Note

# Assessing the Potential Contributions of Reduced Immigrant Viability and Fecundity to Reproductive Isolation

**Cody K. Porter* and Craig W. Benkman**

Department of Zoology and Physiology, Program in Ecology, University of Wyoming, Laramie, Wyoming 82071

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abstract: Reduced fitness of immigrants from alternative environments is thought to be an important reproductive isolating barrier. Most studies evaluating the importance of the relative fitness of immigrants to speciation have focused on reduced survival of immigrants (i.e., immigrant inviability). However, variation in fecundity appears to have a greater impact on variation in fitness than does variation in viability, suggesting that reduced fecundity of immigrants could act as an important yet largely overlooked reproductive isolating barrier. Using a model and a survey of studies of local adaptation, we evaluate the relative strength of reduced immigrant viability and fecundity as potential causes of reproductive isolation. We found that reduced fecundity as compared to reduced viability as a reproductive isolating barrier should increase in importance as the relative costs of reproduction increase. Consistent with the elevated demands of reproduction reported in the literature, we found that reproductive isolation from reduced immigrant fecundity was of similar magnitude or greater than that from reduced immigrant viability, particularly in the early stages of speciation. These results suggest that the important role of differential fecundity in local adaptation extends to speciation.

## Introduction

Despite substantial interest in speciation, surprisingly little is known about the relative contributions of different reproductive isolating barriers to speciation (Coyne and Orr 2004; Sobel et al. 2010). Many more studies of speciation use genomic approaches to identify genomic regions and ecological correlates to lineage divergence. While genomic analyses provide increasingly powerful tools for investigating patterns of divergence (e.g., Wagner et al. 2013), they alone usually provide only indirect information on the isolating barriers and ecological processes causing speciation (Coyne and Orr 2004). Consequently, the direct study of isolating barriers is essential for furthering our understanding of the ecological and behavioral mechanisms underlying species formation. Furthermore, evaluating the contribution of multiple isolating barriers to reducing gene flow between lineages is crucial for elucidating the connections between the fundamental processes of adaptation and speciation (Schemske 2010; Sobel et al. 2010; Nosil 2012).

Justifiably, emphasis has been placed on the importance of identifying the isolating barriers that restrict gene flow between young lineages (Coyne and Orr 2004; Sobel et al. 2010; Nosil 2012; Sobel and Streisfeld 2015). The focus has been on young lineages because isolating barriers evolve during and after speciation, and therefore the isolating barriers that prevent gene flow between established species may be unrelated to the processes that initiate and drive speciation (Coyne and Orr 2004; Sobel and Streisfeld 2015). Although only a handful of relevant studies exist, two patterns are of note. One, prezygotic isolating barriers appear much stronger than postzygotic isolating barriers early in speciation (Coyne and Orr 1989; Jiggins et al. 2001; Ramsey et al. 2003; Nosil et al. 2005; Lowry et al. 2008; Sobel and Streisfeld 2015). Two, isolating barriers closely tied to divergent natural selection (e.g., habitat isolation and immigrant inviability) are often particularly strong early in speciation (Ramsey et al. 2003; Smith and Benkman 2007; Sobel 2014; Sobel and Streisfeld 2015; Ingley and Johnson 2016), supporting the hypothesis that adaptive divergence and speciation are fundamentally linked (Schluter 2000, 2001, 2009; Schemske 2010; Sobel et al. 2010; Nosil 2012).

One form of reproductive isolation receiving increased attention is the reduced viability of maladapted immigrant or nonnative genotypes compared to locally adapted or native genotypes (immigrant inviability; Hendry 2004; Nosil et al. 2005; Giraud 2006; Lowry et al. 2008; Tobler 2009; Ingley and Johnson 2016). This barrier arises when populations experience divergent selection and undergo local adaptation to contrasting environments. Because individuals

* Corresponding author; e-mail: cporte16@uwyo.edu.

**ORCIDs:** Porter, http://orcid.org/0000-0002-6398-5519; Benkman, http://orcid.org/0000-0002-9714-4064.

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that disperse between such populations are likely to suffer higher mortality, gene flow between populations is reduced (Hendry 2004; Nosil et al. 2005). Theoretical and empirical evidence indicate that selection against immigrants is likely to be a strong driver of speciation (Hendry 2004; Nosil et al. 2005; Giraud 2006; Lowry et al. 2008; Tobler 2009; Ingley and Johnson 2016). Indeed, immigrant inviability was among the strongest barriers to gene flow in a survey of reproductive isolating barriers across a wide range of taxa (Nosil et al. 2005). A more recent survey, focused on plants, also found that immigrant inviability was as strong as some more commonly studied forms of reproductive isolation (e.g., pollinator isolation; Lowry et al. 2008).

While immigrant inviability has been estimated in multiple systems, the reduced ability or propensity of immigrants to reproduce has been identified as a form of reproductive isolation in only a single system (immigrant infecundity, per Smith and Benkman 2007), although the importance of reduced fecundity to reproductive isolation has long been appreciated (Coyne and Orr 2004; Harrison 2012). Because of the additional demands of reproduction beyond that required for maintenance, initial divergence might cause a greater depression in reproduction than in viability (Smith and Benkman 2007). Consistent with a greater sensitivity of reproduction than survival to variation in phenotype, fecundity selection is often stronger than viability selection (Kingsolver et al. 2001; Hereford et al. 2004) and is a stronger driver of local adaptation (Hereford 2009).

Here, we develop a model to illustrate the relative importance of reduced immigrant viability and fecundity during divergence along a performance axis (e.g., foraging efficiency). Measures of viability are based on the proportion of individuals that survive, whereas measures of fecundity are based on the fecundity of the surviving individuals. Thus, our measures of fecundity are not confounded by variation in viability (Ramsey et al. 2003; Coyne and Orr 2004). We then present a survey of published studies of local adaptation to investigate the relative strength of reduced immigrant viability and fecundity across taxa, including in the early stages of speciation. Most studies in our survey are reciprocal transplant experiments, which provide a direct test of the fitness consequences of immigration to nonnative versus native environments and are well suited for estimating the potential strength of reproductive isolation arising from the reduced fitness of immigrants (Nosil et al. 2005). We address whether reduced immigrant fecundity potentially acts as a comparable or even stronger barrier to gene flow than that arising from reduced immigrant viability, including during the critical early stages of speciation (Coyne and Orr 2004; Nosil 2012; Sobel and Streisfeld 2015).

We recognize that reciprocal transplant experiments are only a measure of a component of reproductive isolation and that a direct effect of reduced immigrant viability and fecundity on reproductive isolation will be evident only if there is dispersal between habitats (i.e., habitat isolation is not complete; Nosil et al. 2005). Indeed, if immigrants have low fitness in alternative habitats, then there should be strong selection for adaptive habitat choice (e.g., matching habitat choice; Edelaar et al. 2008) reducing the direct net effect of reduced immigrant fitness on reproductive isolation. Thus, one needs to measure immigration rates in addition to immigrant fitness to measure the net effect of each component on reproductive isolation (Sobel et al. 2010). In the absence of data on immigration rates, our goal is to evaluate the relative potential importance of reduced immigrant viability and fecundity to reproductive isolation, whether directly by reducing immigrant fitness or by favoring the evolution of habitat preferences.

## Methods

### *A Model*

We developed a model to illustrate how the strength of reduced immigrant viability and fecundity as potential barriers to gene flow varies as a population diverges from an ancestral population along a performance axis. We focus on the effect of the well-documented elevated demands of reproduction relative to those for maintenance alone (see below). We assumed a standard normal distribution of phenotypes for both the ancestral and derived populations (fig. 1*A*, 1*B*). We characterized variation in performance (e.g., feeding performance) in relation to phenotype using a quadratic equation, which we base on one of the few fitness surfaces having multiple adaptive peaks, and using measures of performance across a range of phenotypes (Benkman 1993, 2003). We set the mean for the ancestral population at the maximum for the performance curve (i.e., we assumed local adaptation; fig. 1*A*) and assumed that the performance curve peaked at a performance value of 0.4, that it had positive values spanning an interval of 5 units of phenotypic standard deviation, and that performance values equaling or exceeding 0.1 and 0.2 were required for survival and breeding, respectively (fig. 1*A*). We assumed that the performance curve remained constant in the ancestral environment and was identical for both survival and reproduction. The form of the performance curve in the derived habitat was not considered, because we used survival and reproduction in the ancestral habitat only to estimate the strength of the reproductive isolating barriers.

The absolute value for survival was arbitrary, but a twofold higher value for breeding (which includes survival) than survival alone approximates the relative energy demands of breeding for a salamander (Fitzpatrick 1973), is at the low end for altricial birds (estimated as 2–5 times maintenance costs; Walsberg 1983), and is less than relative

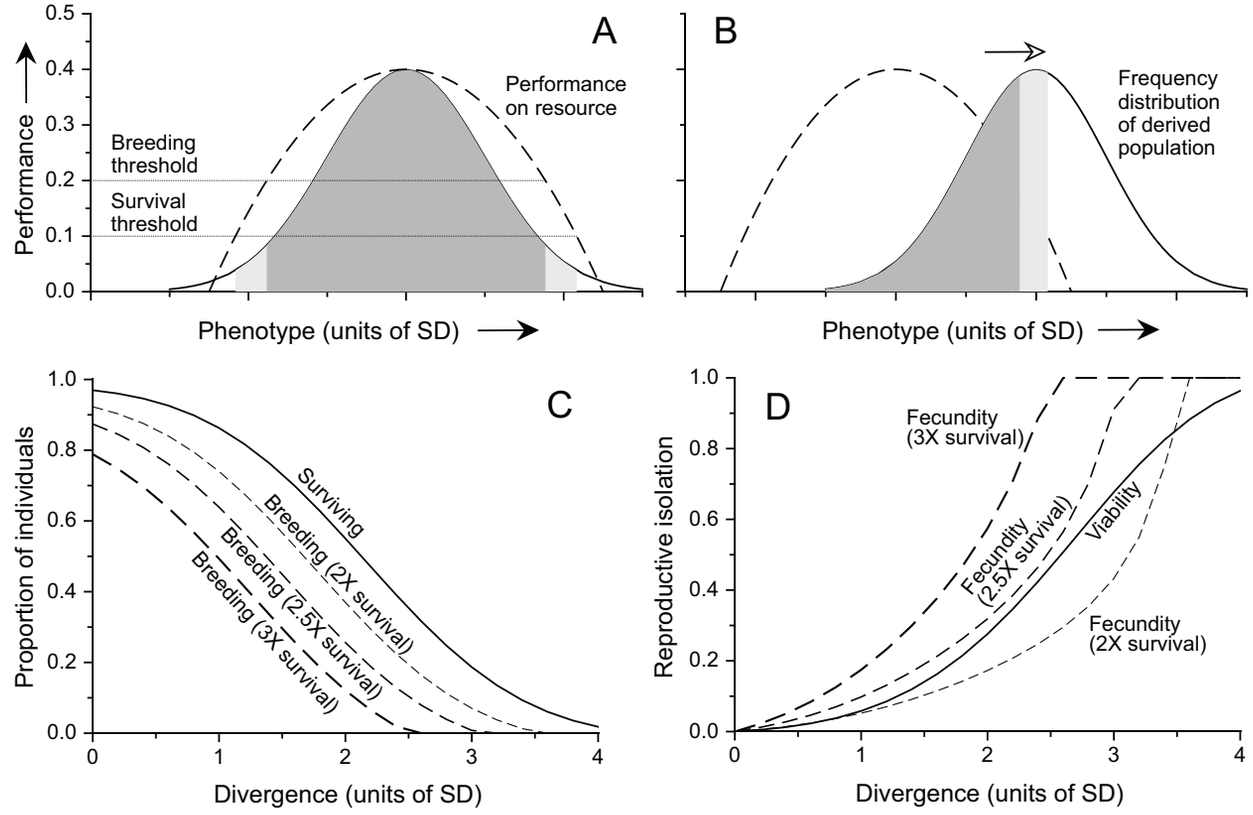


**Figure 1:** Model used to estimate reproductive isolation from reduced immigrant viability and fecundity as a population diverges from its ancestral population. *A*, The phenotypic distribution of the ancestral population is a standard normal centered under a quadratic performance curve with the performance thresholds for survival and breeding shown (dark gray represents individuals able to both survive and breed, and light gray represents individuals able to survive but not breed; see text). As the derived population diverges from the ancestral population (*B*), fewer individuals in the derived population can survive (solid curve) and reproduce (dashed curves) using the ancestral resources (*C*); the three dashed curves in *C* represent, from left to right, breeding thresholds of 0.3, 0.25, and 0.2, respectively. The individual level of reproductive isolation from reduced immigrant fecundity (*D*) increases as the breeding threshold increases. When the breeding threshold is ~2.5 times that required to survive, then reproductive isolation from reduced immigrant fecundity is consistently stronger than that from reduced immigrant survival. Because the proportion of individuals that can breed declines more rapidly than the proportion that can survive, reproductive isolation increases initially more rapidly as a result of reduced immigrant fecundity than as a result of reduced immigrant viability (*D*). Reproductive isolation from reduced immigrant fecundity increases more rapidly with divergence when the relative demands of breeding increase, as illustrated by the three dashed curves in *D* where, from left to right, the breeding thresholds decrease as above.

energy demands for two species of mammals (estimated as ~3 times maintenance costs; Perez and Mooney 1986; Korine et al. 2004). See Begon et al. (2006, p. 30) for a similarly general example analogous to our figure 1*A*. Based on our assumptions, individuals within 2.165 and 1.768 units of standard deviation of the phenotypic mean of the ancestral population (0.970 and 0.923 of the ancestral population) were able to survive and breed, respectively (fig. 1*A*). We then determined the proportion of the derived population that could survive or breed relative to the number that survived on the ancestral resource as it diverged from the ancestral distribution (fig. 1*B*, 1*C*). We also provide estimates for when the energy or resource costs of reproduction are 2.5 times and 3.0 times that for maintenance (breeding thresholds of 0.25 and 0.3; see fig. 1*A*) to illustrate how variation in breeding demands could affect the relative importance of reduced immigrant fecundity.

Our model assumed that the performance curves for both survival and reproduction were identical in the ancestral environment. If there were differences between the optima of these curves, then this could alter the model's predictions depending on the direction of the difference between the two optima relative to the direction of divergence from the ancestral environment. However, unless there is a bias in the direction of the differences between the optima relative to the direction of divergence from the ancestral environment, which we have no reason to expect, our model results should reflect an average expectation. The shape of the per-

formance curves for survival and reproduction could also differ. However, we are unable to envision a general mechanism that would cause such variation to consistently and differentially impact immigrant viability and fecundity. Consequently, we have chosen to ignore such variation in our model.

We used the following general equation to estimate the strength of the reproductive isolating barrier (RI; Sobel and Chen 2014)

$$\mathrm{RI} = 1 - 2\left[\frac{\mathrm{NNat}}{\mathrm{NNat} + \mathrm{Nat}}\right], \quad (1)$$

where NNat denotes the mean fitness of nonnative individuals (those from the derived population) and Nat denotes the mean fitness of native individuals (those from the ancestral population), both while utilizing the resource of the ancestral population. As the mean fitness of nonnative individuals (NNat) decreases toward 0, NNat/(NNat + Nat) decreases and RI approaches 1 (see fig. 1*C*, 1*D*). When the fitness of nonnative individuals is relatively high (NNat ≈ Nat), then RI approaches 0 (i.e., $1 - 2[1/2]$). This equation produces symmetrical values such that positive and negative numbers are directly comparable. A slope of 2 ensures that values of RI range from −1 to 1, representing the proportional reduction in gene flow relative to expectations under random mating (Sobel and Chen 2014). We used equation (1) to estimate RI arising from reduced immigrant viability and fecundity, where the components of fitness were the proportion of individuals surviving and the proportion of individuals breeding relative to those surviving, respectively.

### *Tests of the Model*

We used data from a literature search to test whether the strength of RI from reduced immigrant fecundity is greater than that from reduced immigrant viability overall and during the early stages of speciation. We searched for data that would allow comparison of the fitness of immigrants to residents by surveying the literature on reciprocal transplant experiments and studies of local adaptation using the Web of Science (Thomson ISI). We first conducted two separate searches on "reciprocal transplant" and "local adapt*," restricting the journals searched to *The American Naturalist*, *Biological Journal of the Linnean Society*, *BMC Evolutionary Biology*, *Ecology*, *Ecology Letters*, *Evolution*, *Evolutionary Ecology*, *Evolutionary Ecology Research*, *Journal of Ecology*, *Journal of Evolutionary Biology*, *Oecologia*, *Oikos*, and *Proceedings of the Royal Society of London Series B*. This restriction was necessary as the searches yielded more than 5,000 and 172,000 articles, respectively, largely from irrelevant sources. We conducted a second search on the topics of immigrant inviability and immigrant infecundity without restricting the journals searched. We used the abstracts of articles to identify studies with relevant data and to exclude others. We also searched for relevant citations within each article to either collect additional data on the focal lineage or on other lineages. All searches were conducted on literature published before September 2015.

Within each article, we searched for measures that captured viability or fecundity components of fitness. We used WebPlotDigitizer (Rohatgi 2015) to scan and extract data from figures when necessary. Viability was always measured as some type of survival estimate, whereas fecundity was measured using a variety of metrics of reproductive success (e.g., number of eggs laid, number of flowers). We were careful to ensure that fitness measures did not confound viability and fecundity. Avoiding confounded fitness measures was relatively easy for viability components of fitness, which are measured in ways that are not influenced by variation in fecundity (e.g., number of days survived, percent survival). Estimates of fecundity (e.g., lifetime number of offspring produced) usually confounded viability and fecundity components of fitness, and these studies were excluded from our analyses. However, some studies restricted fecundity analyses to survivors or measured fecundity as mean reproductive output per unit time across the life span of an individual (e.g., mean number of eggs laid per surviving day), so that variation in survival did not directly influence variation in fecundity. When fitness was measured over multiple years, we pooled data across years to obtain a single mean estimate. The majority of studies did not report variances associated with fitness estimates, preventing us from using meta-analytic approaches that weight estimates of the mean by their variance (Gurevitch and Hedges 2001). We estimated the strength of the RI using equation 1. Additional details on estimating the strength of RI from each study are available in appendix A (apps. A, B are available online). All data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.0nm3k (Porter and Benkman 2017).

To test whether the strength of RI from reduced immigrant fecundity was greater than that from reduced immigrant viability overall, we included all estimates of both isolating barriers in one comparison. The distributions of RI values were highly nonnormal, precluding the use of parametric statistics for the overall comparison. Variances also differed between the two groups, which can obscure interpretations about differences in means when certain nonparametric tests (e.g., Mann-Whitney *U*-tests) are used. Therefore, we used a randomization test based on 5,000 iterations to compare the mean strength of RI. In remaining comparisons, we restricted analyses to cases where both isolating barriers could be estimated from the same experiments. We used paired *t*-tests to test for differences between these paired estimates of RI from the same experiments; the paired data met the assumptions required for a paired *t*-test. We

tested for a difference in the early stages of speciation by restricting the paired *t*-test to lineages recognized at or below the subspecies rank (e.g., ecotypes, varieties, populations). We chose this approach because we were not able to obtain age estimates for the majority of the youngest lineages in our sample; thus, restricting analyses to subspecies and lower taxonomic ranks allowed us to focus on the early stages of divergence. All analyses were done in R (ver. 3.02; R Core Team 2013).

We searched the literature for published estimates of lineage ages. In 34 of 49 cases, we found published age estimates based on sequence divergence. In nine cases, age estimates were based on other published data, such as introduction date when nonnative species diversified upon colonization of a new geographic region. In the remaining six cases, we used sequence data from GenBank, where pairwise genetic distances were estimated using MEGA6 (Tamura et al. 2013) after alignment with ClustalW (Chenna et al. 2003), with lineage age estimated using published molecular clocks (Brower 1994; Gaunt and Miles 2002; Kay et al. 2006; Weir and Schluter 2008; Papadopoulou et al. 2010). Details on estimating lineage age are available in appendix B. We converted lineage age into the number of generations since divergence by using data on the number of generations per year for each taxon from the literature.

### *Comparison to Previous Literature Survey*

In a study of local adaptation, Hereford (2009) conducted a literature survey of reciprocal transplant experiments similar to ours. However, our surveys differ in several ways. First, we included 35 field experiments published after Hereford (2009). Second, Hereford (2009) restricted analyses to reciprocal transplant studies in the field, whereas we included nine laboratory studies where the agents of selection proposed to be driving divergence were present. Nosil et al. (2005) similarly included laboratory studies when assessing the potential importance of reduced immigrant viability. Finally, we used 52 of the studies included by Hereford (2009), but because of apparent or potential confounding of viability and fecundity fitness measures, we excluded 22 (30%).

## Results

As the derived population diverges from an ancestral population in our model (fig. 1*B*), the proportion of individuals from the derived population that can reproduce using the resource of the ancestral population is lower and declines more rapidly than the proportion of individuals that can survive (fig. 1*C*). These differences are especially pronounced as the relative demands of breeding increase. When the demands of reproduction exceed two times maintenance and survival costs, the individual level of RI from reduced immigrant fecundity is greater than that arising from reduced immigrant viability early in divergence (fig. 1*D*). Even when discounting RI from reduced immigrant fecundity by the earlier acting reduced immigrant survival ($[1 - \mathrm{RI}_{\text{reduced immigrant survival}}] \times \mathrm{RI}_{\text{reduced immigrant fecundity}}$), the absolute contribution (sensu Ramsey et al. 2003) to RI from reduced immigrant fecundity is higher than that arising from reduced immigrant viability early in divergence and increasingly so as the relative demands of reproduction increase (fig. 2).

We found a total of 125 estimates of immigrant viability and 36 estimates of immigrant fecundity from 97 studies (supplementary material, available online; plants: 67; arthropods: 40; vertebrates: 22; mollusks: 6; algae: 2; and cnidarians: 2). Overall, the strength of RI resulting from reduced immigrant fecundity tended to be stronger than that resulting from reduced immigrant viability (fig. 3*A*; randomization test: $P = .066$), as predicted (fig. 1*D*) if the demands of reproduction substantially exceed that for survival. However, this trend was not detected when controlling for time since divergence (number of generations). The residuals for RI from reduced immigrant fecundity from a re-

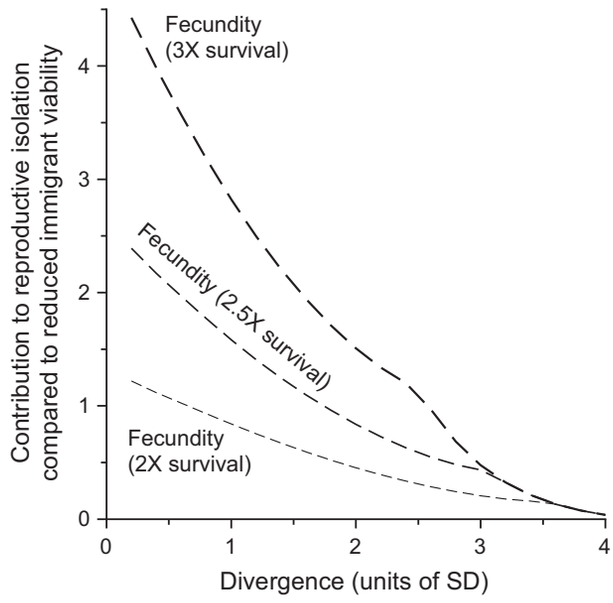


**Figure 2:** Absolute contribution of reproductive isolation arising from reduced immigrant fecundity, as compared to that resulting from reduced immigrant viability, increases with increasing demands for breeding and decreases with increasing phenotypic divergence. The different curves represent the absolute contributions to reproductive isolation resulting from reduced immigrant fecundity ($\mathrm{RI}_{\text{reduced immigrant fecundity}}$ discounted by earlier acting reduced immigrant survival: $[1 - \mathrm{RI}_{\text{reduced immigrant survival}}] \times \mathrm{RI}_{\text{reduced immigrant fecundity}}$) divided by reproductive isolation arising from reduced immigrant viability, where the requirements for breeding are 2, 2.5, and 3 times that required for survival, respectively (data from fig. 1*D*).

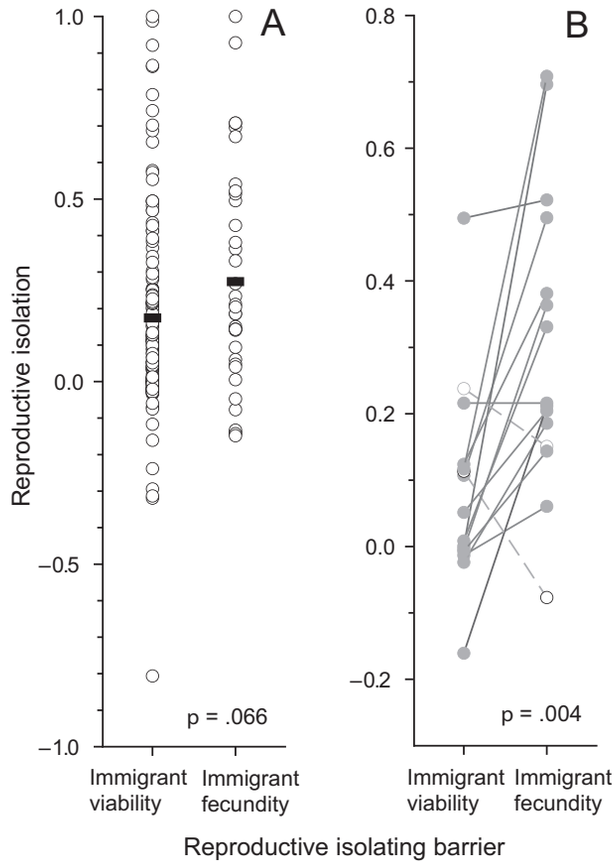


**Figure 3:** Strength of reproductive isolation resulting from reduced immigrant viability and fecundity across all lineages in our literature survey ($n = 125$ and 36, respectively; *A*) and in 15 young lineages (e.g., ecotypes, populations, varieties; *B*) where reduced immigrant viability and fecundity were both measured in the same experiment. *A*, Black bars are the means. *B*, Reproductive isolation from reduced immigrant fecundity was greater than or equal to that from reduced immigrant viability in 15 paired comparisons (solid lines connect estimates [gray circles] from the same experiment), whereas reproductive isolation from reduced immigrant viability was larger in two of the comparisons (dashed lines connect estimates [open circles] from the same experiment).

gression between RI (dependent variable) and time since divergence were not greater than those for reduced immigrant viability (randomization test: $P = .991$). A more powerful test of the relative strength of RI comes from the 18 studies where both forms of isolation could be estimated from the same experiment, and therefore lineage divergence is controlled. In this subset of data, the individual level of RI resulting from reduced immigrant fecundity was greater than that from reduced immigrant viability (paired *t*-test: $t = -2.68$, df $= 17$, $P = .016$). Even after discounting RI by the earlier acting barrier (reduced immigrant viability), the absolute level of RI resulting from reduced immigrant fecundity tended to be greater than that from reduced immigrant viability (paired *t*-test: $t = -2.06$, df $= 17$, $P = .055$).

Reproductive isolation resulting from reduced immigrant fecundity is expected to be stronger than that resulting from reduced immigrant viability, especially early in divergence (figs. 1*D*, 2). Fifteen of the above 18 lineages are at and below the subspecies rank (e.g., populations, varieties, ecotypes). Comparisons of these 15 lineages show that RI from reduced immigrant fecundity was consistently greater than that from reduced immigrant viability early in divergence (fig. 3*B*; paired *t*-test: $t = -3.47$, df $= 14$, $P = .004$).

## Discussion

Our literature survey showed that reduced immigrant fecundity is a stronger reproductive isolating barrier than reduced immigrant viability early in divergence (fig. 3*B*), consistent with predictions from our model (figs. 1*D*, 2). These results are also consistent with previous studies that have found that fecundity selection is generally stronger than viability selection (Kingsolver et al. 2001; Hereford et al. 2004) and that fecundity selection is a stronger driver of local adaptation (Hereford 2009). The emerging pattern of variation in fecundity having a stronger impact than variation in viability on various evolutionary processes (e.g., phenotypic evolution, local adaptation, and potentially speciation) is presumably due to the greater sensitivity of reproduction than survival to variation in phenotype. Indeed, as populations diverge in traits linked to performance (e.g., resource utilization traits), the ability of the derived population to breed in the ancestral environment will be more strongly compromised than the ability to survive because more resources are needed to both survive and breed than to survive alone (e.g., Walsberg 1983). We note, however, that reproductive isolation resulting from reduced immigrant viability will act to reduce gene flow earlier in the life cycle of organisms than that arising from reduced immigrant fecundity, given that a period of survival necessarily precedes reproduction. Although earlier acting barriers have the potential to contribute more to reductions in gene flow than later acting barriers (Coyne and Orr 2004; Sobel et al. 2010), our model (fig. 2) and analyses of reciprocal transplant studies suggest that the higher demands of breeding compared to survival may overcome this effect. Given that RI arising from reduced immigrant viability has been shown to be one of the strongest measured barriers to gene flow (Nosil et al. 2005; Lowry et al. 2008), our work suggests that RI resulting from reduced immigrant fecundity may be just as important or more important for speciation, especially early in divergence (fig. 3*B*) and when the demands of breeding are relatively high (figs. 1*D*, 2).

The vast majority of our estimates of RI were obtained from reciprocal transplant experiments, where individuals

were assigned to alternative environments randomly with respect to their phenotype. This may overestimate the importance of reduced immigrant fecundity and viability relative to other forms of RI, because selection against immigrants is thought to promote the evolution of habitat isolation that will reduce the number of immigrants (Hendry 2004; Nosil et al. 2005), and immigrants might have phenotypes with a higher expected performance than individuals drawn at random from the population (i.e., matching habitat choice sensu Edelaar et al. 2008). Conversely, as habitat choice evolves (e.g., Bolnick et al. 2009), the importance of reduced immigrant fecundity in initiating speciation will be obscured. Because barriers that initiate divergence can be obscured as other barriers evolve, characterizing the evolution of RI early in speciation is difficult (Coyne and Orr 2004; Sobel et al. 2010). Nevertheless, the few estimates of reduced immigrant fecundity from observational studies indicate that this barrier is fairly strong in nature (e.g., Smith and Benkman 2007; C. K. Porter, unpublished data), but more estimates from natural systems are needed to evaluate the generality of this pattern. Future work that directly estimates the relative strength of RI from reduced immigrant viability and fecundity (and all barriers) in young lineages and in groups at varying points along the speciation continuum would be especially useful for further evaluating the relative importance of different factors during speciation (Nosil 2012).

Divergence in traits other than performance might result in different reproductive isolating barriers playing a larger role in speciation. For example, immigrants could be more easily detected than residents by predators (e.g., Sandoval 1994), or immigrants might lack defenses against novel predators in an alternative environment (e.g., Freeman and Byers 2006) but might not suffer reduced reproductive success (Nosil 2004; Sandoval and Nosil 2005). Consistent with this alternative, we find that RI resulting from reduced immigrant viability tends to be greater in lineages that are diverging in antipredatory traits than for lineages diverging in performance traits (randomization test: $P = .076$); this pattern is unlikely the result of a difference in the number of generations since divergence because lineages diverging in antipredatory traits have not diverged over more generations (predation: $688{,}967 \pm 276{,}398$, $n = 5$; other lineages: $1{,}471{,}315 \pm 617{,}891$, $n = 38$; $P = .540$). Unfortunately, we are unable to evaluate the relative roles of reduced immigrant viability and fecundity in lineages prominently diverging in antipredatory traits, because fecundity components of fitness were rarely measured in these studies. However, reduced immigrant fecundity could still play an important role in predator-mediated divergence if, for example, prey respond to the threat of predators by increasing vigilance and reducing feeding behaviors, thus reducing reproductive success (e.g., Lima and Dill 1990). More estimates of fecundity are needed to evaluate the relative importance of reduced immigrant fecundity and viability in lineages diverging in antipredatory traits.

Our work adds to the growing body of literature on reproductive isolating barriers by investigating the relative roles of viability and fecundity components of fitness in causing the low fitness of immigrants from alternative environments. In particular, our findings suggest how divergence onto alternative resources and the high demands of reproduction could reduce gene flow and act to promote speciation. One possibility is that reduced fecundity might contribute more to ecologically mediated reductions in hybrid fitness than reduced viability. Our results also suggest that knowing both the ecological context of divergence, which is widely acknowledged to be critical (Schluter 2000, 2001, 2009; Coyne and Orr 2004; Schemske 2010; Sobel et al. 2010; Nosil 2012), and the demands of reproduction will provide insight into the relative importance of different factors influencing reproductive isolation.

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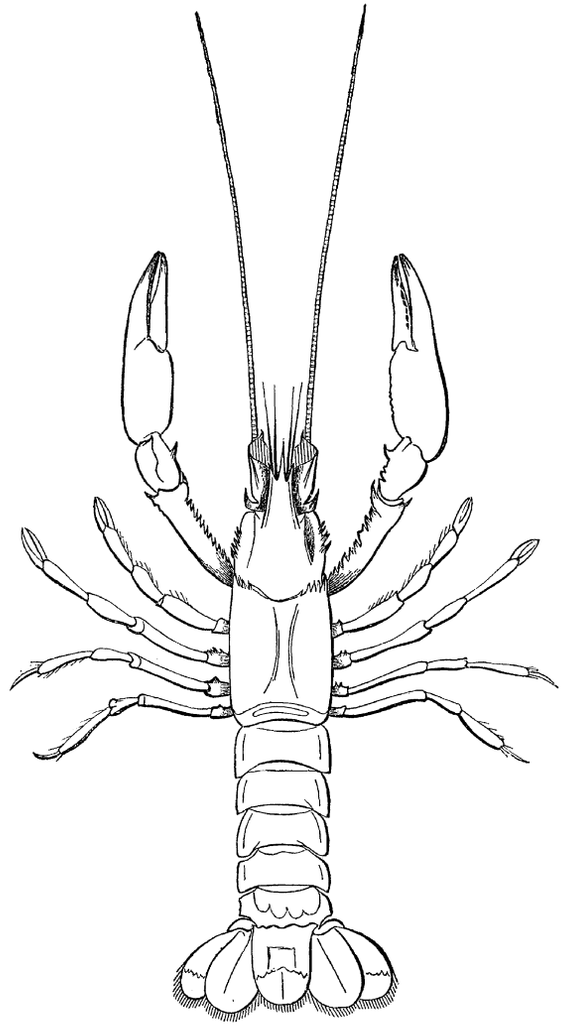

"Next to the blind fish, the blind crawfish attracts the attention of visitors to the cave. This is the *Cambarus pellucidus*" (figured). From "The Mammoth Cave and Its Inhabitants" by A. S. Packard Jr. (*The American Naturalist*, 1871, 5:739–761).