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The maintenance of vocal learning by gene-culture interaction: the cultural trap hypothesis

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Vocal learning has evolved in several groups of animals, yet the reasons for its origins and maintenance are controversial, with none of the theories put forward appearing to apply over a broad range of species. The theory of gene-culture coevolution is applied to this problem taking the specific case of the maintenance of song learning in birds. The interaction between genes underlying the filter for recognizing and learning conspecific song and the culturally transmitted songs themselves sets up an evolutionary force that may maintain vocal learning. We evaluate this hypothesis using a spatial simulation model. Our results suggest that selection that would maintain song learning exists over a wide range of conditions. Song learning may persist due to an evolutionary trap even though the average fitness in a population of learners may be lower than in a population of non-learners.

Keywords: gene-culture coevolution; cultural evolution; vocal learning; birdsong; spatial game theory; song learning

1. INTRODUCTION

Vocal learning is an impressive and well-studied example of cultural transmission in non-human animals (Catchpole & Slater 1995). It seems to be ubiquitous in songbirds (Kroodsma & Baylis 1982), but does not occur in their closest relatives, the suboscines and appears to have evolved separately in two other avian groups (hummingbirds and parrots) and four groups of mammals (see Janik & Slater 1997). However, no widespread functions for learning have been found. Questions about the evolution of song learning can be divided into those about its origin and those about its maintenance. In this paper we address the latter. While learning clearly facilitates the generation of large repertoires, thought to be sexually selected (e.g. Buchanan & Catchpole 1997), many species of songbirds have relatively simple songs with a single type or a small repertoire and no single clear reason has emerged to explain why learning is beneficial for them.

The development of song in oscine birds has been extensively studied: young males of most species produce normal songs only when exposed to conspecific song during a sensitive phase in ontogeny and the resulting songs are usually a very precise copy of the tutor's. This system results in complex and varying patterns of cultural evolution (Lynch 1996; Payne 1996) and, thus, in geographic and temporal variation. Song learning results in several costs. Heterospecific song learning, although occasional, has been reported for many species (Helb *et al.* 1985). This is likely to hinder species recognition, as aspects of song known to be important in species recognition are learned in many species (Becker 1982). There is also the risk that a suitable tutor may not be available. The song developed (isolate song) is discriminated against by the females of many species (Searcy 1992). Finally, song learning requires considerable investment in time before fully crystallized song is produced. To counter these costs, there must be selection maintaining learning. Specific functions for learning have often been proposed (e.g. habitat matching (Hansen, 1979), assortative mating (Nottebohm 1972) and neighbour matching (Payne 1982)). However, while these hypotheses have been supported in some species, none apply to all. Indeed, there are species such as the chaffinch (*Fringilla coelebs*) for which none of the existing hypotheses apply (Slater *et al.* 1999), yet which require song learning for normal song development.

Gene-culture coevolution (Feldman & Cavalli-Sforza 1976; Boyd & Richerson 1985; Laland *et al.* 1993) examines the active role that cultural transmission can play in genetic evolution. Aoki (1989) provided the only previous attempt to apply this theory to the function of song learning. However, his model was highly restricted because it required vertical transmission of song from father to son, for which there is evidence in only a very few species (see Catchpole & Slater 1995). In most species that have been studied, learning appears to occur after independence, notably from territorial neighbours (Payne 1996).

In this paper, we describe a novel hypothesis to explain the evolutionary maintenance of song learning by songbirds and we then evaluate it using a simulation model. First, we introduce the theoretical framework on which our hypothesis is based.

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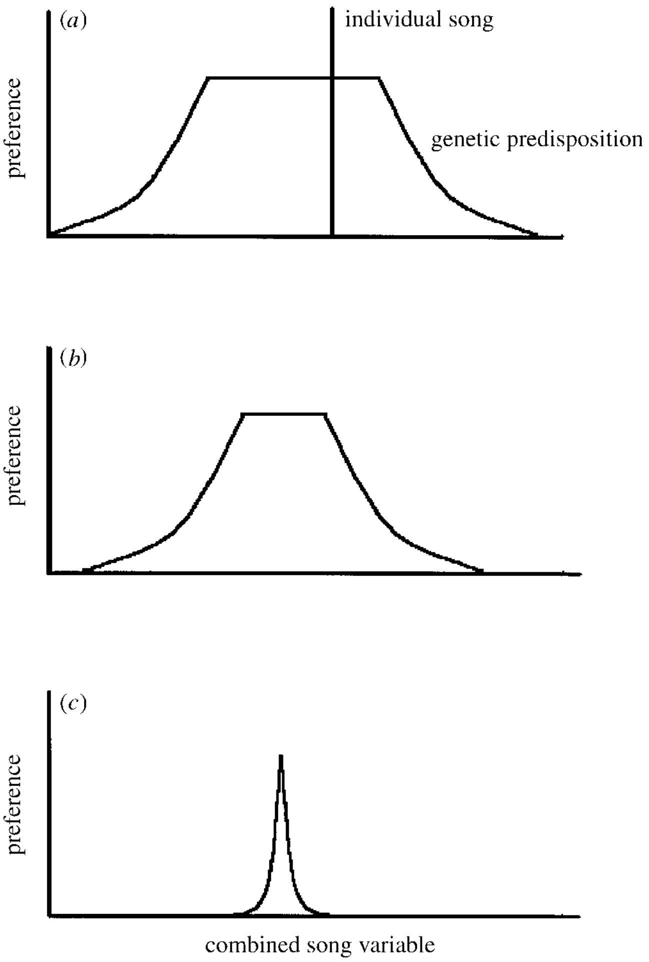

Figure 1. (*a*) The relationship between the genetic filter and learning. The filter leads to variations in the preference of males to learn different songs. Males pick one value in this distribution, an example being shown by the vertical line, as a result of learning. (*a*)–(*c*) Learning would disappear if progressive narrowing of the filter took place.

2. A THEORETICAL FRAMEWORK FOR INVESTIGATING THE EVOLUTIONARY MAINTENANCE OF SONG LEARNING

A realistic theoretical framework is important in the process of evaluating alternative evolutionary hypotheses, particularly in complex situations such as the interaction of genes and culture.

Figure 1*a* suggests the nature of the interaction between genes and culture in song learning. In our model, we have simplified song variation to one dimension, the 'combined song variable'. Song learning occurs as males pick one value on this dimension. A genetic predisposition to learn certain songs exists (Marler & Sherman 1985; Mundinger 1995). This acts as a filter, normally ensuring that only species-specific songs are learned. Within these limits, there is no preference for any particular song over any other. This pattern of neutral transmission of songs has empirical support (Lynch 1996; Payne 1996). Males can learn songs outside these limits, but their tendency to do so decreases progressively as the songs become more unusual. Again, this is based on empirical data: hand-reared birds can be trained to sing heterospecific song in the absence of conspecific song and occasional heterospecific learning ('mixed singing') has been recorded for many species (Helb *et al*. 1985).

We suggest that if song learning were to be selected against, the width of the filter would become progressively narrower, until there was no further potential for variation (figure 1). Clearly, such a complex system as song learning must involve the actions of many genes. However, mutations in single genes could be the basis for narrowing or widening of this predisposition. If there is selection for genes that increase the width of the predisposition, then song learning will clearly be maintained. To assess such selection, we measured the relative success of genes that either narrow or widen the genetic predisposition.

The width of the genetic filter cannot continue to increase indefinitely. It seems likely that the various costs of song learning (e.g. time taken, interspecific confusion and increased metabolism) will rise as the filter width increases. This is likely to create stabilizing selection. To examine this, we have included a direct fitness cost of possessing a wider filter in some of our simulations. Some of the costs may apply more indirectly, but a lack of empirical evidence for them has led us not to include them here.

3. THE CULTURAL TRAP HYPOTHESIS FOR THE EVOLUTIONARY MAINTENANCE OF SONG LEARNING

We have developed a hypothesis to explain the evolutionary maintenance of song learning within the framework described above. The 'cultural trap' hypothesis is based on gene-culture coevolutionary theory and is so named because learning is maintained in an evolutionary trap formed by the interaction between genes and culture.

While in most species only males sing, we assume that females also inherit filters which are used to recognize songs as belonging to conspecifics which might be potential mates, using the same limits within the filter. This assumption seems reasonable since, under hormone treatment, females can be induced to sing (e.g. Pohl-Apel & Sossinka 1984); they also possess many of the brain structures known to be involved in song learning (Nottebohm & Arnold 1976) and the species specificity of females' sexual responses to male song in canaries is removed by a lesion of the higher vocal centre (Brenowitz 1991), which is known to be important in male song learning.

We compare the success of two alleles. The 'wide' allele causes the genetic filter to be wider than does the 'narrow' allele. Therefore, four classes of individual exist in the model: males and females, each with a wide or narrow allele. Males with the wide allele have the potential to learn songs outside the filters of narrow-allele females. If they do so, they may not be recognized by potential mates and will be selected against. Conversely, females with the narrow allele may not recognize some potential mates with the wide allele and will also be selected against. Overall, there should be antagonistic selection against both wide and narrow alleles.

Our hypothesis compares the conditions for the initial increase of either of the alleles. This approach was introduced at the outset of gene-culture coevolutionary models by Feldman & Cavalli-Sforza (1976) and has been used in many subsequent models of this type (e.g. Aoki 1989). In our hypothesis, we essentially compare the stability of equilibria where either the wide or narrow allele is fixed. When the wide allele is rare, males with that allele will be likely to copy songs from the more common narrow-allele males and will thus be recognized by all females present. However, when the narrow allele is rare, it is likely that many males will be singing songs that cannot be recognized by the narrow-allele females and these females will thus be selected against. Therefore, the equilibrium where the wide allele is fixed is likely to be most stable and, through processes of drift, we expect to see our simulations evolve towards this state.

4. DESCRIPTION OF THE MODEL

The aim of our model is to assess whether the cultural trap hypothesis outlined above is likely to generate significant selection for the wide allele in conditions that are realistic for birdsong cultural transmission. We used a spatial simulation model of cultural transmission (Williams & Slater 1990) which consisted of a grid in which each location corresponded to the territory of one pair. The key to our hypothesis is the distribution of unusual songs. Since spatial dynamics are crucial to the cultural transmission of birdsong (Catchpole & Slater 1995; Lynch 1996) our model therefore has to include them, although we also discuss a simpler non-spatial model. We modelled only essential aspects of the life cycle (recruitment, reproduction and death), as well as processes of song learning. These were then iterated for each territory in steps corresponding to one year. The simulation was loosely based on data available for the chaffinch (*F. coelebs*). Although this species has a repertoire of one to six song types, for simplicity a repertoire of one song type was imposed in this model. The simulations were conducted in 12 sets, labelled 'a' to 'm' in the text and in figure 2, in each of which variations in different parameters were examined. The iterated procedures and sets of parameters that we tested were as follows.

(i) Mortality. The probability of mortality was equal for all individuals. For set l, the rate of mortality was varied from 0.05 to 0.5, while for the others it was kept at 0.4 (Goodfellow & Slater 1986). In set f, a fixed mortality cost was applied to all individuals possessing the wide allele. The value of this cost, which was added to the normal mortality rate (0.4) was varied from 0.005 to 0.02.

(ii) Male dispersal. An empty territory could be filled by one of the offspring of the previous year or earlier of a pair in another territory. Dispersal was not biased in any other way. Increased male dispersal was examined in set d. Here, the maximum number of territories a male could cross in dispersal was varied from one to four territories. The probability of dispersing over a given number of territories was equal for all these distances. In a final condition, males could disperse from anywhere within the population.

(iii) Song learning. Males learned song in their first year from any one of their neighbours. The computer sampled all neighbours in random order and the most preferred song was learned. When songs of equal attractiveness to a male were encountered, the first that was sampled was chosen. Increased song learning distances were examined in set b. Here, songs could be learned from a varying maximum distance, from one to four territories and the probability of learning songs from among these distances was set to be equal. In a further condition, songs could be learned from any male in the population. Preference for songs was governed solely by the genetic predisposition for song. The form of the predisposition shown in figure 1*a* is described in equations (1)–(3). Equation (3) describes the central flat part of the graph, while equations (1) and (2) describe the curves on either side. These equations describe the preference, *P*, that a bird shows for learning a song with a value *x* as follows:

$$\text{if } x < \text{min then } P = \frac{\text{prop}}{\text{max} - \text{min}} \times \mathrm{e}^{\frac{2\text{prop}(x-\text{min})}{(1-\text{prop})(\text{max}-\text{min})}}, \quad (1)$$

$$\text{if } x > \text{max then } P = \frac{\text{prop}}{\text{max} - \text{min}} \times \mathrm{e}^{\frac{2\text{prop}(\text{max}-x)}{(1-\text{prop})(\text{max}-\text{min})}}, \quad (2)$$

and

$$\text{if min} \leqslant x \leqslant \text{max then } P = \frac{\text{prop}}{\text{max} - \text{min}}, \quad (3)$$

where min and max are the minimum and maximum limits of the plateau within the filters and prop is the proportion of songs in a given population expected to fall within the limits of the filter. In set j this was varied from 0.9 to 0.05. The wide or narrow alleles change the values of min and max such that the wide allele has a larger range between the two. The midpoint of the two was kept constant. These conditions allowed us to examine overall widening or narrowing of the filter. Set k examined the relative value of the min–max range for the narrow and wide alleles. The narrow:wide ratio for this value was varied between 0.9 and 0.1.

(iv) Cultural mutation. Variation in songs was introduced by including occasional random mutation following the learning process. The rate of cultural mutation was varied from 0.005 to 0.2 in set i, while in all others it was 0.1 (Slater *et al.* 1980). Mutation altered the song score randomly over a range of 0.2 of the min–max range of the genetic predisposition.

(v) Mating. An unmated male territory holder could mate with the offspring of any neighbour, given that those neighbours had been mated the previous year. Set c examined increased female dispersal, as was done for male dispersal (set d). Each year, each male had one mating opportunity. Mating was affected by the allele possessed by the female, i.e. whether she recognized the song, using equations (1)–(3) as before. In set m, the probability of mating, even if a male's song had been recognized, was varied from 0.6 to 1.0, while it was kept at 0.7 elsewhere.

(vi) Inheritance. The inheritance of wide or narrow alleles by males and females followed a simple haploid scheme, i.e. the probability of inheriting the allele from each parent was 0.5.

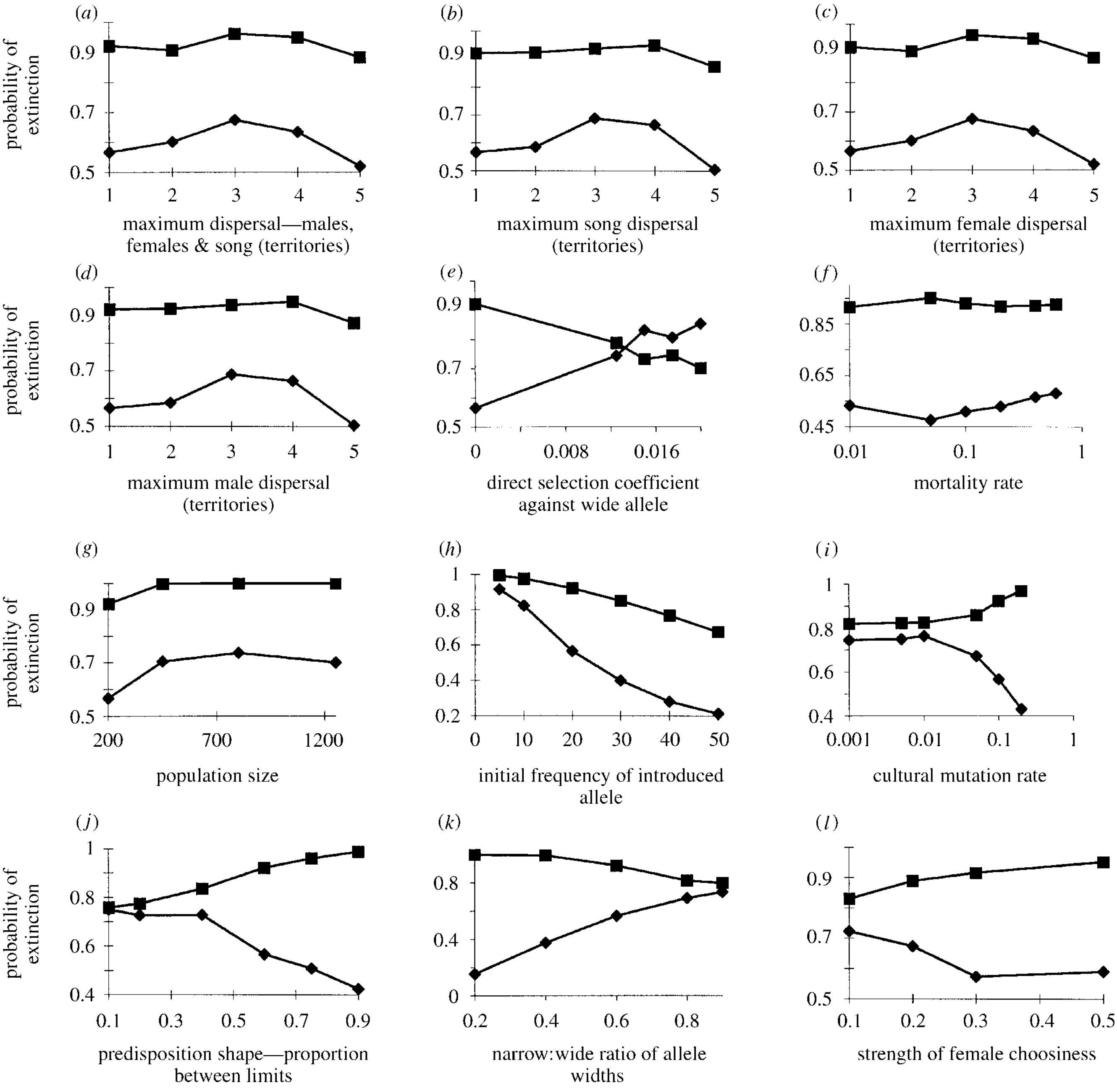

Figure 2. The relative success of wide and narrow alleles under the various parameters tested. In all cases, the squares represent invasion by the narrow allele and the diamonds invasion by the wide allele. The y-axis represents the probability that the invading allele will become extinct. See § 4 for further details on the parameters.

(vii) Grid size. The size of the grid was 10 × 10 territories, except in set g where this was varied from 10 × 10 to 25 × 25 territories. In set a, increased dispersal of males, females and songs together was examined. When dispersal was set to 5, all males, females and songs in the whole population were sampled. This made the model non-spatial.

(viii) A running-in period of 500 years preceded the start of all simulations. This period was experimentally established to be long enough for a steady-state level of cultural diversity to be reached after random seeding. The simulation was started by the introduction of 20 individuals (in two rows of ten), of the opposite type to the rest, into the population. In set h, the initial frequency of 'mutants' was investigated. Here the initial frequency was varied from 0.05 to 0.5, corresponding to 0.5 to five rows of ten territories. Two thousand runs were carried out for each parameter setting: 1000 in which the wide allele was introduced into a population of narrow alleles and 1000 with narrow alleles introduced into populations of wide alleles. Each run proceeded until one or other allele became extinct or until 10 000 years had passed. Fixation within this time-span occurred in all simulations, except when a very low mortality rate was set. This was clearly an artefact of the conditions rather than biological polymorphism. The results of the model were analysed by simply recording the number of instances of extinction of either allele in each condition.

5. RESULTS

Figure 2 summarizes the results and indicates that selection favoured the wide allele under all conditions. Although in some trials the wide allele became extinct as a result of random drift, extinction of the narrow allele after introduction was much more frequent. The wide allele was more successful than the narrow allele over all ranges of dispersal—including the simple case (point 5) where the spatial element of the model was removed altogether (figure 2*a*). Dispersal of three territories produced the smallest difference between the two alleles. Figure 2*b*–*d* shows a similar pattern when male, female and song dispersal were considered independently. Again, dispersal of three territories produced the smallest difference between success of the alleles in all these graphs. Overall, variations in dispersal had only a small effect on the difference between the alleles.

A direct selection coefficient of around 0.013 was required to remove the difference between the alleles entirely (figure 2*e*). This strength of selection would be adequate for rapid evolutionary change, indicating that the effect of the cultural trap hypothesis is significant.

Varying the mortality rate had only a small influence on the effect (figure 2*f*). Lower mortality rates tended to increase the difference between the alleles slightly—except for the lowest value (0.01). This may have been because this was the only condition under which significant numbers of runs did not reach fixation within the allotted maximum time of 10 000 years. Similarly, population size had only a small influence on the outcome (figure 2*g*). The success of the wide and narrow alleles decreased slightly at larger population sizes. However, it should also be borne in mind that the number of genetic mutations in the allele would also be expected to increase in larger populations. Therefore, we would expect wider predispositions in larger populations. Low initial starting frequency clearly reduced the success of both alleles (figure 2*h*)

Higher cultural mutation rates increased the difference in success between wide and narrow alleles (figure 2*i*). At values of 0.01 or less, only a small difference in the success of the two alleles was found. The graph probably did not converge further at the lowest values of mutation because there was not enough time from the random seeding of songs for a steady-state rate of cultural variation to be established. The shape of the predisposition also had a marked effect on the outcome (figure 2*j*). For higher values of this score (which corresponded to nearly rectangular predisposition shapes), the success of the wide allele was greater. For low values of this score (which corresponded to nearly flat predisposition shapes), there was very little difference between the two. Given the low frequency of birds singing markedly unusual songs, a value near the high end of this range is to be expected. If Helb *et al.*'s (1985) estimate of the rate of heterospecific song learning (0.001) was accurate, then our default value of 0.6 may be considered conservative. The relative widths of the wide and narrow alleles also markedly affected the outcome (figure 2*k*). The wider the relative width of the wide allele, the larger its relative success. However, it seems likely that the costs to the wide allele are likely to increase with its relative width, countering this to some extent.

Finally, female choosiness had a small influence on the outcome (figure 2*m*). This value corresponded to the probability that a female would not mate with a male that she recognized and therefore also indicated the relative importance of song recognition in mating. The choosier the females (i.e. the greater the role that song recognition plays in mating), the greater the success of the wide allele. This makes sense, since female mate recognition drives selection for wider alleles in our hypothesis.

6. DISCUSSION

Our hypothesis proposed that the interaction between genes and culture alone might be sufficient to maintain song learning, so that it would persist in a 'cultural trap' without learning leading to an increase in the average fitness in a population. The simulation model confirmed this, as it found selection for the wide allele over a broad range of conditions, which was our requirement for maintaining learning. Therefore, our results provide robust support for the hypothesis, suggesting it may apply to many songbird species.

Previous models of the adaptiveness of culture have concluded that culture can out-compete genetic transmission only under extreme transmission rules (Cavalli-Sforza & Feldman 1983) or high environmental variability (Boyd & Richerson 1988), because of the higher fidelity of genetic transmission. In contrast, in our model it is the low fidelity of cultural transmission that enables it to avoid replacement by genetic transmission. This difference occurs because of the neutrality of cultural traits in our model and because we assume the gradual evolution of a genetic predisposition, as opposed to the direct replacement of a cultural trait with a genetic one.

Our results add to the debate as to whether 'maladaptive' cultural traits can survive in populations (Galef 1996; Laland 1996). The cultural trap hypothesis proposes that the evolution of a wider filter leads to no increase in average fitness. Moreover, since set e showed that the cultural trap effect can overcome significant levels of direct selection against the wide allele, the coevolved traits of unusual songs and wider filters must even be regarded as having the potential to be maladaptive.

Other hypotheses that suggest an adaptive benefit for song learning (Nottebohm 1972; Hansen 1979; Payne 1982) are not excluded by our results. Indeed, it is probable that evolution has led to the exploitation of socially learned information. However, under our framework, it is not certain that any of these hypotheses would be sufficient to maintain song learning by themself.

One goal of this research was to provide a testable hypothesis for the maintenance of song learning. Our results indicate that variations in patterns of cultural evolution, in particular the cultural mutation rate, alter the selection pressure for wider predispositions. The rate at which birds make mistakes in learning might be influenced by ecological variables such as population density and degree of isolation, both of which would be likely to limit experience. If higher cultural mutation rates do indeed lead to wider filters, then the hypothesis will be supported.

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