 134:487–96
- Coyne JA, Orr HA. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43:362–81
- Coyne JA, Orr HA. 1997. “Patterns of speciation in *Drosophila*” revisited. *Evolution* 51:295–303
- Coyne JA, Orr HA. 1998. The evolutionary genetics of speciation. *Philos. Trans. R. Soc. Ser. B* 353:287–305
- Davies N, Aiello A, Mallet J, Pomiankowski A, Silberglied RE. 1997. Speciation in two neotropical butterflies: extending Haldane’s rule. *Proc. R. Soc. London Ser. B* 264:845–51
- Dieckmann U, Doebeli M. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–57
- Dobzhansky T. 1937. *Genetics and the Origin of Species*. New York: Columbia Univ. Press
- Doi M, Matsuda M, Tomaru M, Matsubayashi H, Oguma Y. 2001. A locus for female discrimination behavior causing sexual isolation in *Drosophila*. *Proc. Natl. Acad. Sci. USA* 98:6714–19
- Drossel B, McKane A. 2000. Competitive speciation in quantitative genetic models. *J. Theor. Biol.* 204:467–78
- Feder JL, Opp SB, Wlazlo B, Reynolds K, Go W, Spisak S. 1994. Host fidelity is an effective premating barrier between sympatric races of the apple maggot fly. *Proc. Natl. Acad. Sci. USA* 91:7990–94
- Felsenstein J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35:124–38
- Fisher RA. 1930. *The Genetical Theory of Natural Selection*. Oxford, UK: Clarendon
- Fishman L, Willis JH. 2001. Evidence for Dobzhansky-Muller incompatibilities contributing to the sterility of hybrids between *Mimulus guttatus* and *M. nasutus*. *Evolution* 55:1932–42
- Fishman L, Wyatt R. 1999. Pollinator-mediated competition, reproductive character displacement, and the evolution of selfing in *Arenaria uniflora* (Caryophyllaceae). *Evolution* 53:1723–33
- Gerhardt HC. 1994. Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. *Anim. Behav.* 47:959–69
- Gil D, Gahr M. 2002. The honesty of bird

- song: multiple constraints for multiple traits. *Trends Ecol. Evol.* 17:133–41
- Grafen A. 1990. Biological signals as handicaps. *J. Theor. Biol.* 144:517–46
- Grant BR, Grant PR. 1998. Hybridization and speciation in Darwin's finches: the role of sexual imprinting on a culturally transmitted trait. See Howard & Berlocher 1998, pp. 404–22
- Grant PR. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton, NJ: Princeton Univ. Press. 458 pp.
- Grant PR, Grant BR. 1997a. Genetics and the origin of bird species. *Proc. Natl. Acad. Sci. USA* 94:7768–75
- Grant PR, Grant BR. 1997b. Hybridization, sexual imprinting, and mate choice. *Am. Nat.* 149:1–28
- Hatfield T, Schluter D. 1999. Ecological speciation in sticklebacks: Environment-dependent hybrid fitness. *Evolution* 53: 866–73
- Helbig AJ, Salomon M, Bensch S, Seibold I. 2001. Male-biased gene flow across an avian hybrid zone: evidence from mitochondrial and microsatellite DNA. *J. Evol. Biol.* 14:277–87
- Higashi M, Takimoto G, Yamamura N. 1999. Sympatric speciation by sexual selection. *Nature* 402:523–26
- Hobel G, Gerhardt HC. 2003. Reproductive character displacement in the acoustic system of green treefrogs (*Hyla cinerea*). *Evolution*. 57:894–904
- Holynska M. 2000. Is the spinule pattern on the leg 4 coxopodite a tactile signal in the specific mate recognition system of *Mesocyclops* (Copepoda, Cyclopidae)? *Hydrobiologia* 417:11–24
- Howard DJ. 1993. Reinforcement: Origin, dynamics, and fate of an evolutionary hypothesis. In *Hybrid Zones and the Evolutionary Process*, ed. RG Harrison, pp. 46–69. New York: Oxford Univ. Press
- Howard DJ. 1999. Conspecific sperm and pollen precedence and speciation. *Annu. Rev. Ecol. Syst.* 30:109–32
- Howard DJ, Berlocher SH. 1998. *Endless Forms, Species and Speciation*. New York: Oxford Univ. Press
- Irwin DE, Price T. 1999. Sexual imprinting, learning and speciation. *Heredity* 82:347–54
- Iyengar VK, Reeve HK, Eisner T. 2002. Paternal inheritance of a females moth's mating preference. *Nature* 419:830–832
- Jiggins CD, Naisbit RE, Coe RL, Mallet J. 2001. Reproductive isolation caused by colour pattern mimicry. *Nature* 411:302–5
- Kawata M, Yoshimura J. 2000. Speciation by sexual selection in hybridizing populations without viability selection. *Evol. Ecol. Res.* 2:897–909
- Kawecki TJ. 1996. Sympatric speciation driven by beneficial mutations. *Proc. R. Soc. London Ser. B* 263:1515–20
- Kawecki TJ. 1997. Sympatric speciation via habitat specialization driven by deleterious mutations. *Evolution* 51:1751–63
- Kelly JK, Noor MAF. 1996. Speciation by reinforcement: A model derived from studies of *Drosophila*. *Genetics* 143:1485–97
- King M. 1993. *Species Evolution: The Role of Chromosome Change*. Cambridge: Cambridge Univ. Press
- Kirkpatrick M. 1982. Sexual selection and the evolution of female choice. *Evolution* 36:1–12
- Kirkpatrick M. 2000. Reinforcement and divergence under assortative mating. *Proc. R. Soc. London Ser. B* 267:1649–55
- Kirkpatrick M. 2001. Reinforcement during ecological speciation. *Proc. R. Soc. London Ser. B* 268:1259–63
- Kirkpatrick M, Barton NH. 1997. The strength of indirect selection on female mating preferences. *Proc. Natl. Acad. Sci. USA* 94:1282–86
- Kirkpatrick M, Ravigné V. 2002. Speciation by natural and sexual selection: models and experiments. *Am. Nat.* 159:S22–S35
- Kirkpatrick M, Servedio MR. 1999. The reinforcement of mating preferences on an island. *Genetics* 151:865–84
- Kondrashov AS. 1983. Multilocus model of sympatric speciation I. One character. *Theor. Popul. Biol.* 24:121–35

- Kondrashov AS, Kondrashov FA. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* 400:351–54
- Kondrashov AS, Shpak M. 1998. On the origin of species by means of assortative mating. *Proc. R. Soc. London Ser. B* 265:2273–78
- Lambrechts M, Dhondt AA. 1988. The anti-exhaustion hypothesis—a new hypothesis to explain song performance and song switching in the great tit. *Anim. Behav.* 36:327–34
- Lamnisou K, Loukas M, Zouros E. 1996. Incompatibilities between Y chromosome and autosomes are responsible for male hybrid sterility in crosses between *Drosophila virilis* and *Drosophila texana*. *Heredity* 26:603–9
- Lande R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* 78:3721–25
- Levitan DR. 2002. The relationship between conspecific fertilization success and reproductive isolation among three congeneric sea urchins. *Evolution* 56:1599–609
- Liou LW, Price TD. 1994. Speciation by reinforcement of premating isolation. *Evolution* 48:1451–59
- Lloyd M, Kritsky G, Simon C. 1983. A simple mendelian model for 13-year and 17-year life-cycles of periodical cicadas, with historical evidence of hybridization between them. *Evolution* 37:1162–80
- Lofstedt C, Hansson BS, Roelofs W, Bengtsson BO. 1989. No linkage between genes-controlling female pheromone production and male pheromone response in the european corn-borer, *Ostrinia-nubilalis* Hubner (Lepidoptera, Pyralidae). *Genetics* 123:553–56
- Loftus-Hills JJ, Littlejohn ML. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura: Microhylidae): A reexamination. *Evolution* 46:896–906
- Lorenz KZ. 1952. *King Solomon's Ring*. New York: Crowell
- Lynch A, Baker AJ. 1994. A population mimetics approach to cultural evolution in chaffinch song: differentiation among populations. *Evolution* 48:351–59
- Mallet J. 1995. A species definition for the Modern Synthesis. *Trends Ecol. Evol.* 10:294–99
- Mallet J. 1999. Causes and consequences of lack of coevolution in Mullerian mimicry. *Evol. Ecol.* 13:777–806
- Markow TA. 1997. Assortative fertilization in *Drosophila*. *Proc. Natl. Acad. Sci. USA* 94:7756–60
- McPhail JD. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*)—morphological and genetic-evidence for a species pair in Enos Lake, British Columbia. *Can. J. Zool. Rev. Can. Zool.* 62:1402–8
- McPhail JD. 1992. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*)—evidence for a species-pair in Paxton Lake, Texada Island, British Columbia. *Can. J. Zool. Rev. Can. Zool.* 70:361–69
- Michalak P, Grzesik J, Rafinski J. 1997. Tests for sexual incompatibility between two newt species, *Triturus vulgaris* and *Triturus montandioni*: No-choice mating design. *Evolution* 51:2045–50
- Moore JA. 1957. An embryologist's view of the species concept. In *The Species Problem*, ed. E Mayr, pp. 325–38. Washington, D.C.: Am. Assoc. Adv. Sci.
- Muller HJ. 1942. Isolating mechanisms, evolution and temperature. *Biol. Symp.* 6:71–125
- Munding PC. 1982. Microgeographic and macrogeographic variation in acquired vocalizations in birds. In *Acoustic Communication in Birds*, ed. DE Kroodsma, EH Miller, 2:147–208. New York: Academic
- Nagel L, Schluter D. 1998. Body size, natural selection, and speciation in sticklebacks. *Evolution* 52:209–18
- Naisbit RE, Jiggins CD, Mallet J. 2001. Disruptive sexual selection against hybrids contributes to speciation between *Heliconius cydno* and *Heliconius melpomene*. *Proc. R. Soc. London Ser. B* 268:1849–54
- Navarro A, Barton NH. 2003. Accumulating postzygotic isolation genes in parapatry: a new twist on chromosomal speciation. *Evolution* 57:447–59

- Noor MAF. 1995. Speciation driven by natural selection in *Drosophila*. *Nature* 375:674–75
- Noor MAF. 1997a. Genetics of sexual isolation and courtship dysfunction in male hybrids of *Drosophila pseudoobscura* and *D. persimilis*. *Evolution* 51:809–15
- Noor MAF. 1997b. How often does sympatry affect sexual isolation in *Drosophila*? *Am. Nat.* 149:1156–63
- Noor MAF. 1999. Reinforcement and other consequences of sympatry. *Heredity* 83:503–8
- Noor MAF, Grams KL, Bertucci LA, Almandarez Y, Reiland J, Smith KR. 2001a. The genetics of reproductive isolation and the potential for gene exchange between *Drosophila pseudoobscura* and *D. persimilis* via backcross hybrid males. *Evolution* 55:512–21
- Noor MAF, Grams KL, Bertucci LA, Reiland J. 2001b. Chromosomal inversions and the reproductive isolation of species. *Proc. Natl. Acad. Sci. USA* 98:12084–88
- Nosil P, Crespi BJ, Sandoval CP. 2003. Reproductive isolation driven by the combined effects of ecological adaptation and reinforcement. *Proc. R. Soc. London Ser. B*. In press
- Orr HA. 1987. Genetics of male and female sterility in hybrids of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics* 116:555–63
- Orr HA. 1995. The population genetics of speciation: the evolution of hybrid incompatibilities. *Genetics* 139:1805–13
- Orr HA, Irving S. 2001. Complex epistasis and the genetic basis of hybrid sterility in the *Drosophila pseudoobscura* Bogota-USA hybridization. *Genetics* 158:1089–100
- Ortiz-Barrientos D, Reiland J, Hey J, Noor MAF. 2002. Recombination and the divergence of hybridizing species. *Genetica* 116:167–78
- Palopoli MF, Wu C-I. 1994. Genetics of hybrid male sterility between *Drosophila* sibling species: a complex web of epistasis is revealed in interspecific studies. *Genetics* 138:329–41
- Pantazidis AC, Galanopoulos VK, Zouros E. 1993. An autosomal factor from *Drosophila arizonae* restores spermatogenesis in *Drosophila mojavensis* males carrying the *D. arizonae* Y chromosome. *Genetics* 134:309–18
- Pashley DP, Martin JA. 1987. Reproductive incompatibility between host strains of the fall armyworm (Lepidoptera: Noctuidae). *Ann. Ent. Soc. Amer.* 80:731–33
- Payne RJH, Krakauer DC. 1997. Sexual selection, space, and speciation. *Evolution* 51:1–9
- Pfennig KS, Simovich MA. 2002. Differential selection to avoid hybridization in two toad species. *Evolution* 56:1840–48
- Podos J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409:185–88
- Presgraves DC. 2002. Patterns of postzygotic isolation in Lepidoptera. *Evolution* 56:1168–83
- Price TD. 2003. Causes of post-mating reproductive isolation in birds. *Acta Zoologica Sinica*. In press
- Price TD, Bouvier MM. 2002. The evolution of F1 postzygotic incompatibilities in birds. *Evolution* 56:2083–89
- Powell DP. 1998. Sex linkage and speciation in Lepidoptera. See Howard & Berlocher 1998, pp. 309–19
- Rawson PD, Burton RS. 2002. Functional coadaptation between cytochrome c and cytochrome c oxidase within allopatric populations of a marine copepod. *Proc. Natl. Acad. Sci. USA* 99:12955–58
- Rice WR. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evol. Ecol.* 1:301–14
- Rundle HD. 2002. A test of ecologically dependent postmating isolation between sympatric sticklebacks. *Evolution* 56:322–29
- Rundle HD, Schluter D. 1998. Reinforcement of stickleback mating preferences: Sympatry breeds contempt. *Evolution* 52:200–8
- Rundle HD, Whitlock MC. 2001. A genetic interpretation of ecologically dependent isolation. *Evolution* 55:198–201

- Sætre GP, Borge T, Lindroos K, Haavie J, Sheldon BC, et al. 2003. Sex chromosome evolution and speciation in *Ficedula* flycatchers. *Proc. R. Soc. London Ser. B* 270:53–59
- Sætre GP, Kral M, Bures S, Ims RA. 1999. Dynamics of a clinal hybrid zone and a comparison with island hybrid zones of flycatchers (*Ficedula hypoleuca* and *F-albicollis*). *J. Zool.* 247:53–64
- Sætre G-P, Moum T, Bures S, Kral M, Adamjan M, Moreno J. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* 387:589–92
- Sanderson N. 1989. Can gene flow prevent reinforcement? *Evolution* 43:1223–35
- Sasa MM, Chippindale PT, Johnson NA. 1998. Patterns of postzygotic isolation in frogs. *Evolution* 52:1811–20
- Schilthuizen M, Lombaerts M. 1995. Life on the edge—a hybrid zone in *Albinaria-hippolyti* (Gastropoda, Clausiliidae) from Crete. *Biol. J. Linn. Soc.* 54:111–38
- Schluter D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* 16:372–80
- Schoener TW. 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240–85
- Searcy WA, Yasukawa K. 1996. The reproductive success of secondary females relative to that of monogamous and primary females in Red-winged Blackbirds. *J. Avian Biol.* 27:225–30
- Servedio MR. 2000. Reinforcement and the genetics of nonrandom mating. *Evolution* 54:21–29
- Servedio MR. 2001. Beyond reinforcement: The evolution of premating isolation by direct selection on preferences and postmating, prezygotic incompatibilities. *Evolution* 55:1909–20
- Servedio MR, Kirkpatrick M. 1997. The effects of gene flow on reinforcement. *Evolution* 51:1764–72
- Servedio MR, Sætre GP. 2003. Speciation as a positive feedback loop between post- and prezygotic barriers to gene flow. *Proc. R. Soc. London Ser. B*. In press
- Slabbekoorn H, Smith TB. 2002. Bird song, ecology and speciation. *Philos. Trans. R. Soc. London Ser. B* 357:493–503
- Sota T, Kubota K. 1998. Genital lock-and-key as a selective agent against hybridization. *Evolution* 52:1507–13
- Sperling FAH. 1994. Sex-linked genes and species-differences in Lepidoptera. *Can. Entomol.* 126:807–18
- Swanson WJ, Vacquier VD. 2002. The rapid evolution of reproductive proteins. *Nat. Rev. Genet.* 3:137–44
- Ting C-T, Takahashi A, Wu C-I. 2001. Incipient speciation by sexual isolation in *Drosophila*: Concurrent evolution at multiple loci. *Proc. Natl. Acad. Sci. USA* 98:6709–13
- Trickett AJ, Butlin RK. 1994. Recombination suppressors and the evolution of new species. *Heredity* 73:339–45
- Turelli M, Barton NH, Coyne JA. 2001. Theory and speciation. *Trends Ecol. Evol.* 16:330–43
- Turelli M, Orr HA. 1995. The dominance theory of Haldane's Rule. *Genetics* 140:389–402
- Turelli M, Orr HA. 2000. Dominance, epistasis and the genetics of postzygotic isolation. *Genetics* 154:1663–79
- Vamosi SM, Schluter D. 1999. Sexual selection against hybrids between sympatric stickleback species: Evidence from a field experiment. *Evolution* 53:874–79
- van Doorn GS, Noest AJ, Hogeweg P. 1998. Sympatric speciation and extinction driven by environment dependent sexual selection. *Proc. R. Soc. London Ser. B* 265:1915–19
- Via S, Hawthorne DJ. 2002. The genetic architecture of ecological specialization: Correlated gene effects on host use and habitat choice in pea aphids. *Am. Nat.* 159:S76–S88
- Volterra V. 1926. Variations and fluctuations in the numbers of individuals of animal species living together. *Nature* 118:558–60
- Vos DR. 1995. The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Anim. Behav.* 50:645–53
- Walker TJ. 1974. Character displacement and acoustic insects. *Amer. Zool.* 14:1137–50
- Wasserman M, Koepfer HR. 1977. Character displacement for sexual isolation between

- Drosophila mojavensis* and *Drosophila arizonensis*. *Evolution* 31:812–23
- White MJD. 1969. Chromosomal rearrangements and speciation in animals. *Annu. Rev. Genet.* 3:75–98
- Williams MA, Blouin AG, Noor MAF. 2001. Courtship songs of *Drosophila pseudoobscura* and *D. persimilis*. II. Genetics of species differences. *Heredity* 86:68–77
- Willett CS, Burton RS. 2001. Viability of cytochrome C depends on cytoplasmic backgrounds in *Tigriopus californicus*. *Evolution* 55:1592–99
- Wu C-I, Davis AW. 1993. Evolution of postmating reproductive isolation: The composite nature of Haldane's Rule and its genetic bases. *Am. Nat.* 142:187–212
- Wullschleger EB, Wiehn J, Jokela J. 2002. Reproductive character displacement between the closely related freshwater snails *Lymnaea peregra* and *L. ovata*. *Evol. Ecol. Res.* 4:247–57
- Yoshimura J, Clark CW. 1994. Population-dynamics of sexual and resource competition. *Theor. Popul. Biol.* 45:121–31
- Zouros E. 1981. The chromosomal basis of sexual isolation in two sibling species of *Drosophila*: *D. arizonensis* and *D. mojavensis*. *Genetics* 97:703–18
- Zouros E, Lofdahl K, Martin PA. 1988. Male hybrid sterility in *Drosophila*: Interactions between autosomes and sex chromosomes in crosses of *D. mojavensis* and *D. arizonensis*. *Evolution* 42:1321–31

CONTENTS

EFFECTS OF INTRODUCED BEES ON NATIVE ECOSYSTEMS, <i>Dave Goulson</i>	1
AVIAN SEXUAL DICHROMATISM IN RELATION TO PHYLOGENY AND ECOLOGY, <i>Alexander V. Badyaev and Geoffrey E. Hill</i>	27
PALEOBIOGEOGRAPHY: THE RELEVANCE OF FOSSILS TO BIOGEOGRAPHY, <i>Bruce S. Lieberman</i>	51
THE ECOLOGY OF BIRD INTRODUCTIONS, <i>Richard P. Duncan, Tim M. Blackburn, and Daniel Sol</i>	71
THE EFFECTS OF GENETIC AND GEOGRAPHIC STRUCTURE ON NEUTRAL VARIATION, <i>Brian Charlesworth, Deborah Charlesworth, and Nicholas H. Barton</i>	99
DATA, MODELS, AND DECISIONS IN US MARINE FISHERIES MANAGEMENT: LESSONS FOR ECOLOGISTS, <i>Kenneth A. Rose and James H. Cowan Jr.</i>	127
PARTITIONING OF TIME AS AN ECOLOGICAL RESOURCE, <i>Noga Kronfeld-Schor and Tamar Dayan</i>	153
PERFORMANCE COMPARISONS OF CO-OCCURRING NATIVE AND ALIEN INVASIVE PLANTS: IMPLICATIONS FOR CONSERVATION AND RESTORATION, <i>Curtis C. Daehler</i>	183
GENETIC VARIATION IN RARE AND COMMON PLANTS, <i>Christopher T. Cole</i>	213
THE ECOLOGY AND EVOLUTION OF INSECT BACULOVIRUSES, <i>Jenny S. Cory and Judith H. Myers</i>	239
LATITUDINAL GRADIENTS OF BIODIVERSITY: PATTERN, PROCESS, SCALE, AND SYNTHESIS, <i>M.R. Willig, D.M. Kaufman, and R.D. Stevens</i>	273
RECENT ADVANCES IN THE (MOLECULAR) PHYLOGENY OF VERTEBRATES, <i>Axel Meyer and Rafael Zardoya</i>	311
THE ROLE OF REINFORCEMENT IN SPECIATION: THEORY AND DATA, <i>Maria R. Servedio and Mohamed A.F. Noor</i>	339
EXTRA-PAIR PATERNITY IN BIRDS: CAUSES, CORRELATES, AND CONFLICT, <i>David F. Westneat and Ian R.K. Stewart</i>	365

SPECIES-LEVEL PARAPHYLY AND POLYPHYLY: FREQUENCY, CAUSES, AND CONSEQUENCES, WITH INSIGHTS FROM ANIMAL MITOCHONDRIAL DNA, <i>Daniel J. Funk and Kevin E. Omland</i>	397
PROTECTIVE ANT-PLANT INTERACTIONS AS MODEL SYSTEMS IN ECOLOGICAL AND EVOLUTIONARY RESEARCH, <i>Martin Heil and Doyle McKey</i>	425
FUNCTIONAL MATRIX: A CONCEPTUAL FRAMEWORK FOR PREDICTING PLANT EFFECTS ON ECOSYSTEM PROCESSES, <i>Valerie T. Eviner and F. Stuart Chapin III</i>	455
EFFECTS OF HABITAT FRAGMENTATION ON BIODIVERSITY, <i>Lenore Fahrig</i>	487
SOCIAL ORGANIZATION AND PARASITE RISK IN MAMMALS: INTEGRATING THEORY AND EMPIRICAL STUDIES, <i>Sonia Altizer, Charles L. Nunn, Peter H. Thrall, John L. Gittleman, Janis Antonovics, Andrew A. Cunningham, Andrew P. Dobson, Vanessa Ezenwa, Kate E. Jones, Amy B. Pedersen, Mary Poss, and Juliet R.C. Pulliam</i>	517
THE COMMUNITY-LEVEL CONSEQUENCES OF SEED DISPERSAL PATTERNS, <i>Jonathan M. Levine and David J. Murrell</i>	549
THE ECOLOGY AND EVOLUTION OF SEED DISPERSAL: A THEORETICAL PERSPECTIVE, <i>Simon A. Levin, Helene C. Muller-Landau, Ran Nathan, and Jérôme Chave</i>	575
ANALYSIS OF RATES OF MORPHOLOGIC EVOLUTION, <i>Peter D. Roopnarine</i>	605
DEVELOPMENT AND THE GENETICS OF EVOLUTIONARY CHANGE WITHIN INSECT SPECIES, <i>Paul M. Brakefield, Vernon French, and Bas J. Zwaan</i>	633
FLEXIBILITY AND SPECIFICITY IN CORAL-ALGAL SYMBIOSIS: DIVERSITY, ECOLOGY, AND BIOGEOGRAPHY OF SYMBIODINIUM, <i>Andrew C. Baker</i>	661
INDEXES	
Subject Index	691
Cumulative Index of Contributing Authors, Volumes 30–34	705
Cumulative Index of Chapter Titles, Volumes 30–34	708
ERRATA	
An online log of corrections to <i>Annual Review of Ecology, Evolution, and Systematics</i> chapters may be found at http://ecolsys.annualreviews.org/errata.shtml	