

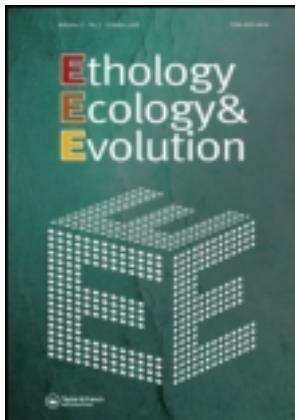
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Bird song learning: causes and consequences

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Bird song learning: causes and consequences *

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This article starts with a brief description of the phenomenon of song learning in birds, and then outlines various consequences that it has for the individuals that show it and the groups to which they belong. Among these are the following features, each of which has been described in at least some species: the sharing of song between kin and between neighbours; changes in song with time; changes with distance, including the phenomenon of dialects. The final section is a discussion of which of these consequences may have functional significance and so be likely to be an advantage of song learning. It is suggested that cultural evolution, geographical variation and dialect boundaries, being features of populations rather than individuals, are epiphenomena without functional significance in themselves. However, song learning may confer advantages stemming from the copying process itself, in interactions with neighbours and in matching song to habitat. The evidence that learnt dialects have a role in assortative mating is less convincing. It is likely both that song learning has different functions in different species, and that it has more than a single function in many of them.

KEY WORDS: birds, song, development, learning, dialect, cultural transmission, communication

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INTRODUCTION

The main aim of this article is to explore the consequences of song learning in birds and discuss which of these are likely to have functional significance.

All aspects of animal behaviour have consequences: feeding leads to a full stomach; grooming cleans the body surface; migration moves the animal to another area. However, it is not always clear whether a particular consequence enhances the inclusive fitness of the individual that shows it. Song is a good example: it occupies time that could otherwise be devoted to other activities and it is likely to attract predators but, on the more positive side, it is known to attract mates and to repel rivals. One must assume that, when the costs and benefits of singing are summed, the advantages would outweigh the disadvantages: it is a matter for empirical study to determine the effects on inclusive fitness, if any, that each of the different consequences has.

The fact that song is learnt also has many consequences. For example, neighbouring birds tend to share songs with each other, songs tend to differ between different places, the songs present in one area tend to change with time. In this article I shall explore these and other consequences of song learning in an attempt to discriminate between those which are simply byproducts of the learning process and those which are of functional significance.

This article is split into three main sections. The first provides a brief outline of the phenomenon of song learning and describes some of its characteristics. In the second will be described the consequences that these processes have for the songs of individuals and of the groups to which they belong. Finally, I shall discuss which of these consequences may have functional significance and so may help us to understand the advantages that song learning has for the individuals that show it.

CHARACTERISTICS OF SONG LEARNING

Basic features

Many experiments have now been carried out in which young birds have been reared in strictly controlled auditory environments. At its most extreme, these experiments consist of taking eggs or chicks from the nest and rearing them in isolation so that the young birds are denied the opportunity to hear others. In such circumstances the song often has certain characteristics in common with that of wild birds of the same species but lacks fine details. For example, in the chaffinch (*Fringilla coelebs*) the song of hand-reared birds is similar in length and in frequency spectrum

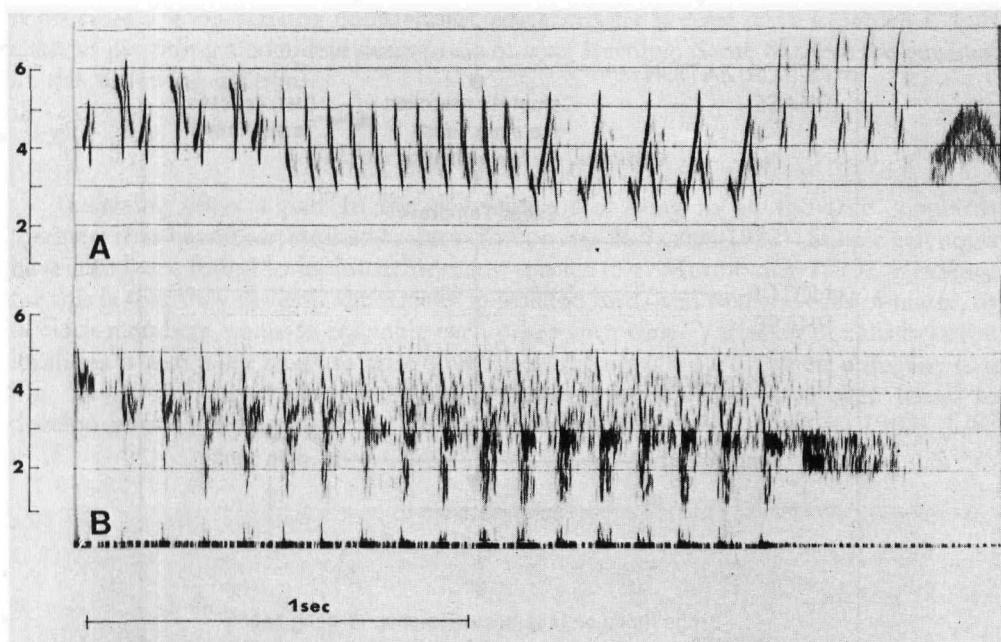


Fig. 1. — Sonogram to illustrate (A) a typical wild chaffinch song and (B) the song of a chaffinch reared in isolation. The frequency scale is in kHz.

to normal, and also consists of a succession of discrete syllables. However, these syllables are simple, they tend to drift in form from one to the next during the song, and the song often peters out at the end (Fig. 1B). By contrast, the songs of wild birds consist of a series of clear phrases within which successive syllables are highly structured and near identical, followed by a more or less elaborate end phrase (Fig. 1A).

Many other studies give similar results. For example, MARLER and PETERS (see MARLER 1987) have found that the songs of song sparrows (*Melospiza melodia*) and swamp sparrows (*M. georgiana*) reared in isolation are simpler than normal but retain certain species-specific characteristics. The song of the swamp sparrow consists of a single series of identical syllables. In isolates there is still a single series but the syllables are simpler. In the song sparrow, by contrast, there is a succession of phrases each with a different syllable type. This is true both of wild birds and of isolates, but the syllable types tend to be simpler in the isolates.

More extreme than isolation is deafening. This has been carried out on young birds either very early in life, before they have had an opportunity to hear others singing, or after the stage when they would have memorized the song of others. In the latter case they are denied the chance to hear their own efforts at singing. Both treatments have drastic effects on song. In some cases rudimentary features of species specificity may be retained, but the structure of the song is drastically modified so that it is little more than a «screech» (MARLER & SHERMAN 1983).

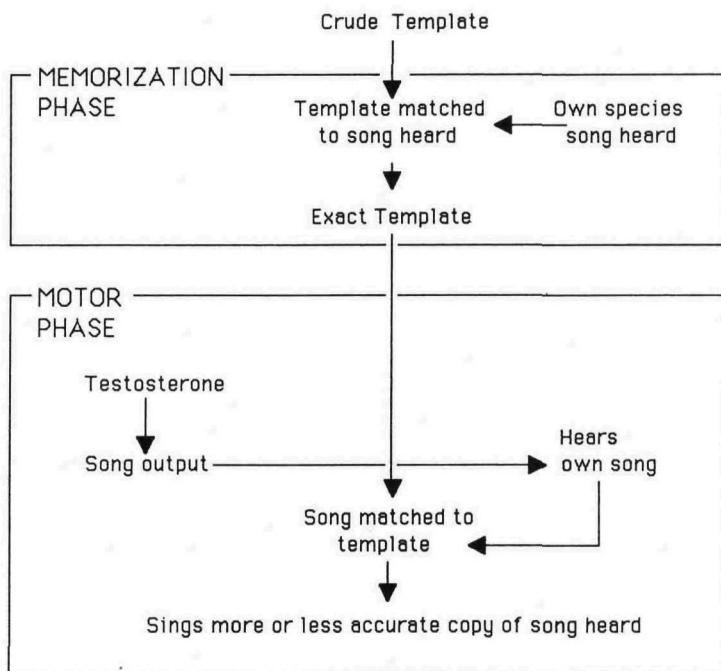


Fig. 2. — The auditory template model of song development. This proposes that the young bird hatches with a «crude template» which predisposes it to memorize the song of its own species. As a result, it forms an «exact template» to which it matches its own output when it starts to sing, so producing a song which is very similar to that which it memorized. Although the memorization and motor phases are shown as separate, in many species they may overlap in time (after SLATER 1983).

Results such as these led MARLER (e.g. 1976) to propose the «auditory template» model of song development (Fig. 2). This proposes that young birds when they hatch are endowed with a crude template which limits the sounds that they may copy. This may be more or less restricting. In many cases only the songs of conspecifics are sufficiently matched to this template to be copied so that inappropriate models are rejected. However, in other cases, of which mimics such as starlings (*Sturnus vulgaris*), mockingbirds (*Mimus polyglottos*) and lyrebirds (*Menura* spp.) are examples, selectivity is less marked and other species may be copied. In the chaffinch, a species which normally only sings songs typical of its own species, THORPE (1958) was able to train young birds to sing tree pipit (*Anthus trivialis*) songs, and argued that this was because the song of this species has several features in common with that of the chaffinch.

The auditory template model proposes that, as a result of hearing songs which match it, the crude template is sharpened up to become an exact template: a neural representation of the fine details of song. When the bird starts to sing itself it is able, by auditory feedback, to match its output to this template and so, through practice, to achieve a song closely similar to that which it has memorized.

Many of the basic features of song learning are incorporated in this model so that

it provides a good starting point. However, there are several ways in which it falls short of providing a complete description of song learning. Some of these are outlined in the following sections.

How widespread is learning?

Learning plays a part in the development of song in all the true songbirds (oscines) that have been studied to date (KROODSMA & BAYLIS 1982). Simple call notes have also been found to be learnt in many species (e.g. MUNDINGER 1979). Evidence for this is that they develop abnormally in isolated birds and that the calls of mates, or of flock members, come to resemble each other with time. Variation of calls between localities is also more likely to arise where learning plays a part in their ontogeny (see Fig. 3). On the other hand, some call notes in non-passerines have been found to develop normally even in birds that have been deafened (e.g. KONISHI 1963). Like

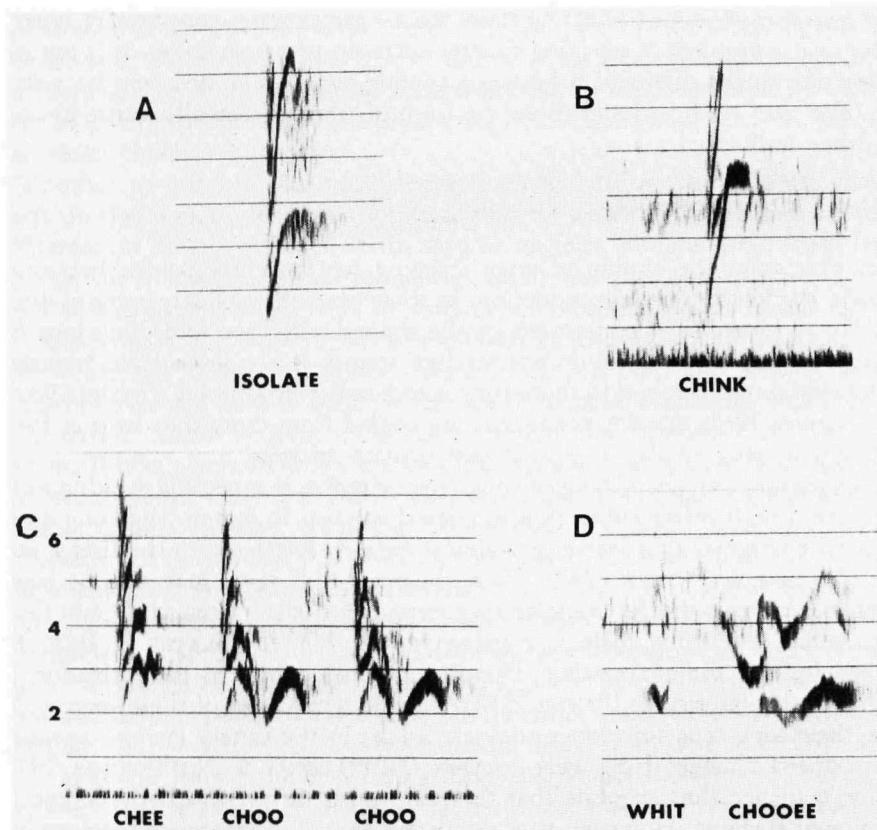


Fig. 3. — Learnt variations in call notes, illustrated by the «chink» call of chaffinches. In Britain and Europe this consists of a single call, often produced in a series (B). Its form is similar in birds reared in isolation, but lacks the pure tonal finish (A). In the Canary Islands race of the same species (*F. c. tintillon*) it is distinctively different (C), and the equivalent call of the blue chaffinch (*F. teydea*), also on the Canary Islands, is again distinct (D) (SLATER unpublished).

oscines, sub-oscine passerines also sing, but here the evidence suggests that learning may not play a role in song development. KROODSMA (1984) reared young willow and alder flycatchers (*Empidonax alnorum* and *E. traillii*) so that they could only hear the song of the other species. Despite this, the songs they produced were those typical of their own species. Some caution is required in interpreting this, however, as the young birds were not taken from the nest until 7-10 days old and, unlike oscines, they started to produce recognisable song at 15-19 days of age. Although no oscine has been demonstrated to learn in the nest, these birds are atypical in singing so early and one cannot therefore discount the possibility that learning takes place earlier as well.

In discussing the generality of learning one must also consider exactly what it is that is learnt. Field data on swamp sparrows suggest that all the song elements that they produce belong to a few basic structures (MARLER & PICKERT 1984). Furthermore, laboratory reared birds sing many more of these elements in sub-song than they do when their full song is finally developed (MARLER & PETERS 1982b). These results have led MARLER & PICKERT (1984) to suggest that all individuals of this species possess all elements and the process of learning does not consist of memorizing those that are to be used, but of selecting these from a pre-existing, much larger repertoire. This hints at a problem of deciding exactly what «learning» involves. It is not easy to see how one might distinguish between sounds selected in this way because they match ones that are heard and those the form of which is actually learnt by copying from other individuals.

Timing

In discussing the timing of song learning we must distinguish between two processes: memorization and production. In some cases these clearly occur at different times. For example, swamp sparrows can be trained with tape recordings long before they start to sing themselves, do not produce sounds in the intervening months and then develop songs matched to those they heard earlier (MARLER & PETERS 1982a). In other instances birds develop songs that are copied from those they hear at the time they begin to sing so the two processes overlap in time.

This diversity in the timing of song memorization is especially striking as it can be illustrated with reference to closely related species. In swamp and song sparrows the evidence suggests that learning is almost entirely restricted to the first 2 months of life (MARLER & PETERS 1982a). Song heard at this stage may also be learnt in chaffinches, but this species may also sing songs heard much later, at 10 months or so of age, when the young male is starting to sing himself (SLATER & INCE 1982). Evidence for the indigo bunting (*Passerina cinerea*) points to memorization being primarily at this later stage (PAYNE 1981). Finally, while most of these species do not change their song repertoire once they are adult, in the canary (*Serinus canaria*) the song produced changes from year to year (NOTTEBOHM & NOTTEBOHM 1978).

The evidence thus suggests that there are great differences between species in the timing of learning. However, it is not always easy to differentiate between its two components. In the canary, for example, while the song changes from year to year in adults, it is not yet certain whether birds memorize new syllables each year or whether they copy many syllables early in life and later call upon a different selection of these to incorporate into the songs they produce each year (see also BAPTISTA & MORTON 1988).

Tutor choice

Within the sensitive phase for song memorization, do young birds exercise any choice in the individuals that they learn from? Many early experiments relied on training birds with tape-recorded songs. While it was possible to provide a standard stimulus in this way it has recently become apparent that some species will not learn from recordings and that, even in those that do, the timing and other characteristics of the learning process may be abnormal. This calls for some reappraisal of these earlier results.

The zebra finch (*Taeniopygia guttata*) is one example of a species where social interaction between the young bird and its tutor is important. Young birds normally become independent of their parents at around 35 days of age and, in the laboratory, the songs of males with which they are housed in the following 5 weeks or so are learnt. If they are exposed to adequate tutoring at this stage they will not produce elements from the father's song which they had heard earlier. However, the parents do have some influence: young birds prefer to learn from a tutor whose song is similar to that of their father (CLAYTON 1987) and, if presented with tutors of different colour morphs, they will also tend to learn from that to which their parents belonged (SLATER et al. in preparation). Thus experience before independence from the parents biases tutor choice afterwards.

Whether or not a young male zebra finch will learn from a particular tutor depends on the amount of interaction it is allowed with that tutor and the form of that interaction (EALES 1989). As with tape recordings, birds will not learn from an adult male which they can hear through an audio link but with which they cannot interact. In this situation they tend to produce song elements heard earlier from their father. Learning is improved if they are allowed to interact vocally but not visually with the tutor, but some of the father's elements are still produced. Only if the young male can both see and hear an adult, in its own or in an adjacent cage, will it copy the song in detail. There is some evidence also that the behaviour of the adult is important. While, above a certain low baseline, song output has not been found to be an important factor, CLAYTON (1987) discovered that young birds given a choice of two tutors tended to learn from that which was most aggressive to them.

These zebra finch results (reviewed more fully by SLATER et al. 1988) illustrate just how complex the effects of experience on song learning can be. As usual, comparison with other species shows that there is also a diversity of patterns. In the swamp sparrow, a species which will learn from tape recordings, MARLER (1987) has found no difference in the timing of learning between birds presented with songs in this way and those exposed to live tutors. On the other hand, white-crowned sparrows (*Zonotrichia leucophrys*), which will not normally learn from tape-recordings after 50 days of age, will learn from live tutors after this stage (BAPTISTA & PETRINOVICH 1986), even to the extent of over-riding songs memorized from recordings heard earlier (PETRINOVICH & BAPTISTA 1987). Social interaction also leads them to learn a wider diversity of sound. While the evidence suggests that they will only learn their own species song from tape-recordings (MARLER 1970), they have been found to learn from some other species with which they are housed (BAPTISTA & PETRINOVICH 1986).

A particularly remarkable case of the influence of interaction on song learning comes from the work of KING & WEST (1983) on brown-headed cowbirds (*Molothrus*

ater), a North American brood parasite. In this species males have been found to develop songs matched to those typical of the sub-species of females with which they are housed. The females do not sing but the males explore a wide variety of sounds during subsong and the females provide reinforcement for those that they prefer by a particular display (WEST & KING 1988).

Accuracy

Accuracy is a final general feature of song copying that deserves discussion but, once again, it is a respect in which species differ to a great extent. Given enough experience of one particular song, in laboratory situations birds will often copy it precisely. However, this does not necessarily mean that precise copies of the songs of single other individuals are made in the wild. Here the young bird may be surrounded by a variety of singing males, with different song types and vocal output. In building up his own song repertoire he may copy one male, or blend the characteristics of several, or improvise to produce variations on the themes he has heard.

The word accuracy can be viewed at several different levels:

(i) An individual might learn its complete song repertoire by accurately copying the songs of a single other individual, or of all the birds in its neighbourhood where all of them sing the same phrase or phrases. Sharing of whole repertoires between neighbouring individuals is most common where repertoires are very small: one song type (white-crowned sparrow, BAPTISTA 1975; redwing, *Turdus iliacus*, BJORKE & BJORKE 1981) or two song types (corn bunting, *Emberiza calandra*, MCGREGOR 1980). However, there are cases where all males in an area share a larger repertoire, as in the village indigobirds (*Vidua chalybeata*) studied by PAYNE (1985).

(ii) Each song might be copied accurately but from a variety of individuals so that the young bird's repertoire differed from that of any one adult that it had heard. This appears to be the case in chaffinches where combinations of song types do not co-occur in the same repertoire more than expected by chance, although individual types are usually copied accurately (SLATER et al. 1980).

(iii) Elements or syllables used to build up songs might be copied accurately but recombined to give songs made up of novel sequences. KROODSMA (1981) gives a good example of this in the wren (*Troglodytes troglodytes*). Another example is shown in Fig. 4, which illustrates changes that can occur through dropping or adding elements, as well as those likely to have arisen through the processes covered in the next point.

(iv) Copying at the level of the element or syllable might be inaccurate so that, while based on sounds that had been heard, the exact relationship was more or less difficult to determine. This is not easy to identify in the field as unrecognised features of song may have been copied outside the area familiar to the observer. The best example comes from work on a small isolated population of saddlebacks (*Philesturnus carunculatus*) by JENKINS (1978), where novel song types were found to arise by inaccuracies of this sort. In laboratory experiments it is easier to control the auditory environment and so identify sounds which cannot have been accurately copied from other individuals: under these circumstances sounds that are produced may be clearly based upon those of tutors but not show a detailed resemblance to them, as in some of our zebra finch song learning studies (SLATER et al. 1988).

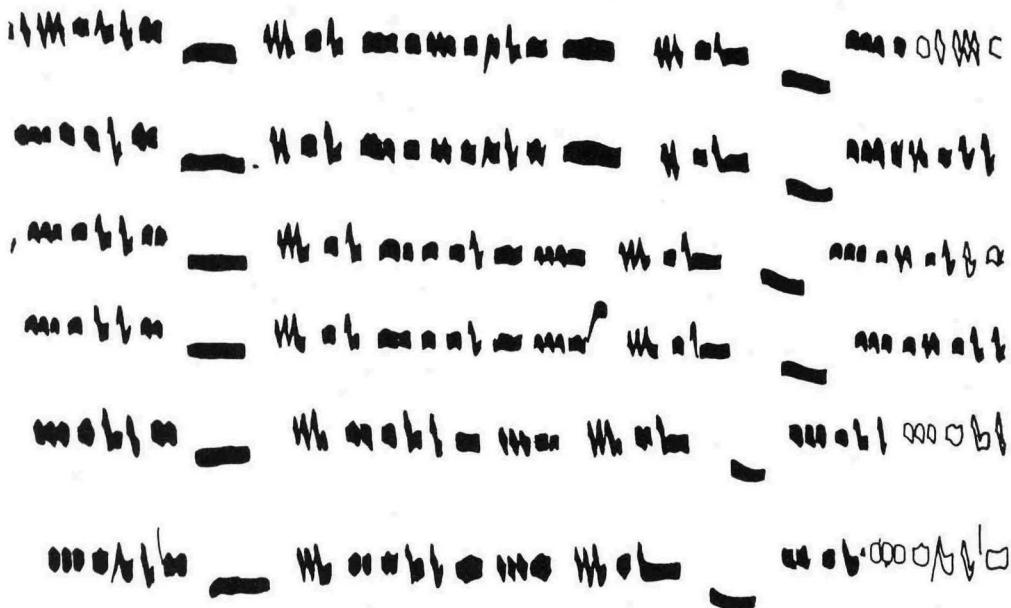


Fig. 4. — A section of the song of six individual grey warblers (*Gerygone igata*) recorded at Riverhead Forest, north of Auckland, New Zealand (30th August 1987). The sequence of elements in the song is repeated and the elements shown in white are repeats of those at the beginning. The section of song shown for each bird is approximately 3.7 sec long. All birds were within 1 km of each other and were recorded along a path in the wood in the sequence shown. While all individuals have features in common, the exact form of song differs between them, and especially between those further apart. In this case the differences are largely attributable to elements being dropped or added in particular positions in the sequence, or to the form of an element in the same position differing between birds (SLATER & JENKINS unpublished).

Factors influencing accuracy of copying have not yet been subjected to detailed study. There are undoubtedly species differences and the timing of exposure may also have an effect. For example, sounds may be copied more accurately when the animal is at its most sensitive. The number of repetitions of a sound that the young bird hears would also be expected to have an influence but the evidence suggest that, beyond a basic minimum, this is not critical. Zebra finches, for example, given a choice of two song tutors often do not learn from the one with the highest output (BOHNER 1983, CLAYTON 1987). There are also documented cases of young birds accurately learning songs they have heard very few times. THIELCKE-POLTZ & THIELCKE (1960) found that blackbirds (*Turdus merula*) copied some phrases heard 50 or fewer times, while others heard much more often were not copied. PETRINOVICH (1985) found that some white-crowned sparrows would learn songs heard as few as 120 times, while other birds did not learn phrases heard twice as often as this. Some of the birds played a particular song as little as this clearly based their own song on it but did not produce an accurate copy.

CONSEQUENCES OF SONG LEARNING

Having outlined some general characteristics of the song learning process, and given an indication of its variability, we can now consider some of the consequences that song learning has.

Kin sharing

An interesting possibility, stemming from the fact that the memorization of song in many species takes place very early in life, is that males might learn from their fathers so that song patterns might be shared amongst close kin. Song might then act as a cue in kin recognition, females choosing mates whose songs diverged from those of their fathers so as to achieve an optimal degree of outbreeding, and males perhaps cooperating more with individuals having similar songs to themselves. The latter idea was put forward by TREISMAN (1978, 1980) very much on theoretical grounds, but criticised by TRAINER (1980) because the behaviour of those species that have been studied is poorly matched to its predictions. It might nevertheless be true in some species that variations in song act as a kinship marker.

Despite these theoretical possibilities, there is little evidence in favour of young males learning from their fathers. Original laboratory results by NICOLAI (1959) on bullfinches (*Pyrrhula pyrrhula*) and of IMMELMANN (1969) on zebra finches suggested that such learning did occur, but may have resulted from the young males being left with their fathers for longer than would be normal in nature. In zebra finches, for example, IMMELMANN found perfect copying when males were separated from their fathers at 80 days of age, while independence usually occurs at about 35 days in the wild. Young males moved from their parents at that age learn from adult males with which they interact subsequently (EALES 1985), although experience before independence may bias them towards learning song like those of their fathers (BOHNER 1983, CLAYTON 1987).

Detailed field studies on indigo buntings (PAYNE et al. 1987, 1988) and on great tits (*Parus major*, McGREGOR & KREBS 1982a) have failed to find evidence that males have songs like their fathers' ones. In view of this, the finding by McGREGOR & KREBS (1982b) that female great tits prefer to mate with males whose songs are slightly different from those of their fathers is of doubtful relevance to kinship.

Firm field evidence of males sharing songs with their fathers more than expected comes from three species of Darwin's finch (*Geospiza* spp.). In one case females have been found to mate with males having songs different from those of their fathers, suggesting that song may be used as a cue in mate choice so that outbreeding is achieved (GRANT 1984). However, in the other two species, studied by MILLINGTON & PRICE (1985), females were found to mate randomly with respect to song type. There is also evidence for kin sharing in the marsh tit (*Parus palustris*, ROST 1987). In this species both members of the pair sing and young birds share many of their song syllables with their parents. Captive studies suggest that the young learn song from their parents shortly after fledging: it is especially intriguing that this is the main time during the breeding cycle that the female sings.

As far as the response of males to song is concerned, playback experiments suggests that males react strongly to songs similar to their own: indeed McARTHUR

(1986) suggests that the response of song sparrows increases the more similar the playback song is to their own. This is the opposite of that would be expected if song provided a measure of kinship and males were less hostile to kin.

In general, therefore, there is only limited evidence that song diverges along kinship lines and is used in kin recognition. While this may be true of some Darwin's finches and of marsh tits, the evidence is against it being a widespread phenomenon.

Neighbour sharing

Neighbouring individuals often share song types, and this is obviously to be expected in cases where young birds learn songs at the time when they set up territories. It is also sometimes the case that birds which move territory in adulthood change their songs to fit in with those of their new neighbours, as in the village indigobird (PAYNE 1985), a species in which groups of up to 20 individuals may share all their songs. A further reason why neighbours may come to share is if young birds learn their songs before setting up their territories but then move only a short distance before settling. In this case neighbours may share because they have both learnt close by. That neighbour sharing can have advantages has been shown by PAYNE (1983, PAYNE et al. 1988), who found male indigo buntings that shared to have better mating, nesting and fledging success.

In other species neighbours have been found to share no more than chance would predict (e.g. chaffinch, SLATER & INCE 1982), or neighbours are reported often to have very different songs while slightly more distant birds sometimes have more in common (RICH 1981, BORROR 1987). Such cases probably result during development in cases where young males learn their songs before dispersal and then set up territories a short distance away. However this does not seem adequate to account for cases where neighbours usually have fewer songs in common than birds further away from each other (e.g. WOLFFGRAMM 1979, BRADLEY 1981). Such results are quite striking because the null hypothesis used in such studies often biasses in favour of finding neighbour sharing. This is because song varies geographically (see section on «Geographical variation») and for this reason alone neighbours, being closer together, are more likely to share than more distant individuals. To compensate for this it is best to compare sharing between birds on neighbouring territories and those with a single territory between them rather than developing a null hypothesis based on more distant individuals.

Where males have less in common with their neighbours than with more distant individuals it suggests that song is learnt before dispersal and that birds may selectively settle on territories where neighbours sing differently from themselves. The advantage this might give them is not yet clear although, if birds are most aggressive to songs they possess themselves, having songs different from neighbours may lead to less fighting. In keeping with the idea that it is advantageous for neighbours *not* to share in these species, GRANT (1984) found that males of the Darwin's finch she studied were more successful if their neighbours had a different song type.

The pattern of sharing amongst neighbours thus shows the full spectrum of possibilities, with some species tending the share, some to show random association and some not to share. Species are likewise liable to differ in the functional significance of sharing for the relationships between individual males.

Cultural evolution

As song learning is not always accurate an individual may produce a song which is different from any which has been sung previously. This may then be copied by other birds and spread through the population. On the other hand, some songs may fail to be copied and, as a result, die out. Thus we expect continual turnover in the songs present in an area. Its rate will depend on various factors, of which accuracy of copying is the most obvious. Another is how often copying takes place. If it is a once in a lifetime affair, birds learning songs when they are young and then using the same repertoire throughout life, turnover will depend on the rate of recruitment to the population and thus on mortality. If birds learn new songs each year it will tend to be more rapid. Although not directly related to accuracy of copying, changes in the songs present in an area will also depend on dispersal patterns: immigrant individuals may introduce new songs to an area that they have learnt elsewhere.

Changes such as these arise because song is culturally transmitted from one individual to another. Given that transmission errors occur, some such changes are inevitable. It does not necessarily mean that the changes have any advantage for the individuals that make them, as is often the case with other examples of cultural transmission. Innovations such as potato washing in Japanese monkeys (*Macaca fuscata*, MIYADI 1964) and milk-bottle top opening in tits (*Parus* spp., FISHER & HINDE 1949) spread rapidly through the populations that showed them because they benefited the individuals that copied them. By contrast, much of the change that takes place in song may be random, the new types being no better adapted than the old. In this section we will consider the characteristics of change with time, whether or not innovation is likely to be beneficial to the individuals showing it and whether or not changes spread through the population more rapidly than chance would predict.

(i) *Do changes take place with time?*

Several studies have now looked at changes in the songs shown within a population which take with time, though few have been able to follow a population from year to year in the detailed way that JENKINS (1978) achieved with saddlebacks. It is more usual for the songs present in a population to be sampled at two points some time apart and a comparison made between them. Some such studies have failed to find differences. For example, THIELCKE (1987) reported the same variants to be present in a population of short-toed treecreepers (*Certhia brachydactyla*) recorded in 1960 and 1983. He attributed this remarkable consistency to two possible influences: that young birds might copy several individuals and thereby achieve an «average» song, and that any tendency to drift in the adult song might be corrected if they emulated one another. Both these factors would certainly lead to greater conservatism.

In the chaffinch, CONRADS (1986) found some song types to persist over a period of 17 years. This confirmed the finding of INCE et al. (1980), who compared songs in the same population 18 years apart and found three identical types. However, this was only a small proportion of the types present (22 recorded in 1960, 35 in 1978), indicating a substantial turnover. They estimate that 15% of the songs sung by young birds are new to the area, either through inaccuracies in copying or immigration.

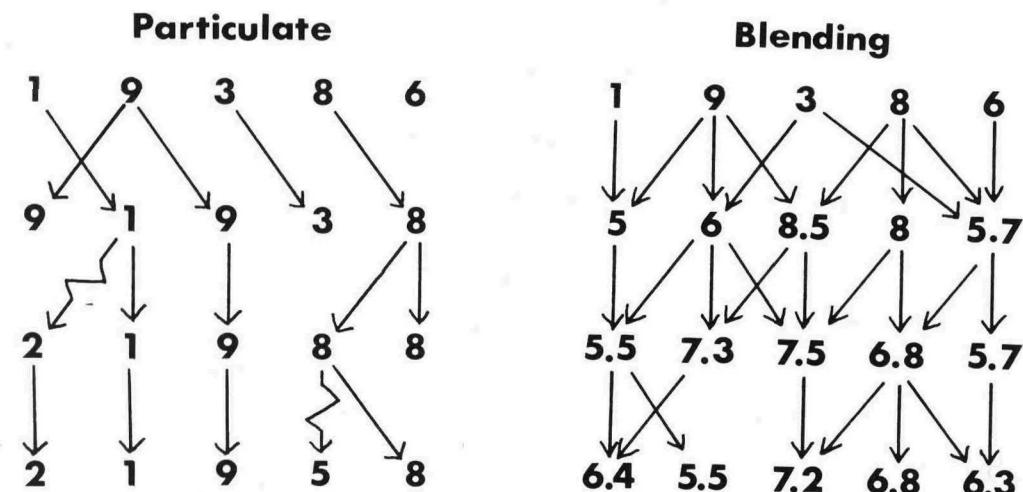


Fig. 5. — Schematic representation of two different forms of song copying. Each row represents a cultural generation, with different song types represented by numbers. In Particulate inheritance birds copy song from single individuals. Copying is usually accurate so that the same song type occurs in the next generation. However, some types are not copied and so become extinct (e.g. 6); other types are copied inaccurately (zigzag arrows) and so give rise to completely new types (2 and 5). In Blending inheritance birds base their song on those of more than one individual. This is symbolised by labelling the song of the young bird as the mean of those it has copied. This process leads to a reduction in variation within the population.

PAYNE et al. (1981) also found substantial turnover in indigo buntings over 10-15 years. They used the measure of exponential half-life to examine how long song types persisted and calculated this as 3.8 years. The equivalent figure for the chaffinch results of INCE et al. (1980) is 6.1 years.

Such studies, involving birds that do not appear to alter their songs in adulthood, involve a substantial degree of change with time. Likewise, in these species many different song types are found over short distances. The key difference from the short-toed treecreeper example may be that chaffinches and indigo buntings tend to learn an individual song type from single other individuals rather than blending the characteristics of several. We can call such transmission «particulate» by analogy with the inheritance of genes. It has the effect of maintaining variety within the population while «blending», of the sort THIELCKE suggests, would rapidly destroy variation (see Fig. 5).

More rapid cultural change still can take place in populations where individuals change their songs from year to year. Such a phenomenon has been described in such diverse organisms as the humpback whale (*Megaptera novaeangliae*, PAYNE & PAYNE 1985) and the village indigobird (PAYNE 1985). In both cases all individuals within a group sing very similar songs in any given year, but the group repertoire changes from year to year. Clearly, such wholesale change could only happen where song learning was not limited to young animals.

(ii) *Are innovations advantageous?*

In deciding whether selection favours innovation we must distinguish between the initial change, where a single individual develops a song distinct from any other, and the copying of that change by subsequent individuals.

As far as the initial change is concerned, there is little evidence to suggest that it incurs advantage to the individual making it. A great deal of song learning is accurate, enabling individuals to match their songs to those of others. It is not easy to see how it could be advantageous to a small proportion of individuals (less than 15%) in chaffinches to diverge, although it is perhaps possible that an argument could be made based on the idea of a balance between alternative strategies.

There are, however, several situations where innovation might be advantageous. First, as discussed above, in some species individuals share songs with neighbour less than expected by chance. This could involve individuals generating new song types that are different from those round about. However, it is more likely that birds learn before settling and choose to settle where the neighboring songs are different from those they already possess. In the group of Darwin's finches studied by GRANT & GRANT (1979) song types were found to alternate in a sequence of territories. These neighbour differences are not therefore due to innovation by individual males once they have settled.

A second possible advantage of innovation is where the song so produced is more attractive to females because it stands out from others. This would be in line with the idea that mate choice involves selecting an individual that is slightly different from those experienced before (BATESON 1978). There is little evidence of this in song. Though female great tits prefer songs which are slightly different from those of their fathers (McGREGOR & KREBS 1982b), in several species familiar song has been found to be preferred (e.g. BAKER et al. 1987a, 1987b). On the other hand, in the laboratory, females of some species have been found to be more attracted to song repertoires (e.g. SEARCY & MARLER 1981, 1984; SEARCY et al. 1982; CATCHPOLE et al. 1984), and there is also some field evidence that males with larger repertoires are more attractive (CATCHPOLE 1980, YASUKAWA et al. 1980). Both innovation at the level of the song type, or by combining song types learnt from several individuals, may enable birds to build up larger repertoires.

A third way in which innovation may be advantageous is if it leads the song of that individual to match the environment better. If song is selected to suit the environment and the environment changes then the most advantageous form of song might also be expected to change. Changes of this sort would then be expected to spread through the population like other cultural changes which confer advantages, and such spread would be the best evidence for innovations of this sort.

(iii) *Do innovations spread?*

The particular songs present in an area can change with time simply because there is a high rate of mutation without novel ones that develop necessarily spreading through the population. SLATER et al. (1980) argue that this is an adequate explanation for the changes in chaffinch song they found and suggest that random innovation, copying and extinction are sufficient to account for their observation without any process of selection being involved. A similar argument is made for cultural

change in indigo bunting song by PAYNE et al. (1988). While song types may change, there is no overall shift with time in any particular characteristic of song.

A few studies do suggest the occurrence of such overall shifts in song characteristics with time. Some of the songs of chaffinches in New Zealand, where the species was introduced in the last century, differ from any so far recorded in Europe, having a shorter trill and longer more elaborate flourish. JENKINS & BAKER (1984) suggest that these features have arisen as an adaptation to the dense coniferous forests in which they were recorded. In members of the genus *Luscinia*, SORJONEN (1986a) reported that song varies with habitat (as has been suggested for many other species: see section on «Habitat matching»), and his subsequent studies suggest that features of song in a population of thrush nightingales (*L. luscinia*) have changed as trees in their habitat have grown (SORJONEN personal communication). Rapid trills and rattles, present at first, have disappeared as one would predict if sounds distorted by echoes were dropped as the habitat became denser.

Another example is provided by BERGMAN (1980) and LEHTONEN (1983) who report that the song of great tits in Finland, which consisted mainly of three syllable phrases before 1950, became simplified over the next 30 years so that most songs now consist of two syllables and some are even reduced to one. The reason for this change is not known, but LEHTONEN suggests that it is most marked in noisy areas and that the explanation may be related to this link.

There is thus only limited evidence that changes in song spread through the population more than processes of random copying and extinction would predict. In all the examples where it has been proposed that change in the population is advantageous the suggested reason is that the songs have thereby retained their adaptation to an environment which is itself changing.

Geographical variation

As well as showing changes through time, the characteristics of bird song frequently also show changes in space, although exceptions have been described (e.g. prothonotary warbler, *Protonotaria citrea*, BRYAN et al. 1987). While the changes observed can be marked, they are within species-specific limits, so that it is usually easy, even for an observer new to an area, to identify a bird by its song. As with song copying, geographical variation can take place at several different levels. Elements, syllables, song types or repertoires may differ from place to place, without there necessarily being a difference at a lower level in this series. For example, in both swamp sparrow (MARLER & PICKERT 1984) and indigo bunting (PAYNE et al. 1981) the repertoire of elements used to construct song appears to be universal, but they can be combined in many ways, so forming different song types in different areas.

Geographical variation is seldom the simple matter that the word «dialect» might imply. This word is often used rather loosely in discussion of song variation, to refer to any form of geographical difference. More strictly, it is used to refer to differences between areas where all the birds in one location share certain song characteristics which lead them to differ from all the individuals in another. This is a much rarer phenomenon. For example, in the chaffinch, a species which was amongst the first to which the word dialect was applied (MARLER 1952), dialects in this strong sense certainly do not exist (SLATER et al. 1984). The array of song types found in an area is quite distinct from that found in others, unless they are close to each other. However,

a wide variety of different song types occurs in each place, and no single feature can be used to separate one place from another. Certain features, while not shared by all individuals, may be common in one place and rare or absent in another. For example, chaffinches on continental Europe often produce a «kit» call after the flourish at the end of their song (THIELCKE 1969), while this has not been recorded in Britain. However, not all of them in a particular area do this, so it does not indicate a dialect in the strict sense, though it is certainly an example of geographical variation.

Dialect boundaries

The most striking examples of dialects are in those species where neighbours share complete repertoires. In this circumstance we would expect all the birds in one area to have features in common and, unless learning is 100% accurate, differences to exist between areas. We would expect to find gradual change with distance, especially if each individual bases its song on listening to several others.

Sharing of whole repertoires is most common where each individual has only one or two song types. In some cases which have been studied in detail a perplexing finding is that of sharp boundaries between dialect areas so that the distribution of song can be described as a patchwork of song neighbourhoods (e.g. BAPTISTA 1975, McGREGOR 1980, BJERKE & BJERKE 1981). One might expect such a mosaic to arise if each young male learns his complete repertoire from a single neighbour. Simulations by GOODFELLOW & SLATER (1986) suggest that this will lead to small groups of sharing males. However, such groups would be unlikely to rise to above 12 or so individuals unless song learning is very accurate and/or mortality is very low compared with known rates (Fig. 6). Nevertheless, this simple means of arriving at sharp dialect boundaries may account for their existence in some species with small song neighbourhoods.

Additional factors must be invoked where song is shared between many more individuals. This is true of the redwing (*Turdus iliacus*, BJERKE & BJERKE 1981), but in this species the existence of sharp boundaries has been questioned by ESPMARK (1982). McGREGOR (1980) describes sharp boundaries in the corn hunting, although in a more recent mapping of territories by McGREGOR et al. (1988) the distribution of song types shown suggests that geographical discontinuities may, at least in part, explain the mosaic pattern. If two populations are separated by a tract of unsuitable habitat over which individuals do not often disperse after learning song it is not surprising to find divergence in their songs. Such geographical barriers need not be greater in width than the distance over which song can be heard provided that juvenile dispersal occurs before song learning and adult males retain the same territory (or at least remain on the same side of the barrier) from year to year.

The most studied, and controversial, example of sharp dialect boundaries is that of the white-crowned sparrow (see BAKER & CUNNINGHAM 1985, with accompanying commentaries). The existence of discontinuities has been questioned even in this case (JENKINS 1989), with the proposal that they result simply as an artefact of choosing some aspects of song rather than others for analysis. However, if the results that have been presented are accepted, they represent large areas with many individuals sharing, sharp boundaries without geographical barriers and boundaries that remain in the same position for many years. These features could only arise if the boundary between areas was actively maintained and, even with this, it is hard to see why the boundary

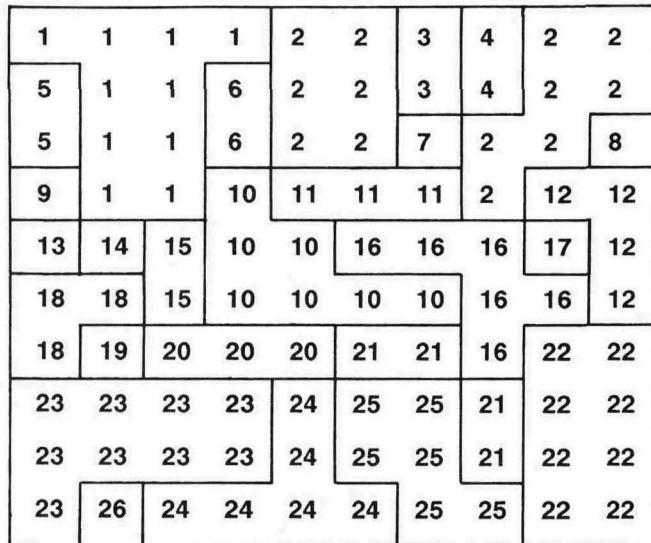


Fig. 6. — A map of «dialect areas» produced by a computer simulation in which each bird occupied a square territory and young birds moving into vacant territories copied song from one of their neighbours. In the example shown 25% of territories became vacant each year and newcomers copied inaccurately, so producing new song types, on 10.6% of occasions. As mortality in passerines is usually greater than this, as is the rate of miscopying in cases that have been studied, the example is likely to overestimate the amount of sharing. Despite this, the commonest song type (2) occurs in only 13 individuals (results of simulations described by GOODFELLOW & SLATER 1986).

would not show random shifts with time unless it was tied to some form of geographical discontinuity. We will return to the idea that dialect boundaries are actively maintained in some way in the section on «Genetic adaptation».

ADVANTAGES OF SONG LEARNING

Now that the various consequences of song learning have been described, we are in a position to consider its adaptive significance. This can be viewed in two different ways. One of these is to consider why song learning arose in the first place (see NOTTEBOHM 1972). The learning of sound has obviously evolved a number of times amongst the birds and, being widespread in the oscines, is likely to have arisen in this group early on in their evolution. Given this, as ANDREW (1985) has pointed out, the reason why it first evolved may be best sought by examining its role in call note development rather than in the more complicated, and recent, phenomenon of song development. The second approach is to examine the current advantages that song learning has for the species that show it to try to discover why it is maintained in the population. This will be our main concern here.

Copying advantages

A number of separate ideas can be put forward under this heading, although all of them are rather speculative and not easy to test. Nevertheless, the following are three possibilities:

(i) Learning allows more precise and accurate transmission. This suggestion contrasts with the more traditional ethological viewpoint that «innate» behaviour, as well as being fixed and inflexible, was also very precise and stereotyped in form. However, it is clear that song learning is proficient at achieving precise copying of highly complex patterns. An advantage of learning may be that it allows *more* precise and detailed copying than would be possible without it. Balanced against this possible advantage is that mistakes in copying are relatively frequent. On average learning may allow greater precision of copying, but the variance is high because the risk of miscopying is greater.

(ii) Learning allows more complexity and variety. Given the role played by learning in the transmission of very simple sounds, such as call notes, this idea would certainly not be a general one. However, some species have very large repertoires of complex sounds, and learning may be favoured as a means of achieving such complexity. The involvement of learning here would certainly be more economical if, as WILLIAMS (1966) argues, selection favours minimising the amount of genetic material.

(iii) Learning allows male-male transmission. In birds the female is the heterogametic sex and transmission of a character by genetic means from male to male without maternal influence is not therefore possible as each male has a «Z» chromosome from his mother as well as his father. In general female birds also disperse further than male birds (GREENWOOD 1980), so that if a male's song was influenced by his mother it would be likely to diverge from that typical of the neighbourhood. Learning from adult males allows young birds to achieve male-male transmission and so match their song to the form typical of the area (see sections on «Social adaptation» and «Habitat matching»).

Genetic adaptation

A more precise and testable suggestion was originally made by NOTTEBOHM (1969, 1972). This proposed that learning led to dialects which acted as population markers, enabling individuals to choose mates from the same population and therefore well matched to themselves. It is argued that adaptation to the local area may be preserved, and breakup of coadapted gene complexes avoided, if individuals from the same dialect area mate with one another. The particular hypothesis put forward here is that like should mate with like, females choosing males with songs typical of the dialect area in which they hatched. It should be noted, however, that song might also have a role in assortative mating in the opposite way, if females chose mates whose songs differed from those in their area of origin, thus achieving outbreeding.

The idea of genetic adaptation has been applied especially to species with sharp dialect boundaries, such as the white-crowned sparrow. However, the existence of such boundaries does not seem prerequisite for song to have a role in assortative mating, nor is it easy to see how the mechanism of mate choice proposed would lead to such boundaries being created. Continuous gradual change in song with distance would seem more likely.

What evidence has been put forward in support of the genetic adaptation idea? There are several lines, most of them deriving from work on white-crowned sparrow, and especially that by BAKER and his collaborators:

(i) Boundaries between dialect areas coincide with shifts in gene frequencies. There is some evidence of a correlation between gene frequency changes and dialect changes in white-crowned sparrows (BAKER et al. 1982) and rufous-collared sparrows (*Zonotrichia albicollis*, NOTTEBOHM & SELANDER 1972). However, this is hardly strong evidence for song limiting gene flow. If any form of barrier to dispersal exists then we would expect both song types and gene frequencies to vary across it.

(ii) Young birds do not usually disperse across dialect boundaries. Some evidence has been put forward that dialect boundaries act as barriers to the dispersal of young birds (e.g. BAKER & MEWALDT 1978), although this is a difficult idea to test and the results have been criticised (e.g. PETRINOVICH et al. 1981). A major difficulty is to generate a random model against which to compare the observed dispersal of young birds. For example, more birds might be expected to stay within the dialect area simply because dispersal distances are short and the bird's own dialect area is obviously closer to its point of origin than are other dialect areas. As KROODSMA et al. (1984) point out, what is needed are more studies of dispersal of birds which hatched close to dialect boundaries and which are therefore roughly equally likely at random to settle on either side.

(iii) Females choose mates which sing the same song as that of the area from which they themselves came. One way of testing this is to inject females with testosterone and ascertain whether the songs they produce are the same as those of their mates, or different so that they indicate that the female came from another area. Unfortunately, the white-crowned sparrow results are conflicting: studies by BAPTISTA & MORTON (1982, 1988) and PETRINOVICH & BAPTISTA (1984) found females often to sing different songs, while 24 out of 25 females studied by TOMBACK & BAKER (1984) used the same song as their mate. The former evidence is, however, more clinching: females using songs typical of a different area have clearly been elsewhere; those singing like their mates may have memorized their song types since pairing even if they did come from elsewhere.

(iv) Males learn song as juveniles and subsequently settle in the same area. The evidence of MARLER (1970) that male white-crowns learn well before setting up their territories, suggested that they must choose to settle within their own dialect area. However, the discovery that birds exposed to live tutors will learn much later (e.g. PETRINOVICH & BAPTISTA 1987), raises the possibility that young birds in nature may learn after settling. The strong similarity between neighbouring birds might thus arise simply because these birds learnt from each other, rather than because they chose to settle next to birds that sang similarly to themselves.

From the above discussion it will be apparent that the evidence so far put forward for the genetic adaptation model is not strong, even in the case of the white-crowned sparrow. Its applicability to the corn bunting, another species with clear dialect areas, has also recently been questioned by McGREGOR et al. (1988). Male corn buntings show no tendency to sing songs of the same dialect as their fathers' ones, and females have mates which tend to sing different dialects from those their father sang. However, it is possible that it applies in other cases which have not yet been studied in sufficient detail. In marsh tits, a species in which both sexes sing, ROST (1987) has

found young birds to learn song from their parents and to mate with individuals that sing very similarly to themselves. There is so far no evidence for sharp dialect boundaries in this species (or for dialects in the strict sense defined above — section on «Cultural evolution» — although there is clear geographical variation), and the similarity of song between mates may simply be a consequence of limited dispersal. Nevertheless, in cases where young birds learn song from their parents, the possibility that it has a role in assortative mating remains an intriguing one.

Social adaptation

The idea that song learning is involved in social adaptation applies particularly in those cases where song is learnt from territorial neighbours and is used in interactions between males. It is related to the argument put forward above (section on «Copying advantages») that learning may enable males to match their songs to those of other males. However, the matter is not a simple one. Only if songs vary from place to place will males gain by learning those of their neighbours when they settle. If songs do not vary males will be able to match anyway. As song learning is thought to be a prime reason why songs come to vary from place to place (LEMON 1975), the argument can easily become a circular one.

Nevertheless, the existence of some degree of spatial variation (whether or not due to learning), perhaps accentuated by individuals having differing repertoires, is likely to lead males that have dispersed some distance from their site of hatching to encounter songs that differ from those they experienced before. If there is an advantage to males in singing songs like those of their neighbours, then those which modify their song through learning after settling will gain. Several lines of evidence, primarily from PAYNE's studies of indigobirds and indigo buntings, are in favour of this idea:

- (i) Males of a number of species have been found to copy the songs of their territorial neighbours when they settle (e.g. JENKINS 1978, PAYNE 1981).
- (ii) Males that move in adulthood may alter their songs to match those of their new neighbours (PAYNE 1985).
- (iii) Groups of males may change their songs from year to year so that they remain matched (PAYNE 1985).
- (iv) In many species, males on neighbouring territories show matched countersinging where individuals have repertoires, a particular song type produced by one being matched by the same type sung in reply (e.g. LEMON 1968, SCHROEDER & WILEY 1983, FALLS 1985).

Despite these points, there are some species that do not match the songs of neighbours (FALLS & KREBS 1975, McGREGOR 1986), or which tend to switch song types when matched by other individuals (HANSEN 1981). The advantage of matching is also open to question. PAYNE (1981) and SLATER (1981) suggested that young males may gain by having songs similar to those used by the previous occupant of their territory: PAYNE & GROSCHUPF (1984) found that male indigobirds removed from their territories were replaced by individuals with matching songs, thus providing evidence for this idea. However, McGREGOR & KREBS (1984a) argue against it applying to great tits, finding that young males do not share more songs than expected with the previous occupant of their territory, nor do they use those that they share

more than expected. PAYNE (1983) tested various hypotheses in indigo buntings and concluded that young males which share songs with older neighbours may gain as they confuse other individuals as to their identity (see also PAYNE 1978). Young birds are thus treated as if pre-established adults. As mentioned earlier (section on «Neighbour sharing»), he also found that males sharing songs with neighbours in this species show greater reproductive success.

There is thus some support for the idea that song learning has a role in enabling neighbouring males to match each other's songs, at least in those species where neighbours share song types and young birds learn when they settle. Several studies have suggested that there is more to the interaction between, neighbouring males than just matching (e.g. KROODSMA 1979, HANSEN 1981, FICKEN et al. 1985). Further study of the role of song in their relationships would certainly be rewarding and is likely to shed light on the role of learning from neighbours and the song matching to which it gives rise.

Habitat matching

Evidence has been accumulating over the past 15 years or so that characteristics of bird song can be influenced by the habitat. Comparisons between species show that those occupying dense forest tend not to use rapid trills, which would be distorted by echoes off the trees, while those in open country do use trills but do not often use pure tones, as these are distorted by wind and temperature gradients (MORTON 1975; WILEY & RICHARDS 1978; SORJONEN 1986a, 1986b). High frequency sounds are particularly subject to distortion through echoes and, in keeping with this, the songs and calls of birds in forests tend to be of lower frequency than those in open areas (CHAPPUIS 1971). The study by MORTON (1975) in central America showed that sounds in the range 1600-2500 kHz (the so called «sound window») attenuated less than expected in transmission through forest, and this is indeed the frequency range within which most forest dwelling bird calls have their main energy peak. The sound window appears to stem from the scattering of high frequency sounds in the atmosphere and foliage and from absorption of low frequencies by the ground. This «ground effect» is itself dependent on habitat: COSENS & FALLS (1984) found it in grassland, but not in marsh. The grassland species they studied also sang with higher frequencies than those from marshy habitats as would be expected if song was selected to minimise attenuation.

These comparisons between species, and studies of the transmission characteristics of different environments, suggest that the structure of song in many species is well matched to the features necessary to minimise attenuation and distortion. There is evidence also that variation within a species, where it occurs in different habitats, may be explained in the same way. Thus, HUNTER & KREBS (1979), in a study covering a wide geographical area, found great tit songs in dense coniferous forests to show less rapid trills than those in more open woodland. NOTTEBOHM (1975) found the song of the rufous-collared sparrow to vary with latitude, altitude and vegetation. At a finer geographic level ANDERSON & CONNER (1985) found differences in the syllables used by cardinals (*Richmondena cardinalis*) in three conifer stands of different foliage characteristics only 4.5 km apart, with some features apparently related to the habitat. For example, rapid frequency modulation was only common in the most open of the three areas. WASSERMANN (1979) found white-throated sparrows to sing more

high frequency songs in field environments than in forest ones as one would expect from the distortion of high frequencies through reverberation and scattering in forest.

There is thus evidence that characteristics of song vary with habitat, both between and within species, in ways that are adaptive. Findings reviewed earlier suggest that the songs present in a population may change as the habitat changes, implying that such changes may occur through the process of cultural transmission from one individual to another. The role of learning in matching song to habitat was more formally proposed by HANSEN (1979). He suggested that, if young birds learn their songs at a distance from the adults they are copying, they will be most prone to memorize the sounds that carry with least attenuation and distortion through the particular habitat in which learning takes place. Thus, with successive cultural generations, song would come to acquire the best characteristics for that environment. An advantage of song learning may thus be to match the song to habitat in the ways that have been described above. The findings of GISH & MORTON (1981) are in line with HANSEN's hypothesis: Carolina wren (*Thyothorus ludovicianus*) songs played back in their habitat of origin showed less degradation over distance than did those from other habitats.

A recent idea put forward by MORTON (e.g. 1986) combines the ideas of habitat matching and social adaptation: this is his so-called «ranging» hypothesis. He proposes that birds use degradation through the habitat to assess the distance away of a singer. That birds are sensitive to degradation has now been amply demonstrated by experiments showing that they respond more to playback of undegraded than of degraded song even when they are matched for amplitude (e.g. RICHARDS 1981, McGREGOR & FALLS 1984, McGREGOR & KREBS 1984b). MORTON goes on from this to argue that birds benefit from producing sounds which degrade little in the environment in which they are singing because these will sound closer than they really are and will thus be more disruptive and threatening to neighbours.

MORTON takes this idea one stage further. He proposes that distance assessment (ranging) may depend on the individual having a song type in its own repertoire so that it compare the distorted version it hears with its own internal representation of the song. He therefore suggests that song learning from neighbours, leading them to share song types, may be a required feature of his hypothesis. However, it seems unnecessary to put forward this additional point as birds may well memorize songs that they do not use themselves (see McGREGOR & AVERY 1986, CLAYTON 1988). Furthermore, experimental results on great tits suggest that their response to degraded song does not depend on whether the type concerned is in their own repertoire provided that it is familiar to them (McGREGOR et al. 1983, McGREGOR & KREBS 1984b).

Even if the ranging hypothesis is wrong in detail, the idea on which it is based, that song learning enables the features of song to be well matched to the habitat so that it carries with minimal attenuation and distortion, is an attractive one which deserves further study.

CONCLUSION

Song learning in birds shows a diversity of patterns and a variety of consequences. In considering its functional significance we must bear in mind the fact that selection acts on individuals and it is the advantage to them of behaving in one way

rather than another that must be sought. Viewed at this level some of the consequences of song learning are epiphenomena: cultural evolution, geographical variation, dialect boundaries. The important question is to discover which are the consequences through which natural selection acts. Several possibilities have been highlighted here. Advantages stemming from the copying process itself, advantages in interactions with neighbours and advantages in the matching of song to habitat, may all be important reasons for learning having a role in song development. There is less evidence for the notion that learnt dialects may have significance in assortative mating. However, there is no reason why song learning should not confer several different benefits, both on the same species and in different species. Indeed, given the wealth of patterns of singing behaviour amongst the passerines, it would be surprising if it did not.

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