

Natural and Sexual Selection Giveth and Taketh Away Reproductive Barriers: Models of Population Divergence in Guppies

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ABSTRACT: The standard predictions of ecological speciation might be nuanced by the interaction between natural and sexual selection. We investigated this hypothesis with an individual-based model tailored to the biology of guppies (*Poecilia reticulata*). We specifically modeled the situation where a high-predation population below a waterfall colonizes a low-predation population above a waterfall. Focusing on the evolution of male color, we confirm that divergent selection causes the appreciable evolution of male color within 20 generations. The rate and magnitude of this divergence were reduced when dispersal rates were high and when female choice did not differ between environments. Adaptive divergence was always coupled to the evolution of two reproductive barriers: viability selection against immigrants and hybrids. Different types of sexual selection, however, led to contrasting results for another potential reproductive barrier: mating success of immigrants. In some cases, the effects of natural and sexual selection offset each other, leading to no overall reproductive isolation despite strong adaptive divergence. Sexual selection acting through female choice can thus strongly modify the effects of divergent natural selection and thereby alter the standard predictions of ecological speciation. We also found that under no circumstances did divergent selection cause appreciable divergence in neutral genetic markers.

Keywords: individual-based model, ecological speciation, adaptive divergence, survival, mating success.

Introduction

Ecological speciation occurs when divergent selection causes adaptive divergence, which then triggers the evolution of reproductive isolation (Schluter 2000). This theory now has considerable support from mathematical models (e.g., Kondrashov and Kondrashov 1999; Fry 2003;

Gavrilets et al. 2007; Thibert-Plante and Hendry 2009), laboratory experiments (review: Rice and Hostert 1993), and natural populations (reviews: Schluter 2000; Rundle and Nosil 2005). Despite this generally supportive body of work, a large number of populations under divergent selection and showing adaptive divergence apparently do not show strong signs of ecological speciation (Crispo et al. 2006; Crispo and Chapman 2008; Berner et al. 2009; Hendry 2009; Nosil et al. 2009). We propose that some of these apparently contradictory outcomes might originate owing to the opposing effects that divergent selection can have on different potential contributors to reproductive isolation.

Divergent selection can influence reproductive isolation through several different routes, including increased site fidelity or host preference (Fry 2003), reduced survival of maladapted immigrants (Via et al. 2000; Hendry 2004; Nosil et al. 2005), reduced mating success of immigrants (Rundle et al. 2000; Nosil et al. 2002), and reduced survival or mating success of hybrids (Hatfield and Schluter 1999; Vamosi and Schluter 1999; Via et al. 2000). The standard prediction of ecological speciation is that any of these potential reproductive barriers should increase with increasing divergent selection. Although this prediction seemingly holds for some natural systems (e.g., Nosil 2007), it is also possible that divergent selection sometimes has offsetting effects on different potential reproductive barriers and thereby limits progress toward ecological speciation (Hendry 2009). One such situation might result from the antagonistic interplay between natural and sexual selection (Ellers and Boggs 2003; Schwartz and Hendry 2006). To illustrate this potential, we turn to Trinidadian guppies (*Poecilia reticulata*), a natural system that shows dramatic adaptive divergence between selective environments without an obvious reduction in gene flow (Magurran 2005; Crispo et al. 2006).

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Trinidadian guppies are a classic example of adaptive divergence in response to selection: they show dramatic differences in behavior, life history, morphology, and male coloration between high- and low-predation sites (Reznick and Endler 1982; Endler 1995; Magurran 2005). We focus here on the effects of male color. In low-predation sites, males are generally more colorful, presumably because females often have preferences for more colorful males (Endler and Houde 1995). In high-predation sites, males are generally less colorful, presumably because colorful males are more susceptible to predation (Endler 1978, 1980; Winemiller et al. 1990; Millar et al. 2006). Females in high-predation sites, however, also seem to often prefer colorful males (Endler and Houde 1995; Rodd et al. 2002; Evans et al. 2004a), although perhaps less strongly so than in low-predation sites (Breden and Stoner 1987; Houde and Endler 1990; Schwartz and Hendry 2007). Exceptions to this classic interpretation, however, are increasingly reported (Millar et al. 2006; Karim et al. 2007; Schwartz and Hendry 2007; Kemp et al. 2008; Weese et al. 2010).

Adaptive divergence in male color might influence several potential reproductive barriers between high- and low-predation guppy populations. Of most relevance here are interactions that occur in high-predation sites—because ongoing dispersal generally occurs from low-predation sites above waterfalls into high-predation sites below waterfalls (Magurran 2005; Crispo et al. 2006; Barson et al. 2009). On the one hand, adaptive divergence should increase reproductive isolation through natural selection against immigrants and hybrids—because fish from low-predation sites are not well adapted for survival in the presence of predators at high-predation sites (O’Steen et al. 2002; Magurran 2005; Gordon et al. 2009). In contrast, males from low-predation sites dispersing into high-predation sites may have increased mating success owing to their high color, provided females at these sites prefer colorful males. If these opposing effects are present, divergent selection on guppies might increase some reproductive barriers (e.g., natural selection disfavoring immigrants) but decrease others (e.g., sexual selection favoring immigrants). The outcome might then be little or no net effect of divergent selection on overall gene flow.

Here we formally test the above hypothesis by grounding individual-based simulation models in key aspects of guppy biology. The reason for this approach is that the devil often lies in the details, which sometimes becomes apparent only in system-specific models (Servedio and Noor 2003). A critical distinction between previous system-specific simulation models of ecological speciation (Gavrilets and Vose 2007; Gavrilets et al. 2007) and our own model is that the former systems were chosen because evidence for ecological speciation is present, whereas our system was chosen because evidence for ecological spe-

ciation is weak or absent. Thus, the two types of models are complementary in helping to determine factors that do and do not promote progress toward ecological speciation.

Methods

We start with an ancestral guppy population from which dispersers colonize a new site that can be characterized by a different predation environment. Based on prior knowledge of colonization patterns in the guppy system (Haskins et al. 1961; Crispo et al. 2006; Barson et al. 2009), we assume that the source population is in a downstream high-predation (HP) site and that the new colonization event is usually of an upstream low-predation (LP) site. This HP versus LP “ecological contrast” is maintained by barrier waterfalls that prevent upstream colonization by the most dangerous guppy predators (Magurran 2005; fig. 1). We then compare ecologically contrasting scenarios (LP vs. HP) to “control” scenarios where the upstream population is also in a high-predation site (HP vs. HP).

We employ a modified individual-based simulation model originally developed by Labonne et al. (2008; http://capsis.cirad.fr/capsis/documentation/docgeneticsmars04_fc.pdf). Individual-based models are fundamentally stochastic, which prevents analytical resolution but allows greater freedom and realism (DeAngelis and Mooij 2005). The model is parameterized and conceptualized using actual data and knowledge of the life cycle (growth and survival), traits (male color), behavior (female sexual preference), and genetics of guppies. Male color and female preference are inherited through an explicit individual polygenic map (similar to Kopp and Gavrilets 2006). Gamete production, meiosis, and crossing over are all simulated, which allows the potential buildup of linkage disequilibrium among alleles at different loci, even if they are not physically linked.

We track the evolution of male color under different levels of dispersal, initial sexual selection (female preference), and natural selection (predation). We then examine the consequences of this color evolution for potential reproductive barriers (survival and mating success), overall reproductive isolation (combined effects of survival and mating success), and neutral gene flow (genetic markers similar to microsatellites). We here report results for the first 100 guppy generations—for two reasons. First, experimental introductions of guppies in different predation environments have demonstrated changes in male color over similar (or shorter) time frames (Endler 1980)—although not always (Karim et al. 2007; Kemp et al. 2008). To the extent that adaptive divergence causes ecological speciation, some initial reproductive barriers should thus emerge on similar time frames (Hendry 2004; Hendry et

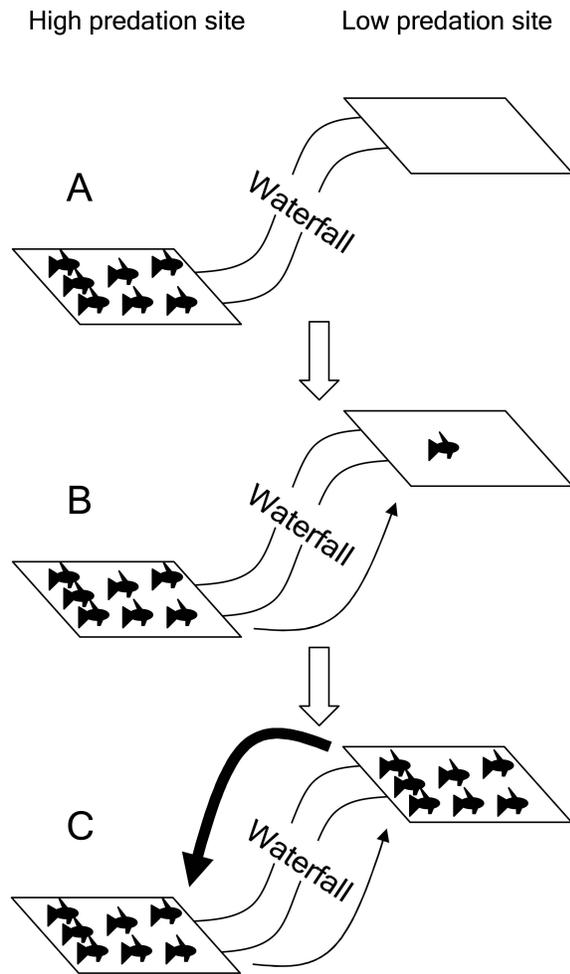


Figure 1: Basic structure and chronology of the model under ecological contrast. Two sites are separated by waterfalls. Specific predators occur only downstream, hence generating divergent selection between sites. Juveniles and adult females have similar life histories in both sites. As an alternative, we also modeled a second structure for control simulations where both sites are under high predation (hence no ecological contrast). *A*, A downstream, demographically stable, high-predation (HP) site initially contains guppies. It is separated by waterfalls from an upstream, low-predation (LP) site that is initially empty. *B*, The HP site sends out dispersers to colonize the LP site. Due to the waterfalls, the upstream dispersal rate is very low (*thin arrow*). *C*, The LP site is now colonized and sends out many dispersers to the HP site (*bold arrow*).

al. 2007; Thibert-Plante and Hendry 2009). Second, short time spans allow us to ignore mutation, reduce simulation processing time, and explore a wider range of parameter space with more replicates. However, all basic conclusions held in a subset of the simulations run through 400 generations (results not shown).

Life Cycle

The length of a time step in our model was 12 days, generating discrete intervals relevant to the life cycle of guppies. The size at birth was 6 mm, maturation size was 14 mm, and individual growth was specified as $y = -0.172x + 4.06$, where y is the growth increment for a 12-day period and x is the standard length (Rodd and Reznick 1997). After maturation, mating could occur in any time step, except for two time steps immediately after a female was inseminated (Liley 1966). The generation length was thus seven time steps, which amounts to approximately four generations per year—a plausible value for guppies (Reznick et al. 1997). Female fecundity (number of offspring) was specified as $\exp[2.7 \times \log_{10}(\text{length}) - 0.2]$, which generates fecundity patterns similar to Rodd and Reznick (1997). The average survival probability over one time step was 0.7 for juveniles and 0.9 for adult females (Rodd and Reznick 1997; Olendorf et al. 2006; Gordon et al. 2009). We assumed that all of the above parameters (except for male survival in relation to color; see below) were the same in both sites (HP and LP). This simplification allowed us to isolate the effects of evolutionary changes in male color.

Dispersal

Natural colonization of sites above waterfalls is likely a very rare event, perhaps accomplished only during very large floods or when a bird predator drops a pregnant female. On the contrary, dispersal from above to below waterfalls is likely quite common, as revealed through genetic analyses (Becher and Magurran 2000; Crispo et al. 2006; Barson et al. 2009). We here examine two probabilities of individual dispersal from an upstream site to a downstream site over a single time step: 1×10^{-2} (high dispersal) and 1×10^{-3} (low dispersal). In each case, the upstream dispersal probability was assumed to be 1% of the downstream dispersal probability. Lower rates of dispersal make colonization events too rare to study in simulations.

Male Color

Male color in guppies is a complex arrangement of spots with different color spectra in different positions (Endler 1978; Brooks 2002; Blows et al. 2003; Kemp et al. 2008). To reduce this complexity, we focused on a single color “trait” (area of orange) that is subject to sexual selection in many populations (Houde and Endler 1990; Kodric-Brown 1993; Endler and Houde 1995; Brooks and Endler 2001). This trait is also under viability selection (Weese et al. 2010) that might differ between natural HP and LP populations (Endler 1980; Millar et al. 2006).

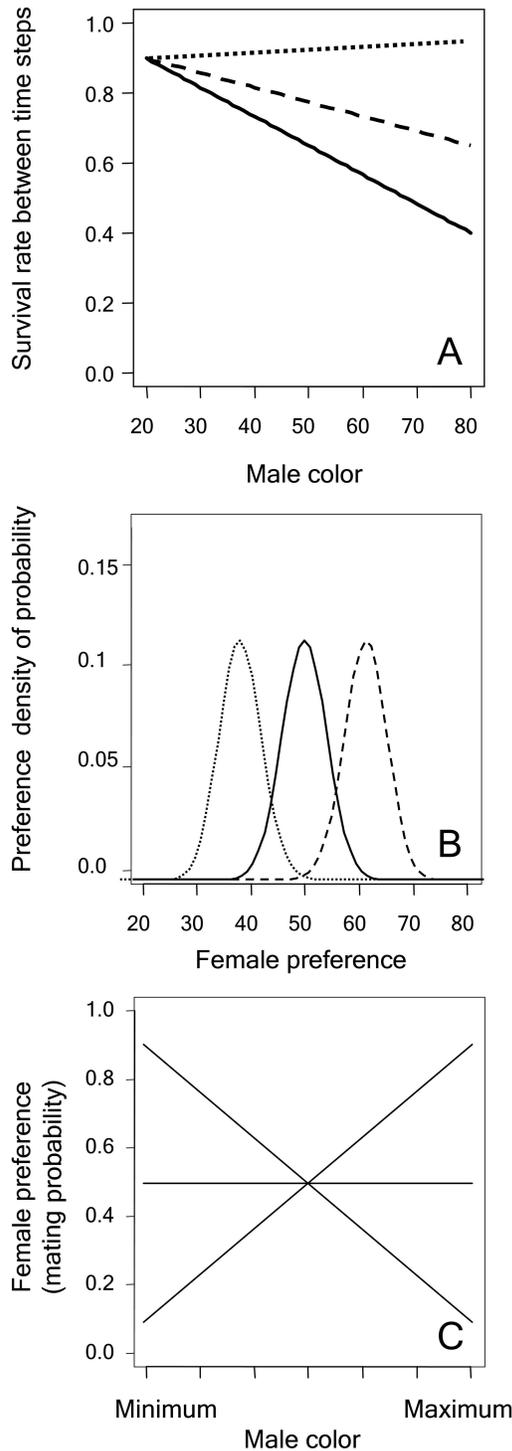


Figure 2: Effect of color on male survival for strong, weak, or absent predation (A), initial distributions of female preference for color in the starting population (B), and examples of positive, flat, and negative female preference for male color (C). A, The effect of color on male survival. The solid line shows a high-predation (HP) site where selection against high color is strong (slope = -0.00833), and the dashed line shows an

In our model, orange area was purely determined by genotype, without any environmental effects (plasticity). This assumption is reasonable given the very strong genetic basis for orange area in guppies (Houde 1992; Brooks and Endler 2001). Male color is at least partly sex linked (Winge 1927; Van Oosterhout et al. 2003; Lindholm et al. 2004; Hughes et al. 2005), and so we assumed that 50% of the color variation originated from unlinked diploid autosomal loci (five loci with four alleles each) and 50% from haploid Y-chromosome loci (10 loci with four alleles each). This proposed polygenic basis for male color fits with recent mapping studies that reveal a number of quantitative trait loci (QTL) on separate linkage groups contribute to orange spots (Tripathi et al. 2009). The color score for one individual was calculated as the sum of the allele scores (1, 2, 3, or 4) across all of the loci and therefore ranged from 20 to 80.

Natural Selection

For the LP site, we assumed that male survival was weakly positively correlated with orange color (fig. 2A), such as in the case of “good genes” postulated for guppies (Evans et al. 2004b). Note, however, that a variety of correlations between color and viability can be found in natural LP populations (Weese et al. 2010). For the HP site, we followed classic work (Endler 1980, 1991; Godin and McDonough 2003) in assuming that male survival decreases with increasing orange color, either at a rapid rate (strong natural selection) or at a slow rate (weak natural selection). These HP survival rates were parameterized by linear selection gradients (Roff 1997) calculated from mark-recapture studies in nature (Weese et al. 2010). The strongest selection gradient those investigators observed against male color was approximately 0.3, which corresponds to an approximately 20% difference in predicted survival rate between males with the highest (65) and lowest (35) color values in the initial range in our simulations.

HP site where selection against high color is comparatively weak (slope = -0.00416). The dotted line represents male survival in a low-predation site, with a slight positive effect of color on survival (good-genes effect). B, Initial distribution of female preference for color in the population. Three different starting conditions are simulated: an initial intermediate distribution, where values are distributed around a flat preference (50; *solid line*), a positive preference distribution with values around a high preference (60; *dashed line*), and a negative distribution around a low preference value (40; *dotted line*). C, Female preferences for male color, for three different genetic values: 20, 50, and 80. The 50 value represents a flat preference, whereas the two other values (20 and 80) represent extreme negative and positive preferences for color. The preference is expressed on the male color range encountered by the female at a given time.

We used this value to establish a function representing strong natural selection against male orange. A lower selection gradient of 0.15, which is seen in some natural HP sites (Weese et al. 2010), was used to establish a function representing weak natural selection (fig. 2A).

Sexual Selection

Most previous work on female preferences for male orange area has used linear functions through the range of male trait values (Endler and Houde 1995; Brooks and Endler 2001; Rodd et al. 2002). In our model, the slope of this function was determined by a diploid individual genetic map (10 unlinked loci with four alleles each). Although the genetic basis of female preference is not known for guppies, it is expected to be polygenic in general (Arnegard and Kondrashov 2004; Seehausen et al. 2008). The phenotypic value of the female preference slope was defined by summing the allele effects across all loci. The initial genetic distributions of preference in the HP population were chosen to represent three contrasted situations: a general positive preference for color, an intermediate (flat) preference (i.e., no preference on average), or a negative preference (fig. 2B). The use of these three scenarios allowed us to consider the influence of initial sexual selection that either counteracted, matched, or reinforced natural selection (fig. 2C). The genetic variation in female preferences also meant that it was free to evolve if it came under sufficiently strong selection, which here would act indirectly through offspring fitness.

In the model, females expressed their choice among 10 males chosen randomly from the females' site. The preference function was first fitted across the observed minimum and maximum colors for these 10 males. Females were then presented with the males (in random order), and mating occurred with a probability that depended on the male's area of orange and the specified female preference function (fig. 2B). This procedure meant that female preferences were "open ended" and potentially very discriminatory. If the female did not mate with a particular male, she assessed the next male. If none of the 10 males was selected, the female remained available for mating at the next time step.

Simulation Scenarios

We ran simulations with an ecological contrast (HP vs. LP) for 12 different scenarios representing all possible combinations of two levels of dispersal (high and low), two levels of natural selection in the HP site (strong and weak), and three levels of initial sexual selection (positive, flat, and negative average female preferences). Control simulations considered identical scenarios, except that

similar natural selection was present in both sites (HP vs. HP). For each scenario, we ran 100 replicate simulations over 100 generations (and a subset for 400 generations), all starting from identical initial conditions: a downstream HP population seeded with 10,000 guppies sampled from a uniform distribution of age (between 12 and 360 days) and sex. Each site was assumed to have a carrying capacity of 10,000 adults, which was maintained by random removal of individuals in cases of overproduction.

Our presentation is based on results for completely unlinked diploid loci for color, preferences, and neutral markers (see Fromhage et al. 2009 for similar approaches). This choice avoided the "magic trait" situations that attend physically linked preferences and traits (Gavrilets 2004). The primary reason for this choice was that many color loci are located on the Y chromosomes and thus cannot show physical linkage with preference loci expressed by females. Moreover, male color loci are located on many linkage groups (Tripathi et al. 2009) and so any physical linkage would likely explain little of the overall variation. Finally, studies using neutral markers for inferring gene flow and reproductive isolation focus on neutral markers unlinked to selected loci (Ogden and Thorpe 2002; Crispo et al. 2006; Gavrilets et al. 2007; Berner et al. 2009).

Measures of Divergence, Reproductive Barriers, and Gene Flow

Population divergence in male color (D_c) and female preference (D_p) was quantified as the proportional difference between the downstream and upstream sites in a given scenario:

$$D_c = \frac{1}{n} \sum_{i=1}^n (C_{LPi} - C_{HPi}),$$

$$D_p = \frac{1}{n} \sum_{i=1}^n (P_{LPi} - P_{HPi}),$$

with C_{LPi} and C_{HPi} representing the scaled mean color values, P_{LPi} and P_{HPi} representing the scaled mean preference values (all for the i th simulation), and n representing the total number of simulations per scenario. The speed of color evolution in each population/simulation scenario was calculated as the amount of change in standard deviation units per generation (i.e., haldanes; Hendry and Kinnison 1999).

Specific reproductive barriers were quantified by comparing the survival (average rate between successive time steps) and mating success (number of females fertilized per male per time step) of residents in the HP site, immigrants into the HP site (from the LP site), and HP-LP

hybrids in the HP site. We calculated the divergence in survival (D_s) and mating success (D_m) as

$$D_s = \frac{1}{n} \sum_{i=1}^n \left(\frac{S_{Ri} - S_{HI/I}}{S_{Ri}} \right),$$

$$D_{mHI} = \frac{1}{n} \sum_{i=1}^n \left(\frac{M_{HI/I}}{M_{Ri}} - 1 \right),$$

with S representing survival, M representing mating success, R representing residents, and H and I representing hybrids or immigrants, respectively. We also computed lifetime reproductive success for each category of male (R , H , I) by multiplying survival rates by mating success (number of offspring per surviving male). We consider this measure to represent “overall reproductive isolation.”

Neutral gene flow was assessed based on divergence in genetic markers at seven simulated unlinked neutral loci, each with 10 possible alleles. Allele frequencies in the starting HP population were determined by drawing at random from a uniform distribution. Divergence between populations in these neutral markers was then estimated as θ (Weir and Cockerham 1984; Sefc et al. 2007). We also calculated θ for the male color loci as a way of estimating gene flow at selected loci. In addition, as an indicator of linkage disequilibrium, we tracked the nonrandom association of alleles between pairs of color and preference loci (D measure; Weir and Cockerham 1978).

Results

Basic Dynamics

We first describe basic dynamics common to all of the simulations. Figure 3 provides a detailed illustration based on a specific scenario: low dispersal, strong natural selection, and positive sexual selection. In all cases, the downstream HP site was demographically stable after only 10 generations with respect to population size (fig. 3A) and age/sex structure (not shown). For high-dispersal scenarios, colonization of the upstream site began as early as the fifth generation, and demographic stability was usually achieved by the thirtieth generation. For low-dispersal scenarios, 50% of simulations showed colonization of the upstream site by the twentieth generation and the remainder by the forty-fifth generation (fig. 3B). All populations were always demographically stable before the fiftieth generation, regardless of the scenario.

No autosomal locus showed any allele loss before the hundredth generation in the downstream HP site. Allelic diversity at the Y-chromosome color loci, however, declined at the downstream HP site by up to 20% in some

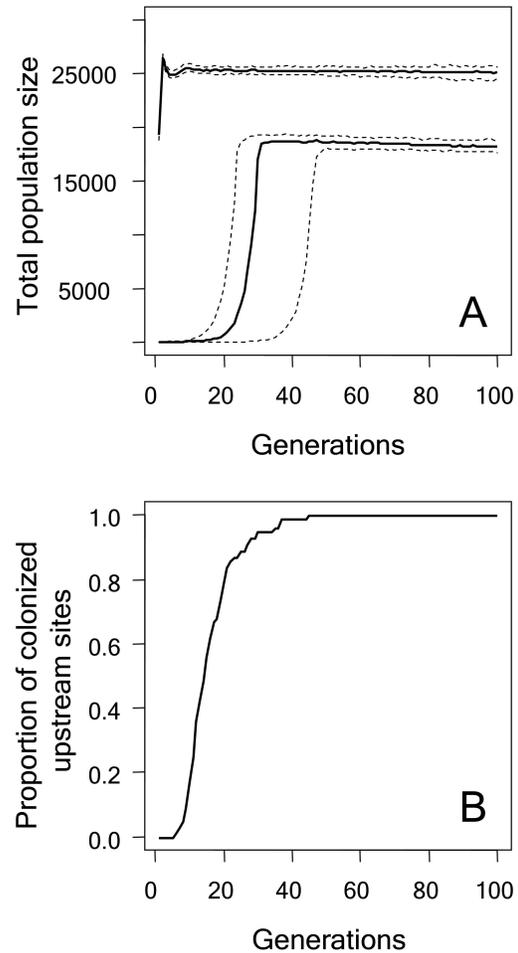


Figure 3: Demographic behavior of the model over 100 generations for a scenario involving low dispersal, strong natural selection, and positive sexual selection. Here we present only the simulations involving ecological contrasts: downstream site is under high predation (HP); upstream site is under low predation (LP) without selection against color. *A*, Median population sizes over the first 100 generations for the downstream HP site (solid line) and the upstream LP site (dashed line). The thin dashed lines show the 5% and 95% quantiles as determined by the 100 replicate simulations. The downstream site reaches a quasi-stable state after fewer than 10 generations. Depending on the variation in colonizing date, the upstream site reaches its carrying capacity in 20–50 generations. *B*, Proportion of the upstream LP sites colonized over the first 100 generations. The proportion is calculated over 100 replicates.

simulations. In the upstream HP or LP site, the dynamics of neutral allelic diversity were more variable because of founder effects and gene flow. By the fiftieth generation, however, recurring immigration had introduced all of the neutral alleles and 50%–80% of the selected alleles.

Divergence in color in the presented scenario began early and progressed rapidly: the two population types showed nonoverlapping distributions (across simulations)

of mean color by the fiftieth generation (fig. 4). Specifically, the HP site showed a slight decrease in mean color, while the LP site showed a large increase in mean color. This divergence was clearly due to the ecological contrast between sites (HP vs. LP), because the control simulation (HP vs. HP) showed much lower divergence in color (fig. 4A). Female preference evolved more slowly: up to 2% divergence after 100 generations (see table A2 in the online edition of the *American Naturalist*) and up to 3.3% divergence after 200 generations (table A6; when using a simpler genetic architecture for preference [two loci only], the speed of preference evolution increased, reaching 5%–6% in 100 generations—but this did not alter the conclusions presented below.)

The dynamics of reproductive barriers are here discussed for the downstream HP site, where HP-LP interactions are most common and therefore most relevant in nature and in the simulations. When an ecological contrast was present, resident HP males had higher survival rates than immigrants from the upstream LP site (fig. 4B). This strong natural selection against immigrants is largely due to the fact that residents are still evolving in an adaptive direction (low color), whereas immigrants are from a population evolving in the opposite direction (high color). In contrast, immigrant males from the LP site attained higher mating rates in the downstream HP population than did the resident HP males (fig. 4C). The reason was that females in this scenario preferred more colorful males, and the LP males were more colorful than the HP males (fig. 4A). Hybrids were intermediate between residents and immigrants in both survival and mating success, which is expected given their phenotypic intermediacy. The above differences are the result of divergent selection because no differences in reproductive barriers are seen in the control HP-HP simulations.

The dynamics of divergence at neutral genetic markers differed qualitatively from the above patterns in that divergence was often initially quite high ($\theta = 0.1$) and then decreased slowly (fig. 4D). The same pattern was seen in the control simulation. These results show that neutral genetic divergence was here mostly independent of divergent selection, instead being driven by strong founder effects that then diminished through ongoing gene flow. Note that genetic diversity did not change appreciably through the simulations, and so these patterns were not the result of changing within-population genetic variation (Sefc et al. 2007).

Effects of Natural Selection, Sexual Selection, and Dispersal

We now summarize differences among the scenarios (different parameter sets) so as to infer the effects of the three

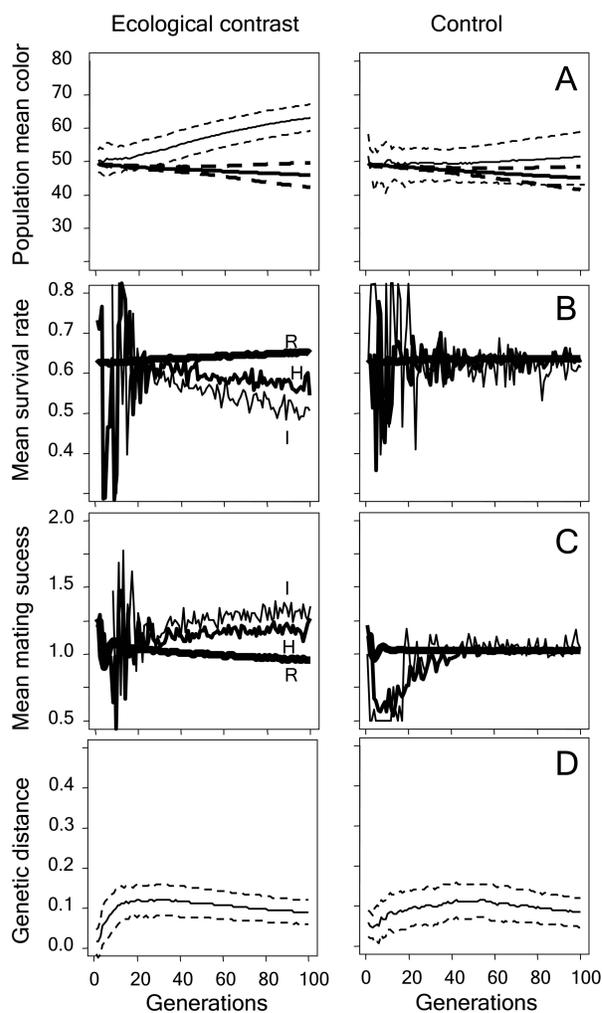


Figure 4: Evolution of phenotypic (A–C) and neutral genetic divergence (D) in the first 100 generations (over 100 replicates) for the scenario involving low dispersal, strong natural selection, and positive sexual selection. *Left column*, the downstream sites are high predation and the upstream sites are low predation (i.e., ecologically contrasted simulations). *Right column*, both sites are high predation (i.e., control simulations). A, The evolution of mean male color in downstream (*bold line*) and upstream (*thin line*) sites. Dashed lines represent standard deviation calculated over 100 replicates. B, Male mean survival in the downstream site for residents (R; *thick line*), hybrids (H; *medium line*) and immigrants from the upstream site (I; *thin line*). C, Male mean mating success in the downstream site for residents (R; *thick line*), hybrids (H; *medium line*), and immigrants from the upstream site (I; *thin line*). D, Neutral genetic distance (measured by q value) between upstream and downstream sites. Full line is the mean value, and dashed lines represent standard deviation calculated over 100 replicates.

predictor variables (natural selection, sexual selection, and dispersal) on several response variables (phenotypic divergence, reproductive barriers, and neutral genetic divergence). Detailed results are presented in appendix tables

A1–A6 in the online edition of the *American Naturalist*. Divergence in male color between HP and LP sites (D_c) ranged from 1.2% to 36.6% (table A1). For a given level of dispersal and sexual selection, color divergence was greater when natural selection acted more strongly against high color in the HP site. This result confirms the expectation that a greater ecological contrast causes greater divergence in selected traits. For a given level of dispersal and natural selection, color divergence was greater when sexual selection was flat (females showed no preference for male color) on average (as opposed to being positive or negative). This was because strong negative sexual selection slowed the evolution of high color in the LP site, whereas strong positive sexual selection slowed the evolution of low color in the HP site. For a given level of sexual and natural selection, color divergence was greater when dispersal was lower, confirming the expected constraining influence of gene flow on adaptive divergence. In control simulations, divergence in color was very low at the high dispersal rate, confirming that the above results are largely driven by the ecological contrast between HP and LP environments. Some divergence was evident in control simulations at the low dispersal rate—but this was because of founder effects.

Survival deficits for LP immigrants into the HP site (D_s) ranged from 0.5% to 23.4% (table A3). Variation in these deficits generally paralleled color divergence, as would be expected. First, survival deficits were generally greater when natural selection acted more strongly against high color in the HP site (i.e., divergent selection was stronger). Second, survival deficits were greater when sexual selection was flat on average (for the reasons described above for color divergence). Third, survival deficits were somewhat higher when dispersal rates were lower (constraints imposed by gene flow were lower). Hybrid survival was generally intermediate between resident and immigrant survival, as was expected given their phenotypic intermediacy. In the control simulations, differences in survival were always less than 5% (results not shown), confirming again that the above results are caused by the ecological contrast.

Mating success differences between residents and immigrants (D_m) ranged from -39.9% (immigrants have lower mating success) to 41.4% (immigrants have higher mating success; table A4). Because female preferences evolved much slower than male color did (table A2), the mating success of immigrants compared to residents was mainly driven by an interaction between the initial conditions of sexual selection and the subsequent color divergence. When sexual selection was positive, the (colorful) immigrants always achieved higher mating success than did the (drab) residents. When sexual selection was negative, immigrants usually had lower mating success than residents. In general, differences in mating success

between immigrants and residents were smaller when the ecological contrast was weaker and when dispersal was higher—as expected because color divergence was lower (as above). Hybrid male mating success was generally closer to immigrant male mating success as a result of their intermediate color superimposed on the observed Gaussian distribution of preferences within the population (table A4).

In summary (fig. 5), divergent selection led to the evolution of one potential contributor to reproductive isolation: survival differences between residents and immigrants. However, when female preferences in the HP site were for males with higher color, sexual selection offset this survival deficit for immigrants by affording them a mating advantage. These opposing effects of natural and sexual selection equalize the fitness of residents and immigrants, despite (indeed because of) their color divergence. In contrast, when female preferences in the HP site are for males with less color, reproductive isolation will be very strong, because natural and sexual selection both act against immigrants. When female preferences in the HP site are flat with respect to male color, sexual selection has very little direct effect on reproductive isolation, because females do not care about male color.

Divergence in neutral genetic markers (θ) was very low after 100 generations in all high-dispersal scenarios (table A5). When dispersal was instead low, neutral genetic divergence was evident after 100 generations ($\theta \approx 0.09$), but this was mostly a carryover from initial founder effects rather than being caused by divergent selection (see fig. 4D). Further insight can be gained by comparing the actual number of immigrants (Nm) to the effective number of immigrants ($N_e m$) at neutral markers and color loci. At low dispersal, $Nm \approx 14$ and $1 < N_e m < 2$ for neutral markers. This difference was the result of deviations from random mating and equal family sizes and was also seen in control simulations. For color loci, $1 < N_e m < 2$ in control simulations and $0.16 < N_e m < 0.4$ in HP-LP simulations. These confirm that selection reduced gene flow at selected markers but not at unlinked neutral markers.

In most scenarios, the level of linkage disequilibrium (D) calculated between two preference and color markers did not change appreciably during the simulations (100 generations, $D \approx \pm 0.001$). In some scenarios where negative sexual selection reinforced the ecological contrast, a small increase in linkage disequilibrium ($D \approx \pm 0.01$) was observed. In other scenarios where positive sexual selection efficiently counteracted ecological contrast (at low dispersal), a further increase in linkage disequilibrium ($D \approx \pm 0.02$) occurred in some, but not all, replicate simulations (fig. A1 in the online edition of the *American Naturalist*).

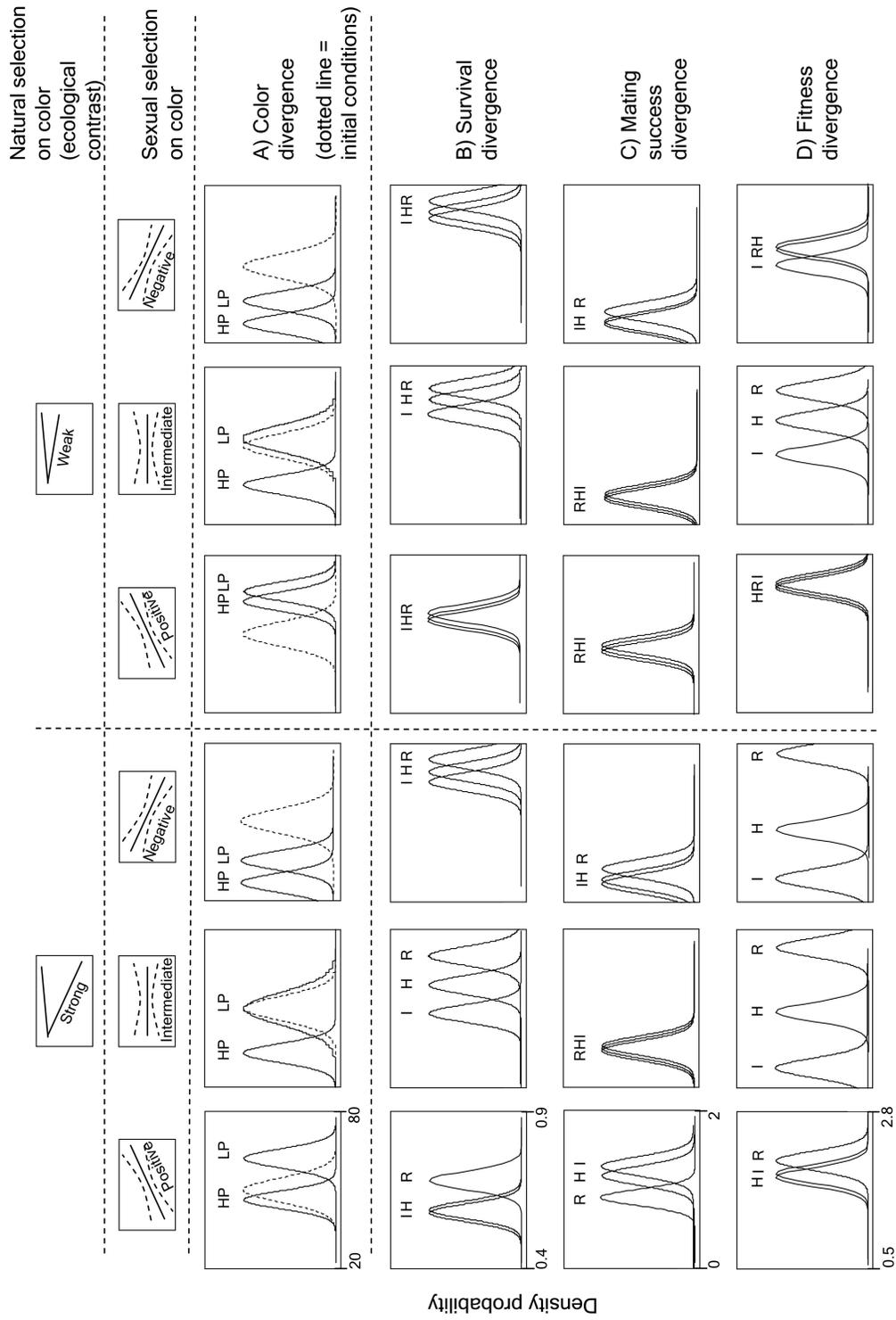


Figure 5: Synthetic figure of divergence of color in HP sites for residents (*R*), hybrids (*H*), and immigrants (*I*) under various simulation conditions: strong or weak natural selection, positive, intermediate, and negative sexual selection. Only results for low dispersal are presented. The abscissa scale is conserved for each horizontal panel to allow comparison.

Discussion

In our simulations, divergent selection often led to noteworthy divergence in male color after only 12–20 generations. The rate of this phenotypic divergence was influenced by dispersal (faster when dispersal was lower), natural selection (faster when divergent selection was stronger), and sexual selection (see below). Interestingly, the rates of adaptive divergence observed in our model were comparable to those observed in nature. Karim et al. (2007) reported rates of male color change following an experimental introduction that ranged from 0.01 to 0.031 haldanes over 13–26 generations. These values fall within the range obtained in our model (between 0.007 and 0.085 haldanes) over 100 generations. Endler's (1980) experiment yielded much higher rates (0.267–0.742), but this is probably due to the shorter time frame (only a few generations), given that evolutionary rates are slower over longer time intervals (Hendry and Kinnison 1999). These observations suggest that our model reasonably captures the natural dynamics of color evolution in guppies.

The nature of sexual selection had a particularly strong influence on adaptive divergence and reproductive barriers, with the possibilities falling into three general cases. (1) When females initially preferred colorful males, adaptive divergence usually took place quickly and became coupled to reduced immigrant survival. At the same time, this color divergence increased relative immigrant mating success, yielding no net effect on overall reproductive isolation (lifetime reproductive success differences of residents vs. hybrids and immigrants). (2) When females initially preferred drab males, adaptive divergence did not proceed very far, because stable sexual selection overwhelmed divergent natural selection. In this case, immigrants had relatively similar survival and mating success to residents, but the product of both (lifetime reproductive success) revealed some overall reproductive isolation (depending on ecological contrast). (3) When female preference was largely absent (flat preference functions, on average), color divergence was highest. In this case, immigrants had reduced survival but mating success similar to that of residents, and so some overall reproductive isolation was evident. In summary, the initial nature of female preference in the population strongly influenced (1) the speed of divergence and the final color phenotypes and (2) the reproductive barriers that lead to reproductive isolation. These results provide a reasonable explanation for why HP and LP guppy populations do not always diverge in color (Karim et al. 2007; Kemp et al. 2008).

One factor that might bring natural and sexual selection in line with each other, and thus enhance overall reproductive isolation, would be for sexual selection to evolve in response to divergent natural selection. In our simu-

lations, however, female preference evolution was minor. We suggest three possible reasons. First, we used a biologically relevant multiallelic polygenic architecture, which makes more difficult the building of linkage disequilibrium between physically unlinked loci (as opposed to biallelic approaches of Kondrashov and Kondrashov [1999] or of Dieckmann and Doebeli [1999]). We feel justified in this choice given that a complex genetic architecture is generally expected for female preferences (Brooks and Endler 2001; Arnegard and Kondrashov 2004; Seehausen et al. 2008). In test simulations with a simplified genetic architecture for female preference (two loci with four alleles each), we observed slightly faster preference evolution, as well as some linkage disequilibrium, but this did not alter any of our basic conclusions. Second, female preferences were not subject to direct natural selection, instead being influenced only indirectly by natural selection acting through offspring fitness. Indirect selection is known to be less effective at driving female preference evolution than is direct selection (Hall et al. 2004; Qvarnström et al. 2006), but no studies have confirmed direct selection in guppies. Third, the evolution of female preference simply might take longer than 100 generations, as is the case in other models (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999; Gavrilets 2004; Thibert-Plante and Hendry 2009). Indeed, we found greater evolution of preference in test simulations run over 200 generations (table A6). Regardless, empirical work in guppies suggests that preference evolution over even long timescales is not strong and consistently different between predation regimes (Endler and Houde 1995; Rodd et al. 2002; Schwartz and Hendry 2007;), and artificial selection on female preferences does not always yield a response (Breden and Hornaday 1994; Hall et al. 2004; but see Houde 1994). In short, our results are generally consistent with those of other models (Kirkpatrick and Nuismer 2004), and with work on guppies, in suggesting that female preferences do not evolve rapidly in response to altered selective regimes.

Our results also inform several other questions about ecological speciation. First, we found that considerable adaptive divergence took place in less than 100 generations and coincidentally caused very strong natural (viability) selection against immigrants and hybrids. These barriers then led to substantial overall reproductive isolation (based on lifetime fitness)—as long as they were not opposed by sexual selection (as described above). The rapidity with which these reproductive barriers can evolve parallels the results of previous models (Hendry 2004; Thibert-Plante and Hendry 2009) and supports previous assertions that substantial ecologically based reproductive barriers can evolve on very short timescales (Hendry et al. 2000, 2007).

Second, our results inform the common practice of using neutral genetic markers to infer ecological speciation.

That is, some analyses suggest that unlinked, neutral markers should flow almost freely between populations in different ecological environments (Via and West 2008; Thibert-Plante and Hendry 2009), whereas others suggest the possibility of a generalized barrier to gene flow (Ogden and Thorpe 2002; Gavrillets 2004; Grahame et al. 2006; Berner et al. 2009). Here we found no evidence that divergent natural selection contributed to divergence at unlinked neutral markers over 100 generations. These findings suggest that the failure to detect selection-associated genetic divergence at neutral markers does not necessarily indicate an absence of progress toward ecological speciation, at least when the time frame is short and the populations are large (ours were about 10,000 individuals). Our results also show that founder effects that cause neutral genetic divergence can give the illusion of reproductive isolation unless a control (populations in similar environments) is included in the analysis.

Assumptions and Their Consequences

For each component of our model, we strove for a reasonable balance (Grimm et al. 2005) between parsimony (simplifying assumptions) and realism (parameter values estimated in natural populations). Reassuringly, our choices yielded reasonable demographic and genetic patterns. Although violations of the assumptions would likely alter the rate and magnitude of evolutionary changes, they probably would not alter our qualitative conclusions.

One major assumption was that life-history traits (age at maturity, pregnancy period, number of offspring) were constant across space and time. In reality, several life-history traits do differ between HP and LP guppy populations (Rodd and Reznick 1997) and can evolve over time frames similar to those modeled here (Reznick et al. 1997; Gordon et al. 2009). If “slower” life histories evolve in the LP site, as would be expected, evolutionary divergence would be slower on an absolute temporal scale (i.e., not generation scale). In addition, life-history differences, as well as other traits, will likely contribute to survival, and perhaps mating, differences in interactions between HP and LP fish (O’Steen et al. 2002; Magurran 2005). It is therefore important to remember that our results consider only two potentially diverging traits (male orange area and female preference for male orange area) and that our approach was to maximize the selective pressure on these traits (whereas it is known that the LP-HP effect on male color does not always apply, as shown by Weese et al. [2010]).

Another set of assumptions simplified the dynamics of mating and reproduction: a single mating event per time step, no sperm storage, no social interactions, and no influence of any male traits apart from orange. In reality, female guppies can mate multiply (Neff et al. 2008) and

store sperm (Houde 1997), prefer rare male phenotypes (Hughes et al. 1999), copy the choices of other females (Dugatkin and Godin 1993), select on other male traits or trait combinations (Kodric-Brown 1993; Brooks 2002; Blows et al. 2003), show “cryptic” mate choice (Magellan and Magurran 2007), and be inseminated through “sneaky” copulations (Magurran 2005). Many of these effects are probably reasonably subsumed in the probabilistic nature of mate preferences modeled here, but some exceptions are likely. For example, multiple mating and sperm storage might reduce founder effects and thus increase the deterministic nature of adaptation. The evolutionary trajectory of male color and female preference might also be altered, but not in ways that are obvious to predict a priori.

A last important assumption was that phenotypic divergence was entirely genetically based. Although this assumption is reasonable for orange area (Haskins et al. 1961; Houde 1992; Brooks and Endler 2001; Brooks 2002; Karim et al. 2007), plastic effects are evident for other aspects of guppy color (Grether et al. 2001; Karim et al. 2007; Schwartz and Hendry 2007; C. Ghalambor, unpublished data). If adaptive, this plasticity might slow the evolution of color differences (Ghalambor et al. 2007) and might influence reproductive isolation (Crispo 2008). For example, adaptive plasticity might positively or negatively influence the survival or mating success of immigrants depending on whether plastic changes occur after dispersal between environments.

Conclusions

Our findings suggest several general implications for the study of ecological speciation. First, studies attempting to infer ecological speciation should examine multiple reproductive barriers (e.g., McKinnon and Rundle 2002; Nosil 2007) because contributions of divergent selection to one potential barrier may be offset by opposing effects on another potential barrier. Second, the predictions of ecological speciation regarding the evolution of reproductive barriers (Schluter 2000) can be heavily influenced by the biological particularities of specific natural systems (Gavrillets and Vose 2007; Gavrillets et al. 2007; Hendry 2009; Nosil et al. 2009), here the nature of female preference. For instance, sexual selection can promote or impede divergence depending on its stability between environments and its interaction with natural selection. We therefore echo the arguments of other authors (Schwartz and Hendry 2006; Svensson and Gosden 2007; Hendry 2009) for a greater consideration of the role of sexual selection in shaping the potential for evolution in general and for ecological speciation in particular.

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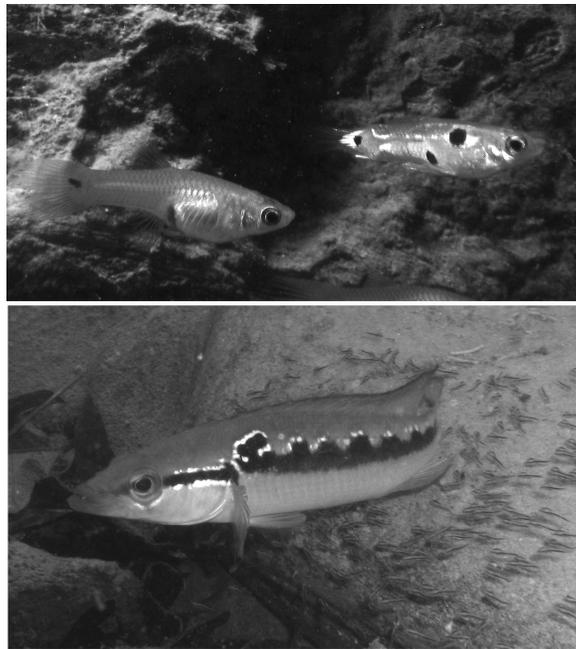
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The conflict between sex and death. *Top*, female guppies often prefer more colorful males. *Bottom*, colorful males are often more susceptible to dangerous predators such as this pike cichlid with babies. Photographs by Paul Bentzen.