The Population Memetics of Bird Song

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Abstract

Two basic requirements for a theory of evolution are variability and her-
itability in the units of change. These requirements are fulfilled in cultural
systems, and therefore it is possible to construct a theory of cultural evolution.
In many species of birds, song is acquired by social learning, and bird song is
often cited as one of the best examples of a culturally acquired trait in animals.
As such, it provides a good subject to develop a model of cultural evolution.

In this paper I examine patterns of differentiation of bird songs within an
evolutionary framework. I identify analogues of the evolutionary forces respon-
sible for frequency changes (mutation, migration, drift and selection) and adopt
methods of population genetics to estimate parameters of population structure
and determine the factors responsible for the origin an maintenance of song
diversity within and between populations.

Cultural evolution can be defined as the change in the frequency of cultural traits
through differential transmission from one generation to the next. This non-genetic
transmission of traits or behaviours across generations can be a powerful source
of variation, so it is important to understand the processes involved in the origin
and maintenance of this diversity. It has been argued that the evolution of cultural
traits is driven by processes analogous to those involved in biological (or genetic)
evolution (Alexander 1980, Mundinger 1980, Cavalli-Sforza and Feldman 1981, Boyd
and Richerson 1985). Many songbirds acquire their specific song patterns by social
learning, and bird song is therefore often cited as one of the best examples of cul-
ture in non-human species (Bonner 1980, Mundinger 1980, Slater 1986). Although
studies of bird-song diversity usually invoke one or more evolutionary forces to ex-
plain the variation within or among populations, in general no attempt is made to
explain cultural evolution quantitatively in terms of the interaction of all possible
evolutionary factors. To be able to describe bird-song diversity in an explicit evo-
lutionary framework, we first need to identify cultural analogues of the well-known
evolutionary forces responsible for changes in gene frequency (mutation, migration,
drift, and selection). Once these forces are identified, we can take advantage of
the well-developed mathematical theory of population genetics to make inferences
about the relative importance of these forces in the origin and maintenance of song
diversity within and among populations. In this paper I will first discuss the main
concepts of cultural evolution by drawing analogies with biological evolution, and I
will describe models adopted from population genetics that are useful in estimating
important parameters of population structure (e.g. mutation and migration rates,

memetic diversity within and among populations). I will briefly illustrate the use of these models with data from a number of passerine species. Finally, I will briefly describe how transfer experiments can be a potentially useful method of obtaining more direct estimates of some of these parameters.

Cultural Evolution of Bird Song

In this section I begin by discussing some important aspects of the transmission of bird songs as they relate to cultural evolution. I then identify analogues of the well known population genetic processes involved in gene frequency changes (mutation, drift, migration and selection) that can be applied to bird-song evolution. Finally, I indicate useful population genetics models that can be borrowed to estimate important parameters of population structure (e.g. mutation and migration rates, diversity within populations, and differentiation among populations). Throughout the section I will point out some important differences between genetic and cultural evolution.

Bird Song Learning

Songs are vocalizations used mainly by male birds during the breeding season for the purpose of defending their territories and attracting mates. Songs are normally distinguished from calls, which are simpler vocalizations used by both males amd females throughout the year for other purposes such as alarm or contact signals.

A song is normally composed of an array of elements called "syllables." Songs that have the same stereotyped configuration of syllables are referred as pertaining to the same "song type." Males of most songbirds sing two or more different song types and are said to possess "song repertoires."

Songs are usually learned during a sensitive period, the timing an duration of which varies among species, lasting from just a few months to several years. Young birds go through a gradual series of stages during song development. They start with a rudimentary stage ("subsong") when they produce variable sounds that are soft and with little structure; by the next stage ("plastic song") the songs are more structured but still quite variable; in the final stage ("crystallized" or "full song") the songs are stable and stereotyped.

We can use the Chaffinch (*Fringilla coelebs*) as a typical example of a passerine species that illustrates several important aspects of its life history as they relate to song transmission. Chaffinch song has been a classic subject of study since the pioneering work of Marler (1952, 1956a, 1956b) and Thorpe (1954, 1955, 1958a, 1958b), and therefore we have a reasonably good understanding of the mechanisms of song transmission through learning in this species (see, c.g., Nottebohm 1968, 1971, 1972; Slater and Ince 1979, 1982; Ince et al. 1980; Slater et al. 1980, 1984; Slater 1981, 1983a, 1983b; Jenkins and Baker 1984). Our understanding of the transmission process of chaffinch song is as follows. Males learn one or more songs (average 2.9; Slater et al. 1980) from other males they interact with either as fledglings before they disperse or in their first breeding season during territory establishment, most

likely from one or several of their neighbors (Slater et al. 1980; Slater and Ince 1982). They do not necessarily copy whole songs (although sometimes they do) but can recombine different elements from different songs from a number of birds. There is therefore linkage between elements in a song, but these can be recombined in a process analogous to genetic recombination during crossing-over (Slater and Ince 1979; Jenkins and Baker 1984).

Transmission of Cultural Traits

Before we can begin the analysis of cultural change, we need to determine what is being transmitted. Dawkins (1976) coined the term "meme" for the unit of cultural transmission, and defined it as "an entity that is capable of being transmitted from one brain to another" (Dawkins 1976:196). We can apply this concept to bird song and define a song meme as a song pattern that is transmitted from one bird to another during the learning process (Lynch et al. 1989).

In some cases whole songs are transmitted (e.g. Slater et al. 1980, Beecher et al. 1994); in others, birds copy individual syllables or blocks of linked syllables from different songs and recombine them with other syllables or blocks to form a new song (Marler and Peters 1982, Jenkins and Baker 1984). A meme can therefore variously be an individual syllable, a group of linked syllables, or a whole song. In any event, these memes are replicators (sensu Dawkins 1976), and it is with their evolutionary fate that I will be concerned. The types of questions I would like to address are as follows: What is the rate of origin of new memes? How much movement of memes occurs among populations? Are some memes more successful than others at producing copies of themselves?

The mode of transmission across generations is a major difference between cultural and biological traits. Genetic transmission is usually strictly vertical (from parent to offspring), whereas cultural transmission can be vertical, horizontal (between members of the same generation), or oblique (from members of a given generation to members of succeeding generations who are not direct descendants) (Cavalli-Sforza and Feldman 1981). Most songbirds learn their songs either before natal dispersal or from their neighbours when establishing territories in their first breeding season (Kroodsma 1982). It is therefore likely that all three modes of transmission occur, although oblique transmission is probably the most common.

Mutation

Mutational input is the ultimate source of variation, so the rate of mutation is an important factor determining the amount of diversity within and among populations. Song transmission is not always accurate: sometimes birds produce imperfect copies of their models. These poor copies can arise due to copy errors as a result of limited exposure to the model, the development of variations on a theme (improvisation), or the invention of totally new types. All these processes can be subsumed under the rubric of "cultural mutations" (Jenkins 1978). Lynch et al. (1989) have distinguished two types of cultural mutations. Point mutations are changes in morphology of the basic elements that compose a song (referred to as elemental improvisation

by Marler and Peters (1982)). Recombinations are the rearrangements of these basic elements within and among songs (combinatorial improvisations of Marler and Peters (1982)). In general, cultural mutation is a common phenomenon, occurring in every generation during the transmission process (e.g. Jenkins 1978, Slater and Ince 1979). In contrast, biological, or gene, mutation is usually a rare event, occurring at a very low frequency per generation. The high rate of cultural mutation makes song a good subject for evolutionary studies because (1) populations will attain equilibrium between mutation and drift relatively quickly after a disruption of their steady-state (e.g. after a population bottleneck), and (2) long-term studies can follow the fate of variants as they arise and spread in a population through time.

Random Drift

When song patterns are transmitted from generation to generation through social learning, some may be lost by accident or sampling error, particularly in small populations. The frequency of a song meme is therefore subject to sampling variation between successive generations. In general, drift reduces the diversity within populations and increases differentiation among populations. An important type of sampling drift occurs during severe reductions in population size, such as during the colonization of new areas by a small number of individuals. During such a founder event birds will likely carry a small set of the total meme pool existing in the original population (e.g. Baker and Jenkins 1987).

The strength of drift depends on population size. Most population genetic models make a number of unrealistic assumptions in connection with the size of the population and therefore with the amount of drift that is expected to occur. For example, it is often assumed that population size is constant from generation to generation, that generations are non-overlapping, and that all individuals have an equal probability of producing offspring. To offset such unrealistic assumptions, Wright (1931) developed the concept of effective population size (N_e), which can be defined as the size of an idealized population that satisfies the above assumptions and has the same diversity as the actual population. The effective population size is usually smaller than the census population size.

In the ideal population no fluctuations in population size occur. If the size of a real population is not constant from generation to generation, then its effective population size will be determined by the harmonic mean of the size in each generation(Kimura 1983). The harmonic mean is dominated by the smallest numbers, and thus extreme fluctuations in population sizes will markedly reduce the effective size.

Ideally, each meme has an equal probability of being copied, so the variance in copying success has approximately a Poisson distribution (Crow and Kimura 1970). The actual number of copies derived from individual memes will vary, but all memes have the same expected number of descendants. In reality, not all memes have the same probability of being copied. For example, individuals differ in their life spans, so the song memes of some individuals will have a higher chance of being transmitted simply because those birds live (and presumably sing) longer. A high proportion of

memes is thus derived from a small number of models, reducing the effective size.

Migration

Populations that are separated will tend to diverge. If contact occurs between those populations, however, memes can spread from one to the other and the populations will therefore remain more or less similar. The effectiveness of migration as a homogenizing factor depends in part on when song is learned. If birds learn at least some of their songs before natal dispersal, then they will carry these songs with them to where they move. If birds learn their songs after they disperse, however, or if they learn new songs when they move to a new area and do not use any songs learned before dispersing, then song elements will not diffuse even with extensive contact between populations. Given the usually high rate of cultural mutations, unless migration rates are exceptionally high they cannot prevent the accumulation of new mutants in different populations before they are dispersed throughout the entire region (Spieth 1974, Lynch et al. 1989).

Selection

Some traits reinforce their own persistence and spread; others do not, and eventually disappear. Cultural selection can be defined as the probability that a given meme will be accepted by a young bird. The selective value will be determined by how acceptable a meme is, and refers to the survival of the memes, not their vehicles. On the other hand, the possession of one meme or another might affect the Darwinian fitness of an individual bird (the carrier or vehicle). The fitness of a meme is determined by its propensity to survive and spread among hosts. The relationship between the cultural fitness of a given meme and the Darwinian fitness of its carrier can be a complex one. For example, the possession of a particular meme might increase the Darwinian fitness of the carrier, which in turn might increase the probability of it spreading its memes. Alternatively, if the probability of a song being copied depends on the frequency with which it is uttered, and if males reduce their song output after mating while unsuccessful males continue singing, young nestlings and fledglings could be preferentially exposed to the songs of these unpaired males, and perhaps would tend to copy their songs. A number of studies have suggested that song memes are functionally equivalent, and that the relative frequencies of memes reflect chance events that made some more frequent than others (e.g. Payne et al. 1981, Slater et al. 1980, McGregor and Krebs 1982, Horn and Falls 1988, Catchpole and Rowell 1993, Lynch and Baker 1993). The results of these studies imply that no selection (or very weak selection) occurs for some memes over others, and we can therefore consider memes as effectively neutral, in the same sense as neutral alleles (Kimura 1983). In this case, the diversity of memes within populations can be explained by an interaction of mutation and migration, both of which introduce new variants, and drift, which tends to eliminate them. It should be stressed that the neutral theory does not ignore selective constraints, and thus is consistent with the presence of purifying selection, which would eliminate

most of the deleterious mutants as they arose and would not contribute much to the diversity in the population (Lynch and Baker 1993).

Two potentially important selective forces in the evolution of song memes are the social and the acoustic environments. The social environment can act in determining the fate of memes in a frequency-dependent manner. For example, common variants might be copied disproportionately often relative to their frequency in the population ("majority-type advantage" or "conformist bias") (e.g. Beecher et al. 1994). This process would lead to a few predominant types, decreasing diversity. Alternatively, if rare variants are copied with higher probability, there will be a more even distribution of types and a concomitant increase in diversity ("rare-type advantage") (Boyd and Richerson 1985).

The acoustic properties of the environment can potentially influence the type and number of song elements that exist within a population. For example, some types that are not transmitted well or are potentially confused may be at a disadvantage (Hansen 1979). Here, the acoustic environment will influence the "realized" mutation rate by affecting the strength of purifying selection (Lynch and Baker 1993). Differences between populations could also be related to differences in the acoustic environment. For example, if different environments have different acoustic properties (e.g. Wiley and Richards 1982), directional selection can promote the acoustic differentiation of populations (e.g. Nottebohm 1975, Hunter and Krebs 1979). Also, it has been argued that populations inhabiting areas with depauperate avifaunas have relaxed pressure for distinctive songs and are therefore more variable (Marler 1960). Note, however, that this process involves different amounts of purifying selection in different populations, and it is therefore consistent with a neutral model (Lynch and Baker 1993).

Estimating Parameters of Population Structure

Two complementary approaches can be used to study song diversity. We can describe patterns of variation within and among populations and then make inferences about the processes that led to these patterns by estimating population parameters such as meme diversity, meme flow, and selection coefficients. This is the approach that I will be using for most of the analyses reported here. Alternatively, given the high rate of change of song elements, it is possible to study this dynamic process directly through time by following the fate of cultural traits as they arise and spread in a population (e.g. Jenkins 1978, Payne et al. 1981, Payne 1996).

Diversity within populations

We can consider song memes as alleles at a single "locus." Given the wide variety of song elements in most species, the two most appropriate models are the infinite alleles model (Kimura and Crow 1964) and the K-alleles model (Kimura 1968). The infinite alleles model assumes a sufficiently large number of possible distinct mutants so that each new mutant is of a type not already represented in the population. The K-alleles model allows for recurrent mutation, and assumes a fixed number

of potential types, K. The rate of mutation from one type to any of the others is $\mu/(K-1)$, where μ is the total mutation rate for a given type. This model is appropriate when similar syllable types can develop independently, for example when birds are limited in the diversity of sounds they can produce (e.g. Tubaro 1991). If S different memes occur in a population of size N, and if the frequency of the kth meme is p_k, then we can define meme identity as

$$I = \sum_{k=1}^{S} p_k^2 \tag{1}$$

This parameter is called homozygosity or gene identity in population genetics (e.g. Nei 1973) and represents the probability that two randomly chosen memes are identical. A useful measure of diversity derived from I is

$$s_e = \frac{1}{I} \tag{2}$$

which is called the effective number of alleles in population genetics (Kimura and Crow 1964). By analogy, it can be called the effective number of memes (Lynch and Baker 1993). It corresponds to the number of different memes that would exist in an ideal population with the same s_e as the real population, and in which all memes had equal frequency $1/S$. This measure is a better index of diversity than the actual number of observed memes in a sample, s_a. The actual number depends greatly on sample size, whereas the effective number is largely independent of sample size. The difference in dependency with sample size arises because larger samples will detect a greater proportion of rare memes, which increase the number of observed memes but contribute very little to s_e. This measure of diversity (s_e) under the infinite alleles model attains an equilibrium value when the input of new types by immigration and mutation is balanced by the elimination of types by sampling drift:

$$s_e \approx 2N_e v + 1 \tag{3}$$

where N_e is the effective population size and v represents the combined effects of mutation (μ) and migration (m) rates. Under a K-alleles model, the relationship is

$$s_e \approx \frac{2N_e v \frac{K}{K-1} + 1}{2N_e v \frac{1}{K-1} + 1} \tag{4}$$

where K is the number of different potential memes (Kimura 1968, Crow and Kimura 1970). Using either equation (3) or (4) as appropriate, one can estimate $N_e v$, the number of new memes entering the population per generation via mutation and migration. It should be noted, however, that if memes fit an infinite alleles neutral model, Ewens (1972) has shown that a better way to estimate $N_e v$ is to use the total number of memes and the number of distinct memes in the sample (see equation (5) below).

Examples

Lynch and Baker (1993) compared levels of within-population variation between continental and Atlantic-island Chaffinch populations. At the level of syllables (memes of length one), no difference was found in diversity (as measured by s_e) between populations from Iberia ($s_{e1} = 23.4$) and the Canary Islands ($s_{e1} = 22.7$). For memes of length 5, however, populations in the Canary Islands had much higher levels of diversity ($s_{e5} = 318.2$ vs. $s_{e5} = 43.8$). These results suggest that the rate of point mutation is the same in both regions, but the rate of recombination is higher in the Atlantic islands. Lynch and Baker (1993) suggested that this increased recombination is the result of looser syntax in the songs on the islands, perhaps because of the depauperate avifauna, and a concomitant relaxation in selective pressure for distinctive songs.

Some species might have a limited repertoire of songs or song elements from which to choose, and a K-alleles model would thus be more appropriate than the infinite alleles model. Wood Thrushes seem to have a limited number of song types, and most songs from the entire species' range can be categorized based on a key developed from a single population (Whitney and Miller 1987). The key could classify 25 distinct song types, so I use 30 as a rough estimate of K, the total number of song types. The average effective number of memes is $s_e = 19.9$, so assuming $K = 30$ and using equation (4), we obtain an estimate of the number of new songs entering the population per generation, $Ne_v = 27.6$. This value likely represents mostly input by mutation rather than immigration, because given the limited number of types available, most immigrant types will already exist in the population.

As a cautionary note, it should be noted that the use of this method to obtain estimates of mutation and migration is limited in several ways. First, we cannot distinguish between new variants that arise from mutations and those that enter the population by immigration. Also, to be able to estimate the rate of input of new variants (v) we need to know the effective population size. Finally, this method of estimating Ne_v is biased because it assumes that all elements that enter the population differ from preexisting ones (barring recurrent mutation). This assumption is true for mutation, but might not be so for migration, especially when mutation rates are low and migration rates high, because types will be shared between populations and some of the immigrant memes will therefore go undetected.

Test of neutrality

A theory of neutral mutations predicts that variation in a population depends upon a balance between the origin of new forms due to mutation and immigration, and the extinction of existing forms by random drift. In such a case, the vast majority of existing forms are functionally equivalent. Ewens (1972) has shown that the total number of distinct alleles (memes, in our case) s in a sample and the sample size n are sufficient to give an expected distribution of allele (or meme) frequencies in a neutral, infinite alleles model. The relationship between the expected number of memes in a sample of size n and the population parameter $\theta = 2N_e v$ is

$$E(s) = \sum_{i=0}^{n-1} \frac{\theta}{\theta + i} \tag{5}$$

where θ is changed iteratively until $E(s)$ equals s. From the expected and observed distributions a number of tests can be used to determine whether the observed sample corresponds with the expected values of the model. Watterson (1978) showed that a good test is to compare the observed and expected values of I. The observed value can be obtained using equation (1); using equation (5) we can obtain θ and from it the expected value of I using the relation $E(I) = 1/(\theta + 1)$. The distribution of I can be obtained by simulation, and from it confidence limits can be calculated (e.g. Whittam et al. 1983, Lynch and Baker 1993).

Examples

I analysed song data from nine different species obtained from the literature (Lynch 1996). Assuming an infinite alleles model, I found good agreement between the observed and expected values of meme identity, I, suggesting that within-population diversity is essentially neutral. This result implies that most variation is maintained by immigration and mutational input, on the one hand, and random extinction of memes on the other, whereby chance plays the major role determining the fate of memes.

Differentiation among populations

Most songbird species display marked geographic variation in their songs. The analysis of such population structure can help us understand the relative importance of different evolutionary factors in the origin and maintenance of memetic diversity. We can measure the degree of population subdivision by comparing the probability of obtaining two memes that are the same (or different) in one population relative to the same probability for two memes in different populations. Two such measures were introduced by Latter (1973). The first, related to the coefficient of kinship and to G_{ST}, is defined as

$$\phi = \frac{I_W - I_B}{1 - I_B} \tag{6}$$

where I_W is the expected probability of identity of memes within a population, and I_B is the expected probability of identity among memes drawn from different populations. This measure, in an island model of population structure (i.e. migration can occur between any pair of populations) and under a neutral model, depends on the rates of migration (m) and mutation (μ) and the effective population size (N_e) according to the following equation:

$$\phi \approx \frac{1}{2N_e(m + \mu) + 1} \tag{7}$$

The degree of differentiation as measured by ϕ is inversely related to m, μ, and N_e. An increase in m will reduce differentiation because of more meme interchange

between populations, while an increase of N_e will reduce the amount of differentiation caused by drift. An increase in μ also will decrease differentiation, which is somewhat counter-intuitive and can make this measure inadequate as an index of population differentiation in certain circumstances (see Lynch and Baker 1994 for details). The second measure of differentiation, called measure of mutational divergence by Latter (1973), is defined as

$$\gamma = 1 - \frac{I_B}{I_W} \tag{8}$$

This measure, in an island model of migration and under a neutral model, is a function of mutational input, which tends to differentiate populations, and the opposing effects of migration, and is independent of population size:

$$\gamma = \frac{1}{\frac{m}{(d-1)\mu} + 1} \tag{9}$$

where d is the number of populations in the region. The probabilities of identity can be estimated using the meme frequencies in each population (Lynch 1991, Lynch and Baker 1994). Although these results are based on an island model, which represents an extreme of long-range dispersal, it has been shown that a two-dimensional stepping-stone model of population structure (where only adjacent populations exchange migrants) results in similar patterns of differentiation (Kimura and Maruyama 1971).

Estimates of meme flow

Slatkin (1985) developed a method to estimate levels of gene flow using the frequency of alleles (memes, in this case) restricted to a single population. If levels of meme flow are high, then only memes that occur at low frequencies will be restricted to just one population ("private" memes). Memes at higher frequencies will have an increased likelihood of spreading to other populations. Conversely, if levels of flow are low, even memes with higher frequencies can be unique to a population. Slatkin's method uses the formula

$$\ln \bar{p}(1) = a \ln (N_e m) + b \tag{10}$$

where $\bar{p}(1)$ is the average frequency of alleles unique to a single population, and $a = -0.505$ and $b = -2.44$ are empirically derived constants. The estimates obtained depend on sample size, and Slatkin therefore proposed an approximate correction method. The value of Ne_m is an estimate of the average number of immigrant memes per generation. The relationship of this value to the number of migrating birds is usually complex, and depends on factors such as the timing of song learning and number of song memes per bird.

Examples

I used data obtained from the literature for four species of passerine birds to study the amount of among-population differentiation (Lynch 1966). I estimated the

amount of meme flow (N_em) using the method of rare alleles (equation (14); Slatkin 1985). Using equation (7) we can estimate the number of new songs entering the population per generation (Ne_v) and, given that the rate of input of new variants is due to the combined effect of mutation and migration ($v = \mu + m$), we can obtain the number of new mutants per generation, $N_e\mu$. In general, the rates of mutation and migration were of the same order of magnitude, indicating that a roughly equal number of memes enter a population by mutation and meme flow. These results are important because they suggest that mutation and migration rates are of the same order of magnitude, at least in these species, and thus we cannot ignore the effect of mutation in subdivided populations, as is commonly done in population genetics (e.g. Crow and Kimura 1970). For two reasons, however, one should be cautious when comparing the levels of differentiation across species: 1) the geographic scale of these studies differs, and 2) song elements are classified subjectively. Both of these factors will affect the observed diversity and therefore the mutation rate estimates.

Transfer Experiments

So far I have used indirect evidence based on the patterns of variation within and among populations to suggest that song elements are neutral, that is, different variants are functionally equivalent (see also Lynch and Baker 1986, 1993, Lynch et al. 1989). Here I present results of a pilot transfer experiment that provide some direct evidence for the neutrality of Chaffinch songs in terms of the fitness effects on their carriers.

Thirty male Chaffinches were captured in Karioi, North Island of New Zealand, and transferred to Kohwai bush, near Kaikoura, South Island. The following spring three of these birds were re-sighted in the area where they were released. All were still singing their North Island songs in unmodified form, but two of them had modified their contact call to resemble the local variant. These two birds had established territories, and at least one of them was mated. The third bird was still using his North Island contact call, and he had not established a territory.

These results suggest that the distinctive North Island songs are functionally equivalent to the South Island ones in the South Island social milieu (that is, it does not matter what one sings, as long as one sings). Contact calls, on the other hand, are probably important in mate acquisition and social interactions with conspecifics in general, and pressure to conform to the local call "dialect" is apparently strong. Although we do not have more detailed information on the reproductive success of the males, the evidence presented here suggests that the particular song variants a male Chaffinch sings do not affect his ability to obtain a territory and a mate (see also Payne et al. 1988, Payne and Westneat 1988). Whether these immigrant song elements are copied by local young birds with probability equal to their frequency in the population, or whether they are discriminated against and therefore driven to extinction, needs to be investigated.

An extension of this experimental approach that seems promising is to introduce birds with distinct song elements into a population and to follow the diffusion of the new cultural variants through time (e.g. Dobzhansky and Wright 1947, Baker

1981). By combining this experimental work with analytical theory and computer simulations relating to the spread of innovations (e.g. Hägerstrand 1967), we could test important aspects pertaining to the theory of cultural evolution of bird song, such as neutrality of song variants and their rate of diffusion, patterns of song transmission across generations, and linkage of elements in a song.

Conclusions

I have attempted to incorporate the different processes of cultural evolution in the study of bird song. I believe that this approach is promising, although more work is needed to be able to make general statements about the relative importance of the different evolutionary factors in shaping the diversity of bird songs. In what follows, I will suggest some of the tasks for the future.

The use of the memetic approach advanced here depends on being able to classify songs or song elements into discrete categories. A major drawback of visual classifications of songs or song elements is their subjectivity, which makes comparisons among studies very difficult. Different investigators classify song elements using different criteria, which will influence the estimated mutation rate. A more objective method of classification of song memes needs to be developed; perhaps digitization of sound patterns (e.g. Miller 1979) combined with the use of methods of pattern recognition could help in this area.

I have borrowed extensively from population genetics theory. Although I believe the models presented here are a good first approximation, bird-song evolution departs in some important respects from genetic evolution, and refinements of these models are required. For example, I assumed that memes were independent of each other. At least two potential sources of linkage occur between memes, however: song elements are linked within songs, and songs might be linked within a repertoire. It might be more appropriate to consider the storage of memes not at just one locus, but at a variable number of loci, within each of which syntactical rules affect the number of elements that can exist and the linkage between them. Also, because some population genetic models assume very low mutation rates, it is difficult to apply them with confidence to the study of bird-song evolution. We need to develop more specific mathematical models or computer simulations that take the peculiarities of the cultural transmission of bird song into account.

It is crucial to conduct long-term studies of banded birds to corroborate the estimates of population structure obtained by means of indirect methods (e.g. see Payne 1996). In particular, transfer experiments like the one described here can be effective to this end, because they provide "marker" memes whose fate can be followed through time and space.

I would like to end with a speculative scenario for the origin and maintenance of diversity in bird songs. The levels of memetic diversity within populations in a number of songbird species seem to be consistent with a random drift-migration-mutation model. I tentatively postulate that each species has a potential mutation rate that is adjusted in different populations according to the acoustic properties of the environment. In this scenario, then, the main importance of selection is to weed

out unsuitable types that appear by mutation or immigration. In general, populations will tend to diverge at random because normal levels of meme flow are not high enough to prevent the accumulation of new variants in different populations due to the high rates of meme mutation. If the acoustic environment changes, however, or if individuals of a given population colonize a new habitat with different acoustic properties, then directional selection can act on the neutral or nearly neutral variants already existent in the population. This phenomenon is what is called in population genetics the "Dykhuizen-Hartl effect" (Dykhuizen and Hartl 1980, Kimura 1983). On the other hand, vocalizations that are important in social situations and that require the need to conform to a local standard might be subject to majority-type advantage (Lynch unpubl. data). This type of frequency-dependent selection will be important in determining which variant predominates in a given area, although different variants might become predominant in different areas.

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