ORIGINAL ARTICLE

EFFECTS ON POPULATION DIVERGENCE OF WITHIN-GENERATIONAL LEARNING ABOUT PROSPECTIVE MATES

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Although learned mate preferences are suspected to have important effects during speciation, theoretical models have largely neglected the effects on speciation and population divergence of within-generational learning, that is, learning based upon prior experience with potential mates. Here, we use population genetic models to address this deficit. Focusing on the situation of secondary contact between populations that still hybridize, we consider models of learning by females and by males under polygyny. We assess the effects of learning to prefer conspecifics from previous conspecific encounters, learning to avoid heterospecifics from previous heterospecific encounters, and learning to prefer familiar types. We examine the amount of population divergence that results from learning in these models. We also assess the effect of learning on the spread of an allele that strengthens assortative mating in both models. We find that learning can have counterintuitive, but logical and understandable effects that differ with the version of the model assessed. In general, population divergence is expected to increase most consistently when females learn to strengthen their preferences for conspecifics from previous encounters with conspecifics. Our results also suggest that within-generational learning will generally inhibit the spread of alleles strengthening assortative mating.

It has been emphasized that premating reproductive isolation may be the most important factor in maintaining species boundaries in the presence of gene flow (Kirkpatrick and Ravigne 2002; Coyne and Orr 2004). Mating preferences and sexually selected traits, which can lead to premating isolation, may thus play an important role in both species maintenance and the speciation process (Panhuis et al. 2001; Ritchie 2007; van Doorn et al. 2009; M'Gonigle et al. 2012; Servedio and Kopp 2012). Coincident with this emphasis on premating isolation, there has been mounting appreciation that mating preferences, and in some cases sexually selected traits, may have a learned component (Immelmann 1975; Irwin and Price 1999; Verzijden et al. 2012b). Interestingly, a type of learning that may be the most amenable to study, within-generational learning based on interactions with prospective mates, has been largely neglected in theoretical studies of the

effect of learning on speciation. We address the effects of this type of learning on the divergence of sexually selected traits during secondary contact, using a series of models where learning occurs in either males or females.

As opposed to the lack of work on within-generational learning, theory suggests that cross-generational learning of sexual signals such as song, mate preference, and habitat choice, can facilitate reproductive isolation and population divergence (Laland 1994; Beltman et al. 2004; Lachlan and Servedio 2004; Beltman and Metz 2005; Servedio et al. 2009; Verzijden et al. 2012b). Perhaps the most attractive empirical system for examining the effects of learning on mate choice, assortative mating, and population divergence is imprinting in birds, in which young learn unique visual and vocal features from parents and perhaps other local adults and ultimately rely on that information for courtship

and mate choice (Immelmann 1975; Irwin and Price 1999; ten Cate and Vos 1999; Price 2008). Learning of parental features, which later affects mate choice, is probably prevalent in mammals (Kendrick et al. 1998) and also occurs in at least some species of fish (Verzijden and ten Cate 2007; Kozak et al. 2011). Indeed controlled experiments involving cross fostering suggest that learning to prefer or express a given signal such as bird song could enhance reproductive isolation (Clayton 1990; Slagsvold et al. 2002; Verzijden and ten Cate 2007). Intriguingly, with a single exception involving the unusual brood parasitic indigo birds (*Vidua* spp.), which imprint on their host (Payne et al. 2000; Sorenson et al. 2003; Balakrishnan et al. 2009), we know of no case where learning has been shown to be a major factor leading to speciation.

One might argue that the lack of empirical evidence for a major role of learning in speciation merely reflects the fact that the model species in question have long generation times, which make experimental evolution studies less feasible. Recent research, however, suggest a role for learning in speciation in fruit flies (*Drosophila* spp.), which are highly amenable to experimental evolution and have been used extensively in speciation research (Coyne and Orr 1989; Coyne and Orr 2004; Noor and Feder 2006). Unlike the imprinting studies discussed above, however, which involve cross-generational learning, learning in fruit flies, and an increasingly documented number of other taxa, occurs within a single generation. In fruit flies, males learn through feedback from females and females learn about the locally available potential mates prior to mating (Dukas 2006). Specifically, male *Drosophila melanogaster* show robust associative learning of the cues associated with receptive females (Siegel and Hall 1979; Ejima et al. 2005). Although males initially indiscriminately court conspecific females and females of the sister species, *Drosophila simulans*, rejection by female *D. simulans* causes males to rapidly and selectively reduce heterospecific courtship (Dukas 2004; Ellis and Carney 2009; Dukas and Dukas 2012). Males of the closely related species pair, *Drosophila persimilis* and *D. pseudoobscura* show the same pattern of initial indiscriminate courtship with subsequent learning to reduce courtship of heterospecifics. This selective decline in heterospecific courtship also leads to a lower frequency of heterospecific matings (Dukas 2008; Dukas 2009; Kujtan and Dukas 2009; Dukas et al. 2012).

Although fruit flies have been the best-studied system in which males show within-generational learning in the context of sexual behavior, such learning may be common. In the brood parasitic cowbirds (*Molothrus ater*), in which males cannot imprint on their biological fathers, sexually mature males learn to refine their courtship displays based on feedback from conspecific females (King and West 1983; West and King 1988). Male Trinidadian guppies (*Poecilla reticulata*) initially attempt to mate indiscriminately with conspecific females and allopatric females

of the closely related swamp guppy (*P. picta*), but learn to restrict mating attempts to conspecific females within a few days (Magurran and Ramnarine 2004). Finally, rearing with mostly heterospecific females enhances conspecific preference in male limnetic and benthic sticklebacks (*Gasterosteus* spp.) (Kozak and Boughman 2009).

Within-generational learning affecting mate choice also occurs in females. Among invertebrates, female fruit flies (*D. melanogaster*) that have previously encountered large males, which they typically prefer, are less likely to mate with less attractive, small males than are females that have previously encountered small males (Dukas 2005). Similarly, in field crickets (*Teleogryllus oceanicus*), females exposed to preferred songs are later less likely to respond to a reference song than are females previously exposed to less-preferred songs (Bailey and Zuk 2009). In wolf spiders (*Schizocosa uetzi*), females prefer to mate with experimentally manipulated male color phenotypes that they experience when immature (Hebets 2003). Females of other species of wolf spiders also modify mate choice based on prior experience (Hebets and Vink 2007; Rutledge et al. 2010). In treehoppers (*Enchenopa binotata* species complex), prior experience with male courtship signals alters females' subsequent selectivity (Fowler-Finn and Rodríguez 2012). Female butterflies (*Bicyclus anynana*) exposed to males with enhanced wing ornamentation are more likely to mate with them than are naïve females (Westerman et al. 2012). Finally, experience plays a role in females' avoidance of heterospecific males in the closely related damselfly species *Calopteryx splendens* and *C. virgo* (Svensson et al. 2010).

In vertebrates, effects of within-generational experience on female mate choice have been documented in a few species of fish. In Trinidadian guppies (*P. reticulata*), females housed with a mixture of males with low and high proportions of orange areas later prefer high over low orange males (Rosenqvist and Houde 1997). Female exposure to males also influences subsequent mate choice in benthic and limnetic sticklebacks (*Gasterosteus* spp.) and in swordtails (*Xiphophorus birchmanni* and *X. malinche*) (Kozak and Boughman 2009; Verzijden et al. 2012a; Kozak et al. 2013).

The above examples indicate that, in a large number of species ranging from fruit flies to birds, both males and females modify their mate choice and mating behavior based on within-generational experience. Both sexes have the opportunity to learn various relevant features of the locally available mates and hence adjust their courtship and mating criteria (Dukas et al. 2006), and males can also learn to improve their courtship behavior. The behavioral data suggest that such within-generational learning can increase the likelihood of reproductive isolation (Dukas 2008; Kujtan and Dukas 2009). We evaluate this possibility using theoretical population genetic analyses, which we hope can provide relevant guidance for future experimental evolution work. We are principally interested in the effects of within-generational learned

preferences on the amount of divergence maintained between two populations in population-specific traits. In some cases, we also examine the effect of this learning on the rate of evolution of stronger assortative mate choice preferences (a measure of the process of reinforcement, Dobzhansky 1940; Servedio and Noor 2003). Using models of both female learning and male learning, we examine both cases where learning reinforces existing species-specific mating biases and cases where familiarity promotes mate preference. In the former scenario, we also consider whether learning occurs based on encounters with conspecifics, heterospecifics, or both. We find that trait differentiation between populations is sometimes enhanced and sometimes decreased by learning. Some of these effects are initially counterintuitive, but the models enable us to pinpoint logical and general reasons why they occur. We also find that the evolution of stronger assortative mating is often inhibited by within-generation learning.

Models

To explore the effects on divergence and speciation of cross-generational learning from potential mates, we analyze separate sets of models in which learning occurred in females and in males. In both of these cases (with the exception of one variant), we assume a mating system of polygyny, in which females have equal mating success, whereas male mating success varies.

For both models, we assume that two large populations have come into secondary contact through the exchange of migrants (a "two-island" model). We assume three haploid loci, each with two alleles, in a deterministic model. The first two loci, N and M, determine population identity, where populations 1 and 2 are characterized by the genotypes N_1M_1 and N_2M_2, respectively. "Hybrid" genotypes at these loci, N_1M_2 and N_2M_1, have low relative fitness ($1-s$) compared to "purebreds," due to Dobzhansky–Muller incompatibilities (e.g., Orr and Presgraves 2000). Purebred phenotypes characteristic of each population are preferred by females above hybrid or foreign phenotypes (in all models we assume hybrid females mate at random). This is a form of a "magic trait" model because the same loci involved in reproductive isolation are under divergent selection due to their role in incompatibilities (Gavrilets 2004; Servedio et al. 2011). The third locus, A, is used in some of the models to examine the evolution of assortative mating, and determines the strength of assortative mating based upon the genotypes at the N and M loci as detailed below.

The life cycle consists of migration (occurring at rate *m*), viability selection against hybrids, mate choice under polygyny (described below), recombination (free recombination is assumed), and offspring production. Exact recursion equations developed from the assumptions described below can be found in the Appendix S1 as well as in the simulation code deposited in Dryad, doi:10.5061/dryad.c0164.

Servedio (2011) demonstrated that in this type of model an intermediate preference strength leads to the maximum amount of divergence between populations in traits that serve as cues for assortative mating (the species identity loci in the current model). In the case of the particular genetic architecture used in this model, there is an optimum preference strength, close to the one that causes the maximum amount of population divergence, that will evolve (Servedio 2011). Populations with preference strengths that are higher than this optimum can be invaded by alleles that reduce the preference strength toward this optimum. As we are interested in effects that may increase population divergence and in the spread of alleles that increase preference strength, we concentrate on the parameter space below this optimum, corresponding to the early stages of speciation. We will find, however, that the effects of learning change the net strength of preferences and occasionally may push it past this optimum.

The data outlined in the introduction indicate that there is large variation between species in the ways within generational learning influences mate choice. To maintain the generality of the model and yet address some biologically realistic examples, we focus on several relevant cases outlined below for each sex.

FEMALE LEARNING MODEL

We assume that two encounters occur during mate choice. During the first encounter females do not yet mate, but instead learn from their experiences. In other words, depending upon the type of initial encounter with a random male, females acquire information that affects their preferences when mating occurs upon the second encounter. Specifically, we assume that purebred females, fixed at the A locus for allele A_1 in these initial analyses, have a basal preference of strength α (where $\alpha > 1$), such that these females are α times as likely to mate with a male that matches their population-specific phenotype (a "conspecific") than with other males if they encounter equal proportions of each. The resulting preferences for each type of male can be modified by learning in several different ways.

Learning increases bias toward conspecifics and against heterospecifics

In the general case explored in the greatest detail, we assume that females receive feedback from their first encounter, which indicates the general suitability of that type of male as a mate. Specifically, when females encounter a conspecific on their first encounter, their basal preference α is increased by a factor γ_1 (Table 1). If a female instead first encounters a "heterospecific" (a pure male of the opposite population), she learns to avoid such a male, so that her probability of mating with a heterospecific upon the second encounter is reduced by a factor γ_2. Finally, a female may also learn from a first encounter with a hybrid, so that her probability of mating with a hybrid upon a subsequent encounter

Table 1. Table of mating probabilities for purebred females, based upon their first encounter.

For M_1N_1 females				
If first encounter is with this type of male →	M_1N_1	M_1N_2	M_2N_1	M_2N_2
then the probability of mating with this type of male↓ is given in the table				
M_1N_1	$\gamma_1\,k\,\alpha$	$k\,\alpha$	$k\,\alpha$	$k\,\alpha$
M_1N_2	1	$1/\gamma_h$	$1/\gamma_h$	1
M_2N_1	1	$1/\gamma_h$	$1/\gamma_h$	1
M_2N_2	1	1	1	$1/\gamma_2$
For M_2N_2 females				
If first encounter is with this type of male →	M_1N_1	M_1N_2	M_2N_1	M_2N_2
then the probability of mating with this type of male↓ is given in the table				
M_1N_1	$1/\gamma_2$	1	1	1
M_1N_2	1	$1/\gamma_h$	$1/\gamma_h$	1
M_2N_1	1	$1/\gamma_h$	$1/\gamma_h$	1
M_2N_2	$k\,\alpha$	$k\,\alpha$	$k\,\alpha$	$\gamma_1\,k\,\alpha$

For A_1 females, $k = 1$; for A_2 females, $k = \kappa$.

is reduced by a factor γ_h. Learning from only a single type of encounter can be studied by setting the appropriate parameters to one (e.g., learning from initial encounters with conspecifics alone can be studied by setting $\gamma_2 = \gamma_h = 1$ and allowing γ_1 to vary). We examined the effects of learning from only conspecifics, only heterospecifics, and both conspecifics and heterospecifics. Unless specified otherwise, we assumed in all runs that $\gamma_h = 1$.

For this case, we also examined the evolution of assortative mating by introducing A_2 at a low frequency. In A_2 females, the basal preference α is increased by a factor κ to be $\kappa\alpha$, and is modified by learning in the same way as for A_1 females.

Preference for familiar types
In the case above, we assumed that females learn based on some characteristics of prospective mates. A feasible alternative is that females learn to prefer male types with which they are familiar. We consider this case by assuming that regardless of whether females initially encounter conspecifics or heterospecifics, they increase their preference for that type by the factor γ. We assume here that females do not learn from encounters with hybrids.

MALE LEARNING MODEL
The loci and alleles in the male learning model are identical to those in the female learning model. The life cycle also proceeds identically through viability selection. As described below, males express their preferences through biases in their courtship, but females are still assumed to make the ultimate mating decision and, in most versions below, have equal mating success (strict polygyny). We allow for the possibility that females may have an underlying preference for conspecific males, which leads to additional variants of the primary version of the model (described

first below). A variant in which females' mating success is based upon the amount of courtship they receive is also included. Unless specified below, we assume that the assortative mating locus is fixed for allele A_1.

Learning increases bias toward conspecifics and against heterospecifics I: Male learning from female identity
Here, we assume that in their first encounter, males receive feedback that indicates species identity. Males thus learn based upon the type of female that they experience through a random initial contact, altering their basal preferences as in Table 1 (with "female" replacing "male" and vice versa throughout the table). In the second encounter, males bias their courtship of encountered females using the preference strengths that have been modified by the first encounter. As in the female learning model, these preferences are a combination of a basal male preference (α) and biases due to learning (γ_1 and γ_2). Specifically, males will bias their courtship toward the preferred type of female, courting her with an intensity (or for a length of time) proportional to the corresponding preference strengths from Table 1. On this second encounter, females choose a mate from among the courting males. We assume that the likelihood that a male will be chosen by a female is proportional to the time/energy that he expends in courting her (Servedio and Lande 2006; Dukas 2008; Kujtan and Dukas 2009).

At the time of mating, females express an innate preference for conspecifics, α_f. We first consider the case where the female preference $\alpha_f = 1$, meaning that females have no inherent mating preferences and their probability of mating with a male of a given phenotype is simply proportional to the effort with which males of that phenotype court those females. Second, we consider that

females have a set inherent preference for conspecific males ($\alpha_f > 1$), which we generally set equal to the basal male preference strength ($\alpha_f = \alpha$). In these cases, female mate choice is ultimately dependent upon all three elements of the frequency of males in the population, the male courtship preference, and the inherent female preference.

In this set of cases, we again consider the evolution of preference strength using the A locus. Here allele A_1 codes for the basal preference in males, α, whereas allele A_2 again changes the preference to $\kappa\alpha$. Both of these preferences are modified by learning as described above. We assume that in cases where females, like males, have a preference ($\alpha_f > 1$), allele A_2 modifies only the male preference strength.

Learning increases bias toward conspecifics and against heterospecifics II: Learning is positively correlated with female preference strength

In the case above, there was a constant value of male learning (the γs). Here, we assume instead that male learning is positively correlated with the magnitude of female preference. This essentially assumes that, in the first encounter, males learn something about their likelihood of being accepted or rejected by that type of female, instead of just learning about the identity of the female. Specifically, we assume that in the case where males learn from conspecifics, males scale their learned increase in preference toward conspecifics, γ_1, as the product $\gamma_1\alpha_f$. Similarly, in the case where males learn to avoid heterospecifics or hybrids, they scale their learned decrease by α_f (such that courtship of heterospecifics is decreased by the factor $\gamma_2\alpha_f$). In this version of the model, we set $\gamma_h = 1$.

Learning increases bias toward conspecifics and against heterospecifics III: Variation in female mating success

In the two sets of cases above, we assumed that females have equal mating success. Here, we relax the assumption of polygyny and assume instead that females have mating success proportional to the frequency with which they are courted (in this model we also assume no female preference, $\alpha_f = 1$). This assumes that mating opportunities for females are limited.

Preferences for familiar types

As for the female learning model, we include a case in which males learn to prefer whatever female type they have encountered previously. We again assume that males increase their preferences for either conspecifics or heterospecifics in this manner by the factor γ, but do not learn from encounters with hybrids.

NUMERICAL ANALYSES

The model was analyzed numerically through iterations of the exact recursion equations, performed in Mathematica (Wolfram

2009). Because the effects of migration and selection against hybrids are well known for two-island reinforcement models (greater selection against hybrids yields more selection for assortative mating, e.g., Liou and Price 1994; Servedio and Kirkpatrick 1997; Servedio 2000), for most of the runs in the model, we have kept $m = 0.01$ and $s = 0.5$ (qualitatively similar results to those reported below were seen with both higher and lower values of m and s in spot checks). Starting with the N_1M_1 and N_2M_2 genotypes initially fixed in populations 1 and 2, respectively, as in a scenario of secondary contact, equilibrium levels of the population-specific alleles at the M and N loci were determined for a given level of sexual selection strength (α) and learning (the γs) by running the simulations until the change in any genotype frequency in a given generation was $<10^{-10}$. In many trial runs, random perturbations of the genotype frequencies were performed after they had reached this equilibrium value to test its stability; equilibria reached in these simulations were always found to be stable by these tests. Examination of the spread of alleles for stronger assortative mating was accomplished by starting a simulation at these equilibrium values for the frequencies of the N_2 and M_2 alleles and the disequilibrium between them, D, and rerunning the simulation with the frequency of A_2 introduced at 0.01 (in linkage equilibrium with the N and M alleles) and κ set at the desired value. Eigenvalues, used as a measure of the rate of spread of the A_2 allele, were calculated from the latter runs numerically using both the rate of change of the A_2 and M_2 alleles (they were considered to have stabilized when these were identical to the second significant digit). We consider assortative mating to have evolved if both the A_2 allele spreads (note that A_2 generally spread to a frequency of at least 0.9 except at the boundaries of the areas of increase) and population differentiation was maintained at the N and M loci (this can happen both with very weak and very strong assortative mating, Servedio 2011).

Results

FEMALE LEARNING MODEL

Learning increases bias toward conspecifics and against heterospecifics

When the net effect of learning from previous encounters by females is to increase bias toward conspecifics, the effects on trait divergence depend heavily on the type of male they learn from. When females learn from encounters with both conspecifics and heterospecifics, our simulations generally find the evolution of more divergence between populations. The allele frequencies of population-specific traits will generally thus be higher in their respective populations (Fig. 1). (Note that although the results reported below all trace the frequencies of a single population-specific allele [e.g., allele N_2 on island 2], qualitatively identical
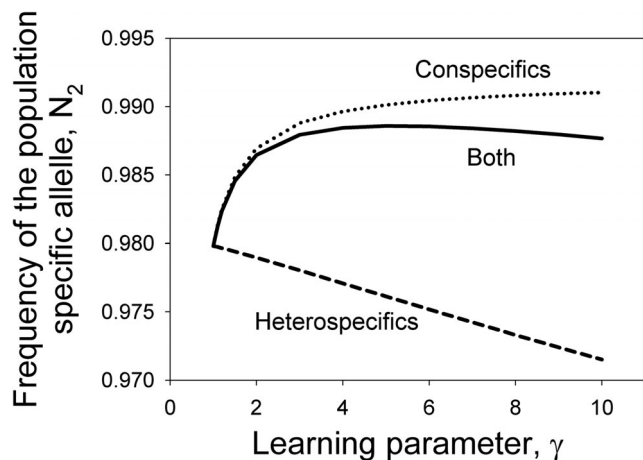
Figure 1. Frequency of the population specific allele N_2 in population 2 as a function of the learning parameter γ (encompassing γ_1 and γ_2, where $\gamma = 1$ means no learning) when females learn from only conspecific males, only heterospecific males, and both conspecific and heterospecific males. The female preference parameter $\alpha = 1.5$; the migration rate $m = 0.01$; and the selection coefficient against hybrids $s = 0.5$. Similar lines result from preference strengths (α) ranging from 1.1 through 2.0 (Fig. S1). Males are assumed to be indiscriminate in their courtship.

patterns were observed in all cases when we instead tracked the frequency of population specific genotypes [e.g., genotype N_2M_2 on island 2, not shown].)

This divergence, however, is a consequence of counteracting forces caused by learning from conspecifics versus heterospecifics. When females only learn to prefer conspecifics from previous encounters with them ($\gamma_1 > 1$, $\gamma_2 = 1$), many females in each population will have the opportunity to learn, because the females characteristic of each population will often encounter common, conspecific males. The strengthened preference for conspecific trait alleles leads to increased sexual selection for such alleles, causing them to spread evolutionarily in each population. A stronger effect of learning (higher γ_1) will increase this effect (Fig. 1). In contrast, when females instead only learn to avoid heterospecifics based on encounters with these phenotypes ($\gamma_1 = 1$, $\gamma_2 > 1$), stronger values of learning (higher γ_2) decrease the frequency of the population-specific trait alleles (Fig. 1). In this case, the females characteristic of each population will seldom encounter rare heterospecific males, whereas females with the heterospecific phenotype that happen to be in the population will frequently encounter the common resident males and learn to avoid them. Consider the effects of these encounters in population 2. Because we assume strict polygyny, both resident and foreign females will have equal mating success. The mating success of foreign males rarely suffers from learning, because a resident female will rarely encounter a foreign male twice (first to learn to avoid him, and then at mating time). Resident males, however, will have poor mating success with foreign females, because it is likely that these females have previously encountered, and hence learned to avoid, these males. This causes selection against the resident male genotype, and it thus arrives at a lower equilibrium frequency when the effects of learning to avoid heterospecifics are stronger. Finally, we further find that when females learn to avoid hybrids upon encounter, trait divergence also increases, but this increase is very slight with increasing γ_h (not shown).

With the parameter values that we explored, the effect on male trait evolution of females learning from conspecifics outweighs the effect of females learning from heterospecifics when both types of learning are present. We note, however, that with very high $\gamma_1 = \gamma_2$, we find that the frequency of the population-specific trait allele begins to drop (this trend can be seen on the curve for "Both" in Fig. 1). This could be a consequence of a shift in the balance of the interactions with very high degrees of learning, or could result from natural decreases in the force of divergent sexual selection that occur when effective preference strengths become too high (Servedio 2011). This effect can also be seen in the decrease in the slope of the lines as the strength of preference α increases in Figure S1.

What effect does learning have on the evolution of assortative mating? We find that, when females learn both from conspecifics and heterospecifics, the net effect of learning is to decrease the rate of evolution of an allele A_2 that slightly strengthens preferences for conspecifics (Fig. 2). The force of selection driving the spread of this allele, selection against hybrids, appears weaker when learned preferences are stronger. This is most likely due to the fact that fewer mistakes are made in mating and hence fewer low fitness hybrids are produced.

Preference for familiar types

When females learn to favor the type of male that they have encountered before, regardless of whether it is conspecific or heterospecific, we find that trait differentiation mimics the case above in which females learn only from encounters with conspecifics (Fig. 3). This is due to the fact that conspecifics are much more common than heterospecifics in each population. Counterintuitively, the frequency of the population-specific traits is slightly higher for a given level of learning in each population when females learn to prefer familiar male types (Fig. 3) versus when they only learn to prefer conspecifics (Fig. 1). Examination of the success of mated pairs shows that this is due to common resident males having disproportionally greater mating success with rare heterospecific females in the case where females learn from familiar types.
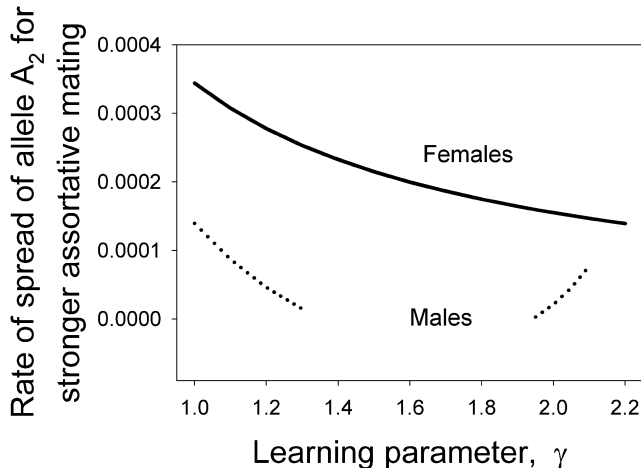
Figure 2. The rate of spread of allele A_2 for stronger assortative mating as a function of the learning parameter, γ, in males and females. The rate is measured as the eigenvalue corresponding to the spread of allele A_2 from a low frequency of introduction. A_2 was only found to spread with very low κ in the male learning case (e.g., $\kappa < 2$, given other parameters in the range shown; in the female learning case, A_2 spread in this range with $\kappa > 10$). In the case of male learning, the evolution of A_2 increased substantially with higher α_f. In general, when A_2 spreads it reaches a very high frequency (1 or close to it, except at the boundaries of where it is lost; in this figure, the only point at which A_2 was lower than 0.999 at equilibrium was with male learning when $\gamma = 1.3$, when $A_2 = 0.36$ at equilibrium). In all cases, $\gamma_1 = \gamma_2$. In the female curve, the female preference parameter $\alpha = 1.7$, and males are assumed to be indiscriminate. In the male curve, the values of both the male and female preference parameters, $\alpha_f = \alpha$, are 1.7. The migration rate $m = 0.01$, the assortative mating strength $\kappa = 1.1$, and the strength of selection against hybrids $s = 0.5$ in both model versions.
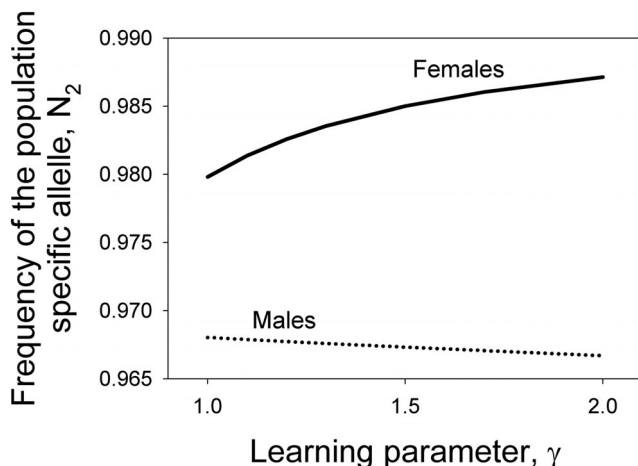

Figure 3. Frequency of the population specific allele N_2 in population 2 as a function of the learning parameter γ (where $\gamma = 1$ means no learning) when females and males learn to prefer familiar phenotypes.

MALE LEARNING MODEL

Learning increases bias toward conspecifics and against heterospecifics I: Male learning from female identity

Our model of male learning yields several differences from the model of female learning. When males choose, learning decreases the frequency of population-specific alleles when polygyny is assumed (Fig. 4A–C). These effects can be understood by a detailed examination of the changes in frequencies of genotypes and mated pairs throughout the life cycle, which yields the following insights.

As a general principle, during polygyny males that bias courtship have a selective disadvantage due to competition (Servedio and Lande 2006; Servedio 2007). For the purposes of understanding the current results, it is important to note that the strength of this competitive disadvantage depends upon the frequencies of male preference and female trait alleles (eq. 7 in Servedio and Lande 2006). The frequency of a male preference allele is particularly important. When there are more males with a preference, there is higher competition for preferred females, strengthening the selection against the male preference allele. In our model, the trait allele combinations N_1M_1 and N_2M_2 themselves face this source of competition when they lead males to have a skew in their courtship due to both inherent preferences for matched female genotypes (α) and learning (γ). When males learn from encounters with conspecifics and females do not have a preference ($\alpha_f = 1$, Fig. 4A), the greatest increase in courtship due to learning occurs in local males courting local females, which are common and thus often encountered. For example, in population 2, M_2N_2 males encounter M_2N_2 females often, so this is the biggest learned preference, resulting in skewed courtship by M_2N_2 males. Coupled with the high frequency of M_2N_2 males, this skewed courtship causes M_2N_2 males to suffer greatly from competition for mates in a polygynous mating system (from the effects described in Servedio and Lande 2006, Servedio 2007). Stronger effects of learning (higher γ_1, Fig. 4A) and higher male preference strengths (higher α, Fig. S2A–C) both increase this disadvantage to local males (Fig. 4A).

When males instead learn to avoid heterospecifics (Fig. 4A), the biggest learned effect in population 2 is that foreign M_1N_1 males learn to avoid local, common M_2N_2 females. Foreign M_1N_1 males thus have a higher skew in their courtship than local M_2N_2 males do. Recall, however, that the disadvantage due to skewed courtship is frequency-dependent. Although the effective preference, in the sense of skewed courtship, of foreign M_1N_1 males is higher than that of local M_2N_2 males, the costs of this skew are low because there are few fellow M_1N_1 males competing for matings with M_1N_1 females (because these females are rare, many M_1N_1 males will court other females despite their courtship preference). Although the relative skew of M_2N_2 males is lower, there are many M_2N_2 males with this slightly biased courtship,
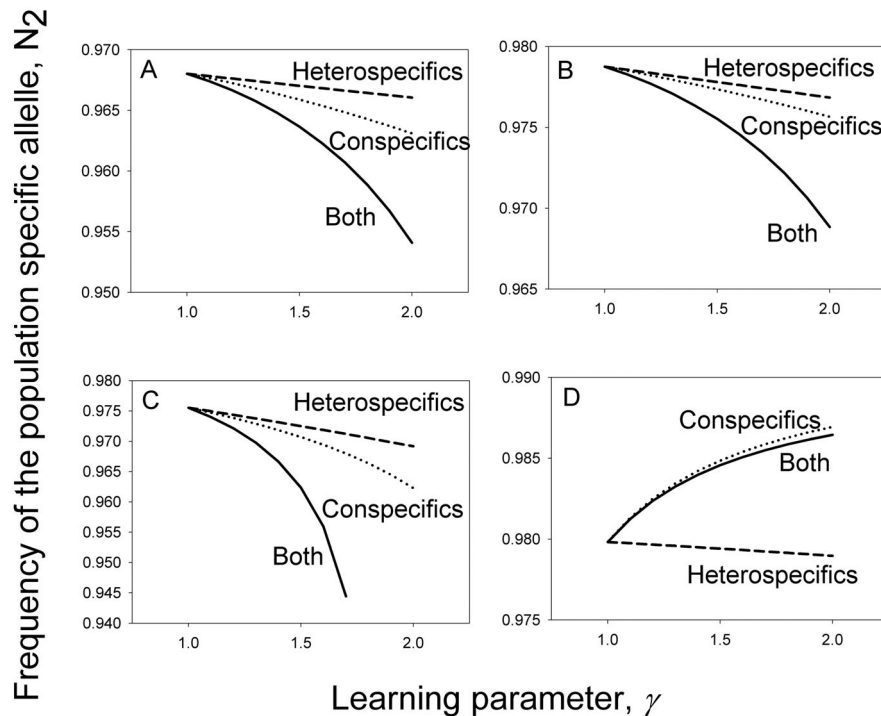
Figure 4. Frequency of the population specific allele N_2 in population 2 as a function of learning strength when males learn from only conspecific females, only heterospecific females, and both conspecific and heterospecific females. In all panels the value of the male preference parameter $\alpha = 1.5$; the migration rate $m = 0.01$; and the selection coefficient against hybrids $s = 0.5$. (A) Females are assumed to be indiscriminate. (B) Both males and females have the same initial preference value of $\alpha = 1.5$. (C) Parameters are as in panel B with the addition that male learning is a function of the feedback they receive from the female's preferences α_f. (D) Parameters are as in panel A except that here, females' mating success is positively correlated with the amount of courtship they receive.

resulting in an overall selective loss of the M_2N_2 genotype. This effect of male preference frequency can be seen by a graphical analysis of a modified version of eq. (7) from Servedio and Lande (2006) in which both types of males have a preference, as in the current model (not shown). It should be noted that the selection due to competition from male preferences described above appears in numerical analysis of the model to be a dominant cause of changes in allele frequencies. However, variation in male mating success due to learning is also present in how often males court hybrid female genotypes, resulting in the interactions being more complicated than are represented here.

When females and males both have an underlying preference for local mates ($\alpha_f = \alpha$), but only males learn, learning again decreases the frequency of local alleles (Fig. 4B), as described above. The effect of increasing preference strength is different, however. When females have no preferences ($\alpha_f = 1$), the frequency of local alleles decreases monotonically as male preference strength increases, as described above (Fig. S2A–C). When females have a preference ($\alpha_f = \alpha$), the sexual selection that this preference imposes on local males (e.g., M_2N_2 males in population 2) increases their frequency. This sexual selection favoring local males interacts with the selection against these males because of their biased

courtship that was described above (seen in Fig. 4A) to produce curves that first increase with stronger preferences and then decrease as preferences become too strong (Fig. S3A–C). The shape of these curves is also consistent, however, with the fact that divergent sexual selection due to phenotype matching decreases in a two-island model when preference strengths become too strong (Servedio 2011). In this case, however, we believe that this latter effect is less likely to explain the decrease in frequency of local alleles than is the presence of more biased male courtship, because drops in the frequency of local alleles do not generally occur with female preferences alone at these preference strengths (Fig. S1). Qualitatively similar results occur when females have a stronger underlying preference for conspecifics than do males ($\alpha_f > \alpha$, not shown), provided that these strengths are not too strong (in which case we again see a drop in the frequency of local alleles as expected from Servedio 2011).

In the case of male preferences, we generally again find slower evolution of an allele A_2 for greater conspecific preference when there is more learning (higher $\gamma_1 = \gamma_2$, Fig. 2), although the dynamics are quite complicated. First consider the effects on A_2 of male versus female choice in the absence of learning. In the male choice model, A_2 has two effects. As in the female choice

model, selection against hybrids is present in this model, which favors the spread of the A_2 allele for stronger assortative mating. A2 also, however, causes a stronger courtship bias in males, which leads to it being selected against. Adding learning, in contrast to the female learning case, *more* hybrids are produced with greater male learning, due to the fact that the frequencies of population-specific alleles become lower as learning increases. The source of the reduction in the spread of A_2 with greater learning is thus not that fewer hybrids are produced (as with female learning), but instead that A_2 is statistically associated with N_2 (again taking the perspective of population 2), which decreases increasingly quickly with greater learning due to its stronger competitive disadvantage (as seen in Fig. 4A–C). Interestingly, the association of A_2 with N_2 can also sometimes be beneficial for the spread of A_2; we find that A_2 is often lost for any value of learning unless females also have a preference ($\alpha_f > 1$) of sufficient strength, which favors N_2 and allows A_2 to increase by association (comparison of different α_fs not shown). Finally, for high but realistic values of learning (high $\gamma_1 = \gamma_2$), there can be a narrow area where A_2 once more increases in frequency (Fig. 2, right), especially when female preference (α_f) is high. Examination of this case in detail shows that here the N_2M_2 genotype takes such a hit due to courtship bias that N_1M_1 becomes relatively more successful (this is seen to occur at the expense of both N_2M_2s and hybrids). Because A_2 is associated with both of these purebred genotypes, the consequence is that A_2 becomes statistically associated with N_1 (from its association with N_1M_1) instead of N_2, and thus A_2 increases as N_2 continues to decrease. With yet higher learning values, variation at the N and M loci is lost (Fig. 2, far right).

Learning increases bias toward conspecifics and against heterospecifics II: Learning is positively correlated with female preference strength

The case where male learning is scaled by female preference strength (simulating learning based upon the expected probabilities of acceptance as a mate) has patterns similar to the case of $\alpha_f = \alpha$ above (Fig. 4C and Fig. S4). When learning is scaled by preference strength, the drops in frequency observed with both a high level of learning γ and high levels of preference α are more pronounced; this is expected since scaling learning by the female preference strength effectively increases the strength of the male's preference (it may also be affected by the additional reduction of courtship toward hybrids in this model).

Learning increases bias toward conspecifics and against heterospecifics III: Variation in female mating success

When female mating success is proportional to how often females are courted, divergence generally increases with male learning; the frequency of local alleles is higher both when males learn from encounters with conspecifics and when they learn both from con-

specifics and from heterospecifics (Fig. 4D). This is simply due to the fact that increased male courtship of conspecifics raises the mating success of conspecific females, and hence the frequency of the conspecific allele (it also counters selection against alleles that cause male preferences, Servedio and Lande 2006). We find that when males learn from heterospecifics, the frequency of the local allele still decreases; although the mating success of heterospecific females decreases in this case, the mating success of the hybrids subsequently increases (males shift their courtship away from heterospecifics toward everybody else), and the hybrids also carry the nonlocal allele.

Preferences for familiar types

As in the female learning case, when males learn to favor familiar types of females, we find similar results to the case of learning from conspecifics alone (Fig. 3 vs Fig. 4A). That is, learning decreases the frequency of population-specific alleles. In the case of male learning, the resulting trait differentiation between populations is a little greater when males learn to prefer familiar types than when they prefer conspecifics (Fig. 3 vs Fig. 4A). The enhanced preferences that males acquire for conspecifics, which are the common type, are moderated by the fact that some males increase their preference for heterospecifics instead. Because strong male preferences cause a competitive cost for that type of male, these relatively weaker conspecific preferences may be leading to a lower cost for conspecific males when males prefer familiar types.

Discussion

Our results help us place in proper perspective the recent data indicating that within-generational learning in the context of mate choice may be prevalent, and give us insight into the possible effects of this phenomenon on species maintenance and speciation. Overall, we find that the effect of within-generational learning on population divergence depends upon the sex and information learned. We are able to pinpoint why these differences occur, which should enable the applicability of our findings to biological situations that differ in certain ways from the assumptions of our models. We also find that the general effect of within-generational learning is to decrease the rate of evolution of stronger assortative mating, which has interesting implications for the occurrence of reinforcement in natural populations.

FEMALE LEARNING

Compared to no learning, within-generational learning increases population divergence when females learn to become more selective in their subsequent mate choice after initial encounters with conspecific males, and this effect is larger with higher values of the learning parameter (Fig. 1). In this case, the resident,

and hence most common, females in each population are most likely to encounter resident conspecific males during the experience phase. They subsequently reduce heterospecific matings, which increases divergence. We find similar results when females learn to prefer familiar males (Fig. 3) due to the fact that females are again most likely to encounter conspecific males.

Counterintuitively, when females can learn only to avoid heterospecifics, learning reduces divergence (Fig. 1). The main reason for this is that it gives rare heterospecific males a relative mating advantage over resident males. Because of the low frequency of heterospecific males, the common resident females rarely learn to avoid them, so the heterospecific males can mate with both heterospecific and conspecific females. In contrast, heterospecific females are very likely to encounter and thus learn to avoid the common resident males, which thus suffer a mating disadvantage.

Overall, the combined effects of females choosing mates based on learning from prior encounters with both conspecifics and heterospecifics are similar to the effect of learning from conspecifics alone because of the much higher frequency of such encounters (Fig. 1). However, although we do not consider it specifically, it is possible that learning from heterospecifics and conspecifics in nature may occur with different strengths. In this case, our results suggest that strong learning to avoid heterospecifics may reduce population divergence even if some learning from conspecifics is also taking place. In general, because the effects of learning to avoid heterospecifics are due to the actions of heterospecific females, it is worth keeping in mind that they may be mitigated by any local adaptation that directly leads to low fecundity of these females in nature.

MALE LEARNING

Unlike the results for female learning, in males, learning from encounters with either conspecific or heterospecific females reduces divergence in all three of the primary model variants considered (Fig. 4A–C). Again, the main reason is that rare heterospecific males have a relative mating advantage over resident males. In the male choice model, this ultimately stems from the competitive disadvantage that learning males put themselves under by increasing biases in their courtship. In the case of males learning from conspecific encounters, the common resident males learn to concentrate courtship on the common conspecific females, increasing competition for these mates. In contrast, heterospecific males are unlikely to encounter rare heterospecific females during the experience phase. They thus do not suffer a competitive disadvantage because they keep courting and mating with both types of females. When males can only learn from encounters with heterospecific females, the effect of learning is stronger in the rare, heterospecific males, which are more likely than resident males to encounter and learn to avoid the other type of females.

However, owing to frequency dependence of competition costs (Servedio and Lande 2006), the smaller effect of learning in the common resident males has an overall larger effect (simply because these males are common) than the larger effect of learning in the rare heterospecific males. Finally, paralleling the female learning case, when males learn to prefer familiar females, the outcomes (Fig. 3) are similar to those in the case of males learning only from encounters with conspecifics (Fig. 4A) because, in both cases, males are most likely to encounter conspecifics.

The fact that the root cause of all of the effects of male learning is increased competition due to biased male courtship suggests that these effects could be reversed in situations where males could avoid or counter courtship costs, such as when they can strategically alter their level of competition (Rowell and Servedio 2009) or when females have an overall preference for more courtship (South et al. 2012). Results from an alternate model of male learning are consistent with this suggestion. We find that when, instead of assuming that all females have equal reproductive success, we assume that female reproductive success is positively correlated with the amount of courtship she receives, male learning from conspecifics increases divergence (Fig. 4D). In this case, local males are likely to learn to focus courtship on the common local females, increasing their mating success and thus lowering the relative fitness of heterospecific females. Indeed, the situation in which female reproductive success is positively correlated with courtship is one in which the benefits of male choice are known to often overcome the costs of courtship (Servedio and Lande 2006; see the case of preferred females having higher fertility, which is mathematically identical to the case considered here). Relaxing the assumption of equal reproductive success for females is realistic and relevant in cases where rare foreign female phenotypes encounter rare foreign male phenotypes at a low frequency. In this case, rare females may delay reproduction or compromise by mating with low quality males (Wilson and Hedrick 1982).

THE EVOLUTION OF ASSORTATIVE MATING

Although learning in the context of mate choice increases divergence under some realistic scenarios (Figs. 1, 3, 4D), it generally decreases the rate of spread of an allele for stronger assortative mating (Fig. 2). As described in detail above, the primary cause of this effect differs between the sexes. With female learning, it is most likely due to the fact that greater learning already decreases the production of unfit hybrids, which is the source of selection for stronger assortment. In contrast with male learning, due to the competitive costs of greater courtship biases in males, stronger learning increases the loss of the population-specific alleles with which the allele for stronger assortment is associated.

Such negative effects on the evolution of learned preferences in particular, and phenotypic plasticity in general, have been noted previously. Robinson and Dukas (1999) reviewed a century of

theory and data and concluded that plasticity and learning can have negative, neutral, or positive effects on rates of evolution. The major cause for plasticity and learning slowing down genetic change was weaker selection on phenotypically adapted individuals. Studies since then often agree with this finding. For example, Price et al. (2003) concluded that intermediate levels of phenotypic plasticity would be optimal for evolution because they permit population survival in a new environment at the realm of attraction of a new adaptive peak, which leads to genetic change. Although high levels of plasticity can speed crossing the adaptive valley, they reduce the rate of genetic change toward the higher peak.

INSIGHTS FOR FUTURE EXPERIMENTAL WORK

The most important insight from our model is that, owing to frequency dependent processes, within-generational learning in the context of mate choice is most likely to enhance population divergence when early encounters with conspecific males make females show a stronger preference for conspecific over heterospecific males. When the critical experience for females is encountered with heterospecific males, within-generational learning in the context of mate choice is less likely to promote divergence. Our results also suggest that within-generational learning by males is less likely to promote population divergence when male choice does not affect the females' reproductive success.

Our results thus suggest that future experimental work seeking to find an effect of within-generational learning on population divergence should focus on identifying a model system in which females learn to increase their preferences for conspecific over heterospecific males based on early experience with conspecific males. Convenient model systems in which females' early experience with males alter subsequent mate choice include fruit flies (Dukas 2005), crickets (Bailey and Zuk 2009), and treehoppers (Fowler-Finn and Rodríguez 2012). It is not clear, however, whether in the species just mentioned, early experience with conspecifics increases assortative mating. As far as we know, in the only model system where this was tested explicitly, female *D. pseudoobscura* did not decrease their frequency of heterospecific matings with males of the closely related *D. persimilis* after early experience with conspecific males (Dukas et al. 2012). Our models suggest that future experimental work in males, which may be promising in systems such as fruit flies, crickets, and treehoppers, should take into account the competitive costs of male mate choice when making predictions about the effects of learning on divergence.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Equations for the female learning model.

Appendix S2. Equations for the male learning model.

Figure S1. Total evolution of N_2 in population 2 as a function of the preference strength, α, for different values of $\gamma_1 = \gamma_2$, where $\gamma = 1$ means no learning and higher values of γ mean greater learning. Females learn from both conspecific and heterospecific males.

Figure S2. Total evolution of N_2 in population 2 as a function of the preference strength, α, for different values of γ with $\alpha_f = 1$ (i.e., no female preference). Males learn from both conspecific and heterospecific females (a), only conspecific females (b), or only heterospecific females (c). See legend for main Figures for other base parameters.

Figure S3. Total evolution of N_2 in population 2 as a function of the preference strength, α, for different values of γ with $\alpha_f = \alpha$ (i.e., female preference = male preference). Males learn from both conspecific and heterospecific females (a), only conspecific females (b), or only heterospecific females (c). See legend for main Figures for other base parameters.

Figure S4. Total evolution of N_2 in population 2 as a function of the preference strength, α, for different values of γ when male learning is a function of female preference strength. Males learn from both conspecific and heterospecific females (a), only conspecific females (b), or only heterospecific females (c). See legend for main Figures for other base parameters.