Sympathy affects the evolution of genetic versus cultural determination of song

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One hypothesis explaining the species richness of the songbirds is based on the fact that these species generally acquire their songs socially rather than genetically. Here we consider the outcome of secondary contact between birds that have developed distinct song dialects in allopatry. We ask 2 questions: 1) given a fixed probability of learning, how do the songs evolve in sympathy and 2) would evolution tend to increase or decrease the genetic, versus cultural, determination of song in this situation? We assume that the 2 local dialects can be both genetically determined and learned via song copying, whereas a third category of song, mixed song, is only learned. We evaluate both questions assuming 5 different ways that mixed song can be generated in addition to learning via copying. We find that when the probability of learning is fixed, local dialects can generally be maintained even when a substantial majority of males produce learned songs. Song differentiation will, however, be lost if song learning itself can evolve. This is partly a result of a positive feedback mechanism; mixed songs are readily accepted by all females, leading to selection favoring an allele which increases the probability that males will produce those songs. This in turn increases the frequency of mixed songs, making it harder for dialects to be maintained. As human disturbance alters species ranges, partially differentiated populations may increasingly come into contact; this work predicts that song differentiation may indeed tend to be lost under a significant proportion of these conditions. Key words: bird song, cultural evolution, learning, mathematical model, secondary contact, sexual selection, song copying, speciation, sympathy. [Behav Ecol 19:594–604 (2008)]

Birds sing in order to communicate, for example, in order to find mates and to defend territories (Searcy and Andersson 1986). The songs that birds produce can be both genetically determined and learned. Oiscines (i.e., songbirds, order Passeriformes, suborder Passeri) in particular are known to learn their songs, at least to some degree, by copying the songs of the adults in the population (Catchpole and Slater 1995). The order Passeriformes comprises roughly 60% of the approximately 9700 known bird species (Sibley and Monroe 1990). The oscines, which contain about 4000 different species, are the larger of the 2 groups in this order. The other group of birds in the order Passeriformes, the Tyranni (less than 2000 species), are not known to learn or copy the songs of singing individuals in the population to any degree (although fewer experiments have been carried out on this group). The fact that songbirds are the most speciose group of birds has led to the hypothesis that song learning can accelerate speciation (Nottebohm 1972). Lachlan and Servedio (2004) developed a theoretical model that supported this hypothesis for allopatric populations. Considering populations that have started to diverge in allopatry, as Lachlan and Servedio (2004) modeled, the question is still open whether song learning will facilitate or prohibit further divergence if these populations were to come into sympathy.

The difference between producing songs that are primarily culturally inherited (“learned” or “copied”) versus genetically determined lies in the degree of flexibility present in the determination of songs by specific individuals. Individuals that inherit their songs culturally copy the songs of the adults in their surroundings and produce songs that are similar to those of these adults, within the confines of genetically determined predispositions. In contrast, individuals that are genetically determined to sing specific songs will do so independently of what is sung in their surroundings. As a result, birds that have genetically determined songs show no or very little variation in their songs within species. Direct evidence for learning appears in the need for tutoring in order for songbirds to produce a song repertoire that is species typical as adults. The degree of tutoring necessarily appears to vary greatly between species (see, e.g., Baptista 1996; Slabbekoorn and Smith 2002). Some songbirds that have been raised in rooms with no sounds can still produce some rudimentary song, song that can be compared more with babbling than with adult vocalizations (Podos et al. 2004). Chaffinches, for example, learn a song that is about the right length and frequency but does not have the details that a normal adult song would have (Catchpole and Slater 1995). However, if their species-specific song is played over speakers, they learn a more species-typical version of the songs sung by their species compared with birds reared in isolation. Experiments have also shown that some birds have a preference for learning conspecific song over heterospecific songs (song sparrows, Marler and Peters 1977; Podos et al. 2004).

Most songbirds have a sensitive phase during which they memorize the songs sung by the adults in the population (Nelson 1998). Chaffinches have been found to use these memories as a frame of reference when they start singing on their own (Catchpole and Slater 1995). This leads to the question of which adult individuals in the population the young birds learn their songs from; specifically, does the father play the biggest role as a tutor (paternal song copying) or does another subset of males in the population influence the chick (oblique song copying; for further details on the definitions of paternal and oblique song copying or imprinting in general, see Cavalli-Sforza and Feldman 1983). The prevalent assumption is that oblique transmission is the primary way for males to learn a song (for chaffinches, Slater and Ince 1982). It has also been shown in a number of songbird species that songs have
a higher resemblance to one another when individuals are closer on a spatial scale than when they are further apart (e.g., Dupont’s lark, Laiolo and Tella 2005), again implying that oblique song copying may play a large role in song acquisition.

Just as in human languages, it has been found that variation exists in bird songs, that is, different dialects, at different geographic locations (e.g., in chaffinches, Baker and Jenkins 1987, in white-crowned sparrows, Marler and Tamura 1964, but see Slater et al. 1984), and at different points in time (e.g., chaffinches, Ince et al. 1980). Females have in some cases developed preferences for the different male dialects, preferring local songs over foreign (e.g., red-winged blackbirds, Searcy 1990, white-crowned sparrows, Baker et al. 1981, but see Riebel and Slater 1998 on chaffinches). Empirical studies on flycatchers (e.g., Haavie et al. 2004; Qvarnström et al. 2006) and Hippolais warblers (Secondi et al. 2003) show that closely related species living in sympathy tend to have converging songs. This means that males inhabiting the sympatric area can learn and produce a mixed song that contains elements of both of the species-specific songs. Females have also been shown to sometimes treat this mixed song as a species-specific song, in some cases leading to hybridization between the 2 species (Qvarnström et al. 2006).

Here we first consider how the presence of various degrees of learning affects the evolution of song in a species where some males primarily learn their songs through song copying, whereas other males acquire song through genetic determination. Second, we look at the evolution of song learning itself in the same setting. We are specifically interested in the situation of sympathy occurring by secondary contact of 2 allopatric populations in which local dialects in song have arisen over time. The answers to these questions thus have ultimate implications for whether further divergence could eventually occur in these populations in sympathy. The song dialects in our model are represented by ranges of population-specific song variants (song “intervals”). An allele specific to each population codes for a different song interval while a third interval (2) will evolution tend to increase or decrease genetic song determination when there is sexual selection for male song. We find that the evolution of song learning versus genetic determination (Question 2) has cascading effects on song evolution (Question 1).

We assume that songs can be assigned to 1 of 3 different song intervals, each of which includes a range of song variants. Two of these intervals (1 and 3) are products of coevolutionary divergence of song and preference for song in allopatry. They thus constitute distinct song dialects representative of each of the allopatric populations. The third interval (2) contains elements of songs from Intervals 1 and 3; the songs in this interval can be thought of as mixed songs originating from mistakes in the song-copying process that occasionally happen in sympathy. We have compared 3 different scenarios for how songs in Interval 2 potentially can arise and be maintained in the population. All 3 scenarios are presented in detail in Song production.

The A locus in our model determines which intervals of songs a male can potentially produce. Males with allele A can produce songs in Interval 1, and males with allele a can produce songs in Interval 3 (see Figure 1a for an illustration); both A and a allele males can produce the mixed songs in Interval 2. The female preference locus P works similarly.

MODEL

We model male bird song where males either 1) are predetermined by their genes to sing songs from within an allele-specific song interval or 2) have a genetic predisposition to learn to sing songs with allele-specific elements, but the specific song they learn, within the intervals allowed by their genetic predisposition, is determined by oblique transmission of song (based on the model of Lachlan and Feldman 2003). We further assume that females chose mates based on male song (e.g., Searcy and Yasukawa 1996; Nowicki and Searcy 2004). Lachlan and Servedio (2004) showed in a similar model that song and preference can coevolve within a population but diverge between allopatric populations. Here we explore the potential outcome of secondary contact between partially diverged populations with different song dialects. Specifically, we ask 2 questions: 1) how do the songs evolve given a fixed probability for a male to learn his songs and 2) will evolution tend to increase or decrease genetic song determination when there is sexual selection for male song. We find that the evolution of song learning versus genetic determination (Question 2) has cascading effects on song evolution (Question 1).

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Figure 1

(a) The 2 alleles A and a and corresponding song intervals produced by males with the respective alleles. (b) The effect of the B and b alleles corresponding to more or less genetic determination of song. In the top part of the graph (representing individuals with the B allele), individuals with the A and a allele have a higher probability of learning (1) in relation to genetic determination of song (G) in comparison with the bottom part of the graph (representing individuals with the b allele). Individuals that learn their songs can learn songs either in the shared interval (2) or in the allele-specific interval (1 or 3), whereas individuals whose song interval is genetically determined can only produce the allele-specific songs.
Females with the allele $P$ prefer males who sing songs from Interval 1 or 2 (coded for by the $A$ allele) compared with males with songs from the opposite dialect, whereas females with allele $p$ prefer males who sing songs from Interval 2 or 3 (coded for by the $a$ allele). However, females cannot differentiate between males carrying the $A$ or $a$ allele when both males are singing songs from Interval 2. Females are $1 + \sigma$ times as likely to mate with a male singing a preferred song compared with a nonpreferred song, assuming equal rates of encounter. The matching of the $P$ and $A$ loci assumes that female preferences have coevolved in allopatria with male song (see Lachlan and Serverud 2004) to produce partial premating isolation between the populations. Songs in Interval 2 are songs that all males who learn their songs potentially can produce and which are preferred by all females because they contain species-specific elements from both dialects.

When song is solely genetically determined, $A$ males will sing songs only from Interval 1 and $a$ males will sing songs only from Interval 3. When a male learns his song, which occurs via oblique transmission, he can produce songs from 1 out of 2 possible intervals (1 or 2, or 2 or 3). Which interval his learned song will fall in will depend on 2 things: the allele, $A$ or $a$, that he carries (see above), which sets a genetic predisposition toward learning a song containing at least some elements specific to his dialect, and the proportions in which the songs exist in the population, which influence the odds that a specific song will be copied (see Song production). The genetic predisposition can thus also be thought of as a constraint that prohibits complete acquisition of songs from the other dialect.

The $B$ locus codes for the extent to which song determination is genetic versus learned. To address our first question, how the amount of song learning affects song evolution, we keep locus $B$ fixed for one specific allele, $b$. To address our second question, concerning the evolution of song learning, we consider 2 alleles at locus $B$, $B$ and $b$, where $b$ is the ancestral allele and we are interested in when $B$ can invade. The effect of these alleles is described by the parameters $w_{bB}$ and $w_{b}$, which correspond to the probability that a $B$ or $b$ male, respectively, will learn songs from the adults in the population (vs. acquire their song genetically). $B$ is always set to correspond to a higher probability for an individual to learn a song than the $b$ allele ($w_{bB}$ is always larger than $w_{b}$, Figure 1b). That is, a population that is fixed for $B$ will have a higher frequency of individuals who are learning their songs compared with a population that is fixed for $b$.

If evolution leads to an increase in the frequency of the $B$ allele, it would mean that the genetic determination of song decreases in the population and learning becomes more prevalent. If $w_{bB} = 0$, individuals who carry allele $b$ would be never have to sing songs from either Interval 1 or Interval 2 depending on their allele at the $A$ locus; their song production will hence be completely genetically controlled. Similarly, if $w_{bB} = 1$, individuals with allele $B$ would always learn their songs; which interval they would end up singing songs from would depend on their genetic predisposition and the representation of songs in the adult generation.

The life cycle

A general description of the life cycle is presented in this and the following section, and all equations including the mating table (Table A1) are presented in the Appendix 1. Our Question 1 can be answered by considering only a subset of the equations (those for changes in the frequency of genotypes with allele $b$) presented here; Question 2 requires assessment of the full model. Every year, females and males mate and produce offspring. We assume discrete generations and a polygynous mating system where all females have equal mating success. The genotype of the offspring (at the $P$, $B$, and $A$ loci) is based on the genotypes of the parents, assuming free recombination between all loci. Male offspring from these crosses acquire song as juveniles via either genetic determination or oblique transmission, as described below. Because individuals are haploid, this leads to 8 female genotypes (PBA, PbA, PaB, etc.) and 16 male phenogenotypes (PBA, PbA, PaB, PaA, PbA, PbB, PbB, etc.), where the subscript describes what song interval the male’s song falls into (a phenogenotype is a combination of a genotype and a learned phenotype).

Song production

The recursion equations presented in Appendix 1 give us the frequencies of the different offspring genotypes. Juvenile male offspring will either be genetically determined to sing songs in Interval 1 or 3 or will learn a song. Juvenile males who are learning their songs will do so by sampling the parental generation and will learn songs in 1 of the 2 intervals that his song allele (i.e., $A$ or $a$) renders possible (either 1 or 2, or 2 or 3), in relation to the frequency in which these songs occur in the parental generation. This corresponds to successful oblique transmission of songs. The mixed songs (Interval 2) are also produced de novo by males who make some kind of a mistake and produce songs with elements from both Intervals 1 and 3. We have below outlined 3 cases of how these mistakes might happen (see Appendix 2 for equations).

Case 1: cultural mutations

Songs in the mixed interval can be continually introduced in the population through mistakes in the learning process, which is, cultural mutations. These cultural mutations happen at a constant rate (1% in the results presented here, but we tested the effect of this mutation rate separately) when juvenile males are unable to make perfect copies of the allele-specific song. This can result in both intrainterval mistakes such as changing the song note order or inclusion of components from the other song interval, changing the male’s songs from song Interval 1 to 2 or from Interval 3 to 2 (note that independently of the type of mistake it leads to mixed songs that are preferred by all females). We assume in this case that individuals do not recognize songs characteristic of the other dialect (e.g., males with allele $A$ do not recognize Song 3) and thus ignore them if they hear them.

Case 2: miscopying

The mixed song interval can be introduced when juvenile males are trying to learn songs from the “wrong” interval. This happens when males perceive all songs as potential songs for him to produce. For example, a male that has the genetic predisposition to learn songs from Interval 1 (i.e., he has the $A$ allele) but hears and tries to produce songs from the Interval 3 will end up singing songs from the mixed Interval 2 (and vice versa for allele $a$ males who try to produce songs from Interval 1).

Case 3: a single introduction

In this case, we assume that songs in Interval 2 originated by a very rare event occurring only on the initiation of secondary contact. In the simulations, songs in the mixed interval are introduced at a low frequency when the 2 populations merge (1%), but after that point, males can only learn mixed songs via oblique transmission. Songs from the wrong dialect are treated in the same way as in Case 1 (they are ignored).

In the first scenario (Case 1) and under a majority of starting conditions for Case 2, songs from the mixed interval are continually reintroduced in the population, whereas in the last case, songs in the mixed song interval will only be introduced once at a very low frequency (1%) in the population. These are just 3 examples of how mixed songs/imperfect songs are
created, and they do not specify what kind of mistakes are occurring (e.g., song note order; frequency, type, etc.). Cases 1 and 2 both represent imperfect learning; however, we have not taken into account a full spectrum of perfect learning to very poor learning. One way to model that spectrum would be to increase the probability for mistakes in Case 1 (for an alternative way of modeling imperfect learning, see Ellers and Slabbekoorn 2003). Because the solutions of the recursion equations for the phenogenotypes are not tractable analytically, we used Matlab to simulate the process. When the frequencies of the different phenogenotypes differ by less than $10^{-14}$ between 2 consecutive years, we assumed that equilibrium was reached. We let the simulation run for 1000 extra time steps once equilibrium was reached in order to assure that our assumption of equilibrium was accurate.

**RESULTS**

**Question 1: song evolution given a constant probability of learning**

Here we consider cases where the allele is fixed. This means that we can examine how the frequencies of the different song intervals change over time given a static probability for male song learning (no evolution of song learning). Particularly, we looked at which songs are present when equilibrium is reached given the different ways songs in Interval 2 can be generated (Cases 1–3) and different starting conditions, such as various combinations of starting frequencies of the female preference allele ($P$ or $p$) and male song allele ($A$ or $a$), different frequencies of song learning ($w_B$), and different strengths of female preference for songs ($\omega$).

Overall, which songs are present at equilibrium is more dependent on the frequency of the $P$ allele than the $A$ allele (Figure 2). We find that, for Cases 1 and 2, all 3 song intervals coexist under roughly the same conditions. Outside of that parameter space (where the 3 intervals coexist), we lose one of the local dialects. In Case 2, this means that there are no songs for males to mimic, and therefore, songs in the mixed interval (Interval 2) are not continuously reintroduced. Without this reintroduction, mixed songs are lost completely for extreme $P$ allele frequencies. In Case 1, where songs in the mixed interval are continuously reintroduced due to cultural mutations, we find both one of the local dialects and mixed songs present at equilibrium. For both cases, the loss of allele-specific songs is due to the fact that either $A$ or $a$ allele is lost at equilibrium. Which allele is lost is determined by which female preference allele ($P$ or $p$) is most abundant when the 2 populations merge (i.e., at the start of the simulation). When either one of the song alleles is lost, the corresponding local dialect is therefore lost because there are no males who have the genetic makeup to produce those songs (loss of $A$ or $a$ allele leads to a loss of songs $1/3$).

In Case 3, where mixed songs are only introduced once at the start of the simulation, mixed songs will be lost, regardless of the strength of female preference ($\omega$), when less than 50% of males learn their songs (Figure 2, last panel in Rows 1, 2, 4, and 5). The effect of this critical frequency can be shown by simplifying our problem somewhat. If the frequencies of all alleles are exactly equal (i.e., the frequency of $P = A = 0.5$), then song Intervals 1 and 3 are going to be equally common in the population and the frequency of songs from Interval 2 at equilibrium (solved from a modification of Equation A7c in Appendix 2) can be described by

$$\text{fr}(\text{Song 2}) = 2\eta(2w - 1),$$  

where $\eta$ is the proportion of individuals that can produce either songs from Interval 1 or 2 and (because of symmetry reasons) songs from Interval 2 or 3 and $w$ is the probability of a male learning his songs. It is easy to see, when all alleles are equally common, $\eta_1 = 0.5$, and hence in order for song Interval 2 to exist in the population, at least 50% learning ($w_B = 0.5$) is needed.

Both the strength of female preference and the probability of song learning affect the likelihood of mixed songs being present at equilibrium in the population. Increasing the strength of female preference will, independently of the case, increase the parameter combinations of $A$ and $P$ that allow for mixed songs to be produced (cf. Figure 2 panels with $\omega = 1$ and $\omega = 5$). An increase in the probability of learning has the same effect (Figure 2, white areas increase as $w_B$ increases). The extreme case is when all individuals learn their songs. Here we lose all variation in songs, and mixed songs are the only songs present (not shown).

When $w_B < 0.5$ (Figure 2, Rows 1, 2, 4, and 5), all 3 song intervals coexist for the same starting conditions in Cases 1 and 2, whereas in Case 3, only the 2 local dialects are present. This opens up the possibility that, when mixed songs are not reintroduced and a majority of the individuals in the population have genetic determination of songs, separate breeding populations can be preserved.

**Song frequencies**

So far, we have only looked at the presence or absence of songs given all possible combinations of $A$ and $P$ allele frequencies, various $\omega$s, and $w_B$s. In Figure 3, we show the frequencies of the local dialects and the mixed songs given different probabilities that males will learn their songs. The patterns of song frequencies given different probabilities of song learning are generally the most similar in Case 1 and Case 3 (and not Cases 1 and 2 as it was when we only looked at presence of songs). Despite the fact that songs in the mixed range are always present in Case 1, for low probabilities of learning, they are generally very low in frequency. This contrasts with Case 2, where songs in the mixed range either are completely missing (with a large skew in the frequency of $P$; Figure 3, Rows 3 and 4) or, if they are present, are more frequent than in Case 1. As a result, learning can be less frequent in the population in Case 2 than under the 2 other cases, but songs in the mixed interval can still be the most common songs.

Increasing the mutation rate for Case 1 increases the amount of mixed songs present at equilibrium substantially, particularly for lower probabilities of song learning (not shown). A higher mutation rate makes Cases 1 and 2 more similar to each other than with a 1% mutation rate. However, neither increases nor decreases in the mutation rate in Case 1 affect the presence or absence of songs at equilibrium, only their frequencies.

**Question 2: evolution of song learning**

In order to see how the frequency of song learning changes over time, we include genetic variation at the B locus. By letting $w_B > w_B$, that is, we let males carrying the $B$ allele have a higher probability of learning their songs than males carrying the $b$ allele. We can then see when selection increases the frequency of song learning by seeing when allele $B$ will spread.

The amount of song learning is determined in any specific generation by a combination of $w_B$, $w_P$, and the frequency of the $b$ and $B$ alleles. Simulations were generally started with a frequency of $B = 0.01$; therefore, almost all males carry the $b$ allele, and hence, the probability for any male in the population to learn his songs at the start of the simulation was almost solely determined by $w_B$. Just as in Question 1: song
evolution given a constant probability of learning above, we tested a wide range and various combinations of different starting frequencies of the female preference allele ($P$ or $p$), male song allele ($A$ or $a$), and the strength of female preference ($\alpha$). We determined which songs were present at equilibrium and when the $B$ allele would go to fixation under the different cases (1–3).

As long as songs in Interval 2 are present at equilibrium, the population becomes fixed for $B$ at equilibrium (Figure 4, Row 1, shows the outcome when $P = A = 0.5$). The difference in the results between the different cases is the greatest when only a minority of the individuals are learning their songs ($w_b < 0.5$). In Case 1 (cultural mutations) and Case 2 (miscopying), the mixed interval is continuously reintroduced and selection favors an increase in the frequency of individuals using the learning strategy, until the point where all individuals are learning their song. In the third case, however, when less than 50% of the individuals learn their song ($w_b < 0.5$), mixed songs will be lost, the $B$ allele will not spread to fixation, and songs from the 2 allele-specific song intervals will eventually be the only ones represented in the population. This can potentially allow further sympatric divergence by processes not included in this model.

The spread of the $B$ allele and existence of Interval 2 are thus tightly linked, following from the assumptions of the model. Sexual selection favors males who sing songs in Interval 2 because they are preferred (over song from the opposite dialect) by all females. Because songs from that interval are primarily produced when males learn them (although they can in Cases 1 and 2 be produced at small rates without males learning the mixed songs specifically), males who have the $B$ allele are favored over individuals with the $b$ allele because they have a higher probability of learning their songs and hence also a higher probability of producing mixed songs. Although song Interval 2 is still present in the population, the $B$ allele spreads, but as soon as the mixed songs are lost...
(as can happen in Case 3), it stops spreading. When this happens, the $B$ allele loses its adaptive value and becomes neutral to selection.

The differences between Cases 1 and 2 under skewed starting frequencies at the $P$ and $A$ loci are very evident (Figure 4, Row 2). In Case 1 where songs in the mixed interval are continuously introduced by cultural mutations, $B$ will always fix. However, in Case 2, songs in the mixed interval are only produced as long as both Intervals 1 and 3 are present; when starting conditions become too skewed (e.g., $P$ more frequent than $p$), one of the song intervals and the corresponding allele, $A$ or $a$, will be lost. The frequency of mixed songs is not essential in determining this outcome. As Figure 3 (Row 3) shows, there is often only a very low frequency of mixed songs for low $w_B$; it is the presence or absence of mixed songs that determines if the $B$ allele can spread. In Case 3, songs in the mixed interval are lost under conditions with less skew than in Case 2, and a higher frequency of learning is now needed for the mixed songs to be present at equilibrium and hence also in order for $B$ to fix. As shown in Figure 4, Row 3, increasing the strength of female preference for songs (from $\alpha = 1$ to $\alpha = 5$) increases the amount of mixed songs in the population. This decreases the effect of the skewed starting frequencies.

Continued evolution of the frequency of learning in the population

In all 3 cases (1–3), until the point where $w_B = 1$ and $B$ is fixed, given that the starting frequencies of $P$ and $A$ are not too skewed, songs from all 3 song intervals can (depending in Case 3 on the value of $w_B$) be represented in the population. But when $B$ is fixed and $w_B$ is exactly equal to 1, all males sing songs from the shared (mixed) Interval 2 and there is no longer any genetic determination of song. This erodes progress toward population differentiation and completely eliminates the possibility for further sympatric divergence in this population. In order to determine whether the conditions of $w_B = 1$ are expected to eventually evolve in the population, we examined whether alleles for successively large probabilities of learning would be likely to spread. For Cases 1 and 2, we started a simulation at $w_B = 0$ and $w_B = 0.1$, equal starting frequencies of $A/a$ and $P/p$ (i.e., $P = A = 0.5$), and all the song intervals at equal frequency; we find that the $b$ allele is not represented at all in the equilibrium population. We therefore started the next simulation with $w_B$ equal to the old $w_B$ value (0.1), increase $w_B$ to 0.2 (again starting $B = 0.01$), and so on. By doing this, we find that evolution tends to increase the value of $w_B$ incrementally, to the point where it is equal to 1, which corresponds to all individuals learning songs from the mixed song interval. For Case 3, we did the same thing, but here we started the first simulation with $w_B = 0.5$ and $w_B = 0.6$, as below $w_B = 0.5$ the $B$ allele does not go to fixation. We again find that alleles for successively high probabilities of learning will spread. Genetic determination of song can thus be eliminated from the population by the successive fixation of alleles for more and more learning.

DISCUSSION

Our joint analysis of the outcome of secondary contact with 1) song evolution given song learning and 2) the evolution of song learning itself has enabled us to draw conclusions about the ultimate evolutionary outcome of sympatric contact between song dialects. Although our results are dependent on
a number of different factors, as a broad summary, we can say that the loss of local dialects is more likely when song learning is more common (from Question 1) and that the evolution of stronger song learning is a very likely outcome (from Question 2). It is therefore likely that local dialects will often be lost. These results are consistent with empirical studies on flycatchers (e.g., Haavie et al. 2004; Qvarnström et al. 2006) and *Hippolais* warblers (Secondi et al. 2003), which find that closely related species living in sympatry tend to have convergent songs.

Specifically, our analysis with fixed song learning demonstrates that the maintenance of local dialects depends both on the probability that a male will copy songs and on how perfect the copying process is. Ultimately, the maintenance of local dialects versus elimination of genetic differentiation between song types within a population depends critically on the continued presence of what we have called the mixed songs. The presence of mixed songs depends in turn on 2 things: how many of the males are learning their songs compared with having genetic determination of songs and how the mixed songs are created. We find that by increasing both the frequency of song learning among males and the strength of female preference, mixed songs become more and more dominant in the population. Additionally, when males make mistakes in the copying process (Cases 1 and 2) compared with a situation of perfect learning (Case 3), it is less likely that local dialects can ultimately be preserved.

We also find that due to the force of sexual selection, songs should tend toward cultural determination, that is, the frequency of learning increases in the population. As long as songs from the mixed interval are present in the population, males who are more likely to produce those songs (i.e., males who learn their songs) are going to have a selective advantage over other males because all females have a preference for the mixed songs (vs. songs from the opposite dialect). This can ultimately lead to a total loss of song differentiation, and the populations that had started to differ in allopatry will mix and become inseparable again in sympatry. Assuming that both song determination alleles \( A \) and \( a \) are maintained, only when the mixed songs are not produced at all at equilibrium (e.g., in Case 3 when half of the males or less produce songs that they have copied from the adult males) can strong genetic
determination of song types can be maintained because learning will not spread as a strategy in the population. Assuming that the genetic variation exists for song learning to potentially fix, some additional mechanism would generally be needed in order to stop the ultimate convergence of songs to the mixed songs. The evolution of song learning could potentially be counteracted if, for example, there would be selection against individuals who mutate culturally or make mistakes in the song-copying process. Selection against these individuals could potentially prevent the spread of the song-learning strategy as well as the convergence to mixed songs.

When the advantage for males who sing songs from Interval 2 is not present, for example, if females have sufficiently stronger preferences for allele-specific songs compared with mixed songs, the importance of song copying would decrease. Data from pied and collared flycatchers, however, indicate that female collared flycatchers have equivalent preferences for species-specific song and mixed song produced by pied flycatchers (Qvarnström et al. 2006). We find that as long as preference for allele-specific song is not more than twice as strong as the preferences for mixed song ($2\sigma_{\text{mixed song}} > \sigma_{\text{allele-specific song}}$), the results of our model (Case 3) remain unchanged (Olofsson H, Servedio MR, unpublished data).

Some components of songs, like duration, rhythm, and frequency interval, have a genetic basis even in species with high levels of plastic song learning (reviewed in Slabbekoorn and Smith 2002). These genetic components lead to the production of rudimentary song even without a tutor, but in order for the song to be recognizable by conspecifics, juveniles must hear adults from their own species (e.g., chaffinches, Catchpole and Slater 1995). Until this point, we have primarily discussed $w$ as the proportion of males in the population that learn their song. Our model should also apply if $w$ determined the proportion of songs that individual males learned versus acquired genetically but only in the situation where a female is choosing a mate on the basis of the song that he happens to be singing when she decides to choose (as opposed to averaging all his songs). Our findings about the evolution of song learning versus genetic determination after secondary contact complement those of previous studies on the evolution of learned song. Aoki (1989) showed that copying of song can evolve in a population given polygyny and a strong enough female preference for new and learned songs. Under these circumstances, a song-learning strategy would be able to invade in a population where all males have a genetically determined song. Lachlan and Feldman (2003) have modeled this in more detail, investigating under what circumstances genetically predisposed songs are favored over more flexible song learning. They conclude that if all songs are equally valuable as signals, then song copying is selected for compared with more restrictive genetic determination of songs. In our model, all songs are not equally valuable; mixed, that is, learned, songs have the advantage of being preferred by females of both incipient species. This also produces an advantage for song copying over genetic determination.

Male song learning is not the only trait that can be learned. Mating preferences can also be acquired through sexual imprinting. In paternal imprinting, for example, juvenile female imprint on their fathers, preferring mates that share their father’s traits later in life (Weisman et al. 1994; but see Setther et al. 2007). Irwin and Price (1999) review the importance of learned mate preferences on speciation, discussing how learning in birds may lead to assortative mating, which in turn can lead to speciation. They conclude that because sexual imprinting is important for species recognition, learning is likely to play a major role in speciation in birds (see also Price 1998; Grant BR and Grant PR 2002; Servedio et al. forthcoming). The role of imprinted preferences in speciation is not, however, clear-cut; if females imprint not paternally, but obliquely (juveniles learn their song in proportion to the occurrence in the entire population), speciation may be inhibited rather than promoted (Kirkpatrick and Digatkin 1994; Verzijden et al. 2005).

Baptista and Trail (1992) also argue that it is very unlikely that learning of songs (as opposed to preferences) will work as an isolating mechanism leading to sympatric speciation. Oblique song copying may also inhibit speciation in this case. The argument is that, given the positive frequency dependence inherent to oblique learning, it would be hard for new and rare songs to spread in the population. If a new song arose by a random mistake in the song-copying process, there would not necessarily be any female preference for that song. Even if that male did produce offspring, his song would occur at such a low frequency that the chances of it being copied would be slim. However, Lachlan and Servedio (2004) showed that song learning could facilitate allopatric speciation. Song learning can mask, to some extent, changes in the genetic predispositions underlying a song. This allows these shifts in predisposition to sometimes reach high frequencies due to drift; when the new song frequencies are high enough, they become favored by selection.

In order for further divergence to occur, differences in the songs produced need to be accompanied by genetic differences between males singing different songs. Ellers and Slabbekoorn (2003) use a spatially structured model and show how song divergence may evolve because of intrasexual selection (male–male interactions) but found that the divergence in phenotypes was not matched with a divergence in genotypes. We have shown that the maintenance of genetically determined song differentiation can occur under some conditions despite the fact that song learning is present in a sympatric population. An interesting extension of this would be to explicitly include the potential for further song or preference divergence, leading to speciation. Selection against hybrids, as in the process of reinforcement (e.g., Dolzhansky 1937), could promote divergence in our situation of secondary contact as well.

Another useful extension of the model would be to include spatial structure. Spatial structure would allow us to incorporate more realistic song learning through copying the songs of local neighbors rather than the population at large. The inclusion of spatial structure would also allow us to model the evolution of local dialects in a more sophisticated fashion. Although local dialects may form via mutations in the learning process, learning may also erase differences between them, as some birds have been shown to change their dialect on migration to a new area (Slabbekoorn and Smith 2002). The effects of learning with finer scale dialect structure may therefore be complex.

In conclusion, we find that when the probability for learning does not evolve, local dialects can potentially be the most common songs sung by males even if there is a substantial chance of producing learned songs. For most cases, song differentiation will, however, ultimately be lost if song learning itself is allowed to evolve. This is partly a result of a positive feedback mechanism, in which the mixed songs are preferred by all females, compared with the local dialects which are only preferred by a subset of the females. This leads to selection of the allele that increases the probability for males to produce those songs. Because learning is oblique, this, in turn, increases the frequency of mixed songs, making it harder for local dialects to be maintained. As human disturbance increasingly alters species ranges, partially differentiated populations may increasingly come into contact; this work would predict that under these circumstances, song differentiation may indeed tend to be lost under a significant proportion of conditions.
APPENDIX 1

We assume that the male phenogenotypes (PBA1, PBA2, PBa2, PBa3, PbA1, etc.) occur with frequencies $x_1, x_2, \ldots, x_{16}$ in the population and female genotypes (PBA, PBa, PbA, etc.) occur with frequencies $x_{17}, x_{18}, \ldots, x_{24}$. The mating table (Table A1) summarizes all the possible matings that can occur in the population. Each number in the table is a reference to a specific equation expressing the frequency of that mating type. Several examples are presented below to illustrate this concept.

Equation A1 corresponds to the mating of PBA1 males with PBA females (recursion Equation 1 from the mating table):

$$eq 1 = \frac{x_1 x_{17} (1 + \alpha)}{(1 + \alpha) (s_1 + s_2) + s_3}. \quad (A1)$$

PBA1 males occur in the population with a frequency $x_1$, and PBA females occur with a frequency of $x_{17}$. PBA females have a preference to mate with PBA1 males, and therefore, the product $x_1 x_{17}$ is multiplied with $1 + \alpha$. The frequency of songs Interval 1 corresponds to $s_1 = x_1 + x_5 + x_9 + x_{13}$ for song Interval 2 $s_2 = x_2 + x_3 + x_6 + x_{10} + x_{11} + x_{14} + x_{15}$, and for song Interval 3 $s_3 = x_4 + x_8 + x_{12} + x_{16}$. Because we assume that each female genotype has equal mating success, we must normalize all the equations (see, e.g., Kirkpatrick 1982).

All the other equations for the mating frequencies will have the same general construction, for example, the frequency of the male phenogenotype times the frequency of the female genotype times the female preference in the cases where females are mating with preferred males.

All females prefer (compared with local song dialects) songs in the shared song interval (Interval 2), independently of which song allele ($A$ or $a$) males carry. This gives us, for example, Equation A2 (recursion Equation 13 from the mating table),

$$eq 13 = \frac{x_2 x_{21} (1 + \alpha)}{(1 + \alpha) (s_2 + s_3) + s_1}. \quad (A2)$$

which is the mating between PBa2 females and PBA females. Note that the normalization factor is different for the equations in the lower half of the mating table compared with the upper half of the mating table due to differences in which songs females prefer (areas marked in gray represent matings where the female has a preference for the male phenogenotype).

Equation A3 (recursion Equation 26 from the mating table) is an example of a mating where the female PBA mates with a male that she does not prefer (a PBa3 male).

$$eq 26 = \frac{x_4 x_{17}}{(1 + \alpha) (s_1 + s_2) + s_3}. \quad (A3)$$

All the equations in the mating table (Table A1) are gathered in a vector, the “mating vector,” $m$.

$$m = [eq 1 \ eq 2 \ \ldots \ eq 128]. \quad (A4)$$

Information about what proportion of offspring genotypes results from each mating type is gathered in a matrix $M$. This matrix has equally many rows as there are equations in the mating table ($8 \times 16 = 128$) and 8 + 8 columns (one for each possible genotype that can come out of the matings, first males and the females; note that males are yet not singing, and therefore, only 8 genotypic equations, not 16 phenogenotypes, suffice to fully describe the males).

The first row in $M$ corresponds to the types of offspring that can come out from the first type of mated pair (Equation A1). Because this is a mating between PBA1 males and PBA females, only 1 type of offspring is produced, PBA, and therefore, 100% of both male and female offspring will be of genotype PBA. However, in the third mating (Equation 3 in the mating table), between PBA1 males and PBA females, 50% of the offspring will be of the genotype PBA and 50% will be of type PbA. Hence, the number 0.5 in the 1st, 3rd, 9th, and 11th columns on the third row.

The vector $m$ is multiplied with the matrix $M$ in order to find out how the genotypes are distributed in the next generation,

$$\begin{bmatrix} x_{t+2} & x_{t+4} & x_{t+6} & x_{t+8} & x_{t+10} \\ x_{t+12} & x_{t+14} & x_{t+16} & x_{t+17} & x_{t+18} \\ x_{t+19} & x_{t+20} & x_{t+21} & x_{t+22} & x_{t+23} & x_{t+24} \end{bmatrix} = \bar{w}M, \quad (A6)$$

where $x_{t+2}$ (at time $t + 1$, not indicated for brevity) indicates the frequency of PBA males that will become $x_1$ and $x_2$ after they have started to sing songs, and so on.

APPENDIX 2

After the new offspring are hatched, males will start to acquire songs. With a probability $1 - w_g$ or $1 - w_b$ (depending on the $B$ allele carried by the individual in question), a male will be genetically determined to sing songs from either Interval 1 or Interval 3 depending on which $A$ allele he has. (For the first question of which songs that are evolving, all individuals carry the $b$ allele.) The rest of the males will learn songs obliquely. We have outlined 3 different scenarios of how song
Females responding to those cases are presented here. 

Case 2: Males miscopy when they try to learn song from the female has a preference for the male phenogenotype. 

<table>
<thead>
<tr>
<th>Females</th>
<th>PB</th>
<th>a</th>
<th>4</th>
<th>12</th>
<th>20</th>
<th>28</th>
<th>36</th>
<th>44</th>
<th>52</th>
<th>60</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pb</td>
<td>a</td>
<td>6</td>
<td>14</td>
<td>22</td>
<td>30</td>
<td>38</td>
<td>46</td>
<td>54</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>pB</td>
<td>a</td>
<td>7</td>
<td>15</td>
<td>23</td>
<td>31</td>
<td>39</td>
<td>47</td>
<td>55</td>
<td>63</td>
</tr>
<tr>
<td></td>
<td>pb</td>
<td>a</td>
<td>8</td>
<td>16</td>
<td>24</td>
<td>32</td>
<td>40</td>
<td>48</td>
<td>56</td>
<td>64</td>
</tr>
</tbody>
</table>

The genotypes of the females are shown down the right-hand side of the table, and the phenogenotypes of the males are shown across the top. Each number represents one specific recursion equation, as described in Appendix I. The gray markings correspond to matings where the female has a preference for the male phenogenotype.

learning might happen in the main text—the equations corresponding to those cases are presented here.

Case 1: Cultural mutation occurs from songs in Intervals 1 and 3 to songs in Interval 2. The resulting male phenogenotypes will then be as follows:

\[
x_1 = x_1(1 - wB) + (1 - \mu)x_1 \left( \frac{s_1}{s_1 + s_2} \right),
\]

\[
x_2 = x_2 + \frac{s_2}{s_1 + s_2} wB + x_1 \left( \frac{s_1}{s_1 + s_2} wB \right),
\]

\[
x_3 = x_3 + \frac{s_3}{s_1 + s_2} wB + x_1 \left( \frac{s_3}{s_1 + s_2} wB \right),
\]

\[
x_4 = x_4 + \frac{s_4}{s_1 + s_2} wB + x_1 \left( \frac{s_4}{s_1 + s_2} wB \right),
\]

\[
x_5 = x_5 + \frac{s_5}{s_1 + s_2} wB + x_1 \left( \frac{s_5}{s_1 + s_2} wB \right),
\]

\[
\cdots
\]

\[
x_{16} = x_{15}(1 - wB) + (1 - \mu)x_{15} \left( \frac{s_3}{s_2 + s_3} \right),
\]

where \(\mu\) is the mutation rate.

Case 2: Males miscopy when they try to learn song from the wrong allele-specific interval:

\[
x_1 = x_1(1 - wB) + x_1 \left( \frac{s_1}{s_1 + s_2} \right),
\]

\[
x_2 = x_2 + \frac{s_2}{s_1 + s_2} wB,
\]

\[
x_3 = x_3 + \frac{s_3}{s_1 + s_2} wB,
\]

\[
x_4 = x_4 + \frac{s_4}{s_1 + s_2} wB - x_3 \left( \frac{s_3}{s_1 + s_2} wB \right),
\]

\[
x_5 = x_5 + \frac{s_5}{s_1 + s_2} wB - x_4 \left( \frac{s_4}{s_1 + s_2} wB \right),
\]

\[
\cdots
\]

\[
x_{16} = x_{15}(1 - wB) + x_{15} \left( \frac{s_3}{s_2 + s_3} \right).
\]

Case 3: Songs in Interval 2 are introduced at a low frequency at the start of the simulation:

\[
x_1 = x_1 + \frac{s_1}{s_1 + s_2} wB,
\]

\[
x_2 = x_2 + \frac{s_2}{s_1 + s_2} wB - x_1 \left( \frac{s_1}{s_1 + s_2} wB \right),
\]

\[
x_3 = x_3 + \frac{s_3}{s_1 + s_2} wB - x_2 \left( \frac{s_2}{s_1 + s_2} wB \right),
\]

\[
x_4 = x_4 + \frac{s_4}{s_1 + s_2} wB - x_3 \left( \frac{s_3}{s_1 + s_2} wB \right),
\]

\[
\cdots
\]

\[
x_{16} = x_{15}(1 - wB) + x_{15} \left( \frac{s_3}{s_2 + s_3} \right).
\]

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