

# HOW BIRDS DEVELOP SONG DIALECTS

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This paper considers how dialects develop in the songs of territorial oscines. The term "dialect" implies on the one hand some similarities in the repertoires of sound patterns, here called "syllables," and their sequences in songs of birds on neighboring territories. It also implies some dissimilarities among birds of different localities. Much evidence indicates that copying is the major basis of the similarities, while the dissimilarities arise from a variety of sources. These include active generation of new syllables and new sequential combinations, and the interaction of time-limited copying and dispersal. Hence, where dialects occur they result from opposing tendencies toward conformity and toward individuality of repertoires. Not all species can be said to exhibit dialects (indeed the term itself is used quite imprecisely); but species obviously vary in the extent to which their songs conform within a population. In spite of this variation, the bases of development seem the same throughout the species studied, although there is varying emphasis one way or another. An important source of variation and confusion is the size of the repertoire and the number of sequences in which the items are presented.

Most emphasis in this paper is placed on the family Fringillidae because this group shows a wide range in the expression of dialects and is the best studied of any avian family with regard to song development. I shall first describe the situation as noted in the Cardinal (*Cardinalis cardinalis*), for this species has been studied in both field and laboratory, and it sings in a manner that is easy to appreciate in the visual displays of sound spectrograms. Findings in this species are related to other fringillids and finally to other oscines. The consequence of these considerations is a general model of song development for oscines.

## AN EXAMPLE OF DIALECTS

The Cardinal is a common bird of gardens and woodlands, especially in the eastern United States, southern Ontario and Mexico. Both males and females sing well, although the males sing much more frequently as part

of their territorial proclamations throughout the breeding season. Both sexes have a repertoire of several distinctive songs, as many as 8 to 12 being used frequently by each individual (Lemon 1965, Lemon and Herzog 1969). They also have a repertoire of calls used for communication at close distances and in different contexts (Lemon 1968a).

The songs consist of repetitions of sound patterns called syllables, each type consisting of one to three individual sound units. For example, the first syllables of all three males in figure 1—A1, B1, and C1—have one part only, whereas in A5, and B5, the syllables have three parts. Any particular song consists of one to three types of syllables occurring in definite orders or permutations as seen in A2, A3, A4, and others. Each of these permutations is called a "song type." In the present examples only about half of the song types of each bird are shown.

Neighboring Cardinals have very similar songs which are often different from those of Cardinals elsewhere. Of the examples from three males shown in figure 1, two of the males were neighbors on immediately adjacent territories at London, Ontario, while the other resided near Melbourne, about 32 km direct flight from the former location. The similarities of the songs of birds A and B are obvious although some individual differences are evident in A6 and B6.

In some cases, little or no difference is detectable among the songs used in different localities, as is shown by the songs in A1, B1, and C1. In fact, some syllables and song types occur widely throughout Ontario and adjacent United States with little change.

On the other hand, differences between local populations that are the expressions of dialects are also obvious and can be considered under three categories (Lemon 1966). First, the syllables are very similar, yet there are slight and consistent differences occurring locally. Such differences are seen in the syllables of rows 2 and 3. On the other hand, the syllables may be so different that they can hardly be considered of the same class, as in rows 4 and 6. Of course, there are many examples in which the distinction between

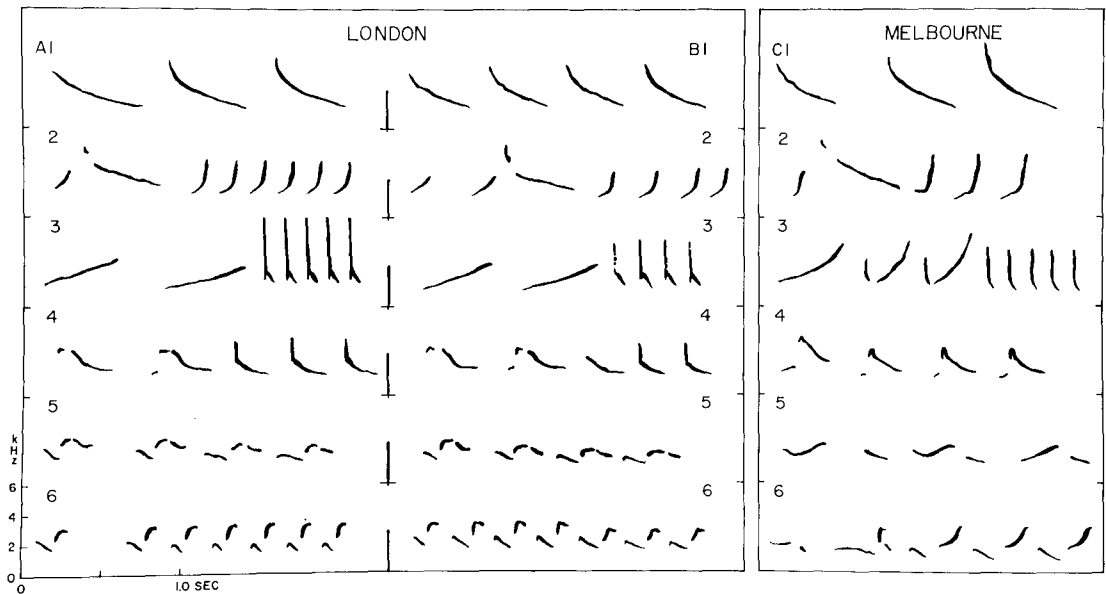


FIGURE 1. The similarities and dissimilarities of songs of two male Cardinals from contiguous territories at London, Ontario, and one from about 35 km away near Melbourne, Ontario. Songs toward the upper half of the figure show those syllables and song types most similar among the two places. Only about half the repertoires are shown. (In this and subsequent figures, the unnumbered base marks are 0 kHz. Exceptions are indicated otherwise, as in some examples in Figures 2, 7 and 8.)

different classes becomes quite arbitrary; indeed this is to be expected since I shall argue that new syllable classes arise through the modification of existing forms. Finally, the syllables may occur in combinations and permutations peculiar to a locality, as seen in row 3. Further examples of these differences will be shown later.

#### BASES OF COMMON PATTERNS

In considering the development of dialects, we shall deal first with those aspects that contribute to the sharing of patterns by neighboring territory holders. We shall examine first the developmental processes, leaving the ecological features till later. The occurrence of patterns common to several individuals could result from copying or from the inheritance of influences among birds of common lineage. The evidence supports the view that both aspects are involved, although that for copying is much clearer.

Evidence of copying or imitation is seen both in wild Cardinals and in birds reared under controlled conditions (Lemon and Scott 1966, Dittus and Lemon 1969). Young male Cardinals were captured in their first winter and were isolated from further exposure to the songs of other Cardinals. The following spring they sang most of the syllables common to the locality, an example being shown in figure

2A. This bird had been color-banded as a nestling and had accompanied his banded father for the next three months after leaving the nest; obviously this young male had been exposed to the local songs.

I took several Cardinals from the nest approximately five days after hatching and let them hear recorded songs including some from localities other than their own. Eventually they reproduced the foreign patterns, as in figure 2B. Conversely, individuals taken from the nest but isolated from song failed to reproduce the syllables and song types of their parents, with a few exceptions to be considered later. Instead, they developed repertoires that were smaller than those of wild Cardinals; the syllables produced were usually one-parted only, lacking two or three temporal subdivisions characteristic of many sung in the wild, and most were slurred in one direction in their frequency sweeps, as in figure 2C1. When reared together, these isolated Cardinals developed syllables of which most were common to all birds in the group. When reared separately, they had repertoires mainly unique to each bird.

Evidence of copying was noted also in the wild in two young males that settled in territories immediately adjacent to an older male that had certain peculiarities of song, two of which subsequently appeared in their songs. The young birds reproduced a syllable

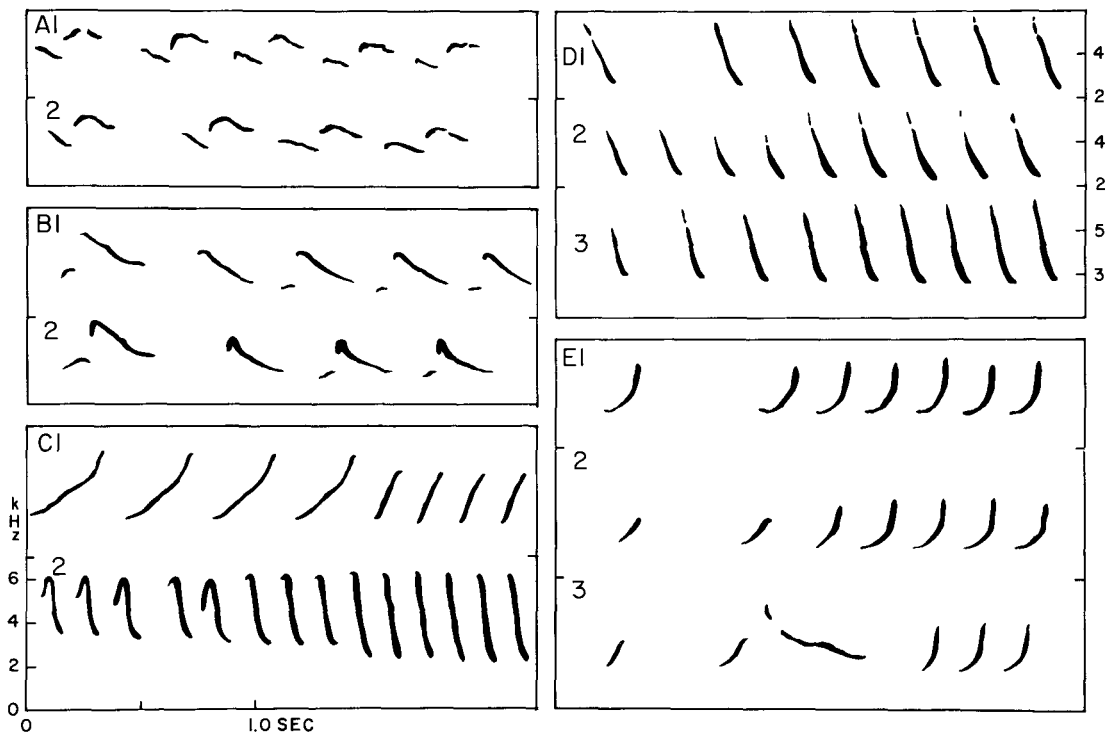


FIGURE 2. Examples of Cardinal songs illustrating copying and improvisation. A1 is the song of a wild Cardinal reproduced as in A2 by his male offspring the spring after the latter left the nest. B1 is a model song played from a tape recorder and B2 is a copy of it reproduced by a tutored male. C1 and 2 are songs improvised by captive males reared in the absence of model songs from wild Cardinals. The first syllables in C1 are similar to syllables sung by some wild Cardinals. D1 is a song that was peculiar to a certain banded wild Cardinal and D2 and D3 are apparent copies of the same as reproduced by two young males which settled on territories adjacent to the first male. E1 is a sequence of syllables that was peculiar to the same adult male as in D1 and that was reproduced as in E2 by one of the young males which settled beside him. The more usual form of song is that in E3.

which up to that time had been peculiar to the older bird (fig. 2D) and they omitted a syllable which most birds in the area, except the older neighbors, sang with another (fig. 2E).

The copying process terminates with the final development of the motor patterns. Until this time, the Cardinals are open to influences from other individuals both during their first summer and in the following spring. Hence, a young Cardinal settling on a territory for the first time may copy much from his immediate neighbors if he settles before motor development is complete. Four young males exposed to one set of recorded songs in summer and to another set the following spring copied from both sets. The subject which copied least from the first tape was least exposed to it. The period when Cardinals first become sensitive to songs is not known precisely but a young male captured three weeks after leaving the nest later reproduced some of the peculiarities of the dialect where he was captured.

When acquiring a territory for the first time, if the young Cardinals settle early, say in February or March, then song development will be completed on the territory. However, if they settle later, in April and May, development may already be completed. Once developed, the songs remain stable, as was noted in wild adults over as long as five or more years.

The foregoing evidence indicates the importance of sensory information in the development of song. Further evidence of this is seen from the effects of experimental deafening. Cardinals deafened after exposure to songs but before motor development failed to reproduce what they had heard (fig. 3A1) (Dittus and Lemon 1970). Such birds developed very small repertoires and the syllables were sung quietly (in some instances they were sung with great vigor but in silence), they were less pure with strong harmonics and were accompanied by many short pulses or clicks somewhat reminiscent of certain calls (fig. 3A2). There was also

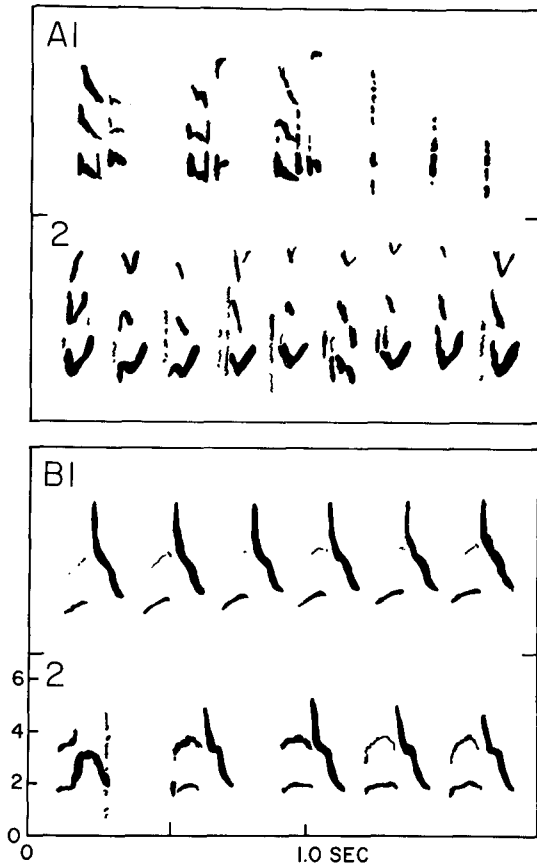


FIGURE 3. Songs of deafened Cardinals. A1 and A2 are those sung by Cardinals reared in isolation without singing experience before deafening. Some portions of the syllables are reminiscent of calls, especially those at the end of A1. A2 had exposure to song but had not developed song before deafening. B1 is the song of a Cardinal before deafening while B2 is a version of the same song months after deafening. Although generally the same afterward, there is some hesitancy evident in the first syllable and the harmonic on the first part of the syllable is more emphatic.

some deterioration of songs in birds deafened after motor development, but much of this was in the loss of purity of tone through the addition of stronger harmonics. In such birds the original patterns remained recognizable (fig. 3B).

Features of the motor system are probably also important in determining various aspects of song, but the forms of sounds produced by different song birds are not correlated closely with the structure of the syrinx, which is essentially the same throughout oscines (Miskimen 1951). In Cardinals the sounds of deafened birds had roughly the same frequencies emphasized as those of wild birds, between 1.5 and 4 kHz and this may relate in part to the syrinx and its dimensions. Other features, however, probably reflect con-

trols exerted by the central nervous system. Such features might include the tendency to repeat syllables in numbers inversely proportional to their duration, to repeat the song types in long series or bouts, and to organize the sequences of syllables and song types into predictable sequences (Lemon and Chatfield 1971). Even here, sensory information probably has an effect. In other words, the sensory and motor systems probably function together rather than independently. For example, the songs of one Cardinal can influence the choice of song type and the number of repetitions of such by another (Lemon 1968b).

Further comment is needed on the songs of Cardinals reared in isolation from an early age. Syllables of such birds generally differed in configuration from those of their parents, although they were typically pure whistles. Some syllables, however, had practically the same configurations as those of wild Cardinals. In certain cases such syllables were occasionally identical to those of the birds' parents but perhaps more often they were the same as those of birds located considerable distances away. Two examples can be seen in fig. 2C: The first syllables in C1 are similar to those shown in figure 1, A3, B3, C3; and the last syllables in C2 are similar to those in 2D. Syllables like this were widespread in Ontario but I did not find them in the repertoires of all isolates. These syllables were apparently improvised. They might have been innate, but more probably they arose through improvisation in which limits to the possible outcome were set so that some syllables developed in this way turn out to be the same as those in the wild. This point is elaborated further under improvisation.

The picture that emerges from these results is that during development of song, a Cardinal reproduces the model of song provided normally by other individuals. A memory of the model may be retained for some months after exposure or may be established during the period of motor development itself. In the absence of a model provided from another individual, Cardinals reared in isolation improvise their own syllables and song types, which usually differ from those of wild Cardinals. However, there are enough similarities in syllable form and in the general features of whistling and repetition to indicate that inherited influences determine these features to some extent. These influences are partly sensory and partly motor or the interaction between the two. Further elaboration on developmental processes is given in the next section.

## DIFFERENTIATION OF DIALECTS: DEVELOPMENT OF NEW SYLLABLE TYPES

Aside from the sharing of song patterns among individuals, it is characteristic of dialects that the vocal patterns are distributed locally. Hence we must also deal with the question of how the local repertoires become differentiated with respect to each other.

Since copying is the major source of the similarities of neighbors' songs, local differences develop first in individuals and then spread to others through copying. Hence I shall describe sources of individual variation and thereby show that each singer may contribute to the differentiation of song in the locality where he is situated. There are several possible sources of individual peculiarities, beginning with the least important.

Because copying involves matching of the motor output with a particular model, hypothetically one might anticipate errors in the process, either through improper storage of the model because of faulty hearing or because of noisy conditions. Also, since Cardinals may develop their songs some months after actual exposure to the model, there may be problems of recall.

All of these points are speculative and it is very difficult to find examples that might be considered errors; in fact, only one example seems reasonable. Most Cardinals sing syllables of relatively pure tone without prominent harmonics. One male Cardinal produced what was apparently a copy of a common syllable but with exceptionally strong harmonics (fig. 4A), even though the rest of his repertoire was normal.

In spite of the possibility of errors, evidence indicates that other sources of variation are more important. One of these is the effect of the duration of sensitivity and its interaction with dispersal. As noted, song development ends when the motor patterns are stabilized. Cardinals have a long breeding season in Ontario and young may leave the nest from early May to September in the extreme. A few Cardinals exhibiting juvenal plumage of the year and unaccompanied by adults have been heard to sing fairly well late in the season in August. This may indicate that individuals leaving the nest earlier might develop their patterns earlier the following spring than other individuals and because of that might be less susceptible to new patterns at that time. The few experimental Cardinals exposed to two series of recorded songs in autumn and spring differed in the extent to which they

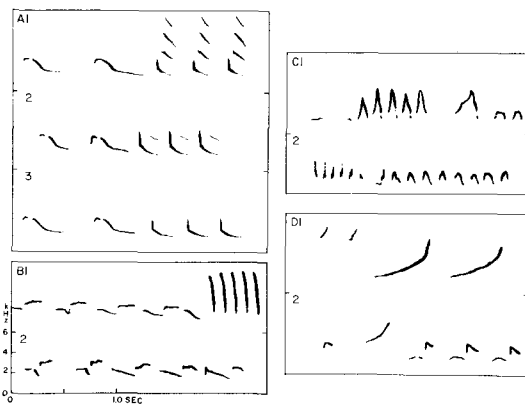


FIGURE 4. Some individual peculiarities of song. A variant of the second syllable in A1 with strong harmonics as sung by one Cardinal only. A2 and A3 show the more common form with little or no evidence of harmonics. In B1, from a bird reared in isolation and tutored from tape recordings, a syllable from a recorded song is sung in the same song with a syllable apparently improvised. The model song with the first syllable type is shown in B2. C1 and C2 are syllables from wild male Cardinals captured during their first winter. The syllables differ from those heard in the locality where captured and adjacent areas and were apparently improvised as in the same manner as with the isolates. D1 and D2 show the inclusion of syllables of unusually high frequency found in the songs of two wild Cardinals.

copied from each series, those with more experience with the earlier recordings copied more from them.

Related to this problem is the time at which the birds actually achieve or become holders of territories. Cardinals may acquire territories as early as January and as late as May, and those which are later may have completed their development before settling.

Another source of differences among individuals and dialects is evident in captive birds but is more difficult to assess in wild individuals. The repertoires of captive Cardinals exposed to model songs included not only copies or variants of these models but also syllables that were more similar to those developed by totally isolated birds. Again such syllables were usually complete without subdivisions in time, and their slurring was most often in one direction only such as the second syllable in fig. 4B1. Hence, in addition to copying, these birds apparently improvised from models other than those provided by the recorded songs played to them. In four males exposed to two sets of recorded songs in both autumn and spring, the improvised syllables accounted for one third of the total repertoires, while in birds exposed to one set only, they comprised almost half.

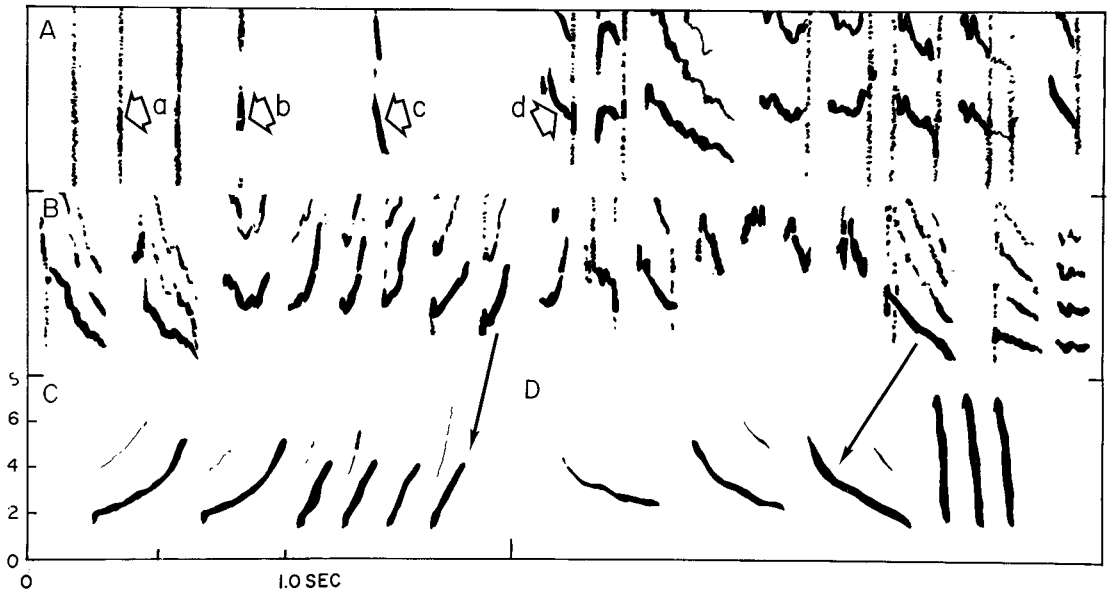


FIGURE 5. The emergence of developed song from subsong in a Cardinal isolated from five days after hatching and without further exposure to Cardinal songs. A shows a portion of subsong beginning with a series of calls, a) to d), and beginning song elements apparently occurring with the calls. B is a portion of subsong one week later than A showing syllables that appear to be the forerunners of those stabilized in C and D, the latter recorded seven months later. Evidence of calls decreases throughout. The structure of the song syllables seems related to the immediately preceding syllables.

Improvisation of this sort may happen under natural conditions also. Cardinals captured in the wild during their first winter after exposure to song the previous summer not only reproduced copies of the local dialect, but also produced syllables not found in the locality nor at several places in Ontario (fig. 4C). Nor were the syllables considered copies of songs from other species. If such improvised syllables are retained in wild Cardinals, they would be difficult to distinguish from similar syllables copied from models unless they had some distinguishing peculiarity. One such peculiarity would be a syllable of exceptionally high frequency, for although during development sounds of relatively high frequency are produced, say of 6 kHz or more, most emphasis in the final repertoire is at lower frequencies. Two birds in Ontario sang peculiarly high syllables not shared by their neighbors and which may have had the origin just described (fig. 4D).

#### IMPROVISATION OF SYLLABLES

The foregoing has shown that development of song involves either the replication of a model based on memories of songs of other birds, or alternatively the improvisation of a repertoire of syllables without the aid of such models. Although these two possibilities seem unrelated, they probably involve the same pro-

cesses, two of which are elaborated here. First is the use of calls, which are well developed by the time of song development, to provide an initial basis for comparison and to facilitate the motor processes through auditory feedback. Second is the modification of the calls and early song elements by a phenomenon called "drift," named after the process as seen in the domestic fowl (Andrew 1969). In drift, the elements are immediately repeated but with some modification; the result is a variant of an earlier form that may eventually become stabilized as a new syllable.

In Cardinals four calls commonly used in subsong are similar in form and occur in similar contexts. The *chuck* is a short broad-frequency pulse with lower frequencies emphasized; the *chip* is similarly short but of more restricted and higher frequency of 4 to 8 kHz; the *chitter* is a series of short repeated pulses but is of high frequency, 6 to 10 kHz; and the fourth, the *pee-too*, differs somewhat in being slightly longer with downward slurring and in having two separate portions of high and low frequency. The *chip* is a contact call used by pairs and flocks. All four calls are used in agonistic encounters within the species, while the *chip* is also used in mobbing predators and the *chitter* is also a warning of aerial predators.

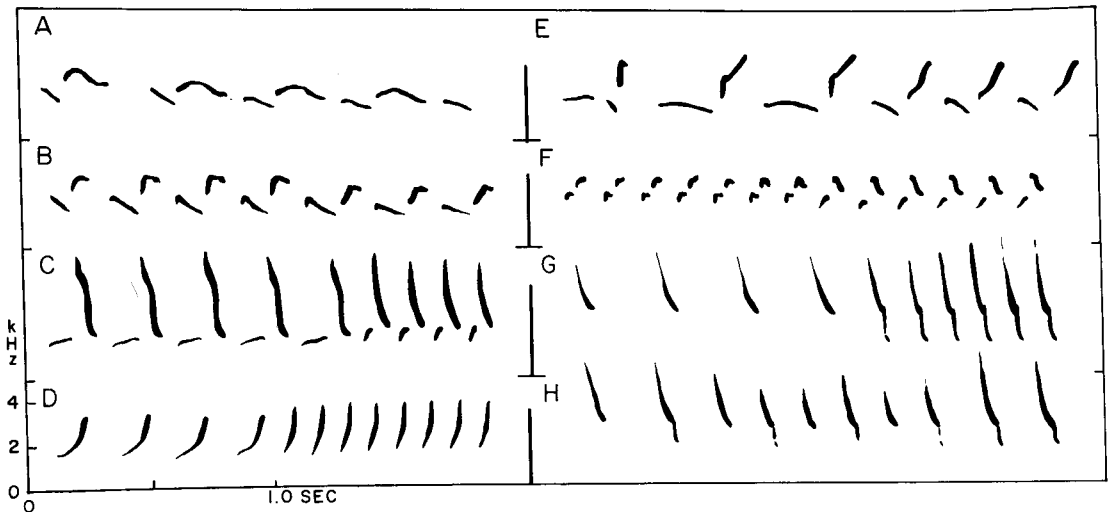


FIGURE 6. Drift of syllables in the songs of adult wild Cardinals. A to D show drift related to acceleration with associated decreases in frequency in A and B and increases in C and D. E and F show changes in overall configuration; G and H show the addition of parts to the syllables as the songs progress, although in H the additions are often incomplete.

The interaction of the calls and drift can be seen in portions of developing song or subsong of an individual reared without exposure to songs from other birds or recordings. The bout of subsong shown in fig. 5A begins with three chucks, (a), followed by a chip, (b), the pee of pee-too, (c), and the same followed immediately by a chip, (d). There follows a series of calls and varied elements which are more truly the beginning elements of song. These elements are not random expressions of sound but rather each is usually related to the immediately preceding element although they show some variation from it, and although some of the variation probably reflects lack of motor control. The structure of the chuck calls in the first sample is such that they are indistinguishable from other transient sounds with emphatic beginnings and endings, but their occurrence in the middle of syllables suggests they are indeed calls. In view of the two voices frequently heard in songs, a call and a song element could occur simultaneously from different sources.

The occurrence of the described calls was very noticeable in bouts of developing song in wild Cardinals even when they sang clearly recognizable syllables (Lemon and Scott 1966).

A later portion of a bout (fig. 5B) shows more immediate repetition and more gradual modification or drift. At this time there appear the forerunners of syllables of the final repertoire as shown in fig. 5C and D. In these later samples the calls are less obvious or entirely absent. Note also that each of the two

songs shown has two syllables of essentially the same slurring, as if one had developed through drift from the other.

#### DRIFT IN DEVELOPED SONGS

Certain forms of drift can be seen clearly in developed songs of Cardinals where the effects may be gradual (fig. 6A) or rather abrupt (fig. 6B-E). The result of the drift is often a form similar to the original as in these examples, or it may be a syllable more different as in fig. 6F where the second part of the syllable is eventually slurred downward whereas initially it was upwards. In fig. 6G, H, are examples where parts are added to syllables as the songs progress, although in H this addition was not always complete, as if reflecting incomplete facilitation of the singing process.

Where drift does not involve the addition or omission of parts, conceivably it could result through a change in the rate of singing such as one can alter the frequency/time relationships of recorded sounds by varying the speed of playback. When this is done changes in speed have directly proportional effects on frequency and inversely proportional effects on time periods.

In fig. 6C the drift in this two-part syllable involved both a shortening of the syllable and the interval between syllables as well as an increase in frequency (pitch). The intervals between syllables before the shift were about 0.06 s and 0.03 to 0.035 s after, while the durations of the syllables were approximately 0.21 s before and 0.11 s after. As an index of change

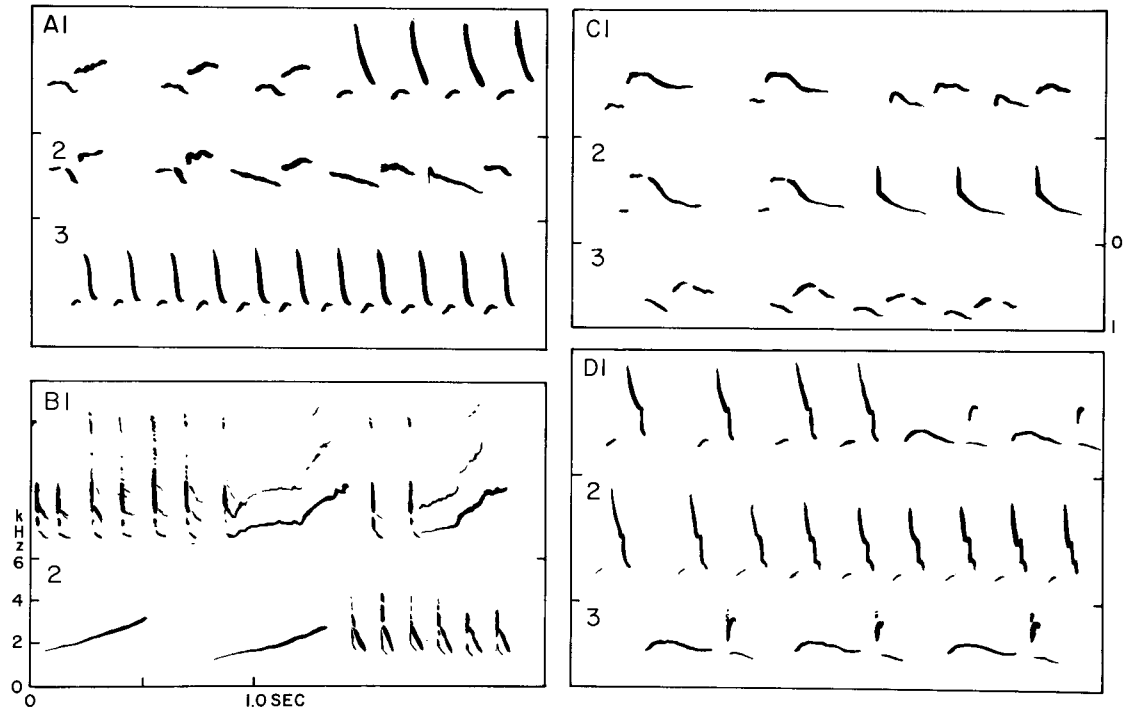


FIGURE 7. The reordering of syllable sequences. A1 is the combination of two syllable classes by a captive bird tutored with the two separate songs in A2 and A3. B1 is an unusual sequence of syllables in a young captive wild Cardinal which had some months in the wild before capture. The more usual sequence is in B2. C1 is an unusual combination in a captive bird as in B1 with the more usual combinations of the particular syllables in C2 and C3. D1 is an example similar to C1 but as recorded from a Cardinal in the wild.

in frequency only the lower limit of the second part of the syllable was measured, the value being approximately 1.9 kHz before the shift and 2.3 kHz after. The changes in both intervals and durations were roughly equal after the shift, being about one-half the original value, but the change in frequency was much less than expected by the simple acceleration model because the minimum frequency of the second part of the syllable should have been approximately 3.8 kHz instead of 2.3 kHz. Note also that the maximum frequency of the second part of the syllable is lower rather than higher after the drift.

In fig. 6D a similar situation applies. The durations of the syllables were reduced from about 0.13 s before drift to about 0.05 s after; although it was difficult to obtain accurate measures of minimum and maximum frequencies, it is clear that the increase in frequency was hardly proportional to the change in duration. Also, the successive intervals between syllables shortened progressively from 0.15 s to 0.08 s without appreciable change in the form of the syllable until the interval became about 0.06 s.

In the example of more gradual drift shown

in fig. 6A, the duration of successive intervals decreased, but the syllables became longer in time and lower in frequency. The maximum frequencies of the four successive syllables were 3.3, 2.7, 2.6, and 2.5 kHz, while the durations of the syllables were 0.28, 0.32, 0.35, and 0.37 s. The successive intervals were 0.17, 0.07, 0.06, and 0.07 s. Figure 6B shows another example of a drop in maximum frequency (from 3.4 to 2.9 kHz) and an increase in duration (from 2.1 to 2.4 s), although in this case the intervals also shortened (from 0.06 to 0.05 s).

Drift in developed songs may occur at different positions in consecutive songs. For example, the sudden change noted in fig. 6C in four successive songs by the same bird occurred between the following syllables numbered from the beginning of each utterance: 9-10, 12-13, 13-14, 12-13. In some examples, although not in this one particularly, the usual sudden change did not always occur even in relatively long utterances.

These examples show that changes in the duration and frequency of the syllable correlate with changes in the rate of singing. Sometimes, however, this correlation is positive and sometimes it is negative so that it is



not exactly as one would expect by the simple acceleration model. Of course, this model takes no account either of the situation where parts are added or omitted to syllables or of further changes in configuration. In conclusion, it seems possible that what is described as drift may result from several underlying influences.

Although the examples considered here have been taken from the developed songs of Cardinals, they reflect influences present earlier in the development of song. There is reason to believe that these influences play an important part in the development of new syllable types as is described in the next section.

#### SEPARATION AND REORDERING OF SYLLABLE TYPES

Once new variants of syllables have been produced by drift, they may be either separated and sung alone in separate song types or recombined with other syllables into new song types. This separation process can be observed in the developing song or subsong. Initially the calls and developing syllables are often presented in long series lasting several seconds overall but as development progresses the utterances shorten to an average duration of only two to four seconds in the Cardinal, and fewer kinds of syllables are sung in the same utterance. Thus the different syllables come to be sung either alone or with only one or two other types in the same song.

Examples of the separation of syllable types were seen in experimental birds provided with model songs containing two syllable types which the birds sang independently (fig. 7A). Evidence of this reordering of syllables was noted too in birds captured in the wild during their first winter. In fig. 7B1 is a different sequence of syllables sung by such a bird whereas the more usual sequence is seen below. At the time of recording, this Cardinal had not stabilized its singing completely and was still singing exceptionally long sequences. In fig. 7C1 is yet another example of an unusual sequence from a Cardinal captured in the wild, which was formed from syllables taken from two otherwise separate songs heard from other birds in the area (C2, C3).

This final sorting of sequences was noted also under natural conditions. Using symbols to represent the syllables (Lemon and Scott 1966) two young males were heard singing the following long utterances: the first sang utterances of AWCZCY and AWXSYCAW, the number of syllables not being recorded; the second sang  $W_1A_1W_{12}A_5T_5W_8$ , the sub-

scripts representing the number of repetitions. The usual sequences in this area were WBW, C, UY, with Z following at the end of many permutations, and for the second WBW, A, and T. Incidentally, both of these males accompanied these songs with series of calls.

Gradually more certainty in the sequences of syllables is established and less frequent permutations and combinations are eliminated. In one example I heard a wild male sing 35 permutations during his first season but only 18 in the second season, only about half of which were used commonly. Figure 7D1 shows an unusual combination from another bird consisting of two syllables usually sung alone, as shown in D2 and D3. The uncommon permutations which remain usually result from two syllables which are more often sung separately and less often in the same song type. Lemon and Chatfield (1971) showed detailed examples, particularly from one Cardinal called "Chambers," which included syllables designated A and T which were most often sung alone, but were also sung in combination as AT or TA and ATA.

Whether the permutations and combinations are determined by any rules relating to the forms of the syllables is difficult to determine. Most often a Cardinal achieves a combination used by the bird he copies, but often long syllables are associated with short syllables as in fig. 1B and C. This may partly explain why the permutations seen in these two examples occur widely throughout southern Ontario and the adjacent United States.

#### EMERGENCE OF NOVEL SYLLABLES

If the foregoing model is true, then we should expect to find in the repertoires of individual Cardinals syllables that are very similar and yet are used independently. Two examples are presented here that apparently reflect these processes.

Near Melbourne, Ontario, most Cardinals used two very similar syllables, examples from four individuals being shown in fig. 8A. The syllables on the left half of the figure were sung at rates of roughly three to four per second while those on the right were sung at nearly five per second. Often there were consistent differences in these syllables between individual birds, but among the group as a whole the only consistent difference was that the initial part of the syllables swept upwards more rapidly in those syllables sung faster. In some syllables, however, as seen in the first three individuals especially, certain portions were either present or absent.

Another example shows even more combina-

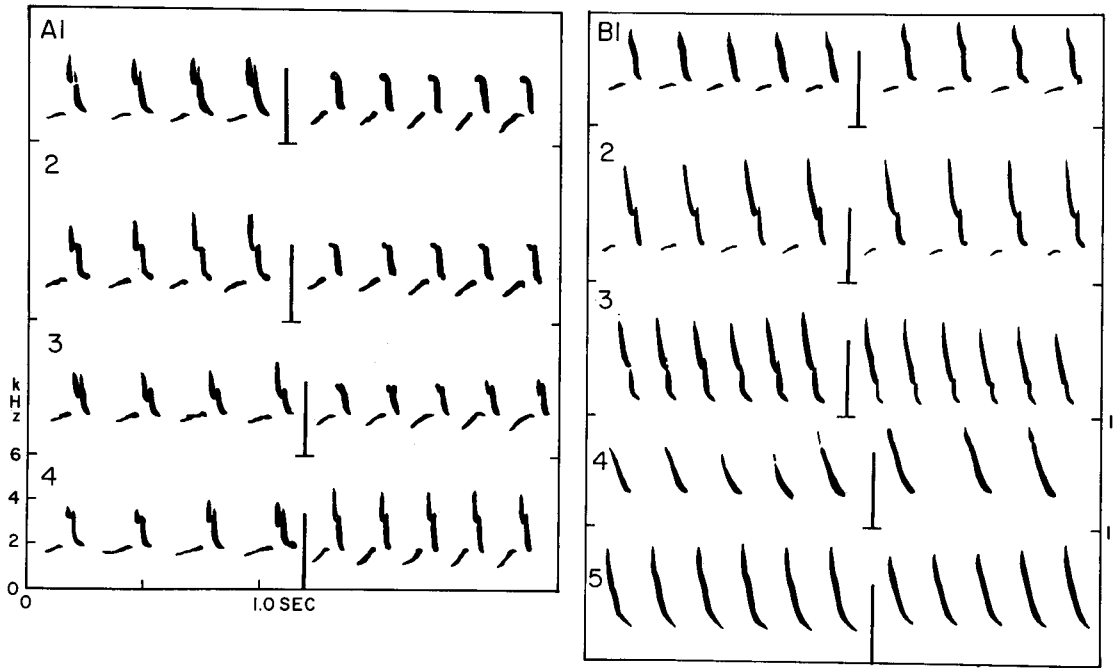


FIGURE 8. The emergence of new syllable classes in Cardinals. In A the songs are presented in pairs on the left and right, each pair being from one of four birds from Melbourne, Ontario. The two similar syllables were sung by each bird in separate songs. One consistent difference between them was that the syllables on the right side of A were shorter and were sung at a faster rate than those on the left. In B, songs are again shown in pairs, but in this figure the songs of each pair come from a different bird at London, Ontario. Each pair shows one of five arrangements of syllables differing by the presence or absence of common parts, B1 to 4, or in the fusion of parts as in 5. Birds in the locality usually had B1 and 2 and most also had one of the following three.

tions of variation, all being recorded from birds at London, Ontario, and living within a small area. Again a syllable similar to that in fig. 8A is shown in 8B1, with examples from two different birds. In this figure variation is seen more definitely as the presence or absence of certain parts of the syllable. Two parts occur in the syllables in B1; a third part is added in B2; one is absent in B3; two parts are absent in B4; while in B5, it appears that two parts have been fused. All male Cardinals in the area had at least two of the syllables and many had three.

It is possible that examples of a new syllable type copied by young neighbors shown earlier in figure 3 and shown again here in figure 8B4, arose originally when a Cardinal dropped some portions of a syllable already in the area. Alternatively the simplicity of this syllable in question suggests that it was improvised without regard to any model from another individual.

#### LIFE HISTORY ASPECTS RELEVANT TO DIALECTS

For dialects to occur, there must be some basis of separation of the local populations or at

least of establishing their integrity. Otherwise, constant mixing of populations would mediate against local peculiarities. Obviously geographic barriers may play an important role in some species. For the Cardinal in eastern North America, however, such barriers are often only minor, if present at all. Hence we must look to other factors.

Cardinals are essentially sedentary or non-migratory, although the adults may leave their territories in winter to join feeding flocks. They are highly loyal to their breeding territories from year to year; D. M. Scott (pers. comm.) has found that of 100 to 200 adults banded, none was found to change his breeding territory any farther than the distance of one territory from the original held. Further there is a relatively high return of adults from year to year, about 70%, obviously reflecting a relatively low mortality over winter. Of those birds acquiring territories for the first time, a large number are the offspring of local parents and may settle between 2 and 10 or 12 territories distance from the territory where they were reared (P. Smith, from D. M. Scott). Less detailed, but similar results were reported by Laskey (1944) in Tennessee closer to the center of distribution of the species.

TABLE 1. Certain fringillid species grouped according to the degree of conformity seen in the songs of males on immediately adjacent territories. Identical superscriptions (a to d) indicate species that are congeneric or nearly so. + or — indicates presence of dialects as determined by reports in the literature.

Group 1 High Conformity		Group 2 Moderate Conformity		Group 3 Low Conformity	
<sup>a</sup> Cardinal	+	Chaffinch	+	<sup>d</sup> Oregon Junco	—
<sup>b</sup> Pyrrhuloxia	+	<sup>c</sup> White-throated Sparrow	—	<sup>d</sup> Mexican Junco	—
<sup>b</sup> Rufous-sided Towhee	+	<sup>b</sup> Rufous-sided Towhee		<sup>b</sup> Brown Towhee	—
<sup>c</sup> White-crowned Sparrow	+	<sup>c</sup> Rufous-collared Sparrow	+	Chipping Sparrow	—
		Song Sparrow	+		
		Indigo Bunting	—		
		Rose-breasted Grosbeak	?		

Cardinals are relatively recent in Ontario, having been reported first in 1901 at Point Pelee at the western end of Lake Erie. From that area many Cardinals apparently moved into Ontario by following the Thames River, which offered suitable habitat for breeding and winter survival. As a result the first Cardinals occurred at London in 1915 and by mid-1930's they were fairly common in that area. Other Cardinals apparently entered Ontario via the Niagara Peninsula.

From an analysis of banding records principally from the United States, Dow and Scott (1971) found that 13% of 1500 recaptures were outside the 10 minute block of latitude and longitude in which they were banded. Of course these data do not indicate what proportion of the population actually disperses. More birds dispersed during their first year than during their second and they travelled farther. Most of these dispersed less than 30 miles but the upper limit was 550 miles. Hence, most Cardinals disperse to areas where some of the songs will be very similar to those they had heard from their parents. Yet the occurrence of some local differentiation at even shorter distances (Lemon 1966), indicates how effective some sources of differentiation of song must be, particularly the modification through drift.

Although many males acquire their territories and mate successfully during their first full season after leaving the nest, some young males fail to acquire mates and in subsequent years they are found on a different territory. Other young males appear to wander through their first potential breeding season without holding a territory, at least permanently. It has been suggested that for other species at least, young birds might be influenced in their choice of nesting area by the similarity of the songs of that area relative to those of the selecting individuals' home area. It is important to note that because of the widespread distribution of much of the repertoire of Car-

dinals (Lemon 1966), a member of this species would have to travel perhaps some hundreds of miles to get to an area where most of the repertoire is unfamiliar. Of course this need not be so with other species.

In conclusion, the basis of dialect integrity in Cardinals is found principally in the habits of territorial fidelity and a low rate of annual mortality. Dispersal occurs, but most often over short distances. Over longer distances it probably accounts for widespread similarities of song as noted with figure 1.

#### DEVELOPMENT OF DIALECTS IN OTHER FRINGILLIDS

Having considered the development of dialects in one species in some detail, I wish next to examine other species, first dealing with those of the same family, particularly since the fringillids have been studied better than any other group.

We have seen that in Cardinals the situation with regard to dialects is complex because some syllables and song types are widespread while others are local. This raises the question as to whether there is any precise definition of dialects. Actually there is not. I shall not review in detail the literature on this matter because some authors take account of whole song types, or just certain syllables at certain positions in the song types. Also, the birds' own assessment of differences in songs is not likely to coincide with ours. Indeed, in playback experiments we sometimes find that species differ in their responses and in ways that are sometimes surprising. Some examples will be cited in the next sections.

My primary concern here is to account for the conformities and non-conformities in the repertoires of birds on neighboring territories and in other localities. Therefore, we need to consider to what extent different species show conformities; we will also consider the interpretations of the researchers on whose studies the analysis is made as to whether the species

show dialects. The assessment of the degree of conformity in the songs of birds on neighboring territories is here made according to three levels, high, medium, or low. This arrangement is arbitrary and does not take account of the wide differences in the sizes of the repertoires. A summary of the species considered (table 1) also shows the occurrence of dialects.

Those species showing high conformity have both syllables and sequences of syllables in song types essentially identical. Those in the medium category have some syllables in common and possibly also some sequences of same, while those in the low category apparently have no syllables in common and hence no sequences either. The degree of conformity and the occurrence of dialects need not agree, for there may be widespread conformity without local differences. Closely related species may occur in different groups, supporting the view that the bases of song development are the same although reflecting differences in emphasis.

#### GROUP 1. HIGH CONFORMITY

This group includes species clearly considered to have dialects. These are the Cardinal and its close relative, the Pyrrhuloxia (*Pyrrhuloxia sinuata*), the Rufous-sided Towhee (*Pipilo erythrophthalmus*), and the White-crowned Sparrow (*Zonotrichia leucophrys*). The first three species have several song patterns per bird, each consisting of repetitions of one to three syllable types; both syllables and their permutations in the songs are strikingly similar among different individuals. Cardinals have 9 to 12 commonly used songs, most often of two syllable types (Lemon 1965, Lemon and Herzog 1969); Pyrrhuloxias have 10 to 15 songs of mostly one syllable type (Lemon and Herzog 1969); Towhees in western United States have nine songs or sometimes fewer, each consisting of two syllable classes (Kroodsma 1971). The White-crowned Sparrow differs with usually only one or sometimes two songs per bird, each beginning with whistles of sustained frequency followed by two trills of repeated and rapidly slurred syllables (Marler and Tamura 1962).

With Cardinals and White-crowned Sparrows, playing songs that are obviously different from those of the locality concerned evokes significantly less response than the local song (Lemon 1967, Milligan and Verner 1971). In the first three species, individuals frequently interact by matching each other's choice of song type (Lemon 1968b, Lemon and Herzog 1969, Kroodsma 1971).

Copying as the basis of conformity has been clearly established in the White-crowned Sparrow (Marler and Tamura 1964, Marler 1972). In this species, however, copying appears restricted to patterns heard only during the first one to seven weeks. Some of the songs developed by isolated White-crowned Sparrows in the absence of models from other birds are reminiscent of the songs of White-throated Sparrows (*Zonotrichia albicollis*) in being comprised entirely of whistles of sustained rather than modulated frequency. Hence there may be some inherited influence on this aspect. Some of the published audiospectrograms have examples suggestive of drift in this species. The importance of auditory feedback for normal song development in White-crowned Sparrows was demonstrated by Konishi (1965a). Development has not been studied in the Pyrrhuloxia or the Rufous-sided Towhee, nor is drift immediately evident from the published audiospectrograms. However, many of the syllables used in separate songs are strikingly similar, as if from a common origin.

Information on population dynamics is available from White-crowned Sparrows. They may be either migratory as in populations in the Sierra mountains of California (Morton, Horstmann and Osborn 1972), but in the San Francisco area they are often permanent residents (Blanchard 1941). In both areas there is a high degree of return to the same territory in successive years. The annual mortality of adult birds in both areas is roughly 50%.

#### GROUP 2. MODERATE CONFORMITY

This group contains species that have considerably more individuality than was shown in the previous group, but some of which still show evidence of dialects. They show more conformity than species in the third group to be considered.

The Chaffinch (*Fringilla coelebs*) of Europe has been considered to exhibit dialects but there is also apparently a considerable amount of individual variation. One problem in assessing the situation is that published audiospectrograms are limited and the principal study on geographic variation (Marler 1952) was done by ear. Each male has two to five song types each consisting of two or three phrases of repeated syllables followed by a non-repeated terminal flourish. The songs of neighboring Chaffinches may be sufficiently similar to exhibit the matching characteristic of Cardinals and towhees (Marler 1956), but there is also much individual variation with the result that the chief similarity is in the terminal flourish.

In studies of song development, Thorpe (1958a, 1958b, 1961) and Nottebohm (1968) demonstrated that imitation was the chief basis of similarity among Chaffinches and that isolated individuals developed song patterns which in complexity of syllable structure and sequence were clearly related to the exposure that they had received. Those birds without exposure improvised songs with very simple rapidly slurred syllables and simple terminal flourishes. The period of sensitivity seems similar to that of Cardinals, lasting normally until motor development in the first spring after leaving the nest. Nottebohm (1969a) subsequently showed that the development could be delayed by castration but may be resumed with injections of testosterone. There is evidence that Chaffinches exhibit subsong each spring as adults, but it is probable that this reflects low motivation rather than true development of song. There is evidence also that in subsong, Chaffinches may incorporate sounds employed by other species but that these are excluded from the final repertoire (Thorpe 1961). Drift is not explicitly described in the species but is indicated in the audiospectrograms.

Two members of the genus *Zonotrichia* fall within this group, the White-throated Sparrow of eastern North America and the Chingolo or Rufous-collared Sparrow (*Z. capensis*) of South America. The songs of the White-throat consist almost entirely of whistled syllables of sustained frequencies, although successive syllables may shift in frequency relative to each other. As noted, sustained whistles are characteristic of White-crowned Sparrows, and they are also a feature of other North American members of the genus, the Golden-crowned Sparrow (*Z. atricapilla*), and Harris' Sparrow (*Z. querula*). The Chingolo does not show this tendency, though, for its songs begin with varied sequences of non-repeated slurred whistles, followed by a trill of rapidly slurred syllables.

Neighboring Chingolos frequently differ in their initial parts of the songs, although there are instances where one form may predominate locally, but the claim of dialects in this species (Nottebohm 1969b) is based primarily on the terminal trill, which does vary locally (see also King 1972).

White-throated Sparrows offer a different situation. In the region of Algonquin Park, Ontario, most individuals follow a few sequences of amplitude-modulated whistles. However, in coastal localities in New Brunswick there is much greater individuality, with the result that no particular sequence predominates

(Lemon and Harris 1974). The syllable classes are the same in this species over wide geographic areas (Borror and Gunn 1965) and are much the same in the two areas just mentioned. Hence, in this species although neighbors may or may not share the same syllable sequences, if they do, there is yet no clear evidence of dialects, although significant differences occur in the frequencies of syllables.

Playback experiments in Algonquin Park revealed greater responses to songs from birds on non-neighboring territories than to those of immediate neighbors which were familiar to the experimental subjects (Falls 1969). The same applied to birds in New Brunswick, which also failed to show any differential responses to songs from other localities (Lemon and Harris 1974).

The Song Sparrow (*Melospiza melodia*) is important in our considerations for it has been fairly well studied, its organization indicates an intermediate position in its degree of conformity between neighbors and the results of these studies have led to some confusion.

Song Sparrows live in open areas with relatively small trees, shrubs, and patches of grass; in such areas near open water they often occur in high densities with territories much less than 1 acre in size (Tompa 1963, Harris and Lemon 1972). Each male has several song patterns, up to 15 in California (Mulligan 1966) and up to 9 or 10 in Quebec. The songs are complex, perhaps the most complex of all fringillid songs. They consist of many varied syllables, some whistled with many sub-parts, some tremolos, and some very brief sounds. Some syllables are repeated in trills. The same syllable may occur in different songs of the same bird, but this applies only to a small portion of the total of an individual's repertoire. Male Song Sparrows on neighboring territories rarely have identical songs, but they share some syllables (Borror 1965, Mulligan 1966, Harris and Lemon 1972).

Although dialects in Song Sparrows are not as evident to human observers as those in other species, Song Sparrows have shown significantly less response to songs of their own species from only a few miles distance as compared to songs from the experimental subjects' own locality (Harris and Lemon 1974). This difference in response was more noticeable than that to non-neighbors' and neighbors' songs from the subjects' own localities, in spite of the obvious individual variation in the songs (Harris and Lemon, in preparation).

Mulligan (1966) studied the development of song in this species. Some individuals were placed while in the egg under an incubating

Canary, (*Serinus canaria*) and were subsequently reared by Canaries, while others were hand-reared after having been taken from the nest after hatching. These individuals were eventually reared either separately or together in groups, with no major differences in the results. Mulligan concluded of the songs developed by these birds that, "If one were to mix these songs with recordings from wild Song Sparrows, it would be difficult to distinguish them from the latter." However, it is also clear that the repertoires were smaller than those of wild birds, both in numbers of syllables and song types, and there were additional quantitative differences as well. Also, three siblings reared by the Canaries sang quite different songs. There was no attempt to assess whether the syllables were identical in form with those of the parents or members of the wild population (Mulligan, pers. comm.), although some presumably could have been. Some individuals who were allowed to hear tape recordings of Song Sparrow songs showed clear evidence of copying. This fact plus the occurrence of similar syllables in immediate neighbors in the wild gives strong evidence that imitation normally plays a role in the development of song in this species. One individual who was deafened before song development eventually sang, but his repertoire was relatively small and the syllables differed in quality from those developed by other isolates and wild Song Sparrows.

Song Sparrows in the San Francisco area where Mulligan studied are highly sedentary and distinct populations have been recognized. From year to year there is little change in the territorial positions of particular males (Johnston 1956). Dispersal of young is often over short distances with a median of 185 m, about 100 m less than in Ohio. In Ohio, where Song Sparrows are more migratory, there is also a high incidence of return to the same territory, but there appears to be more movement than is seen in Cardinals (Nice 1937).

In the literature, the Song Sparrow has been treated as a special case with a development of song different from that of other fringillids (Marler 1967, Nottebohm 1972b). As an example, Konishi and Nottebohm (1969) wrote, "These birds produced songs indistinguishable from the average song of wild Song Sparrows. . . . This is, perhaps, the first and only reliable study of passerine birds in which the audiospectrograms did not show any qualitative difference between isolate and wild-type songs." Actually, audio-spectrographic evidence showing syllables of isolated Cardinals remarkably similar to certain syllables of wild

Cardinals was published earlier (Lemon and Scott 1966). This point aside, however, their statement implies far more than has been demonstrated.

My own interpretation is that Song Sparrows are no different from other fringillids, all of which show evidence of copying and improvisation. Where they differ is in the degree to which each of these influences prevails. Probably Song Sparrows in isolation actually develop some syllables essentially identical to those of their parents or others. But as noted, wild Song Sparrows share only a portion of their repertoires. Also, the size of the repertoire and the complexity of the patterns produced help to obscure the similarities with other species.

Another species considered in this group is the Indigo Bunting (*Passerina cyanea*). Members of the genus vary in the number of syllable types per song and in the tendency to repeat the syllables within the song (Thompson 1968). Indigo Buntings usually have one song type per bird, consisting on the average of four syllable types (called "figures" by Thompson) which are repeated one to three times each. In local populations, the number of syllables in all individuals together seems relatively constant at approximately 60 to 80 (Thompson 1970, Shiovitz and Thompson 1970, Emlen 1971a). However, none of these syllables is common to all birds in each population; in fact, the mean number of individuals in which a syllable occurred in a sample of 38 to 46 buntings in Michigan was about 6. Not surprisingly therefore, there is relatively little sharing of entire sequences of syllables, which in the same samples was limited to less than 25% of all birds. In another sample from New York from 36 birds, the figure was less at 7%. Where the syllable sequences were the same, more often than not, the buntings sharing them held contiguous territories. In spite of the large number of syllables in each sample there was about 90% sharing among each of three sites in Kentucky, New York, and Michigan. In this respect this species is like the White-throated Sparrow.

Within a population of buntings, many of the syllables are similar, as if derived from the same origin. Shiovitz and Thompson (1970) cited a case of a bird which had two very similar syllables yet apparently employed them differently in the song. Evidence from buntings reared under controlled conditions (Rice and Thompson 1968) indicates that the details of the syllables are normally copied from other birds, and isolates develop songs which exhibit syllables different from those in the

wild. The captive birds showed ability to copy throughout the spring after leaving the nest for a longer period of time than observed in captive Chaffinches and Cardinals. Whether such is the case in the wild is not known.

Thompson (1970) suggested that the similarities of syllables are the result of copying that may begin when the young birds leave the nest but may also continue the following spring, when they settle on a territory. He ruled out the possibility of effect of the territory while the buntings winter in Central America and during their return migration. It is possible that some young return to territories adjacent to those of their fathers, but he thought this unlikely as a general rule.

Perhaps more so than with Cardinals, young Indigo Buntings do not necessarily retain the territories first acquired, but instead change in the second year. This could account for the relatively low sharing of sequences in a population. The individuality in the songs is apparently involved in the markedly greater response levels to songs of non-neighbors than to songs of immediate neighbors (Emlen 1971b).

Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) sing songs with syllables of variable order, which are predictable on first and second order Markov chain models (Lemon and Chatfield 1973). The repertoires may have over 20 syllables per bird, roughly a third of which may be common to neighbors.

Konishi (1965b) reared Black-headed Grosbeaks (*Pheucticus melanocephalus*) in isolation and also deafened one. The isolates were fairly normal in their syllables although they did not sing any of the syllables found in the single wild individual studied. The deafened bird also sang but his syllables were not as stable as those of the birds with hearing.

Rufous-sided Towhees may also be considered in this group as well as in that of high conformity, for in the eastern United States they show considerable individual diversity in syllable sequences, although some syllables are shared (Borror 1959b).

### GROUP 3. LOW CONFORMITY

This group contains species in which individual variation clearly predominates over group similarity. The main examples are from the genus *Junco*, which is considered closely related to *Zonotrichia* and *Melospiza*. Two species studied, the Oregon Junco (*J. hyemalis oregonus*) (Konishi 1964a) and the Arizona Junco (*J. phaeonotus*; Marler and Isaac 1961) differed in that the former usually had one

syllable type repeated in each song while the latter employed three to four syllable types per song. Although accurate samples were not taken, some individuals have more than one song type. Syllables in populations show a high degree of individuality, no two birds being found to have the same. Therefore, no evidence of dialects could be found.

The Oregon Juncos raised in two groups in two seasons each developed songs, the larger repertoires occurring in the larger group (Marler et al. 1962). Some of the songs consisted of two syllables. In the smaller group, the syllables differed among all the birds, whereas in the larger group, at least three syllables were shared by two or three birds. These birds also showed evidence of copying songs from sparrows and towhees. Some individuals also developed new syllables during their second season, based on material copied from others, sometimes of another species, or modified from a syllable sung previously. At least one published audiospectrogram shows evidence of drift.

In the Arizona Juncos, the situation was somewhat different, for most juncos reared together had songs of fewer syllable classes than those of the wild population (Marler 1967). Birds reared together developed songs with a number of syllables comparable to those in the wild population, while an isolated individual had fewer syllables per song. There was evidence of copying among the group reared together as well as in the bird exposed to recorded songs.

The importance of auditory feedback in the development of song in these species was shown by Konishi (1964b), and deafened birds lacked stability in the syllables developed. Differences between the species occurred but these may reflect differences in the experimental procedure (Konishi and Nottebohm 1969).

Hence in these species we see not only a high degree of individual variation in natural populations, but also evidence of copying in captive birds. Therefore, the juncos do not differ radically from the species previously considered. The significance of the individuality of song is not known. I have observed singing by flocks of migrating Slate-colored Juncos (*J. h. hyemalis*) where there might be an emphasis on individuality. The rapid modulations of the syllables also suggest that the prime information used may not be frequency but rather amplitude modulations in time.

Other species such as the Brown Towhee (*Pipilo fuscus*) (Marler and Isaac 1960) and

the Chipping Sparrow (*Spizella pusilla*) (Borror 1959a) have been described as showing much individual variation but little is known of the development of their songs.

#### COPYING, DRIFT AND CALLS IN SONGS OF OTHER SPECIES

We may ask how generally the results so described apply to song birds other than fringillids. Copying has been shown in a variety of species (Lanyon 1960, Thorpe 1961, Marler and Hamilton 1966). The older literature also refers to innateness of song, often meaning the general characteristics of song and not necessarily the precise configurations of the syllables, although there may be some valid exceptions. A few relevant examples including aspects additional to copying are discussed here.

Copying combined with improvisation of new syllables has been well documented in the European Blackbird (*Turdus merula*) (Thielcke-Poltz and Thielcke 1960, Hall-Craggs 1962). Calls are also important in development. The organization of the song is probably similar to that of fringillids in that although the repertoire is large, the sequences are often highly ordered. A highly ordered sequence is seen also in the close relative the Mistle Thrush (*Turdus viscivorus*) (Isaac and Marler 1963), which also shows local variations of repertoire. Blackbirds also show frequent alternations between syllable classes (Todt 1970), somewhat in the same form as the alternations of song types in short bouts by Cardinals.

Dialect variation is claimed in Short-toed Treecreepers (*Certhia brachydactyla*) (Thielcke 1969, 1972). Drift is evident in successive syllables with intergrades occurring between the most different syllable types. Calls appear to be the forerunners of syllables in *Certhia* and the syllables of *C. brachydactyla* and *C. familiaris* are very similar; some calls and elements in songs appear to be homologous (Thielcke 1964).

In the Old World warblers of the genus *Phylloscopus* excellent examples of drift can be seen (Thielcke and Linsenmair 1963). Indeed much of the variation seen occurs about a basic plan somewhat similar to the additions or subtractions to the syllables noted earlier in Cardinals.

Indian Hill Mynahs (*Gracula religiosa*) (Bertram 1970) not only show high conformities in the calls among neighbors relative to birds of other localities, but also the conformities are confined to members of the same sex. Males and females have repertoires

of calls that are apparently the counterparts of territorial songs. Neighboring males share much of their repertoires independently of the females. Males or females when interacting often select calls similar to those sung by their partner, but when mates interact they usually select calls that are different. In development it appears that partners actively avoid copying the calls of the opposite sex. How recognition of a Mynah's sexual role is determined is not known and the species are monomorphic.

In certain African shrikes, males and females develop special repertoires by which they interact with great precision. Although the repertoires are often unique, the uniqueness in some species at least is primarily in the sequences of syllables in the songs; birds of a locality may share a common repertoire of syllables (Thorpe 1972, Wickler 1972). Thorpe attributed to shrikes an ability to improvise syllables based on musical principles.

African indigobirds (Viduinæ) exhibit song dialects copied partly from their brood hosts as well as from their own species (Payne 1973). Payne attributed differences between birds and dialects to errors in copying although evidence seems limited. Drift as a basis of syllable variation seems evident in Splendid Sunbirds (*Cinnyris coccinigaster*; Grimes 1974).

#### SOCIAL INFLUENCES ON SOURCES OF MODELS

One other important aspect in the development of song in birds is that of the social influences on the selection of material to copy. The selection of material can be important in maintaining species isolation, especially for close relatives, the songs of which are often rather similar, probably because of common inherited influences as well as originating from a particular repertoire. Examples of similarities are seen in creepers (Thielcke 1964), Cardinals, and Pyrrhuloxias (Lemon and Herzog 1969).

There are many examples where birds fail to observe their species limits but instead copy other species, sometimes unrelated. Such examples occur in fringillids (Borror 1968, Baptista 1972), meadowlarks (*Sturnella*) (Lanyon 1957), and wrens (*Troglodytes* and *Thryomanes*) (Kroodsma 1973). In some related species, however, copying the other species' repertoire may be useful in repelling them, as may be the case in tits (*Parus*) (Thielcke 1969) and creepers (Thielcke 1970, 1972).



Mimicry of other species or sources has occurred among captive birds reared with others of a different species (Scott 1902, Lanyon 1960). Of course, it also occurs naturally among some species such as the Mockingbird (*Mimus polyglottos*), which has a large repertoire (Borror and Reese 1956). Mimicry by nest parasites of songs and calls of their host species occurs regularly in African viduine finches (Nicolai 1964, 1973, Payne 1973).

These results indicate that the association of auditory and visual stimuli is an important basis of determining which sounds a species copies, except in the mimics like the Mockingbird. Confirming experimental evidence of this conclusion comes from the studies of Immelmann (1969) in the cross-rearing of estrildid finches. Zebra Finches (*Taeniopygia guttata*), when reared by Bengalese Finches (*Lonchura striata*), copied songs only from the foster father even when they could see and hear their true father. The only exception to this was a case where a Zebra Finch began to assist the rearing of the young wherein they copied from the conspecific parent.

#### A GENERAL INTERPRETATION

The song repertoires of birds may be considered a multi-dimensional form of behavior. Some dimensions are the numbers of syllables of the repertoire, and the sequential and temporal rules governing them. Another is the degree to which the repertoires conform among birds of the same species, and yet another is the geographical distribution of the previous dimensions. Our main concern here is with the last two, especially with the behavioral bases for the conformities and non-conformities among the songs of birds on neighboring territories and in different localities.

Whether dialects occur depends in part on the degree of conformity in the songs of neighbors and also on the extent to which the local populations diverge. To some extent, the concept of dialect is artificial, for many citations of dialects fail to consider the actual geographic distributions of the patterns; that is, the differences between localities could be disjunctive or clinal. A further complication is that derived from dimensions of the repertoires cited above. As a result, situations such as that described by King (1972) for Chingolos may be so complex that the concept is difficult to apply. Instead, one sees clines, mosaics and other disjunctions, and even changes of repertoire with the season. The dialects as defined by researchers may not

TABLE 2. A schema relating variation in bird song to developmental processes.

A. NATURAL VARIATION IN REPERTOIRES	
Conformity $\longleftrightarrow$ Individuality	
B. DEVELOPMENTAL INTERACTIONS	
Imitation $\longleftrightarrow$ Improvisation	(Time-Dependency of Copying,
(Copying)	Dispersal of Young, Drift,
	Reordering of Syllables)
C. CONSTRAINTS	
1. Sensory—motor	
2. Social	
3. Behavioral—Ecological	

agree with the birds' own perception of the songs they hear. Hence, to human observers the great diversity of song in Song Sparrows obscures differences between populations that are apparently evident to the birds themselves as judged by their lessened response to foreign songs (Harris and Lemon 1974). In spite of these criticisms, the concept has brought attention to the bases of variation of repertoires and their behavioral and evolutionary significance (Thielcke 1970).

Local differences of song may fail to appear in two cases: either the conformity is widespread, or there is practically no local conformity at all. White-throated Sparrows may show both features, tending more toward conformity in the repertoire of syllables and their sequences in the center of their range in Ontario, but toward individuality at the periphery in New Brunswick; in both areas they use essentially the same repertoire of syllables. Somewhat similarly, the Indigo Bunting populations seem to have the same repertoires in New York, Kentucky, and Michigan; however, the songs of individuals usually differ except for some pairs and trios of buntings which are most often on immediately adjacent territories. In this case, the movement of males to new territories in their second breeding season may be the basis of the individuality established after copying has occurred in the first season.

In these two species, the limits to the variations of the syllables may reflect certain limits on the particular frequency-time configurations. In White-throated Sparrows, the songs are varied primarily by amplitude modulations only. The result is a repertoire of only five or six syllable classes in a population. Indigo Buntings modulate their whistles in the frequency dimension also, so that the number of syllables is much larger. There is a caution about assuming limits to the amount of varia-

tion, for the assessment of the number of syllable classes is somewhat arbitrary as the classifier recognizes distinct groups. If the evidence were considered more thoroughly, variation might seem more continuous. In Cardinals, classifying syllables within a local population is fairly easy, whereas the syllable classes often intergrade between localities (Lemon 1966). In spite of this comment, syllables in different geographic areas are often similar, apparently because of the interaction of imitation with dispersal.

The sharing of repertoires by neighbors on adjacent territories is obvious in some cases and includes most or all of the repertoires; in other cases it is less obvious. The extent to which the conformity exists is seen as the outcome of two main developmental interactions, imitation and improvisation (table 2).

Imitation is the copying, usually by young, of the songs of adults, often the copiers' own parents. The copying most often occurs in the first few months of life and perhaps in most species is confined to the period that ends with the motor development of the songs. Therefore, it coincides approximately with the time when young males first acquire a territory. Imitation is also influenced by social constraints which result more often in the exclusion of sounds from individuals and members of species of no social consequence to the copying individual. There also appear to be sensory and motor constraints on the kinds of material that may be copied by particular species. This might lead to the conclusion that there are "species-specific" differences which determine the variation among species. No doubt this is true to some extent. For example, the hearing of juncos and House Sparrows (*Passer domesticus*) differs considerably (Konishi 1969, 1970). However, closely related species, especially of the same genus, are not likely to differ much in their sensory or motor systems, particularly when such systems must remain flexible enough to handle variation resulting from experience.

Individuality in the repertoire occurs from several causes, chiefly generating new syllable types through drift and reordering of syllable sequences in the songs. The models used for the syllables may be those provided by other individuals and copied from them, or they may arise through gradual development based on drift applied initially to calls. Other factors influence individuality, particularly the interaction of copying with dispersal, with the temporal limits on development, and with the relative annual changeover of populations.

Development of song is a complex process

that involves the replication by the motor system of a model obtained normally through audition. Auditory feedback plays a dominant role in the development of the songs as shown by experiments where lack of audition has been forced upon a bird either through deafening or exposure to very loud noise (Marler et al. 1972). The importance of hearing is undoubted, but proprioceptive information should also be available during development of the motor patterns, not only from the syrinx, but also from the rib cage musculature, and may be the main source of information for those birds which develop their songs after deafening. There is a suggestion, too, of proprioception from the results of sectioning of mixed nerves to the syrinx. Sectioning of the left nerves in Chaffinches (Nottebohm 1970, 1971) greatly distorts the sounds. In White-throated Sparrows (Lemon 1973) there is evidence of not only qualitative distortion but also of changes in the durations of the syllables, especially at the beginning of the song.

It has been suggested that there is an innate template which is the basis of the songs of deafened birds (Marler 1964, 1972, Konishi 1965a). Konishi suggested that the song developed by a deafened Song Sparrow was evidence of such a template, but it could also have developed through proprioception and improvisation. Also one might ask what becomes of the innate template in birds which develop their songs normally.

The concept of a template that is innate or otherwise is also misleading because it does not distinguish between sensory and motor information. During development, when a bird reproduces the song it has heard from another individual, it is reproducing information that is basically sensory in origin. If the model of development presented here is correct, however, replication may involve initially the application of this information to the calls. The calls in some deafened birds appeared to develop normally (Dittus and Lemon 1970) and on this basis they may have been innate, in the sense of the classical isolation experiment (Lorenz 1965). Other evidence suggests that experience is involved in development of calls (Nottebohm 1972a, Mundinger 1970), and it is possible that the calls which occur while the birds are still in the egg have an influence which is essential to normal development of those calls which appear later. In a bird which is deafened, these calls could be the basis of improvisation and might be described as the innate template. This template, however, is motor, not sensory, although it may be con-

verted to sensory information via feedback. The template concept also fails to recognize the importance of drift, reordering of syllables, and repetition of syllables, all of which are probably mainly motor in their control.

Much of the research on development discussed here, including my own, was done under the influence of the historical context, where one of the prime questions of ethologists was whether behavior was innate or learned. There has been much discussion of this problem, which need not be reviewed here. As far as the studies of development are concerned, however, the very nature of the question supposes answers in the same framework: namely, that song is either innate or learned. Thus observations made were applied to this framework, whether the application was valid or not.

There have been claims that song or parts of song are innate (Lanyon 1960). It is not clear in these examples though, how the innateness is derived. Is it through the coding of information in the central nervous system which programs muscle contractions in the syrinx and associated respiratory structures, or is it related also to the structures of the syrinx?

For example, the crows of domestic fowl (*Gallus gallus var. domesticus*) (Konishi 1963) and the calls of Ring Doves (*Streptopelia risoria*) (Nottebohm and Nottebohm 1971) appear normal even in birds deafened at an early age. These particular calls, however, should not be equated to the song elements of oscines, for the former often have strong harmonics and show little or no rapid and highly precise frequency modulation so characteristic of song elements in the latter. There are exceptions to this. Certain alarm shrieks of oscines when held in the hand have strong harmonics, (e.g. Cardinals) (Dittus and Lemon 1970), as do the sounds produced by oscines after the hypoglossus has been sectioned, shown especially clearly in White-throated Sparrows (Lemon 1973). These last two examples show the lack of precise control of the syrinx so characteristic of song syllables. Other examples are the short contact calls or chips of Cardinals (Dittus and Lemon 1970). Although more sophisticated analysis may yet reveal some differences, these calls seem normal in deafened birds. But this normality may simply reflect the relative simplicity with which the sounds can be produced, that is, a quick passage of air over tightened membranes, followed immediately by damping, and the frequency structure is probably related to the dimensions of the membranes as well as to the tension applied to them.

My point is that the apparent innateness in the calls of fowl and doves may reflect a much simpler situation than in oscines where normally the song elements require a much higher level of neuromuscular control. Indeed, probably this is the reason why such innateness is not readily apparent in higher oscines. To make a crude analogy, the natural sound of a violin string can be obtained when plucked by either a musician or an untrained novice, but only the musician can make the strings vibrate in a harmonically controlled fashion over a length of time.

This discussion need not pose a threat to the recognition that some aspects of vocal behavior may be common to oscines and others, such as drift in calls of chicks, although the underlying bases of drift may be somewhat different. The occurrence of drift in fowl should also raise the question of how it is related to the calls of adults.

Of related practical problems, one is that the standards for comparing the songs of experimental birds have not been chosen consistently. The best standards would surely be the songs of the experimental birds' own parents, and barring those, of other members of the parental populations when conformity in such populations is obvious. In many cases members of the population are not a valid standard because of the large degree of individuality in the songs of some species, so the idea of an average song of a species may hardly apply.

Also, experimental birds often vary greatly in their responses under controlled conditions and the unnaturalness of the tutoring from a tape recorder does not help.

Much of the confusion in the literature lies in the nature of song itself and in the fact that repertoires may be so complex that simple understanding is difficult, as in the Song Sparrow. Also, even closely related species differ greatly in the size of the repertoire and the degree of conformity. There seems little doubt that the size of the repertoire is determined to a great extent by inherited influences, although proof is limited to obvious differences between species. However, as noticed in Cardinals, a strong tendency to conformity has a restrictive influence on the inclusion of certain patterns from unimportant individuals or of improvised models. On the other hand, in experimental situations where the material available to copy is relatively low, a bird may include material that would otherwise be excluded. Further, where social stimulation is missing, the repertoire may never develop to its normal extent.

## SUMMARY

1. Individual songbirds frequently share, in varying degrees, their repertoires with others on neighboring territories. Hence birds within a locality show some degree of conformity in their songs. At the same time, repertoires differ between localities, giving expression to the term "dialect." This paper considers how dialects form, illustrating first with the Cardinal, and then considering other species, especially fringillids.

2. Conformity is seen principally as the result of copying by young, a process which is limited in most species to a period from the time when the young leave the nest until the motor patterns develop the following spring. Reared without experience of song, birds develop some features such as general structures of syllables and repetitions of syllables and songs. These facts suggest inherited motor and sensory influences.

3. Individuality of songs is determined by a variety of influences, the major ones being: the interactions of the time-limited copying process with dispersal of the young arising from the area of rearing to their new place, the active modification of syllables through drift, and the reordering of syllables within songs. These individual characters are in turn copied by young males. In this way local peculiarities are built up within a population.

4. The integrity of a local dialect is maintained in Cardinals by a high return of adults to their territories from year to year and low annual mortality. Also, young often disperse to relatively short distances from home nests. However, many individuals disperse over considerable distances and probably introduce novel patterns to certain localities. Such dispersal also probably has the countering effect of making some patterns widespread over fairly large areas as in Ontario.

5. In other species, conformity varies from high to low, although in all groups there is evidence of copying and improvisation. The differences depend to a great extent on which tendencies dominate.

6. A model of development based on calls, copying, improvisation and reordering of syllables is presented. This model is seen to apply to oscines in general.

7. Problems associated with the development of song are discussed, particularly those based on the concept of innateness.

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