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## PERSPECTIVE: REPRODUCTIVE ISOLATION CAUSED BY NATURAL SELECTION AGAINST IMMIGRANTS FROM DIVERGENT HABITATS

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**Abstract.**—The classification of reproductive isolating barriers laid out by Dobzhansky and Mayr has motivated and structured decades of research on speciation. We argue, however, that this classification is incomplete and that the unique contributions of a major source of reproductive isolation have often been overlooked. Here, we describe reproductive barriers that derive from the reduced survival of immigrants upon reaching foreign habitats that are ecologically divergent from their native habitat. This selection against immigrants reduces encounters and thus mating opportunities between individuals from divergently adapted populations. It also reduces the likelihood that successfully mated immigrant females will survive long enough to produce their hybrid offspring. Thus, natural selection against immigrants results in distinctive elements of premating and postmating reproductive isolation that we hereby dub “immigrant inviability.” We quantify the contributions of immigrant inviability to total reproductive isolation by examining study systems where multiple components of reproductive isolation have been measured and demonstrate that these contributions are frequently greater than those of traditionally recognized reproductive barriers. The relevance of immigrant inviability is further illustrated by a consideration of population-genetic theory, a review of selection against immigrant alleles in hybrid zone studies, and an examination of its participation in feedback loops that influence the evolution of additional reproductive barriers. Because some degree of immigrant inviability will commonly exist between populations that exhibit adaptive ecological divergence, we emphasize that these barriers play critical roles in ecological modes of speciation. We hope that the formal recognition of immigrant inviability and our demonstration of its evolutionary importance will stimulate more explicit empirical studies of its contributions to speciation.

**Key words.**—Ecological speciation, habitat isolation, host races, hybrid fitness, isolating mechanisms, local adaptation, reproductive barriers, sexual isolation.

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Scientists expect their conceptual terminology to provide precise and complete descriptions of the phenomena to which they are applied. Terminological ambiguity impedes scientific progress because concepts often structure the thought, motivate the research, and influence the interpretations of scientists (Keller and Lloyd 1992). Concepts play a particularly important role in evolutionary biology (Mayr 1997). Consider the classification of reproductive isolating mechanisms laid out by Dobzhansky (1937) and Mayr (1942, 1963; see Table 1), a conceptual structure that has profoundly influenced thinking about the speciation process and the history of speciation studies (Coyne and Orr 2004). This classification aims to present, in chronological order of occurrence, the totality of intrinsic biological tendencies that might im-

pede the mating of individuals from two populations and the meeting and mixing of their alleles across generations. It also illustrates how the naming of concepts affects our thinking.

For example, the term “isolating mechanism” was itself originally coined to reflect the view that reproductive isolation functioned as an adaptation that preserved coadapted gene pools (Fisher 1930, p. 130; Dobzhansky 1937). However, criticism of this adaptive interpretation of reproductive isolation and of the continued use of isolating mechanism terminology (e.g., Paterson 1982) motivated the introduction of the term “reproductive barrier” as an adaptively neutral alternative. Nonetheless, the original conceptual classification has continued to motivate various research programs to evaluate the roles of traditionally recognized reproductive

TABLE 1. An extended classification of intrinsic reproductive barriers, or isolating mechanisms. Novel additions to the traditional classification are presented in boldface. This paper treats immigrant inviability; papers discussing other novel barriers are cited below.\*

Form of reproductive isolation	Description
Premating, prezygotic barriers	
Temporal, allochronic isolation	reduced encounters of potential mates due to different mating times
Habitat, ecological isolation	reduced encounters of potential mates due to different mating sites
<b>Immigrant inviability, premating</b>	reduced encounters of potential mates due to mortality of maladapted immigrants
Sexual, behavioral, ethological isolation	reduced mating due to divergent courtship signals, mate preferences
Postmating, prezygotic barriers	
Mechanical isolation	reduced transfer of sperm during mating due to poor genitalic compatibility
Gametic incompatibility	reduced fertilization of eggs by ill-suited sperm
Postmating, postzygotic barriers	
<b>Immigrant inviability, postmating</b>	reduced production of offspring due to mortality of mated, maladapted immigrants
Zygotic mortality	reduced survival of zygotes soon after fertilization
Hybrid inviability (genetic)	reduced survival of hybrid offspring independent of the environment
<b>Hybrid inviability (ecological)<sup>1</sup></b>	reduced survival of hybrid offspring where viability is environment dependent
<b>Sexual selection against hybrids<sup>2</sup></b>	reduced mating success of hybrid offspring
Hybrid sterility	reduced fertility of hybrid offspring
F <sub>2</sub> breakdown	reduced survival or fertility of subsequent hybrid generations

\* Modified from Mayr (1963), Futuyma (1998).

<sup>1</sup> Schluter (2000), Rundle and Whitlock (2001).

<sup>2</sup> Schluter (2000), Naisbit et al. (2001).

barriers in speciation (Coyne and Orr 2004). For example, much recent work on the ecology of speciation has specifically focused on demonstrating the consequences of ecological population divergence for mating time (temporal isolation) and place (habitat isolation) and for hybrid inviability (Arnold 1997; Schluter 2000; Berlocher and Feder 2002; Drès and Mallet 2002; Funk et al. 2002; Rundle 2002).

If the suite of currently classified reproductive barriers is truly comprehensive, then empirically evaluating each of them should allow the accurate quantification of total reproductive isolation between populations and of the relative contributions of particular reproductive barriers (e.g., Ramsey et al. 2003). But what if it is incomplete? In this paper, we describe and evaluate a distinct yet unnamed and understudied category of reproductive barrier.

#### THE CONCEPT OF IMMIGRANT INVIABILITY

In providing the first widely read definitions of what Mayr (1963, p. 92) would later refer to as “prematuring” isolating mechanisms, Dobzhansky (1937, p. 231–232) offered the following descriptions: (1) ecological isolation (“habitat isolation” as used by Mayr [1963] and throughout this paper) exists when “the potential parents are confined to different habitats (ecological stations) in the same general region, and therefore seldom or never come together, at least during the reproductive age or season”; (2) temporal isolation exists when “the representatives of two or more species reach the adult stage at a different season, or the breeding periods fall at different times of the year”; and (3) sexual isolation exists when “copulation does not occur because of the lack of mutual attraction between the individuals of different species.”

Thus, following Dobzhansky and Mayr, a knowledge of the willingness of two populations to mate in each others’ habitats, their overlap in mating time, and their acceptance of each other as mates should be sufficient to predict the overall frequency of matings between them and thus their degree of prematuring isolation. However, this is not neces-

sarily the case. To understand why, imagine the following scenario: two populations mate over the same time period, migrate to and mate within each others’ habitats as readily as their own, and accept mates from each population with equal frequency. Guided by the traditional classification, one would expect random mating between these populations. However, imagine further that due to genetically based adaptive differentiation of these populations, individuals migrating to the foreign habitat survive there at a lower rate than do the native residents of that habitat. Under this scenario, interpopulation matings will be reduced relative to intrapopulation matings because some proportion of immigrants will die in the less-suitable foreign habitat prior to mating. In this way, gene flow will be restricted through a degree of positively assortative mating (Table 1). Furthermore, those immigrant females that do survive and mate may nonetheless perish before they have produced all or any of their potential offspring, further reducing potential opportunities for genetic exchange through hybrid progeny.

Following Futuyma’s (1998) definition of an isolating mechanism as “a genetically determined difference between populations that restricts or prevents gene flow between them,” the lowered survivorship of ill-adapted unmated or mated immigrants constitute legitimate reproductive barriers, which we dub prematuring and postmating “immigrant inviability,” respectively. In many respects, immigrant inviability barriers represent prezygotic analogs to the postzygotic hybrid inviability that results when ecologically divergent parents produce ecologically ill-adapted hybrid offspring (e.g., Rundle 2002). Thus, we find it striking that the former has received little explicit attention as a reproductive barrier per se, whereas the latter has been the focus of appreciable recent study (for review, Arnold and Hodges 1995; Arnold 1997; Emms and Arnold 1997; Wang et al. 1997; Hatfield and Schluter 1999; Campbell and Waser 2001; Rundle and Whitlock 2001; Rundle 2002). These observations notwithstanding, Coyne and Orr (2004) have recently included hab-

itat-associated fitness differences as contributors to prezygotic isolation. These authors classify these contributions under habitat isolation, thus pooling them with the habitat preference traits more traditionally associated with this reproductive barrier.

Although we agree with Coyne and Orr's consideration of these novel elements of reproductive isolation, we also believe that they should be considered and classified separately from habitat isolation because habitat isolation and immigrant inviability are biologically and chronologically distinct. Whereas Dobzhansky (1937) and Mayr (1963, p. 12) described habitat isolation in terms of a lack of migration to foreign habitats, immigrant inviability reflects the reduced survival of those individuals that do indeed successfully migrate to the foreign habitat (Table 1). This biological difference can be further appreciated by the fact that habitat-associated preference and viability traits may often result from different genes, as reflected in their treatment as independent variables in many speciation models (e.g., Coyne and Orr 2004, p. 130). This biological independence means that these two types of barriers can act in isolation of each other, such that studying one may possibly provide no insight on the other and the contributions of each must be independently assessed. Such independent assessments of habitat isolation and immigrant inviability will facilitate study of the important evolutionary interactions between them that are discussed later in this paper. None of these insights are possible if these distinctive phenomena are not appropriately distinguished. This is not merely a semantic distinction, but an important ontological one.

At this point, we should be clear about the relationship between the concerns of this paper and the contributions of previous students and models of speciation, many of which have invoked habitat-associated fitness differences between populations. For example, as pointed out by Coyne and Orr (2004, p. 131), various models of sympatric speciation, from the classic work of Maynard Smith (1966) and Felsenstein (1981) onwards, treat speciation as the evolution of particular combinations of assortative mating, niche preference, and niche adaptation (i.e., habitat-associated fitness). In these models, habitat-associated fitness differences are described as contributing to speciation primarily through their pleiotropic association with or by being in linkage disequilibrium with traits causing assortative mating (i.e., forms of reproductive isolation other than immigrant inviability). However, habitat-associated fitness is not itself described as a source of reproductive isolation per se in these models. Hybrid zone and parapatric speciation models come closer to treating habitat-associated fitness differences as an isolating barrier in their incorporation of selection against ill-adapted alleles and their recognition of the reduction in gene flow that results (e.g., Slatkin 1973; Endler 1977; Barton 1983; Gavrilets 2000, 2004). Here, we call for the more widespread and explicit recognition that habitat associated fitness differences, in and of themselves, are a source of reproductive isolation that act through the above-described mechanisms of immigrant inviability.

We should also be clear that some other authors have implicitly or explicitly recognized selection against immigrants as a cause of reproductive isolation (for theoretical treatment

see Hendry 2004). For example, elevated predation on *Heliconius* butterfly mimics that immigrate to regions occupied by different wing-pattern races has long been identified as a cause of reproductive isolation (e.g., Mallet 1989; Mallet and Barton 1989; Mallet et al. 1998). Via and coworkers have distinguished between host plant choice (i.e., habitat isolation) and selection against immigrants as complementary causes of host-associated reproductive isolation between clover- and alfalfa-associated pea aphids (Via 1999; Via et al. 2000). Funk (1998) coined the term "physiological isolation" to describe the premating and postmating reproductive isolation resulting from the death of ill-adapted insect immigrants on unsuitable host plants prior to mating or ovipositing, respectively. Other workers have undoubtedly made related observations (e.g., Young 1996; Nagy and Rice 1997; Hendry et al. 2000; Riechert and Hall 2000; Riechert et al. 2001; Nosil 2004).

Why then has immigrant inviability not been more generally recognized as a reproductive barrier? Perhaps this is because most students of divergent adaptation are understandably less interested in reproductive isolation, while students of prezygotic barriers focus on the reproductive behavior of living individuals rather than on the selective processes determining who survives to mate. Perhaps this is because of the foreignness of the concept of selection *as* reproductive isolation, which describes immigrant inviability, as opposed to the more familiar idea of selection *promoting* the evolution of reproductive barriers. Perhaps this simply reflects the fact that these barriers have not previously been named (but see Funk 1998) and so have not been highlighted as a defined subject of study. Here, we recommend formally inserting the premating and postmating elements of immigrant inviability within the accepted classification of reproductive barriers (Table 1).

#### THE PREVALENCE AND IMPORTANCE OF IMMIGRANT INVIABILITY

For the reasons described above, there exists little in the way of literature that explicitly quantifies the contributions of immigrant inviability to reproductive isolation. However, the role of immigrant inviability in a given study system can nonetheless be quantified given published data on relative viability in native versus foreign habitats that are occupied by potential mates, plus data on additional reproductive barriers.

#### *Literature Survey I: Identifying Studies on Adaptive Population Divergence*

We identified study systems with data appropriate for these calculations by surveying the literature on reciprocal transplant experiments and local adaptation. Such investigations often provide estimates of immigrant and resident viability for each study population with regard to their respective habitats and are thus designed to detect the divergent adaptation that results in immigrant inviability. To identify pertinent literature, we conducted two searches using the Web of Science (Thomson ISI). For the first, we searched on the topic of "reciprocal transplant\*" with no restrictions on journal of publication. For the second, we searched on the topic of

“local\* adapt\*” while restricting the journals searched to *The American Naturalist*, *Ecology*, *Evolution*, *Evolutionary Ecology*, *Evolutionary Ecology Research*, *Journal of Evolutionary Biology*, *Oecologia*, and *Oikos*. This restriction was necessary because more than 16,000 papers were recovered otherwise, almost entirely from irrelevant sources. Using the abstracts of papers from both searches, we eliminated non-pertinent papers (i.e., those that did not present studies of adaptive divergence in congeneric populations). For each of the remaining papers, we conducted a further literature search to identify any studies of reproductive isolation conducted on the focal species. Thus, we searched on the topic of “[species name] AND (isolation or barrier\* or gene flow or speciation\*)” and then scanned titles and abstracts to identify appropriate literature. In this way, we identified taxa for which data had been collected that were relevant to immigrant inviability plus at least one other reproductive barrier.

#### Quantifying Contributions to Reproductive Isolation

In general, we quantified each reproductive barrier as described below. Sexual isolation was estimated as described because data on all four possible sex  $\times$  population mating combinations were not available for many studies, precluding the use of more powerful estimators (Rolán-Alvarez and Cabarello 2000). When a reproductive barrier was studied more than once in a system, we averaged results across studies. These cases did not appreciably affect our conclusions, however, because separate studies tended to yield similar results. See online Supplementary Materials (available at <http://dx.doi.org/10-1554/04-428.1.s1>) for details concerning each study system.

The values of reproductive barriers were calculated as follows: habitat isolation (choice experiments) =  $1 - (\% \text{ of trials where foreign habitat was chosen})$ ; habitat isolation (no-choice experiments) =  $1 - (\% \text{ of trials where foreign habitat was accepted})$ ; immigrant inviability =  $1 - (\text{immigrant viability/resident viability})$ ; sexual isolation =  $1 - (\text{heterotypic mating frequency/homotypic mating frequency})$ ; floral (pollinator) isolation =  $1 - (\text{no. cross-species foraging bouts/total no. foraging bouts})$ ; pollen competition =  $1 - (\text{no. hybrids in mixed pollination crosses/no. parentals in homotypic crosses})$ ; hybrid inviability (genetic) =  $1 - (\text{hybrid viability/parental viability})$ ; hybrid inviability (ecological) =  $1 - (\text{hybrid ecological fitness/parental ecological fitness})$ ; sexual selection against hybrids =  $1 - (\text{hybrid mating success/parental mating success})$ .

For each of our study systems, we calculated the individual, absolute, and relative contributions of each studied barrier to reproductive isolation, as well as the total reproductive isolation between study populations (Tables 2, 3). These values may range from negative infinity through zero (no reproductive isolation) to one (complete reproductive isolation). Negative values indicate increased gene flow relative to the random expectation, as, for example, under negatively assortative mating. Individual contributions indicate the magnitude of reproductive isolation caused by a particular reproductive barrier if it were to act in isolation. Absolute contributions indicate the magnitude of reproductive isolation caused by a particular reproductive barrier considering

the restrictions on gene flow already contributed by previously acting barriers. Thus, if the individual contribution of two reproductive barriers are equal, the barrier that acts later in a species' life history will make a smaller absolute contribution because the earlier barrier will have already reduced the number of individuals that might potentially be removed by the later barrier. As suggested by Ramsey et al. (2003), the absolute contribution (AC) of a component of reproductive isolation (i.e., of the individual contribution, RI) at stage  $n$  in the life history was calculated as:

$$AC_1 = RI_1, \quad (1)$$

$$AC_2 = RI_2(1 - AC_1), \quad \text{and} \quad (2)$$

$$AC_3 = RI_3[1 - (AC_1 + AC_2)], \quad (3)$$

and more generally

$$AC_n = RI_n \left( 1 - \sum_{i=1}^{n-1} AC_i \right). \quad (4)$$

Total reproductive isolation can be calculated either by multiplying across the individual contributions of all barriers or by summing across the absolute contributions of all barriers, an approach proposed by Coyne and Orr (1989) for two components of reproductive isolation and extended to  $n$  components by Ramsey et al. (2003). Thus, for  $m$  components of isolation, total reproductive isolation (T) may be calculated as:

$$T = \sum_{i=1}^m AC_i. \quad (5)$$

Finally, the relative contribution of a particular barrier to total reproductive isolation indicates the proportion of the total reproductive isolation due to the absolute contributions of that barrier. The relative contribution (RC) of an individual component at stage  $n$  in life history is thus:

$$RC_n = \frac{AC_n}{T}. \quad (6)$$

We calculated these measures of reproductive isolation using the Excel (Microsoft, Redmond, WA) spreadsheet employed by Ramsey et al. 2003, available at <http://www.plantbiology.msu.edu/schemske.shtml>.

#### Results

The existence of ecologically divergent and locally adapted populations is now well documented and widely recognized (e.g., Mopper and Strauss 1998). Furthermore, the great biological generality of this phenomenon was suggested by a literature review (Schluter 2000) that identified evidence for local adaptation in 36 of 42 pertinent studies. Our own literature review further suggests that the direct relevance of such divergent adaptation for reproductive isolation is rarely evaluated. To wit, of 145 plant and metazoan genera recovered by our literature search on reciprocal transplant experiments testing for local adaptation, only 13 included species that have also been studied with respect to specific reproductive barriers. By including some additional systems not recovered by our searches, we assembled 20 pertinent pop-

TABLE 2. Study systems for which contributions of multiple reproductive barriers to reproductive isolation were quantified (see Tables 3, 4). These represent taxa for which data from both reciprocal transplant experiments and additional assays of reproductive isolation were available. This table presents information on the populations, species, or forms compared; the aspect of fitness assayed; the site of the transplant experiments; and the putative source of selection yielding the observed divergent adaptation.

Study system	Common name	Form 1	Form 2	Fitness measure(s)	Lab or field?	Putative agent(s) of selection	Pertinent references
<i>Acyrtosiphon pisum</i>	pea aphids	clover host race	alfalfa host race	fecundity	field	physiological adaptation	Via 1999; Via et al. 2000
<i>Agelenopsis aperta</i>	desert spider	arid land	riparian	survival	field	food availability, predation risk	Riechert and Hall 2000; Riechert et al. 2001
<i>Artemisia tridentata</i>	big sagebrush	basin subspecies	mountain subspecies	survival, growth	field	—	Wang et al. 1997
<i>Bombina</i> spp.	toads	pond-adapted <i>B. bombina</i>	puddle-adapted <i>B. variegata</i>	survival, growth	both	biophysical conditions, predation	MacCallum et al. 1995, 1998; Kruuk and Gilchrist 1997; Kruuk et al. 1999a
<i>Eurosta solidaginis</i>	galling fly	<i>E. s. altissima</i> race	<i>E. s. gigantean</i> race	survival	lab	physiological adaptation	Craig et al. 1993, 1997, 2001
<i>Galerucella nymphaeae</i>	water lily leaf beetle	Nymphaeaceae race	Polygonaceae race	survival	lab	physiological adaptation, feeding ability	Pappers et al. 2002a,b
<i>Galerucella</i> spp.	water lily leaf beetle	<i>G. nymphaeae</i>	<i>G. sagittariae</i>	survival	lab	physiological adaptation	Nokkala and Nokkala 1998
<i>Gasterosteus aculeatus</i>	freshwater stickleback	limnetic	benthic	growth, survival	field	foraging efficiency, competition, predation	Schluter 1993, 1994, 1995; Hatfield and Schluter 1999; Rundle 2002; Vamosi 2002
<i>Gilia capitata</i>	herbaceous plant	inland subspecies	coastal subspecies	survival	field	biophysical conditions	Nagy 1997a,b; Nagy and Rice 1997
<i>Heliconius erato</i>	mimetic butterflies	postman	rayed	longevity	field	visual predation	Mallet 1989; Mallet and Barton 1989; Mallet et al. 1998
<i>Ipomopsis</i> spp.	phlox	<i>I. aggregata</i>	<i>I. tenuituba</i>	survival	field	biophysical factors	Campbell and Waser 2001; Campbell 2003; Campbell et al. 2003
<i>Iris</i> spp. 1	perennial flowers	<i>I. douglasiana</i>	<i>I. innominata</i>	survival	field	biophysical factors	Young 1996
<i>Iris</i> spp. 2	perennial flowers	<i>I. fulva</i>	<i>I. hexagona</i>	survival	field	—	Emms and Arnold 1997
<i>Littorina saxatilis</i>	intertidal snails	upper shore	lower shore	survival	field	physical factors, predation	Johannesson et al. 1993; Roldán-Alvarez et al. 1997
<i>Mimulus</i> spp.	monkeyflower	<i>M. lewisii</i>	<i>M. cardinalis</i>	survival, ecogeographic isolation <sup>1</sup>	field	climatic conditions	Hiesey et al. 1971; Ramsey et al. 2003
<i>Mitoura</i> spp.	butterfly	host races	host races	survival	lab	physiological adaptation	Forister 2004
<i>Neochlamisus bebbianae</i>	leaf beetles	<i>Acer</i> host form	<i>Betula</i> , <i>Salix</i> host forms	survival	lab	physiological adaptation	Funk 1998
<i>Polemonium viscosum</i>	alpine flower	Krummholz low elevation	Summit high elevation	survival	field	climatic conditions	Galen and Kevan 1980; Galen 1985; Galen et al. 1991
<i>Rhagoletis</i> spp.	fruit flies	<i>R. mendax</i>	<i>R. pomonella</i>	survival	lab	physiological adaptation	Bierbaum and Bush 1990
<i>Timema cristinae</i>	cryptic walking-sticks	<i>Ceanothus</i> host form	<i>Adenostoma</i> host form	survival	field	visual predation	Sandoval 1993, 1994a,b; Nosil et al. 2002, 2003; Nosil 2004; Nosil and Crespi 2004

<sup>1</sup> See online supplementary material (<http://dx.doi.org/10.1554/04-428.1.s1>) for explanation.

TABLE 3. Individual components of reproductive isolation for focal study systems (see Table 2). Note that environment-independent (genetic) and environment-dependent (ecological) aspects of hybrid inviability are treated separately. Values may range from negative infinity through zero (no reproductive isolation) to 1.0 (complete reproductive isolation). The negative values in this table indicate cases where hybrid viability exceeded that of parents, a phenomenon that would actually increase gene flow. See text for details of calculations.

Study system	Habitat isolation	Immigrant inviability	Sexual/floral isolation	Pollen competition	Hybrid inviability (genetic)	Hybrid inviability (ecological)	Sexual selection on hybrids
<i>Acyrtosiphon pisum</i>	0.927	0.970	—	—	0.000	0.470	—
<i>Agelenopsis aperta</i>	—	0.632	0.06	—	-0.15	—	—
<i>Artemisia tridentata</i>	—	0.900	—	—	—	-5.250	—
<i>Bombina</i> spp.	0.660	0.437	—	—	0.190	—	—
<i>Eurosta solidaginis</i>	0.962	0.877	0.365	—	0.000	0.344	—
<i>Galerucella nymphaeae</i>	0.855	0.772	0.000	—	0.000	0.322	—
<i>Galerucella</i> spp.	0.904	0.938	—	—	0.000	-0.710	—
<i>Gasterosteus aculeatus</i>	—	0.363	0.633	—	0.000	0.255	0.777
<i>Gilia capitata</i>	—	0.704	—	0.800	0.813	—	—
<i>Heliconius erato</i>	0.000	0.520	0.000	—	0.000	0.450	—
<i>Ipomopsis</i> spp.	—	0.429	—	—	0.000	-0.125	0.155
<i>Iris</i> spp. 1	0.000	0.955	0.000	—	-0.620	—	—
<i>Iris</i> spp. 2	—	0.087	—	—	—	-0.008	—
<i>Littorina saxatilis</i>	0.742	0.691	0.518	—	0.000	-0.259	0.000
<i>Mimulus</i> spp.	—	0.587	0.976	0.833	0.415	—	—
<i>Mitoura</i> spp.	0.696	0.208	—	—	0.000	—	—
<i>Neochlamisus bebbianae</i>	0.947	0.990	0.720	—	—	—	—
<i>Polemonium viscosum</i>	—	0.795	0.140	—	—	—	—
<i>Rhagoletis</i> spp.	0.555	0.368	—	—	—	0.606	—
<i>Timema cristinae</i>	0.252	0.340	0.222	—	—	—	—

ulation comparisons for our calculations, representing arthropod, mollusk, vertebrate, and plant taxa (Table 2).

These calculations reveal that immigrant inviability commonly represents a strong reproductive barrier, often stronger than more conventionally studied barriers such as sexual isolation (Tables 3, 4, Fig. 1). Indeed, among reproductive barriers evaluated in more than two study systems, only the contributions of habitat isolation were found to be comparably high. Our analyses thus suggest that immigrant inviability commonly represents a biologically important reproductive barrier. This conclusion does not depend on the high absolute contribution of immigrant inviability, which partly reflects the early life-history stage at which these reproductive barriers act. Although absolute and relative contributions are indeed high, so too are individual contributions, which are the data we present in Figure 1. These individual contributions show that immigrant inviability, even when acting alone, is capable of considerably restricting gene flow between divergently adapted populations.

#### HYBRID ZONES AND IMMIGRANT INVIABILITY

Hybrid zones can be profitably exploited for studies of speciation and the contributions of various reproductive barriers to reproductive isolation (Harrison 1990). The inherently spatial nature of hybrid zones provides opportunities to address the role of immigrant inviability because the structure of hybrid zones depends on the strength of reproductive isolation and rate of dispersal. Selection against immigrants (i.e., immigrant inviability) may therefore play a major role in the structure and maintenance of hybrid zones. Mosaic hybrid zones (Harrison and Rand 1989), those with genetic structures that are spatially patchy rather than clinal, are of particular relevance to immigrant inviability. Mosaic hybrid zones can be formed by long-distance dispersal into the pre-

viously unoccupied region between two advancing populations (Nichols and Hewitt 1994; Ibrahim et al. 1996). However, when a close correspondence between particular genotypes and discernible environmental patches is observed, this explanation is implausible (Barton and Hewitt 1985). In such situations, the patchiness of these zones is more readily attributed to some combination of active habitat preference on the one hand and selection against immigrant alleles on the other.

Reciprocal transplant experiments that demonstrate the divergent ecological adaptation of hybridizing taxa to their respective habitat patches provide direct evidence for the role of immigrant inviability in maintaining mosaic hybrid zones. Phenotypic differentiation of these populations that is apparently associated with divergent habitats provides more indirect evidence of this phenomenon. Additional indirect evidence is found when genetic structure is associated with habitat patches, yet experiments reveal no evidence for divergent habitat preferences in the hybridizing populations. In such instances, immigrant inviability seems the most plausible alternative explanation even in the absence of explicit tests of habitat-associated fitness. Furthermore, because habitat preferences are unlikely to evolve in the absence of local adaptation (Rice and Hostert 1993), it could be argued that the demonstration of divergent habitat preferences itself constitutes indirect evidence for immigrant inviability.

#### Literature Survey II: Identifying Studies on Mosaic Hybrid Zones

We identified mosaic hybrid zone study systems through a Web of Science search on the topic of "mosaic\* AND hybrid\* AND zone\*" and through following references listed in these papers. Among the recovered studies, we selected those study systems for which hybrid zones were explicitly

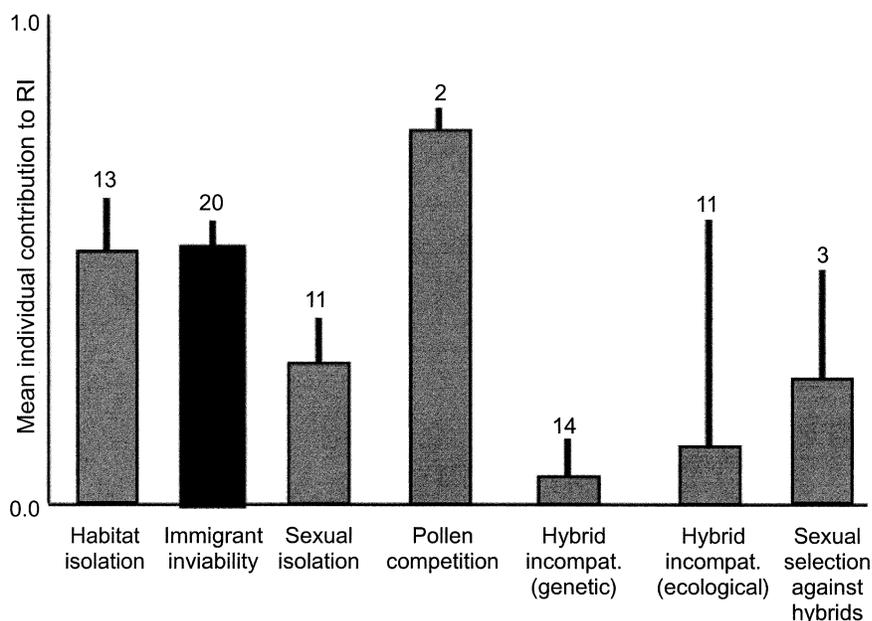


FIG. 1. Mean individual contributions ( $\pm$  SE) to reproductive isolation across reproductive barriers. Each bar represents mean values across those study systems for which data for that barrier were available (see Table 3 for raw data). Numbers above bars indicate number of systems contributing data. One extreme datapoint was excluded in the calculation for the bar for ecological hybrid inviability. Including this datapoint (from a study in which hybrid fitness was much higher than parental fitness) yields a mean value slightly less than zero. Note the high value for immigrant inviability relative to traditionally recognized reproductive barriers.

described as mosaics by authors or that presented a map showing one or more spatial patches within the hybrid zone. For each such study system, we investigated associated literature to determine whether authors observed evidence for the following with respect to parental genotypes: (1) a spatial correspondence between an environmental variable and phenotypes within the zone; (2) divergent habitat preferences (e.g., MacCallum et al. 1998; Vines et al. 2003); and (3) habitat-associated performance/viability differences or phenotypic divergence suggestive of same.

#### Results of Literature Survey

Our second literature survey identified 27 mosaic hybrid zones (Table 5). Twenty of these (74%) are habitat associated, a pattern that itself is highly suggestive of a common role for ecological adaptation in hybrid zone maintenance. This proportion may overestimate or underestimate the fraction of mosaic zones that are truly habitat associated, depending on which is more likely to be overlooked and understudied: habitat-independent zones or cryptic mosaic-associated environmental variables, respectively. Our primary interest, however, was in how commonly immigrant inviability appears to act in habitat-structured zones.

On this point, our survey revealed that only two of these 20 hybrid zones exhibited clear evidence of divergent adaptation and thus direct evidence for immigrant inviability. However, eight more zones showed putatively adaptive phenotypic divergence, providing indirect evidence for this phenomenon. Studies on an additional six zones provided evidence against divergent habitat preferences, leaving anti-immigrant selection as the most plausible cause for the habitat association. Of the remaining four habitat-associated zones,

three have not been evaluated for either habitat preference or divergent adaptation. Thus, of 17 habitat-associated mosaic hybrid zones in which the necessary data have been collected, direct or (mostly) indirect evidence for immigrant inviability has been found in 16. Although this survey indicates the need for additional and direct experimental investigations on divergent adaptation in mosaic hybrid zones, it also is highly consistent with a general role for immigrant inviability in their maintenance.

#### THEORETICAL AND POPULATION GENETIC ASPECTS

From a population-genetic perspective, selection against immigrants has generally been regarded as roughly equivalent to selection against heterozygotes with respect to maintaining reproductive isolation in the face of migration (Barton and Gale 1993; Kruuk et al. 1999b). This position stems from the observation that clines maintained by a balance between migration and either form of selection are the same width under a wide range of conditions (Kruuk et al. 1999b). However, there are several theoretical reasons why selection against immigrants may be able to maintain population differentiation under higher levels of migration than selection against heterozygotes.

Consider a simple mainland-island model, where the island population receives immigrants at rate  $m$  from the mainland population. These two populations differ at a single biallelic locus. The frequency of allele  $A$  is denoted by  $p$ , and its frequency is initially assumed to be close to 1.0 on the island. The frequency of the alternative allele  $a$  is denoted by  $q$  and is assumed to be fixed on the mainland. Under this scenario, when selection only acts against heterozygotes it must be relatively strong to maintain the local allele. For example,

TABLE 4. Absolute and relative contributions to total reproductive isolation of investigated barriers from focal study systems (see Table 2). Also presented are estimates of total reproductive isolation that were calculated both with and without the contribution of immigrant inviability. Note that environment-independent (genetic) and environment-dependent (ecological) aspects of hybrid inviability are treated separately. These calculations assume that immigrant inviability occurs prior to sexual/floral isolation during life history. However, for systems where sexual/floral isolation has been evaluated we also provide estimates (in parentheses) of the lower bound on the contribution of immigrant inviability assuming that sexual/floral isolation acts prior to immigrant inviability. Values ordinarily range from negative infinity through zero (no reproductive isolation) to 1.0 (complete reproductive isolation). The negative values in this table indicate cases where hybrid viability exceeded that of parentals, a phenomenon that would actually increase gene flow. The values that are >1.0 represent unusual artifacts of the method of calculating relative/absolute contributions to reproductive isolation when certain individual components are negative. See text for details of calculations.

Study system	Habitat isolation	Immigrant inviability	Sexual/floral isolation	Pollen competition	Hybrid inviability (genetic)	Hybrid inviability (ecological)	Sexual selection on hybrids	Total isolation	Total isolation (no immigrant inviability)
<i>Acyrtosiphon pisum</i>									
absolute	0.927	0.071	—	—	0.000	0.001	—	0.999	0.961
relative	0.928	0.071	—	—	0.000	0.001	—		
<i>Agelenopsis aperta</i>									
absolute	—	0.632 (0.594)	0.022 (0.060)	—	-0.052	—	—	0.602	-0.080
relative	—	1.05 (0.986)	0.04 (0.10)	—	-0.086	—	—		
<i>Artemisia tridentata</i>									
absolute	—	0.900	—	—	—	-0.525	—	0.375	-5.25
relative	—	2.400	—	—	—	-1.400	—		
<i>Bombina</i> spp.									
absolute	0.660	0.148	—	—	0.036	—	—	0.844	0.725
relative	0.781	0.176	—	—	0.040	—	—		
<i>Eurosta solidaginis</i>									
absolute	0.962	0.034 (0.021)	0.002 (0.014)	—	0.000	0.001	—	0.998	0.984
relative	0.964	0.034 (0.021)	0.002 (0.014)	—	0.000	0.001	—		
<i>Galerucella nymphaeae</i>									
absolute	0.855	0.112	0.000	—	—	0.011	—	0.978	0.902
relative	0.875	0.115	0.000	—	—	0.011	—		
<i>Galerucella</i> spp.									
absolute	0.904	0.090	—	—	0.000	-0.004	—	0.990	0.836
relative	0.914	0.091	—	—	0.000	-0.004	—		
<i>Gasterosteus aculeatus</i>									
absolute	—	0.363 (0.133)	0.403 (0.663)	—	0.000	0.060	0.135	0.961	0.939
relative	—	0.378 (0.139)	0.419 (0.658)	—	0.000	0.062	0.141		
<i>Gilia capitata</i>									
absolute	—	0.703	—	0.238	0.048	—	—	0.989	0.963
relative	—	0.711	—	0.240	0.049	—	—		
<i>Heliconius erato</i>									
absolute	0.000	0.520	0.000	—	0.000	0.216	—	0.736	0.450
relative	0.000	0.707	0.000	—	0.000	0.293	—		
<i>Ipomopsis</i> spp.									
absolute	—	0.429	—	—	0.000	-0.071	0.100	0.457	0.049
relative	—	0.938	—	—	0.000	-0.156	0.218		
<i>Iris</i> spp. 1									
absolute	0.000	0.945	0.000	—	-0.028	—	—	0.926	-0.619
relative	0.000	1.030	0.000	—	-0.030	—	—		
<i>Iris</i> spp. 2									
absolute	—	0.0868	—	—	—	-0.008	—	0.079	-0.008
relative	—	1.092	—	—	—	-0.092	—		
<i>Littorina saxatilis</i>									
absolute	0.742	0.179 (0.086)	0.041 (0.134)	—	0.000	-0.010	0.000	0.953	0.843
relative	0.779	0.188 (0.090)	0.043 (0.141)	—	0.000	-0.011	0.000		
<i>Mimulus</i> spp.									
absolute	—	0.587 (0.014)	0.403 (0.976)	0.008	0.001	—	—	0.999	0.998
relative	—	0.588 (0.014)	0.403 (0.977)	0.008	0.001	—	—		
<i>Mitoura</i> spp.									
absolute	0.696	0.063	—	—	0.000	—	—	0.759	0.696
relative	0.917	0.083	—	—	0.000	—	—		

TABLE 4. Continued.

Study system	Habitat isolation	Immigrant inviability	Sexual/floral isolation	Pollen competition	Hybrid inviability (genetic)	Hybrid inviability (ecological)	Sexual selection on hybrids	Total isolation	Total isolation (no immigrant inviability)
<i>Neochlamisus bebbianae</i>									
absolute	0.947	0.053 (0.015)	0.000 (0.038)	—	—	—	—	1.000	0.985
relative	0.947	0.053 (0.015)	0.000 (0.038)	—	—	—	—		
<i>Polemonium viscosum</i>									
absolute	—	0.795 (0.684)	0.029 (0.140)	—	—	—	—	0.824	0.140
relative	—	0.965 (0.830)	0.035 (0.170)	—	—	—	—		
<i>Rhagoletis</i> spp.									
absolute	0.556	0.163	—	—	—	0.170	—	0.889	0.825
relative	0.625	0.184	—	—	—	0.191	—		
<i>Timema cristinae</i>									
absolute	0.252	0.254 (0.198)	0.110 (0.166)	—	—	—	—	0.616	0.418
relative	0.409	0.413 (0.321)	0.178 (0.269)	—	—	—	—		

under random mating, the fitness of heterozygote hybrids must be about 92% that of homozygotes (i.e.,  $s \sim 0.08$ ) to preserve the local allele when  $m$  is only 0.01. The minimum value of  $s$  increases to about 0.62 when  $m = 0.1$ , and when the migration rate exceeds 0.2, even a hybrid fitness of zero cannot preserve the local allele. This is because some  $AA$  individuals are inevitably involved in  $AA \times aa$  matings each generation and produce offspring that die, resulting in the loss of  $A$  alleles. This problem does not affect  $aa$  genotypes because their numbers are more than replenished every generation by migration. Furthermore, given  $p < 0.5$  prior to migration, any amount of selection against heterozygotes will actually decrease the frequency of the island allele. In contrast, if selection favors genotypes that are adapted to the island environment, then, providing there is no dominance, selection will be capable of countering higher immigration rates because both  $Aa$  and  $aa$  will have low fitness. Indeed, Haldane (1932, p. 122) showed that as long as  $s > m$  the island allele will be maintained, and thus any amount of immigration can potentially be countered by selection (see also Slatkin 1981; Vines et al. 2003).

These observations indicate that selection against immigrants may play a critical role in facilitating speciation in the face of gene flow. They show that populations can more readily diverge adaptively and maintain critical levels of reproductive isolation when immigrant inviability is acting to counter the potential effects of migration on gene flow.

#### FURTHER IMPLICATIONS OF IMMIGRANT INVIABILITY

So far, we have pointed out that divergent ecological adaptation commonly results in strong reproductive barriers that we refer to as “immigrant inviability.” Like other reproductive barriers, immigrant inviability restricts gene flow between populations and in this way may obviously and directly contribute to speciation. In this section, however, we discuss some additional evolutionary implications of immigrant inviability for population differentiation and speciation (Fig. 2).

For example, immigrant inviability can select for population divergence in mating preferences through forms of selection that are analogous to reinforcement (e.g., Servedio 2001). In this case, it is not the threat of producing unfit

hybrid offspring that selects for discrimination against foreign (i.e., immigrant) mates (Dobzhansky 1937; for review, see Servedio and Noor 2003); instead, it is the increased likelihood that one’s immigrant mate will die before producing offspring. The same logic applies if residents themselves exhibit reduced survival as a function of mating with immigrants. Studies of *Timema* stick insect populations associated with two host plants provide examples of both these phenomena (Nosil et al. 2003). Two points are relevant: each host-associated population of these insects has a pattern that is more cryptic on its native host, and these animals mate for extended periods of time. The result is that matings between residents and immigrants yield elevated rates of predation on the ill-camouflaged immigrants as well as on residents while they are in copula with their conspicuous mates. Furthermore, the reduced viability of immigrants in foreign habitats should favor alleles that increase the degree of preference for the native habitat and thus reduce immigration to foreign habitats, yielding increased habitat isolation (for theory, see Balkau and Feldman 1973; Rice and Hostert 1993; Kruuk and Gilchrist 1997; Via et al. 2000). Because local adaptation appears to be common, this strengthening of habitat isolation should be a general phenomenon, though empirical tests are lacking.

Immigrant inviability also participates in various feedback loops that may influence the evolutionary dynamics of the speciation process. Consider, for example, the selection for increased habitat preference discussed above. Such increased restriction to a particular habitat should increasingly result in specialized adaptations to that habitat as countervailing selection pressures associated with other, increasingly ignored, habitats correspondingly decrease. This process will thus promote increased adaptive divergence and immigrant inviability between populations in a positive feedback loop. However, the strength of this feedback should ultimately fade due to decreasing numbers of immigrants, and thus diminishing selection for habitat preference, each generation (Hendry 2004).

Like any reproductive barrier, immigrant inviability restricts the homogenizing force of gene flow (Slatkin 1987; Lenormand 2002), facilitating reinforcement (for review, see

TABLE 5. Evidence on ecological divergence in mosaic hybrid zones. HA, habitat-associated genetic structure; HP, evidence for divergent habitat preferences; DA, evidence for divergent ecological adaptation. The term "indirect" in the DA column denotes evidence for local adaptation stemming from phenotypic divergence (see text for details). A question mark indicates an absence of pertinent data. Patch type refers to the environmental feature putatively responsible for the mosaic.

Hybridizing taxa	Type	HA?	Patch type	HP?	DA?	Source
<i>Allonemobius fasciatus</i> × <i>A. socius</i>	cricket	yes	temperature	?	?	Howard 1986; Britch et al. 2001
<i>Ambystoma tigrinum</i> subspecies	tiger salamander	yes	elevation and vegetation	?	?	Jones and Collins 1992
<i>Baptisia sphaerocarpa</i> × <i>B. leucophaea</i>	false indigo	yes	soil type	no	?	Alston and Turner 1963; Leebens-Mack and Milligan 1998
<i>Bombina bombina</i> × <i>B. variegata</i>	fire-bellied toad	yes	aquatic habitat	yes	indirect	MacCallum et al. 1995, 1998; Kruuk et al. 1997; Vines et al. 2003
<i>Bufo americanus</i> × <i>B. fowleri</i>	toad	yes	vegetation type	?	?	Green and Parent 2003
<i>Chamerion angustifolium</i> diploid × tetraploid	fireweed	?	n/a	no	?	Husband and Schemske 1997
<i>Chorthippus brunneus</i> × <i>C. jacobsi</i>	cricket	yes	vegetation	no	?	Bridle et al. 2001; Bailey et al. 2004
<i>Gryllus pennsylvanicus</i> × <i>G. firmus</i>	cricket	yes	soil type	?	indirect	Rand and Harrison 1989
<i>Iris fulva</i> × <i>I. brevicaulis</i>	iris	yes	light and soil water	no	indirect	Cruzan and Arnold 1993; Johnston et al. 2001
<i>Iris fulva</i> × <i>I. hexagona</i>	iris	yes	light and soil water	no	yes	Arnold and Bennett 1993; Emms and Arnold 1997
<i>Limnoperus dissoritis</i> × <i>L. notabilis</i>	water strider	no	—	no	?	Sperling and Spence 1991
<i>Littorina saxatilis</i> morphs	snail	yes	humidity and exposure	yes	yes	Otero-Schmitt et al. 1997; Rolán-Alvarez et al. 1997
<i>Monobella grassiei</i> subspecies	springtail	no	—	no	?	Deharveng et al. 1998
<i>Mus musculus domesticus</i> chromosomal races	mouse	no	—	no	?	Hauffe and Searle 1993
<i>Mytilus edulis</i> × <i>M. galloprovincialis</i>	mussel	yes	exposure and salinity	yes	indirect	Bierne et al. 2003
<i>Nucella lapillus</i> races	dog whelk	yes	humidity and exposure	?	indirect	Kirkby et al. 1997
<i>Palaemonetes kadiakensis</i> type A × type B	grass shrimp	?	—	?	?	Garcia and Davis 1994
<i>Papilio canadensis</i> × <i>P. glaucus</i>	butterfly	yes	host plants and temperature	?	indirect	Hagen 1990; Scriber 2002
<i>Piriiqueta caroliniana</i> × <i>P. viridis</i>	piriqueta	yes	soil type	no	?	Martin and Cruzan 1999
<i>Polystichum imbricans</i> × <i>P. munitum</i>	fern	yes	light and soil water	no	?	Kentner and Mesler 2000
<i>Quercus affinis</i> × <i>Q. laurina</i>	oak	yes	elevation and soil type	no	indirect	Ganzález-Rodríguez et al. 2004
<i>Quercus grisea</i> × <i>Q. gambelii</i>	oak	yes	elevation and soil type	no	?	Howard et al. 1997
<i>Ranunculus lappaceus</i> group (7 species)	buttercup	yes	soil water	no	?	Briggs 1962
<i>Sceloporus grammicus</i> chromosomal races	lizard	yes	oak/pine	yes	?	Sites et al. 1995
<i>Solenopsis invicta</i> × <i>S. richteri</i>	fire ant	no	—	no	?	Shoemaker et al. 1996
<i>Triturus cristatus</i> × <i>T. marmoratus</i>	newt	yes	aquatic habitat	yes	indirect	Arntzen and Wallis 1991
<i>Triturus vulgaris</i> × <i>T. montandoni</i>	newt	no	n/a	no	?	Babik and Rafinski 2001

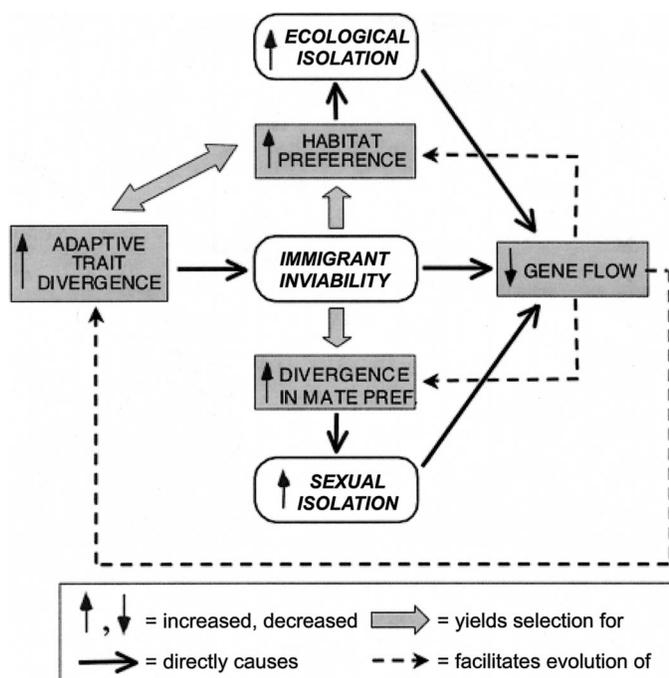


FIG. 2. A diagrammatic summary of the various direct and indirect effects of immigrant inviability on other aspects of adaptive divergence and reproductive isolation and of the resulting evolutionary feedback loops in which it participates. See text for details.

Servedio and Noor 2003), divergent adaptation, and increased immigrant inviability. Notably, this increased adaptive divergence may itself indirectly (pleiotropically) contribute to the evolution of any reproductive barrier (Mayr 1942, 1963; Funk 1998; Hendry et al. 2000, 2001; Schluter 2000; Jiggins et al. 2001; Nosil et al. 2002, 2003; Presgraves et al. 2003). These relationships describe additional feedback loops (Hendry 2004) that, together with those described above, may have complex dynamics and interactions, with important consequences for speciation. Additional theoretical treatment of all these issues is needed.

Lastly, it is perhaps in the context of the recent renaissance in the study of ecological speciation (Schluter 2000; Funk et al. 2002) that immigrant inviability will be of the broadest interest to evolutionary biologists. Many reproductive barriers may evolve in the absence of ecological divergence, such as through environment-independent sexual selection, sexual conflict between the sexes (Arnqvist et al. 2000; Martin and Hosken 2003) or genetic drift (Templeton 1980). In contrast, premating and postmating immigrant inviability (along with ecological hybrid inviability: Schluter 2000; Rundle and Whitlock 2001; Rundle 2002) should usually evolve only when populations have ecologically diverged, and thus are inherently ecological reproductive barriers. Intriguingly, immigrant inviability also softens theoretical objections to sympatric speciation, in two respects. First, because selection itself is the cause of reproductive isolation (i.e., reduced gene flow), the same genes affecting fitness also affect reproductive isolation. Thus, a pleiotropic relationship exists between reduced (immigrant) fitness and assortative mating (due to immigrant mortality) that obviates

the oft-cited need for a genetic association between separate loci controlling habitat-associated fitness and mating preferences (Felsenstein 1981; for reviews of speciation models see Kirkpatrick and Ravigne 2002; Gavrillets 2004). Second, it represents direct selection on genes promoting reproductive isolation and so should be more effective than indirect selection acting through imperfect genetic associations (Kirkpatrick and Barton 1997).

#### CAVEATS AND QUALIFIERS

Before concluding this paper, we raise a few issues that bear on the importance of immigrant inviability as compared to other reproductive barriers. Most basically, it should be reiterated that, like other reproductive barriers, immigrant inviability is not an all-or-nothing phenomenon at the population level, even though it may be thought of in these terms (life vs. death) at the individual level. Rather, partial immigrant inviability may be said to act even when some immigrants survive to mate and reproduce in the foreign habitat, as long as the overall rate of immigrant survivorship and reproduction is lower than that of the resident population.

However, it is quite important to recognize that immigrant inviability will come into play only to the extent that migration between habitats occurs, providing the immigrants on which selection might act. Thus, one might predict immigrant inviability to restrict gene flow the most in taxa with particular tendencies, such as: frequent dispersal of both sexes to foreign habitats and a willingness to settle in them; occupation of regions that are ecologically heterogeneous; and a tendency to disperse early in the life history, such that immigrants must long endure habitats they find stressful. Thus, the potential role of immigrant inviability will be intimately linked to the biology of the taxon. For example, it may play a relatively small role in angiosperms that disperse through pollen (e.g., Arnold et al. 1991) rather than the seeds that produce immigrant plant individuals. Nonetheless, this issue is not special to immigrant inviability. Rather, there are particular circumstances and taxa for which each reproductive barrier is relatively more or less likely to play an active role in restricting gene flow. Furthermore, barriers that do not presently restrict gene flow despite their potential to do so should not be overlooked, given the possibility of future changes that might bring them to bear, such as secondary contact between currently separated populations.

On this point, one might argue that the geographic scale of successful migration is relevant for determining whether foreign habitats are reached in the first place. Issues of spatial scale are certainly critical to an understanding of how all premating barriers restrict gene flow. However, an adequate treatment of this issue is beyond the scope of the present paper. Furthermore, we examined how intrinsic factors (i.e., those reflecting genetic variation) rather than geographic factors influence reproductive isolation between coexisting populations. The spatial scale that implicitly underlies our arguments is that of divergent habitats existing within the ordinary movements or cruising ranges of populations. Thus, we are primarily concerned with what happens to immigrants once they have arrived at the foreign habitat, rather than with the factors (e.g., spatial) influencing whether they get there

(for further discussion of geographic vs. reproductive barriers to gene flow see Coyne and Orr 2004).

Finally, a critical but often overlooked issue for speciation studies is the fact that the current contributions of particular reproductive barriers are not necessarily indicative of the historical role they have played in speciation. Consider that, while reproductive barriers evolving early in the speciation process may play a particularly large role in promoting speciation, barriers that evolve after speciation has reached completion may presently obscure the contributions of those earlier barriers. For example, if immigrant inviability drove speciation between two populations, after which strong habitat isolation evolved, a modern investigator might mistakenly conclude that habitat isolation was largely responsible. Evaluating the likely time course for the evolution of reproductive barriers through comparative studies (Etges 2002; Coyne and Orr 2004) will thus be necessary to accurately evaluate the role of immigrant inviability or any reproductive barrier as an actual contributor to speciation.

#### CONCLUSIONS

Collectively, the lines of evidence presented here suggest that the reduced survival of immigrants to foreign environments represents a form of reproductive isolation that likely plays important and diverse roles in the ecology of speciation. We suggest the formal recognition of the twin pre-mating and post-mating elements of immigrant inviability in an extended classification of reproductive barriers. We also hope for increased empirical study of these barriers for their own sake but also in conjunction with other reproductive barriers to further tease apart the relative contributions of each (e.g., Ramsey et al. 2003). The many consequences of immigrant inviability for adaptive differentiation, the evolution of other reproductive barriers, and gene flow provide opportunities for theoretical investigations of the little-studied feedback loops among these phenomena and how these play into speciation dynamics. Increased attention to all these issues will help further our understanding of the complex processes of speciation.

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#### LITERATURE CITED

- Alston, R. E., and B. L. Turner. 1963. Natural hybridization among four species of *Baptisia* (Leguminosae). *Am. J. Bot.* 50:159–173.
- Arnold, M. L. 1997. Natural hybridization and evolution. Oxford Univ. Press, Oxford, U.K.
- Arnold, M. L., and B. D. Bennett. 1993. Natural hybridization in Louisiana irises: genetic variation and ecological determinants. Pp. 115–139 in R. G. Harrison, ed. Hybrid zones and the evolutionary process. Oxford Univ. Press, Oxford, U.K.
- Arnold, M. L., and S. A. Hodges. 1995. Are natural hybrids fit or unfit relative to their parents? *Trends Ecol. Evol.* 10:67–71.
- Arnold, M. L., C. M. Buckner, and J. J. Robinson. 1991. Pollen-mediated introgression and hybrid speciation in Louisiana irises. *Proc. Natl. Acad. Sci.* 88:1398–1402.
- Arnqvist, G., M. Edvardsson, U. Friberg, and T. Nilsson. 2000. Sexual conflict promotes speciation in insects. *Proc. Natl. Acad. Sci. USA* 97:10460–10464.
- Arntzen, J. W., and G. P. Wallis. 1991. Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. *Evolution* 45:805–826.
- Babik, W., and J. Rafinski. 2001. Amphibian breeding site characteristics in the western Carpathians, Poland. *Herpetol. J.* 11: 41–51.
- Bailey, R. I., C. D. Thomas, and R. K. Butlin. 2004. Premating barriers to gene exchange and their implications for the structure of a mosaic hybrid zone between *Chorthippus brunneus* and *C. jacobsi* (Orthoptera: Acrididae). *J. Evol. Biol.* 17:108–119.
- Balkau, B. J., and M. W. Feldman. 1973. Selection for migration modification. *Genetics* 74:171–174.
- Barton, N. H. 1983. Gene flow and speciation. *Heredity* 50:213–223.
- Barton, N. H., and K. S. Gale. 1993. Genetic analysis of hybrid zones. Pp. 13–45 in R. G. Harrison, ed. Hybrid zones and the evolutionary process. Oxford Univ. Press, Oxford, U.K.
- Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16:113–148.
- Berlocher, S. H., and J. L. Feder. 2002. Sympatric speciation in phytophagous insects: Moving beyond controversy? *Annu. Rev. Entomol.* 47:773–815.
- Bierbaum, T. J., and G. L. Bush. 1990. Genetic differentiation in the viability of sibling species of *Rhagoletis* fruit flies on host plants, and the influence of reduced hybrid viability on reproductive isolation. *Entomol. Exp. Appl.* 55:105–118.
- Bierne, N., F. Bonhomme, and P. David. 2003. Habitat preference and the marine-speciation paradox. *Proc. R. Soc. Lond. B* 270: 1399–1406.
- Bridle, J. R., S. J. E. Baird, and R. K. Butlin. 2001. Spatial structure and habitat variation in a grasshopper hybrid zone. *Evolution* 55:1832–1843.
- Briggs, B. G. 1962. Interspecific hybridization in the *Ranunculus lappaceus* group. *Evolution* 16:372–390.
- Britch, S. C., M. L. Cain, and D. J. Howard. 2001. Spatio-temporal dynamics of the *Allonemobius fasciatus*–*A. socius* mosaic hybrid zone: a 14-year perspective. *Mol. Ecol.* 10:627–638.
- Campbell, D. R. 2003. Natural selection in *Ipomopsis* hybrid zones: implications for ecological speciation. *New Phytol.* 161:83–90.
- Campbell, D. R., and N. M. Waser. 2001. Genotype-by-environment interaction and the fitness of plant hybrids in the wild. *Evolution* 55:669–676.
- Campbell, D. R., R. Alarcon, and C. A. Wu. 2003. Reproductive isolation and hybrid pollen disadvantage in *Ipomopsis*. *J. Evol. Biol.* 16:536–540.
- Coyne, J. A., and H. A. Orr. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43:362–381.
- . 2004. Speciation. Sinauer, Sunderland, MA.
- Craig, T. P., J. K. Itami, W. G. Abrahamson, and J. D. Horner. 1993. Behavioral evidence for host-race formation in *Eurosta solidaginis*. *Evolution* 47:1696–1710.
- Craig, T. P., J. D. Horner, and J. K. Itami. 1997. Hybridization studies on the host races of *Eurosta solidaginis*: implications for sympatric speciation. *Evolution* 51:1552–1560.
- . 2001. Genetics, experience, and host-plant preference in *Eurosta solidaginis*: implications for host-shifts and speciation. *Evolution* 55:773–782.
- Cruzan, M. B., and M. L. Arnold. 1993. Ecological and genetic associations in an *Iris* hybrid zone. *Evolution* 47:1432–1445.
- Deharveng, L. A., A. Bedos, and C. Gisclard. 1998. Environmental factors, microgeographic patterns of endemism and hybrid zones in *Monobella grassei* (Insecta: Collembola: Neanuridae). *Biol. J. Linn. Soc.* 64:527–554.

- Dobzhansky, T. 1937. Genetics and the origin of species. Columbia Univ. Press, New York.
- Drès, M., and J. Mallet. 2002. Host races in plant-feeding insects and their importance in sympatric speciation. *Philos. Trans. R. Soc. Lond. B* 357:471–492.
- Emms, S. K., and M. L. Arnold. 1997. The effect of habitat on parental and hybrid fitness: transplant experiments with Louisiana irises. *Evolution* 51:1112–1119.
- Endler, J. A. 1977. Geographic variation, speciation and clines. Princeton Univ. Press, Princeton, NJ.
- Etges, W. J. 2002. Divergence in mate choice systems: Does evolution play by rules? *Genetica* 116:151–166.
- Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35:124–138.
- Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, U.K.
- Forister, M. L. 2004. Oviposition preference and larval performance within a diverging lineage of lycaenid butterflies. *Ecol. Entomol.* 29:264–272.
- Funk, D. J. 1998. Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. *Evolution* 52:1744–1759.
- Funk, D. J., K. E. Filchak, and J. L. Feder. 2002. Herbivorous insects: model systems for the comparative study of speciation ecology. *Genetica* 116:251–267.
- Futuyma, D. 1998. Evolutionary biology. 3rd ed. Sinauer, Sunderland, MA.
- Galen, C. 1985. Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination and resources. *Ecology* 66:792–797.
- Galen, C., and P. G. Kevan. 1980. Scent and color, floral polymorphisms and pollination biology in *Polemonium viscosum*. *Nutt. Am. Midl. Nat.* 104:281–289.
- Galen, C., J. S. Shore, and H. Deyoe. 1991. Ecotypic divergence in alpine *Polemonium viscosum*: genetic structure, quantitative variation, and local adaptation. *Evolution* 45:1218–1228.
- Garcia, D. K., and S. K. Davis. 1994. Evidence for a mosaic hybrid zone in the grass shrimp *Palaemonetes kadiakensis* as revealed by multiple genetic markers. *Evolution* 48:376–391.
- Gavrilets, S. 2000. Waiting time to parapatric speciation. *Proc. R. Soc. Lond. B* 267:2483–2492.
- . 2004. Fitness landscapes and the origin of species. Princeton Univ. Press, Princeton, NJ.
- González-Rodríguez, A., D. M. Arias, S. Valencia, and K. Oyama. 2004. Morphological and RAPD analysis of hybridization between *Quercus affinis* and *Q. laurina* (Fagaceae), two Mexican red oaks. *Am. J. Bot.* 91:401–409.
- Green, D. M., and C. Parent. 2003. Variable and asymmetric introgression in a hybrid zone in the toads, *Bufo americanus* and *Bufo fowleri*. *Copeia* 2003:34–43.
- Hagen, R. H. 1990. Population structure and host use in hybridizing subspecies of *Papilio glaucus* (Lepidoptera: Papilionidae). *Evolution* 44:1914–1930.
- Haldane, J. B. S. 1932. The causes of evolution. Longman, New York.
- Harrison, R. G. 1990. Hybrid zones: windows on evolutionary process. *Oxf. Surv. Evol. Biol.* 7:69–128.
- Harrison, R. G., and D. M. Rand. 1989. Mosaic hybrid zones and the nature of species boundaries. Pp. 110–133 in D. Otte and J. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, MA.
- Hatfield, T., and D. Schluter. 1999. Ecological speciation in sticklebacks: environment dependent hybrid fitness. *Evolution* 53:866–873.
- Hauffe, H. C., and J. B. Searle. 1993. Extreme karyotypic variation in a *Mus musculus domesticus* hybrid zone: the tobacco mouse story revisited. *Evolution* 47:1374–1395.
- Hendry, A. P. 2004. Selection against migrants contributes to the rapid evolution of ecologically dependent reproductive isolation. *Evol. Ecol. Res.* 6:1219–1236.
- Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516–518.
- Hendry, A. P., T. Day, and E. B. Taylor. 2001. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* 55:459–466.
- Hiesey, W. M., M. A. Nobs, and O. Bjorkman. 1971. Experimental studies on the nature of species. V. Biosystematics, genetics, and physiological ecology of the *Erythranthe* section of *Mimulus*. Carnegie Institute of Washington Publication no. 628.
- Howard, D. J. 1986. A zone of overlap and hybridization between two ground cricket species. *Evolution* 40:34–43.
- Howard, D. J., R. W. Preszler, J. Williams, S. Fenchel, and W. J. Boecklen. 1997. How discrete are oak species? Insights from a hybrid zone between *Quercus grisea* and *Quercus gambelii*. *Evolution* 51:747–755.
- Husband, B. C., and D. W. Schemske. 1998. Cytotype distribution at a diploid-tetraploid contact zone in *Chamerion (Epibolium) angustifolium* (Onagraceae). *Am. J. Bot.* 85:1688–1694.
- Ibrahim, K. M., R. A. Nichols, and G. M. Hewitt. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansions. *Heredity* 77:282–291.
- Jiggins, C. D., R. E. Naisbit, R. L. Coe, and J. M. Mallet. 2001. Reproductive isolation caused by colour pattern mimicry. *Nature* 411:302–305.
- Johannesson, K., B. Johannesson, and E. Rolán-Alvarez. 1993. Morphological differentiation and genetic cohesiveness over a microenvironmental gradient in the marine snail *Littorina saxatilis*. *Evolution* 47:1770–1787.
- Johnston, J. A., R. A. Wesselingh, A. C. Bouck, L. A. Donovan, and M. L. Arnold. 2001. Intimately linked or hardly speaking? The relationship between genotype and environmental gradients in a Louisiana iris hybrid population. *Mol. Ecol.* 10:673–681.
- Jones, T. R., and J. P. Collins. 1992. Analysis of a hybrid zone between subspecies of the tiger salamander (*Ambystoma tigrinum*) in central New Mexico, USA. *J. Evol. Biol.* 5:375–402.
- Keller, E. F., and E. A. Lloyd. 1992. Keywords in evolutionary biology. Harvard Univ. Press, Cambridge, MA.
- Kentner, E. K., and M. R. Mesler. 2000. Evidence for natural selection in a fern hybrid zone. *Am. J. Bot.* 87:1168–1174.
- Kirkby, R. R., R. J. Berry, and D. A. Powers. 1997. Variation in mitochondrial DNA in a cline of allele frequencies and shell phenotype in the dog-whelk *Nucella lapillus* (L.). *Biol. J. Linn. Soc.* 62:299–312.
- Kirkpatrick, M., and N. Barton. 1997. The strength of indirect selection on female mating preferences. *Proc. Natl. Acad. Sci. USA* 94:1282–1286.
- Kirkpatrick, M., and V. Ravigne. 2002. Speciation by natural and sexual selection: models and experiments. *Am. Nat.* 159: S22–S35.
- Kruuk, L. E. B., and J. S. Gilchrist. 1997. Mechanisms maintaining species differentiation: predator mediated selection in a *Bombina* hybrid zone. *Proc. R. Soc. Lond. B* 264:105–110.
- Kruuk, L. E. B., J. S. Gilchrist, and N. H. Barton. 1999a. Hybrid dysfunction in fire-bellied toads (*Bombina*). *Evolution* 53: 1611–1616.
- Kruuk, L. E. B., S. J. E. Baird, K. S. Gale, and N. H. Barton. 1999b. A comparison of multilocus clines maintained by environmental adaptation or by selection against hybrids. *Genetics* 153: 1959–1971.
- Leebens-Mack, J., and B. G. Milligan. 1998. Pollination biology in hybridizing *Baptisia* (Fabaceae) populations. *Am. J. Bot.* 84: 500–507.
- Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends Ecol. Evol.* 17:183–189.
- MacCallum, C. J., B. Nurnberger, and N. H. Barton. 1995. Experimental evidence for habitat-dependent selection in a *Bombina* hybrid zone. *Proc. R. Soc. Lond. B* 260:257–264.
- MacCallum, C. J., B. Nurnberger, N. H. Barton, and J. M. Szymura. 1998. Habitat preference in a *Bombina* hybrid zone in Croatia. *Evolution* 52:227–239.
- Mallet, J. 1989. The genetics of warning colour in Peruvian hybrid zones of *Heliconius erato* and *H. melpomene*. *Proc. R. Soc. Lond. B* 236:163–185.
- Mallet, J., and N. H. Barton. 1989. Strong natural selection in a warning-color hybrid zone. *Evolution* 43:421–431.

- Mallet, J., W. O. McMillan, and C. D. Jiggins. 1998. Mimicry and warning color at the boundary between races and species. Pp. 390–403 in D. J. Howard and S. Berlocher, eds. *Endless forms: species and speciation*. Oxford Univ. Press, Oxford, U.K.
- Martin, L. J., and M. B. Cruzan. 1999. Patterns of hybridization in the *Piriqueta caroliniana* complex of central Florida: evidence for an expanding hybrid zone. *Evolution* 53:1037–1049.
- Martin, O. Y., and D. J. Hosken. 2003. The evolution of reproductive isolation through sexual conflict. *Nature* 423:979–981.
- Mayr, E. 1942. *Systematics and the origin of species*. Columbia Univ. Press, New York.
- . 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge, MA.
- . 1997. *This is biology: the science of the living world*. Harvard Univ. Press, Cambridge, MA.
- Maynard Smith, J. 1966. Sympatric speciation. *Am. Nat.* 100: 637–650.
- Mopper, S., and S. Strauss. 1998. Genetic variation and local adaptation in natural insect populations: effects of ecology, life history and behavior. Chapman and Hall, New York.
- Nagy, E. S. 1997a. Frequency-dependent seed production and hybridization rates: implications for gene flow between locally adapted plant populations. *Evolution* 51:703–714.
- . 1997b. Selection for native characters in hybrids between two locally adapted plant subspecies. *Evolution* 51:1469–1480.
- Nagy, E. S., and K. J. Rice. 1997. Local adaptation in two subspecies of an annual plant: implications for migration and gene flow. *Evolution* 51:1079–1089.
- Naisbit, R. E., C. D. Jiggins, and J. Mallet. 2001. Disruptive sexual selection against hybrids contributes to speciation between *Helioconius cydno* and *Helioconius melpomene*. *Proc. R. Soc. Lond. B* 268:1849–1854.
- Nichols, R. A., and G. M. Hewitt. 1994. The genetic consequences of long distance dispersal during colonization. *Heredity* 72: 312–317.
- Nokkala, C., and S. Nokkala. 1998. Species and habitat races in the chrysomelid *Galerucella nymphaeae* species complex in northern Europe. *Entomol. Exp. Appl.* 89:1–13.
- Nosil, P. 2004. Reproductive isolation caused by visual predation against migrants between divergent environments. *Proc. R. Soc. Lond. B* 271:1521–1528.
- Nosil, P., and B. J. Crespi. 2004. Does gene flow constrain adaptive divergence or vice versa? A test using ecomorphology and sexual isolation in *Timema cristinae* walking-sticks. *Evolution* 58: 102–112.
- Nosil, P., B. J. Crespi, and C. Sandoval. 2002. Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* 417:441–443.
- . 2003. Reproductive isolation driven by the combined effects of ecological adaptation and reinforcement. *Proc. R. Soc. Lond. B* 270:1911–1918.
- Otero-Schmitt, J., R. Cruz, C. Garcia, and E. Rolán-Alvarez. 1997. Feeding strategy and habitat choice in *Littorina saxatilis* (Gastropoda: Prosobranchia) and their role in the origin and maintenance of a sympatric polymorphism. *Ophelia* 46:205–216.
- Pappers, S. M., G. Van der Velde, N. J. Ouborg, and Van J. M. Groenendael. 2002a. Genetically based polymorphisms in morphology and life history associated with putative host races of the water lily leaf beetle, *Galerucella nymphaeae*. *Evolution* 56: 1610–1621.
- Pappers, S. M., G. Van der Velde, and N. J. Ouborg. 2002b. Host preference and larval performance suggest host race formation in *Galerucella nymphaeae*. *Oecologia* 130:433–440.
- Paterson, H. E. 1982. Perspective on speciation by reinforcement. *S. Afr. J. Sci.* 78:53–57.
- Presgraves, D. C., L. Balagopalan, S. M. Abmayr, and H. A. Orr. 2003. Adaptive evolution drives divergence of a hybrid inviability gene between two species of *Drosophila*. *Nature* 423: 715–719.
- Ramsey, J., H. D. Bradshaw, Jr., and D. W. Schemske. 2003. Components of reproductive isolation between the monkeyflowers *Mimulus lewisii* and *M. cardinalis* (Phrymaceae). *Evolution* 57: 1520–1534.
- Rand, D. M., and R. G. Harrison. 1989. Ecological genetics of a mosaic hybrid zone: mitochondrial, nuclear, and reproductive differentiation of crickets by soil type. *Evolution* 43:432–449.
- Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on speciation: What have we learned in 40 years? *Evolution* 47: 1637–1653.
- Riechert, S. E., and R. F. Hall. 2000. Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. *J. Evol. Biol.* 13:541–550.
- Riechert, S. E., F. D. Singer, and T. C. Jones. 2001. High gene flow levels lead to gamete wastage in a desert spider system. *Genetica* 112–113:297–319.
- Rolán-Alvarez, E., and A. Caballero. 2000. Estimating sexual selection and sexual isolation effects from mating frequencies. *Evolution* 54:30–36.
- Rolán-Alvarez, E., K. Johannesson, and J. Erlandsson. 1997. The maintenance of a cline in the marine snail *Littorina saxatilis*: the role of home site advantage and hybrid fitness. *Evolution* 51: 1838–1847.
- Rundle, H. 2002. A test of ecologically dependent postmating isolation between sympatric sticklebacks. *Evolution* 56:322–329.
- Rundle, H. D., and M. Whitlock. 2001. A genetic interpretation of ecologically dependent isolation. *Evolution* 55:198–201.
- Sandoval, C. P. 1993. Geographic, ecological and behavioral factors affecting spatial variation in color or morph frequency in the walking-stick *Timema cristinae*. Ph.D. diss. Univ. of California, Santa Barbara, CA.
- . 1994a. The effects of relative geographic scales of gene flow and selection on morph frequencies in the walking-stick *Timema cristinae*. *Evolution* 48:1866–1879.
- . 1994b. Differential visual predation on morphs of *Timema cristinae* (Phasmatodeae: Timemidae) and its consequences for host range. *Biol. J. Linn. Soc.* 52:341–356.
- Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecology* 74:699–709.
- . 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* 266:798–800.
- . 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* 76:82–90.
- . 2000. *The ecology of adaptive radiation*. Oxford Univ. Press, Oxford, U.K.
- Scriber, J. M. 2002. Latitudinal and geographic mosaics in host plant preference as shaped by thermal units and voltinism. *Eur. J. Entomol.* 99:225–239.
- Servedio, M. R. 2001. Beyond reinforcement: the evolution of pre-mating isolation by direct selection on preferences and post-mating, prezygotic incompatibilities. *Evolution* 55:1909–1920.
- Servedio, M., and M. Noor. 2003. The role of reinforcement in speciation: theory and data. *Annu. Rev. Ecol. Syst.* 34:339–364.
- Shoemaker, D. D., K. G. Ross, and M. L. Arnold. 1996. Genetic structure and evolution of a fire ant hybrid zone. *Evolution* 50: 1958–1976.
- Sites, J. W., N. H. Barton, and K. M. Reed. 1995. The genetic structure of a hybrid zone between two chromosome races of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae) in Central Mexico. *Evolution* 49:9–36.
- Slatkin, M. 1973. Gene flow and selection in a cline. *Genetics* 75: 733–756.
- . 1981. Pleiotropy and parapatric selection. *Evolution* 36: 263–270.
- . 1987. Gene flow and the geographic structure of natural populations. *Science* 236:787–792.
- Sperling, F. A. H., and J. R. Spence. 1991. Structure of an asymmetric hybrid zone between two water strider species (Hemiptera: Gerridae: *Limnoporus*). *Evolution* 45:1370–1383.
- Templeton, A. R. 1980. The theory of speciation via the founder principle. *Genetics* 94:1011–1038.
- Vamosi, S. 2002. Predation sharpens the adaptive peaks: survival trade-offs in sympatric sticklebacks. *Ann. Zool. Fenn.* 39:1–28.
- Via, S. 1999. Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. *Evolution* 53:1446–1457.
- Via, S., A. C. Bouck, and S. Skillman. 2000. Reproductive isolation

- between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. *Evolution* 54:1626–1637.
- Vines, T. H., S. C. Köhler, M. Thiel, I. Ghira, T. R. Sands, C. J. MacCallum, N. H. Barton, and B. Nürnberger. 2003. The maintenance of reproductive isolation in a mosaic hybrid zone between the fire-bellied toads *Bombina bombina* and *B. variegata*. *Evolution* 57:1876–1888.
- Wang, H., E. D. McArthur, S. C. Sanderson, J. H. Graham, and D. C. Freeman. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IV. Reciprocal transplant experiments. *Evolution* 51:95–102.
- Young, N. D. 1996. An analysis of the causes of genetic isolation in two Pacific Coast iris hybrid zones. *Can. J. Bot.* 74: 2006–2013.

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