



Bird Songs and Mate Selection

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ALTHOUGH BIRD SONGS have been the subject of much attention, particularly in recent years, there is hardly any *direct* information about how they actually function. In this respect bird studies are less advanced than, for example, those on Orthoptera (e.g. Perdeck 1957, Walker 1957), and there is no doubt that the greatest single need in studies of avian communication is for experiment in this field and in particular, on the value of songs as reproductive isolating mechanisms. This subject must therefore be discussed at present in terms of indirect evidence, not all of which is as clear as is sometimes assumed.

Ornithologists are often impressed by the distinctiveness of the songs of species which live together. Often song is more useful for field identification than the morphology, and at least once has provided the first clue to the separation of new species (White, 1879) (Fig. 1). This fact of specific distinctiveness in songs seems to carry the implication that they serve as reproductive isolating mechanisms, either in establishing or perpetuating a bond between breeding birds, thus being subject to a selective pressure encouraging specific distinctiveness. Leaving aside for the moment the question whether specific distinctiveness of songs in sympatric species is in fact universal, we can make certain deductions about some of the characteristics which bird songs should have, when functioning in this way.

ACKNOWLEDGMENTS

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² Recordings illustrating this chapter are on Side II, Band 3 of the Demonstration Record.

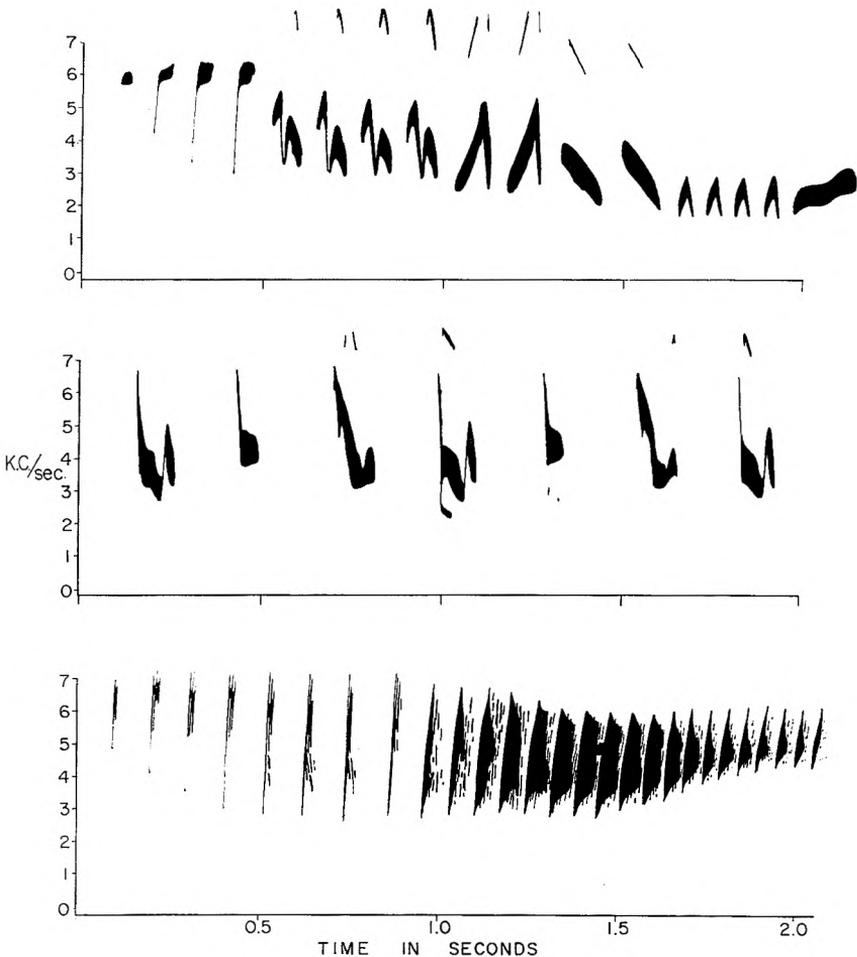


FIG. 1. The songs of three European *Phylloscopus* warblers, used by Gilbert White as the first evidence that they are distinct species. The two upper birds, the willow warbler (*Phylloscopus trochilus*—top, May 1957) and the chiffchaff (*P. collybita*, May 1957) are particularly similar morphologically but have quite different songs. The first has a short regular song, repeated at intervals, while the second rambles on continuously, improvising on two basic notes. The lower record is a wood warbler song (*P. sibilatrix*, May 1954).

REPRODUCTIVE ISOLATION AND SPECIFIC DISTINCTIVENESS

We should not forget, as Ernst Mayr has often reminded us (1942), that there is a wide variety of methods of achieving reproductive isolation. In any one species several factors of varying importance may

contribute and this must be as true of birds as of other animals. So the following discussion is based on the hypothesis, that *the structural characteristics of loud and conspicuous song play a dominant role in reproductive isolation of the species*, leaving aside for the moment the effects of such factors as *when* or *where* the song is given, and ignoring other functions of the song, such as defense of the territory.

This hypothesis implies that the kind of *sound environment* within which a bird lives, exerts a selective pressure on its song, encouraging the development of a type which is conspicuously different from the sounds making up the background against which it must be used. This in turn has important implications for the study of geographical song variation.

GEOGRAPHICAL VARIATION OF SONG

Although the geographical variation of bird songs has often been noted (Benson, 1948; Marler, 1952; Saunders, 1935) no explanation is usually advanced to suggest why variation takes a particular form in a given case. However many species live with different companions in different parts of their range, and from our hypothesis their songs would be expected to vary. If we know sufficient of the various *sound environments* it should even be possible to predict in detail the direction in which the song is likely to vary. The task of describing all the sounds in a given area during the course of a year is huge, though not insuperable. It has not yet been attempted in a normal mainland environment, but a start has been made in the simpler situation presented by small islands.

Lack and Southern (1949) drew attention to the interesting differences in songs of the same or closely related species between Britain and the Canary Islands, in the Atlantic off the coast of North Africa. Small island avifaunas are always poorer in species than those on the adjacent mainland, and the *sound environment* will therefore be simpler. Selection pressure on the songs of resident birds should be relaxed, compared with mainland, as the observations of Lack and Southern did indeed seem to imply. The single *Parus* species for example, as compared with six in Britain, has a very variable song, which seems to encompass many of the sounds made by the British species. In the Azores the goldcrest, *Regulus regulus*, also has much more varied calls than the British bird (Marler and Boatman, 1951).

BIRD SONGS IN THE CANARY ISLANDS

In 1956 the writer was able to visit the Canary Islands with a tape recorder, making possible a more detailed comparison of songs with the

mainland. The situation proved to be more complex than had been expected. Some songs showed no significant change, some were simpler, and others were more variable, but none were more complex, in the sense of being more elaborate while still remaining reasonably stereotyped.

For example, the songs of the turtle dove, *Streptopelia turtur*, the great spotted woodpecker *Dryobates major*, the corn bunting *Emberiza calandra*, the blackcap, *Sylvia atricapilla*, and the blackbird, *Turdus merula*, do not seem to differ consistently from those of their close relatives in Britain, on the basis of the small samples examined. (Fig. 2.) Why some species should be unaffected by island conditions is not clear. Of the above, all but the turtle dove have sub-specific status, and presumably have been living on Tenerife long enough for changes in song to occur. It may be that we have to postulate an *inertia* in the mechanisms controlling song form in some species. Alternatively, the function of song may differ in species which show island variation and in those which do not.

Two species of chaffinch live on Tenerife, the endemic blue chaffinch, *Fringilla teydea* and *Fringilla coelebs tintillon*, a subspecies of the mainland form. Recordings were only obtained of blue chaffinch song, but Lack and Southern suggest that *tintillon* song is similar. The comparison with the British chaffinch shows a simpler song on the islands, which has a closer resemblance to the innate song of isolated chaffinches than to the more elaborate normal songs of wild birds (Thorpe, 1954, 1958).

The same applies to the song of the Azores chaffinch, *Fringilla coelebs moreletti* (Marler and Boatman, 1951). It looks as though island conditions have reduced the need for the learned elaboration of chaffinch song which takes place in Britain (Thorpe, 1954, 1958), and this in spite of the fact that two species of *Fringilla* are present instead of one. Perhaps the relative ecological isolation of the two Tenerife chaffinches is significant here.

The trend to increased variability is illustrated by the blue titmouse, *Parus caeruleus* and the chiffchaff, *Phylloscopus collybita*. The *Parus* has an extraordinary range of different songs or calls, one succeeding the other in the same individual with bewildering variety (Fig. 3). Many of these bear a resemblance to songs of the coal tit, *Parus ater*, in Britain but some are more like those of other *Parus* species. In the same way, the chiffchaff sometimes sounds like the corresponding species in Britain, but at other times sounds like its close relative, the willow warbler, *Phylloscopus trochilus*, which is not present in the Canary Islands (Fig. 4).

In seeking the reason for this increased variability in the island situation, which contrasts with the greater simplicity in the chaffinches, we

can only speculate. It almost seems that while the chaffinch in Britain is under pressure to elaborate its song, the blue tit and chiffchaff must restrict themselves to a small portion of their potential repertoires. Under island conditions, with the selection pressure on specific distinctiveness relaxed, there are changes in opposite directions. Yet both of these would result in a loss of efficiency if they occurred in Britain.

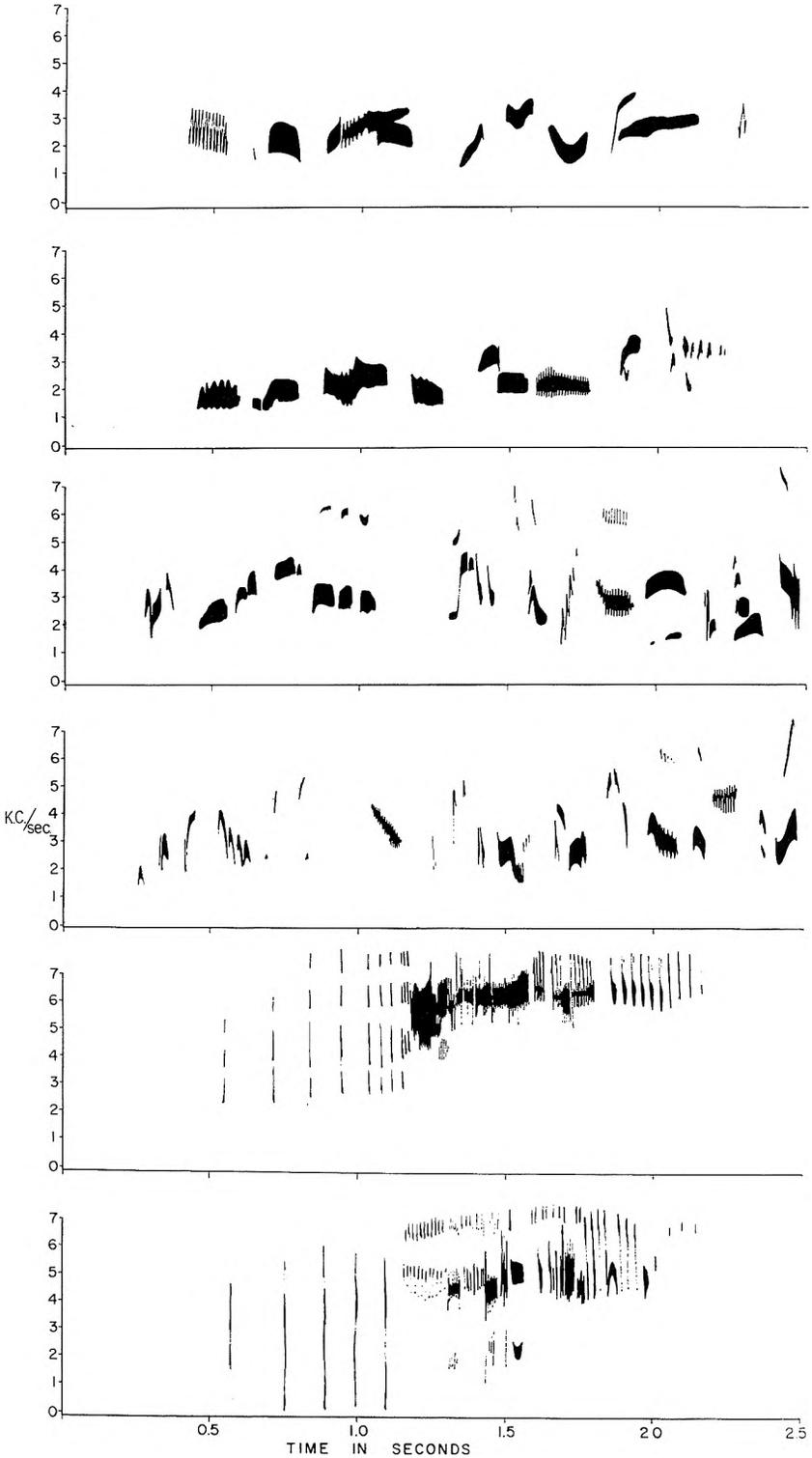
At present the evidence reveals no correlation between island variation and the relative contributions of learning and inheritance to song development in the mainland forms. Both in the European corn bunting (Thorpe, 1956), and chiffchaff (Heinroth, 1924) the inherited elements seem to predominate in the song, yet the former hardly sounds different on Tenerife, while the other is distinctly changed. There may be considerable plasticity in the genetic mechanism controlling chiffchaff song, for variations are known to occur in other parts of Europe (Lynes, 1914). Learning plays a greater role in normal song development of the black-bird in Europe (Messmer, 1956) yet there is little difference between Britain and Tenerife. However, it may be significant that of all the species involved, it is in the development of chaffinch and blue tit song that learning is most important in Europe (Thorpe, 1954, 1958; Promptoff and Lukina, 1945). We should expect that learned song traditions would be the most ready to vary in response to change in selection pressure.

Much more information is needed here, but careful studies of geographical variation may eventually throw considerable light on the kind of selection pressures to which bird songs are subject. Other types of variation are also worthy of attention.

SONG DIALECTS

We must take care to distinguish between the broad geographical variation of the song of a species and the variations which can be observed between adjacent populations living under similar conditions. These are often considerable and have led to the proposal of an analogy with dialects in human speech. In the chaffinch for example, there are community song-characteristics which change as you pass into the next community, particularly if there is a barrier to hinder movement. The situation is well illustrated in some of the more isolated Scottish glens, each with its own chaffinch *dialect* (Marler, 1956).

FIG. 2. A comparison of songs of close relatives in Europe and on the Canary Islands. In each case the upper record is from Tenerife in the Canary Islands. Note the similar basic patterns of song in *Turdus merula* (top, April, 1956, April, 1953), *Sylvia atricapilla* (center, April, 1956, June, 1951), and *Emberiza calandra* (bottom, April 1956, May 1938).



There are similar observations on other species such as the snow bunting, *Plectrophenax nivalis* (Tinbergen, 1939), blackbird, song sparrow, *Melospiza melodia* (Nice, 1943), the white-crowned sparrow, *Zonotrichia leucophrys*, (Blanchard, 1941) and the eastern and western meadowlarks *Sturnella magna* and *S. neglecta* (Lanyon, 1957). In the chaffinch we know that the *dialects* arise because young males learn their songs from older birds in their first year and then return to breed in the same area in subsequent seasons. This encourages the persistence in one area of a limited number of song types. The effect is aided by the habit of countersinging in which a male tends to reply to another with a similar song type, if he possesses one, so that songs uncommon in the area tend to fall into disuse.

It is difficult to see what function is served by this dialect variation, but we may note that learned traditions of this type may be as susceptible to natural selection as entirely inherited songs and may adjust more readily, especially if there is a certain *inertia* in the genetic mechanism underlying innate songs.

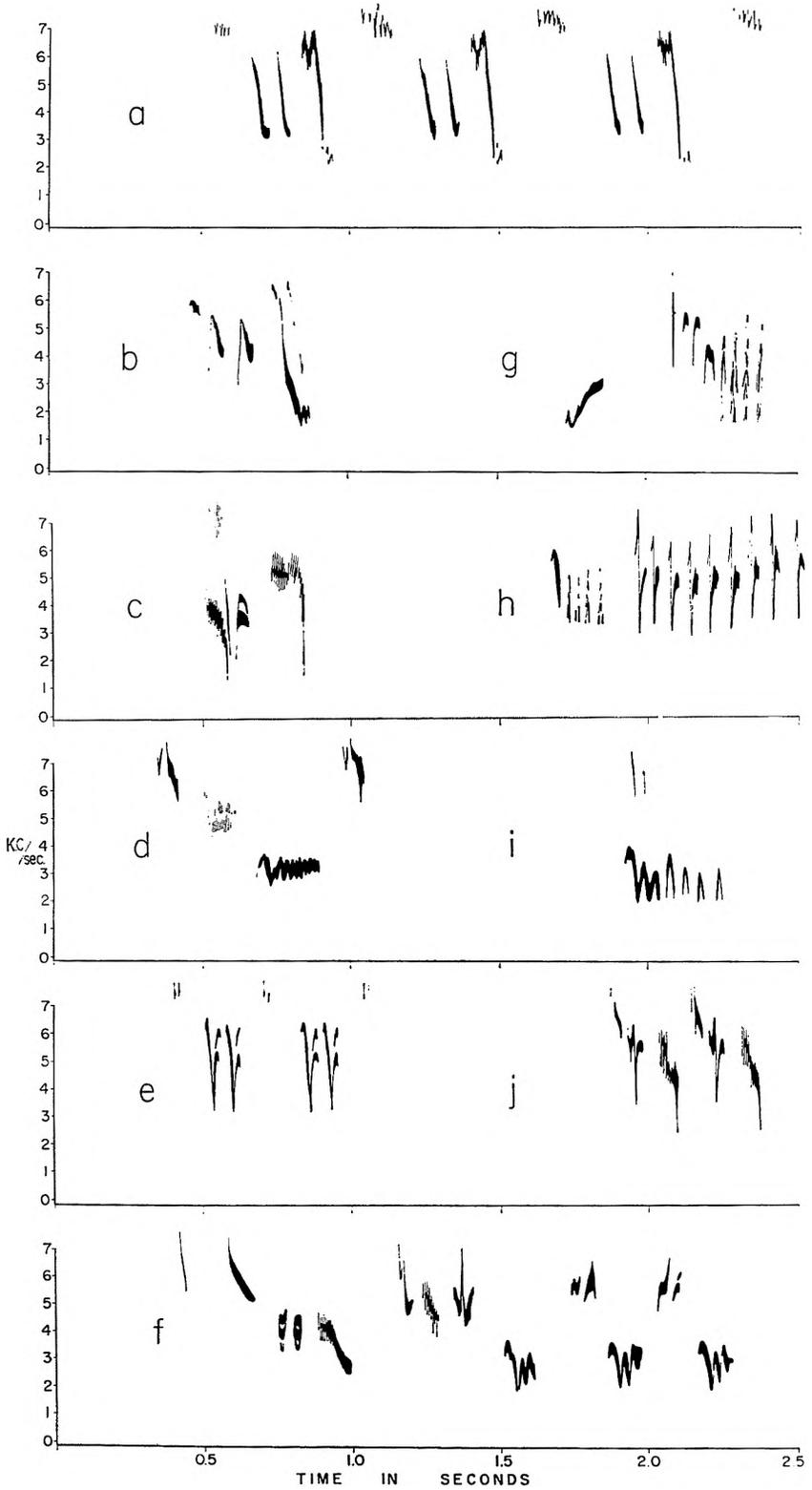
VARIATION WITHIN A POPULATION

One of the difficulties in describing song variation is that, even within a population, there are so many song types that large samples are necessary. This is all the more surprising when we reflect that if the facilitation of specific sexual recognition were the only function song had to perform, there should be an ideal for this purpose to which all members of the population should conform. The rarity of this condition—if it exists at all—only serves to emphasize our ignorance of song function.

It is not uncommon for songs of different individuals to differ with sufficient consistency that an observer can use them for individual identification. Mrs. Nice found this with the song sparrow (1943) and the same is true of meadowlarks (Lanyon, 1957), the chaffinch, yellow bunting, *Emberiza citrinella*, Mexican junco, *Junco phaeonotus*, and brown towhee, *Pipilo fuscus*. Leaving aside the excessive variation on small islands which has already been mentioned, the range of variation within mainland populations may be surprisingly wide.

In the chaffinch a considerable number of types can be discerned by ear alone (Marler, 1952). More extreme is the situation recently found in the Mexican junco in the Durango pine forests, in Mexico. Songs of some seventy individuals were recorded, and on analysis no two of them

FIG. 3. A sample from the great variety of songs heard from *Parus caeruleus* in Tenerife (April 1956). Some are similar to the corresponding European species (g,h) while others resemble *Parus cristatus* (d,i) and *Parus ater* (a,b,c,e).



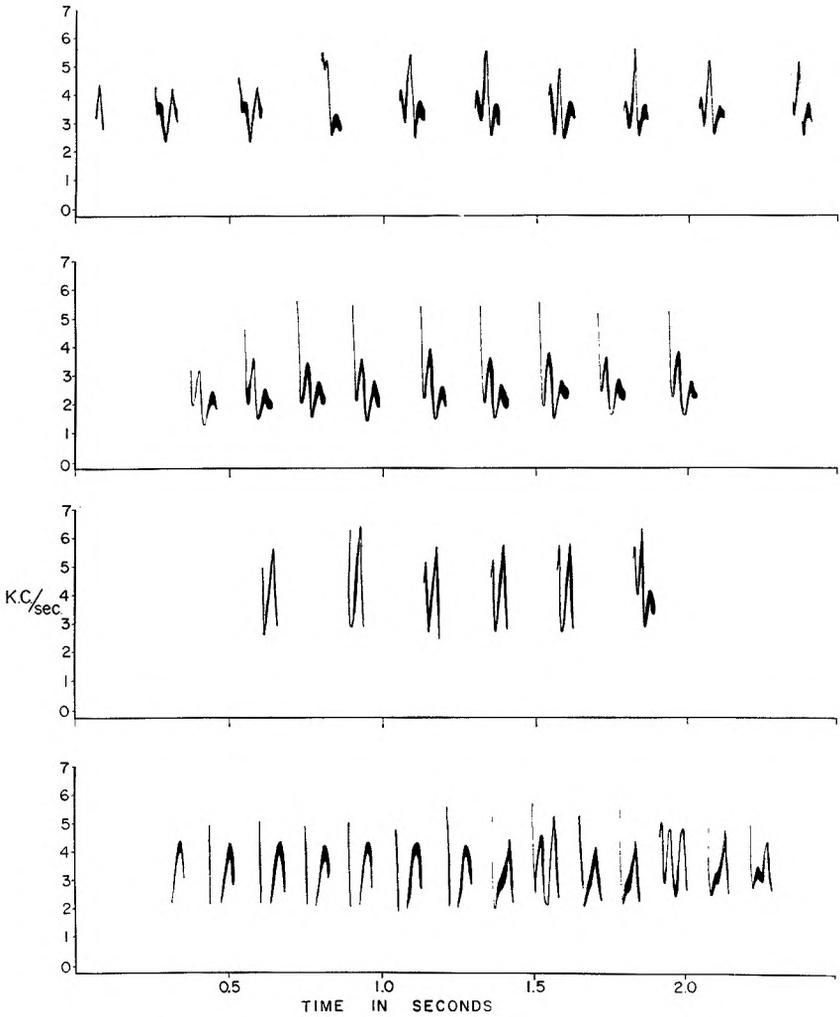


FIG. 4. Some song variations of the Tenerife chiffchaff, *Phylloscopus collybita* (April 1956). While the individual notes are often similar to those of the European bird, at times they are arranged into a short two-second song, particularly clear in the bottom record, reminiscent of the European willow warbler (cf. fig. 1).

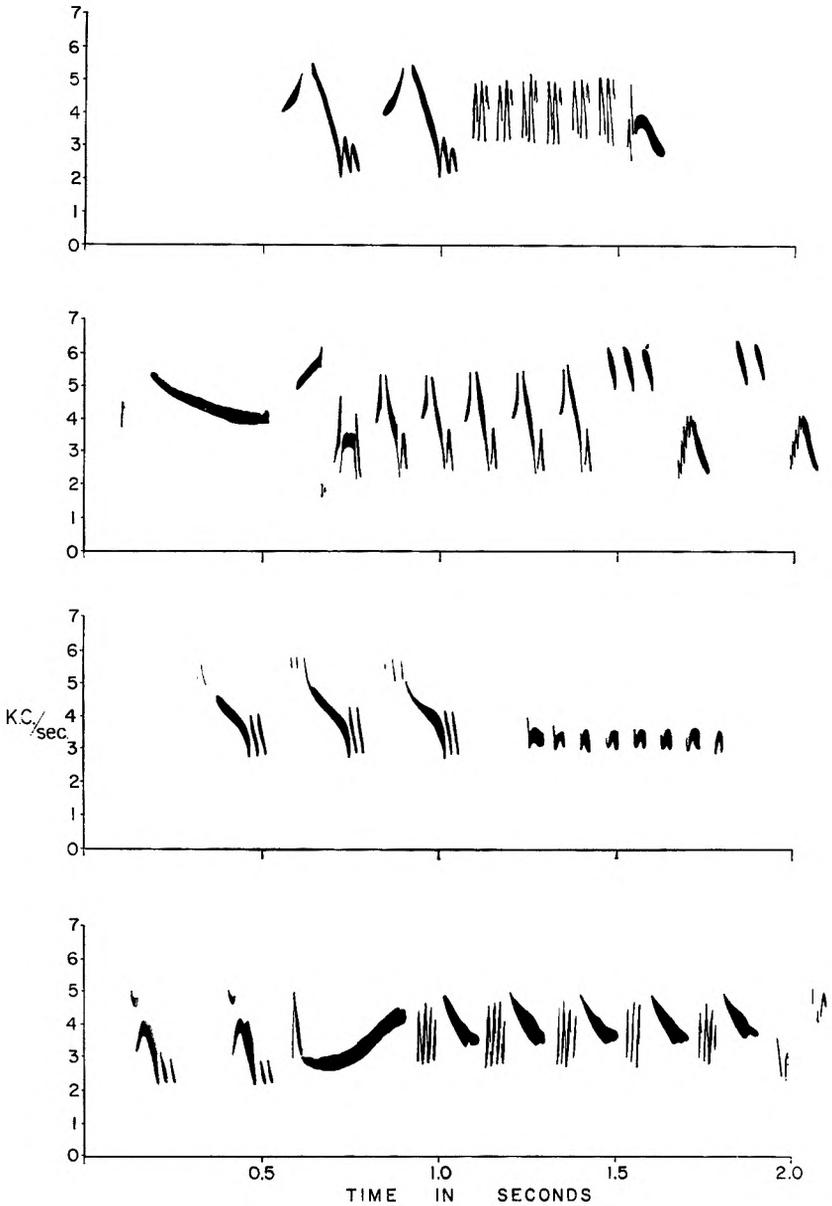


FIG. 5. Songs of four neighboring Mexican juncos (*Junco phaeonotus*) recorded in the pine woods near El Salto in Durango, Mexico. Although there are marked differences between each one, they all have one similar pattern of notes in common (Selection 1, July 1958).

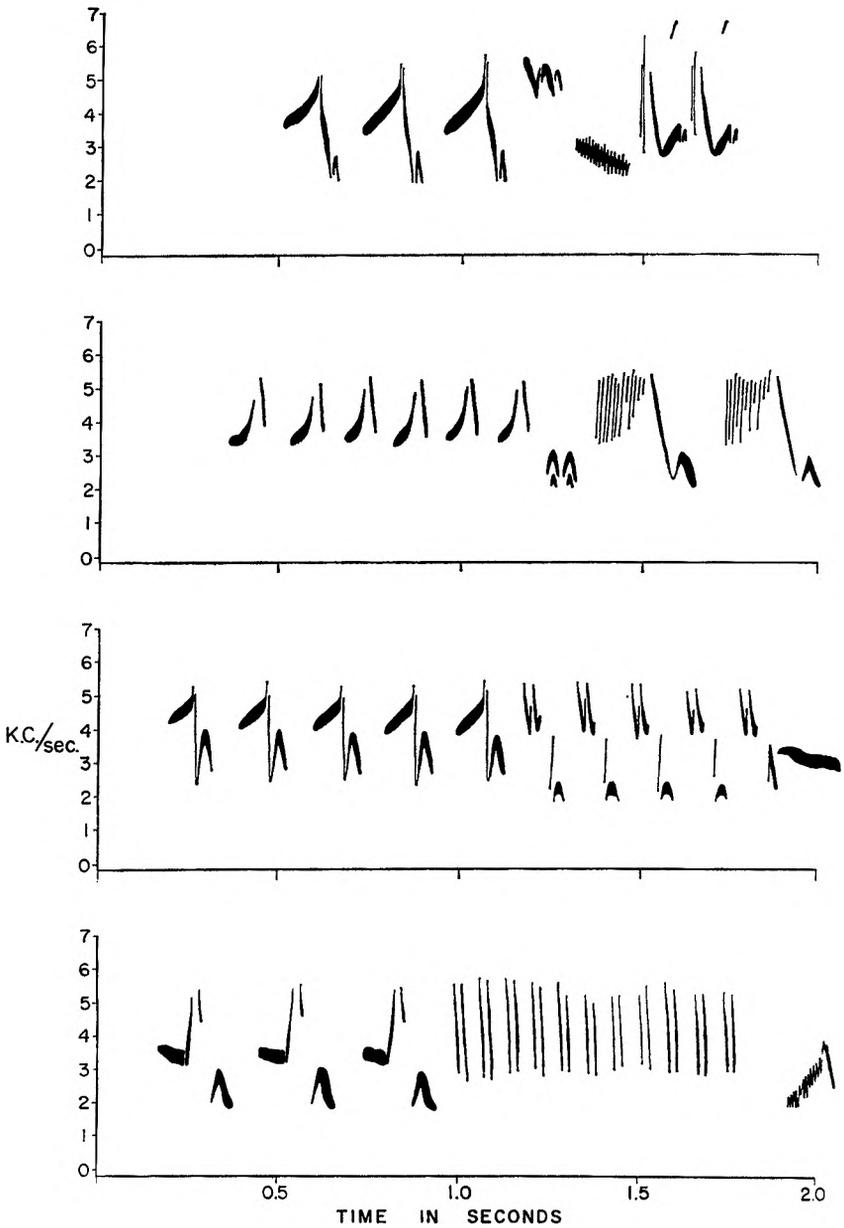


FIG. 6. Songs of four more adjacent Mexican juncos from another part of the same pine wood. Here the variations on the shared note pattern are more free, but share the same basic form (Selection 2, July 1958).

were identical (Selections 1 and 2 on the Demonstration Record). Adjacent birds sometimes shared certain characteristics (Figs. 5 and 6), which are reminiscent of the dialects discussed above (although in an ecological sense, the whole sample was drawn from one population). The songs which contrasted most strongly were so different that it was at first difficult to believe that they came from members of the same species. Another example of divergence within a population comes from brown towhees in Mexico (Fig. 7 and Selection 3), and even songs as homogeneous as those of the chipping sparrow, *Spizella passerina*, show considerable variation in detail.

What is the explanation for this variation in song which seems to hinder the usually accepted function of specific recognition? Again only experiment can give the answer, but a hint is provided by the help which the variation gives ornithologists in identifying individual birds. It is conceivable that it facilitates individual recognition for the birds themselves, both between rival males, and between mates. The evidence for this recognition is at present only circumstantial (Marler, 1956). But we can see how it might come to have survival value by enabling males to distinguish between new intruders and old rivals, and by helping females to locate males with whom they have previously bred.

Individual identification of chaffinches is made easier by the possession of more than one song type, some contrasting more strongly with the songs of neighbors than others. Occasionally a particular combination of song types may serve to identify a bird, even though each of them may be shared with other individuals.

REPERTOIRES OF INDIVIDUAL BIRDS

Perhaps even more surprising than variation within a population is this variation in the individual. Apart from the slight variations of repetition or omission, many birds have several distinct themes. If this were only an occasional phenomenon it would hardly be worth remarking on. But it is noticeable how few birds sing exactly the same theme all the time, even among those which one tends to regard as monotonous singers. The European willow and wood warblers usually have several themes, so does the yellow bunting. Among a group 71 chaffinches the mean number of song themes per birds was 2.8 (Marler, 1956). Mrs. Nice (1943) found from 6 to 24 themes in the repertoire of individual song sparrows. A Carolina wren, *Thryothorus ludovicianus*, gave 22 themes in 24 bursts of singing (Borrer, 1956). Up to nine songs per bird are recorded for western meadowlarks, and many more for the eastern form (Lanyon, 1958). Among more versatile singers the repertoire may be still larger, the greatest recorded so far being 173 themes used

by a song thrush, *Turdus ericetorum*, near Cambridge, England (Marler, 1959). The way in which these various themes are constructed is of great interest, but it would be out of place to discuss it here. The point which concerns us is the function of this variation. Is it simply a manifestation of aesthetic exercise without any special significance, or does it have survival value?

SPECIFIC CHARACTERS VERSUS INDIVIDUAL CHARACTERS

If song variation within a population is an aid to individual recognition of other members of the species, is it not possible that variation within the individual is another contribution to this function? Within

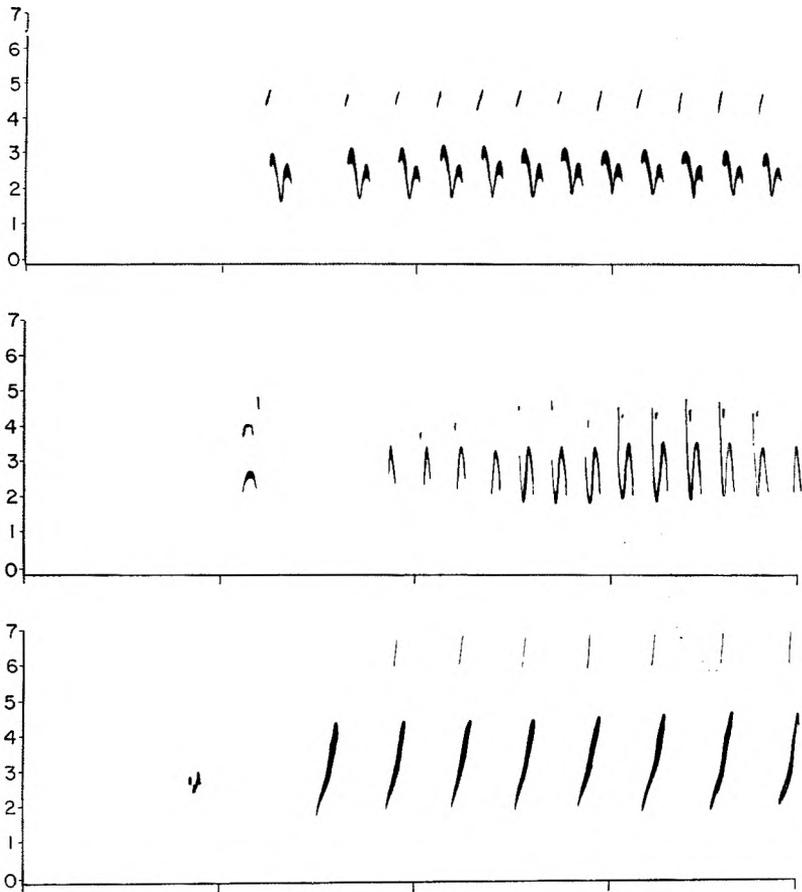


FIG. 7. Songs of six brown towhees (*Pipilo fuscus*) from the same population at La Labor, near Calvillo, in Aguascalientes, Mexico (Selection 3, July 1958).

the repertoire, each additional theme varies but little, and so adds to the clues on which individual recognition can be based.

Again, we have the apparent conflict between the use of variations for individual recognition and the need for stereotyped characteristics for species recognition. However, we ourselves can usually identify the species even of the most varied singers and we must impute to the birds themselves at least an equal ability in this regard. This implies that some constant characteristic survives through the variations. In fact it seems as though the conflict is resolved in many cases by relegating

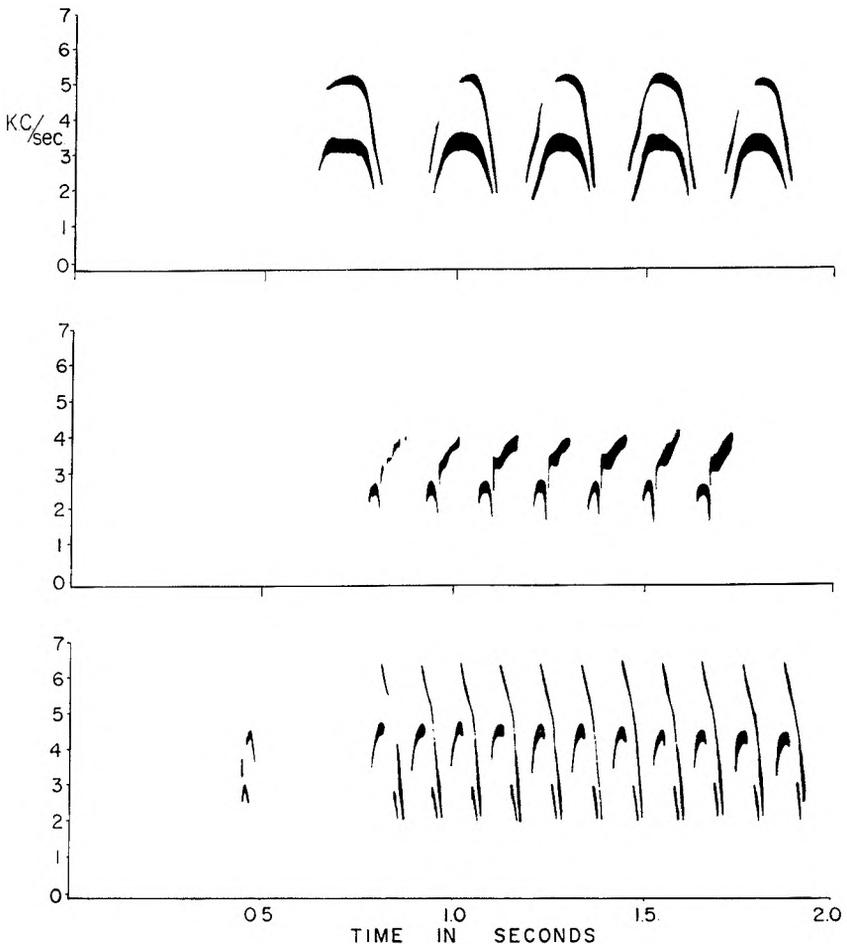


FIG. 7. (Continued)

specific and individual characteristics to different parameters of the song. Often it looks as though the specific properties lie in the overall time pattern of the song while individuality is portrayed by the detailed changes of frequency. The situation in the *Hylocichla* thrushes seems consistent with this (Stein, 1956), though there are undoubtedly alternative methods as well.

THE SIGNIFICANCE OF SONG LEARNING

Dr. Lanyon has discussed elsewhere the roles of learning and inheritance in the development of song, but one aspect bears on the present discussion. We have no satisfactory explanation of why some birds elaborate their innate song by learning from others. It may be that this provides an alternative means of responding to selection pressure, without relying on the rather slower selection of genetic mutations. As pointed out by Huxley (1942), learned traditions are equally susceptible to selection effects. From the studies so far carried out, it appears that the copying of another's song is never quite precise, so that learning may also facilitate the development of individual characteristics. To achieve a similar effect with an innate song would require either some kind of polymorphism, or an element of indeterminacy in the ontogenetic process through variable expressivity of the genes concerned, both possibilities to be born in mind in studies on the development of song.

SOME EXAMPLES OF SPECIFIC "INDISTINCTIVENESS" IN SONGS

It was pointed out at the beginning of this paper that the assumption on which all of this discussion is based, that loud and conspicuous songs, where used, play a dominant role in reproductive isolation, is unproven in the strictest sense; though Dilger (1956) has clearly demonstrated in *Catharus* and *Hylocichla* thrushes the role of song in territorial defense. There is little doubt that great differences will in fact be found in the functions of song, and it is already clear that the meadowlarks do not fit into this simplified picture (Lanyon, 1957). The strongest line of indirect evidence is the specific distinctiveness of sympatric species (Marler, 1957). During a study of the songs of some Mexican birds in the summer of 1958, two cases of a relative lack of specific distinctiveness were noted.

In the pine woods of Durango three species live within earshot, with rather similar songs: the chipping sparrow, *Spizella passerina*, the striped sparrow, *Oriturus superciliosa*, and the Hartlaub's warbler, *Vermivora superciliosa* (Fig. 8 and Selection 4). Although there are differences, I suggest that these songs are less distinct than we should

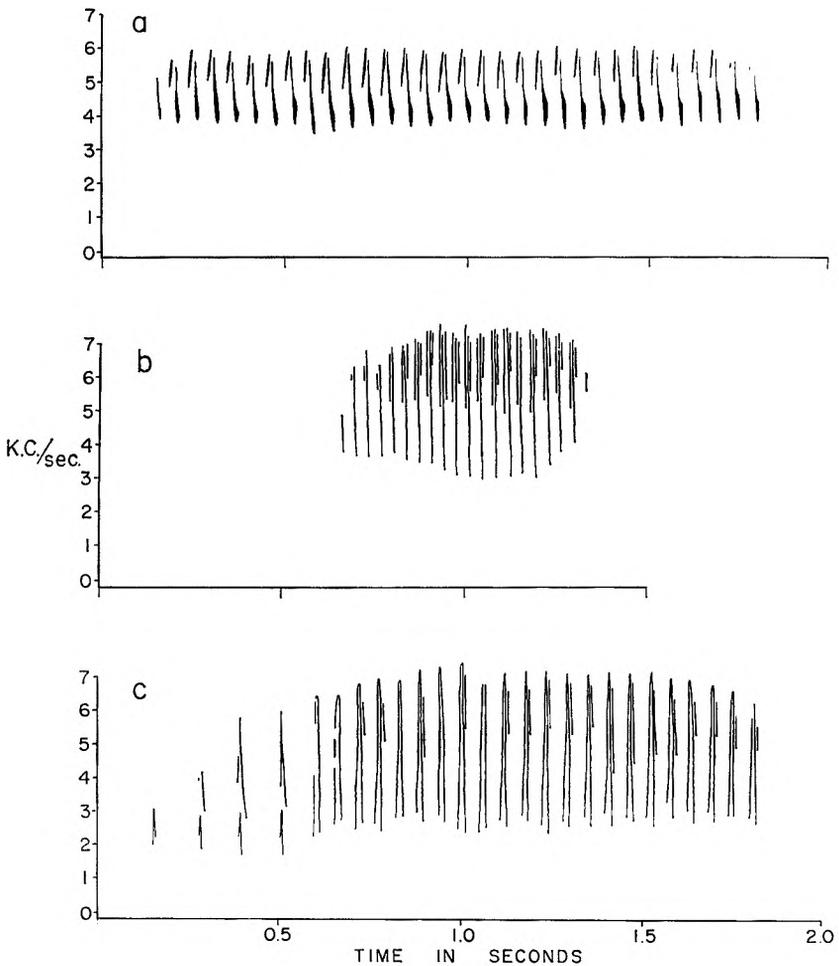


FIG. 8. A comparison of songs of three species, (a) the chipping sparrow (*Spizella passerina*), (b) Hartlaub's warbler (*Vermivora superciliosa*) and (c) the striped sparrow (*Oriturus superciliosa*) illustrating their relative lack of specific distinctiveness (Selection 4, July 1958). These were all recorded near El Salto in Durango, Mexico.

expect if they played a dominant role in reproductive isolation of these species. In fact those three species are rather different ecologically, which may help to keep them apart.

In a rocky wooded valley in Aguascalientes four species with rather similar songs were observed, three of them engaging in what seemed to be interspecific countersinging. These were the brown towhee, *Pipilo fuscus*, the cactus wren, *Campylorhynchus brunneicapillus*, and the

ladderback woodpecker, *Dendrocopus scalaris*, the fourth being the yellow-breasted chat, *Icteria virens* (Fig. 9, and Selection 5). Again, there are differences, and the chat has other themes which are quite different. But the relatively limited specific distinctiveness is worthy of note.

OTHER FUNCTIONS FOR SONG THAN MATE SELECTION

It is possible that the slight differences between the songs of these species are adequate for quick and accurate specific recognition, though we would still need to explain why a relatively slight specific distinctiveness suffices here, and not in other cases. On the other hand we must not forget that song may serve other functions which are not necessarily aided by specific distinctiveness.

The repulsion of intruders from the territory is often accomplished by song. When such defense is restricted to members of the same species a highly specifically-distinct song will be suitable, and can serve for reproductive isolation as well. If song is freed from this latter function, however, selection may favor a different situation. Specific distinctiveness becomes at less of a premium, for nothing is lost if a song repels other species as well. If there is the slightest degree of competition with other species selection may shift in favor of a degree of resemblance between their songs. The similarities in voice between species of *Parus*, described by Dixon, in areas where they overlap, may be such a case, for the territories are mutually exclusive (Dixon, 1950), and voice plays an important role in territorial defense (Dixon, 1949). The resemblances between the threat displays of many species (Marler, 1957) is no doubt related to these same considerations.

There may also be variation in the role which song plays in the relationship between male and female. Specific distinctiveness will be crucial if the song is concerned with establishment of the bond which leads to copulation. In species where the pair bond lasts a long time, song may also be concerned with its maintenance. In this case it may be important to the female to recognize her mate's song individually, thus encouraging the different types of variation discussed earlier in this paper. As pointed out, this too may run counter to the trend towards a stereotyped species specific song. In the same direction, stimulation of the female as an aid to synchronization of the physiological cycles of the pair may be achieved in part by song, again, likely to be related to individual characteristics as well as to specific ones.

Extreme specific distinctiveness in bird song is therefore unlikely to be a general rule, since in a given species the same song may serve several of the functions discussed above. The hypothesis with which this paper

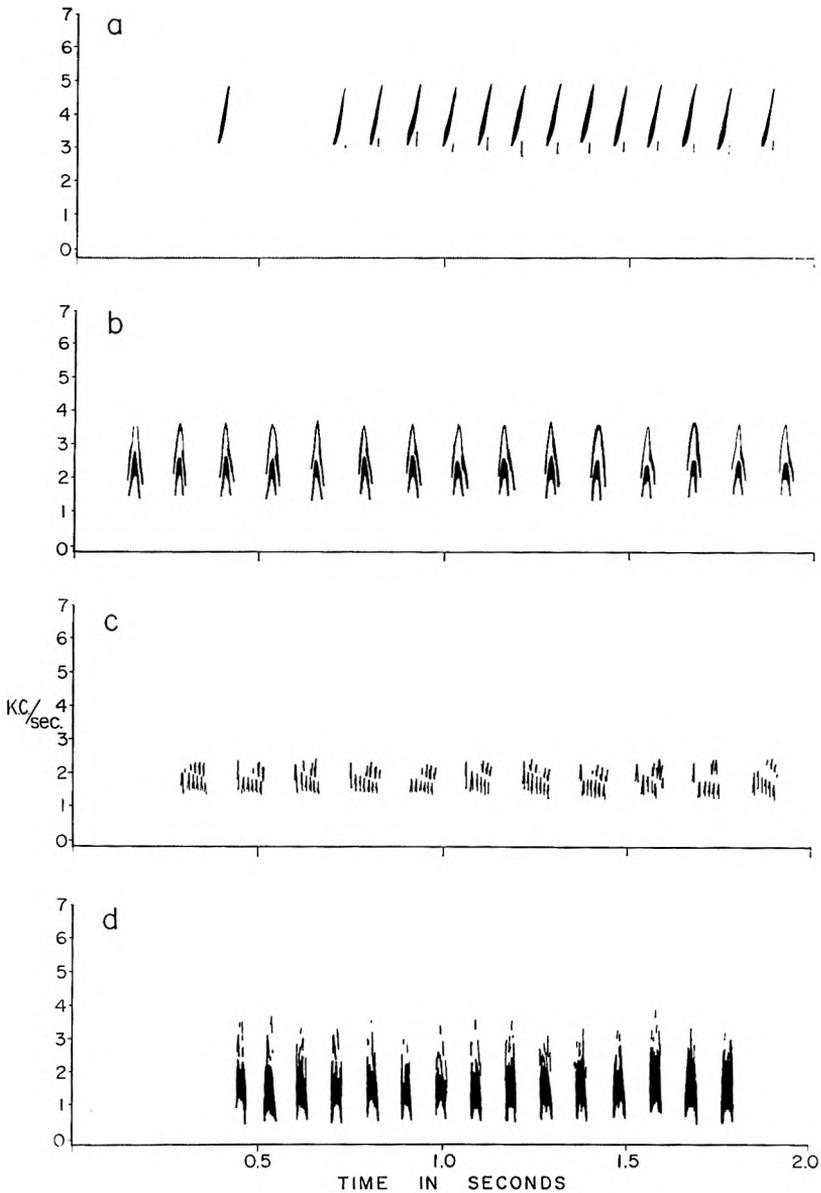


FIG. 9. Songs of (a) a brown towhee (*Pipilo fuscus*), (b) a ladderback woodpecker (*Dendrocopus scalaris*), (c) a cactus wren (*Campylorhynchus brunnei-capillus*), and (d) a sample from a yellow-breasted chat (*Icteria virens*), recorded within earshot of each other, at La Labor, near Calvillo in Aguascalientes, Mexico (Selection 5, July 1958).

opened, that the structural characteristics of loud and conspicuous song play a dominant role in reproductive isolation of the species, is clearly an oversimplification. The extent to which we are able to understand the evolution of bird song in the future depends on how far we can establish the precise functions which it serves, and this calls for a different approach than that used in this paper; that is, experimental rather than simple observational methods are necessary.

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CAPTIONS TO SELECTIONS ON DEMONSTRATION RECORD

Selection 1. Songs of four neighboring Mexican juncos (*Junco phaeonotus*) recorded in the same part of a pinewood near El Salto in Durango, Mexico. Although there are marked differences between each one, they all have one similar pattern of notes in common (see Fig. 5).

Selection 2. Songs of four more adjacent Mexican juncos from another part of the same pine wood. Here the variations on the shared note pattern are more free, but share the same basic form (see Fig. 6).

Selection 3. Songs of six brown towhees (*Pipilo fuscus*) from the same population, at La Labor, near Calvillo, in Aguascalientes, Mexico (see Fig. 7).

Selection 4. A comparison of similar songs of three species which may be heard at the same time and place: Bird 1—the striped sparrow (*Oriturus superciliosa*); Bird 2—Hartlaub's warbler (*Vermivora superciliosa*); Bird 3—the chipping sparrow (*Spizella passerina*). This illustrates their relative lack of specific distinctiveness. Recorded near El Salto in Durango, Mexico (see Fig. 8).

Selection 5. Similar songs of a brown towhee, *Pipilo fuscus* (Bird 1); a ladderback woodpecker, *Dendrocopus scalaris* (Bird 2); a cactus wren, *Campylorhynchus brunneicapillus* (Bird 3); and a yellow breasted chat, *Icteria virens* (Bird 4). The latter is selected from a variable song, some parts of which are quite different from songs of the other three species. Recorded within earshot of each other, at La Labor, near Calvillo in Aguascalientes, Mexico (see Fig. 9).



ANIMAL SOUNDS AND COMMUNICATION

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