# SONG VARIATION IN A POPULATION OF BROWN TOWHEES

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With the advent of new methods of analysis, the study of variation in bird song can be approached with more objectivity than has hitherto been possible. As with morphological characters, careful study of variation may throw some light on the kind of selective influences to which vocal signals and other communicatory behavior are subject. The problem of describing variation in behavior is confounded by the extensive variation which we sometimes find within the same population and even within the same individual at different times.

In a previous paper (Marler and Isaac, 1960) we have given a preliminary description of the situation in a simple case, the song of the Chipping Sparrow (*Spizella passerina*), in which variation within the individual is minimal. The singing of the Brown Towhee (*Pipilo fuscus*) is somewhat more complex and it is our intention in this paper to establish the limits of variation in the songs of the individual and in a sample of a number of individuals from the same geographical area.

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## METHODS

The methods of recording and physical analysis are the same as those described previously for the Chipping Sparrow (Marler and Isaac, *op. cit.*). Once again three types of analyses are presented, all made with a Kay Electric Company Sonagraph. Most of the data come from frequency/time sonagrams, using the wide band-pass setting, and amplitude/time analyses were also made of some songs. The results of frequency/amplitude serial sectioning of single syllables will be published separately.

The field recordings were made between July 11 and 23, 1958, all within the small state of Aguascalientes in west-central México. The majority, 55 song types from 31 birds, were made within a 10-mile radius of Calvillo. The remainder, 6 song types from 6 birds, were recorded in the neighborhood of Rincon de Roma, about 40 miles from Calvillo. Most of the recordings comprise only a few selected songs from each bird, and these two samples are in general grouped together for analysis. An additional series of 53 songs was recorded from one individual on July 20, 10 miles west of Calvillo and is referred to as Calvillo B24. Songs of this bird are analyzed separately and are excluded from the analyses of the general sample. Two of the songs were recorded at slow speed and are excluded from the detailed analyses. Variability figures, unless otherwise specified, are given as the arithmetic means plus or minus one standard deviation.

## SONG

*General description of the song pattern.*—A typical song of the Brown Towhees in the study area consists of two basic parts. First, a single soft introductory *chip*, then a pause, and then a louder, regular trill of some 5–20 syllables, lasting about 1.5 seconds (see fig. 1 A–D). The introductory syllable was not seen on some sonagrams. In the general sample, 40 had introductory syllables and 21 did not. Upon rechecking the re-

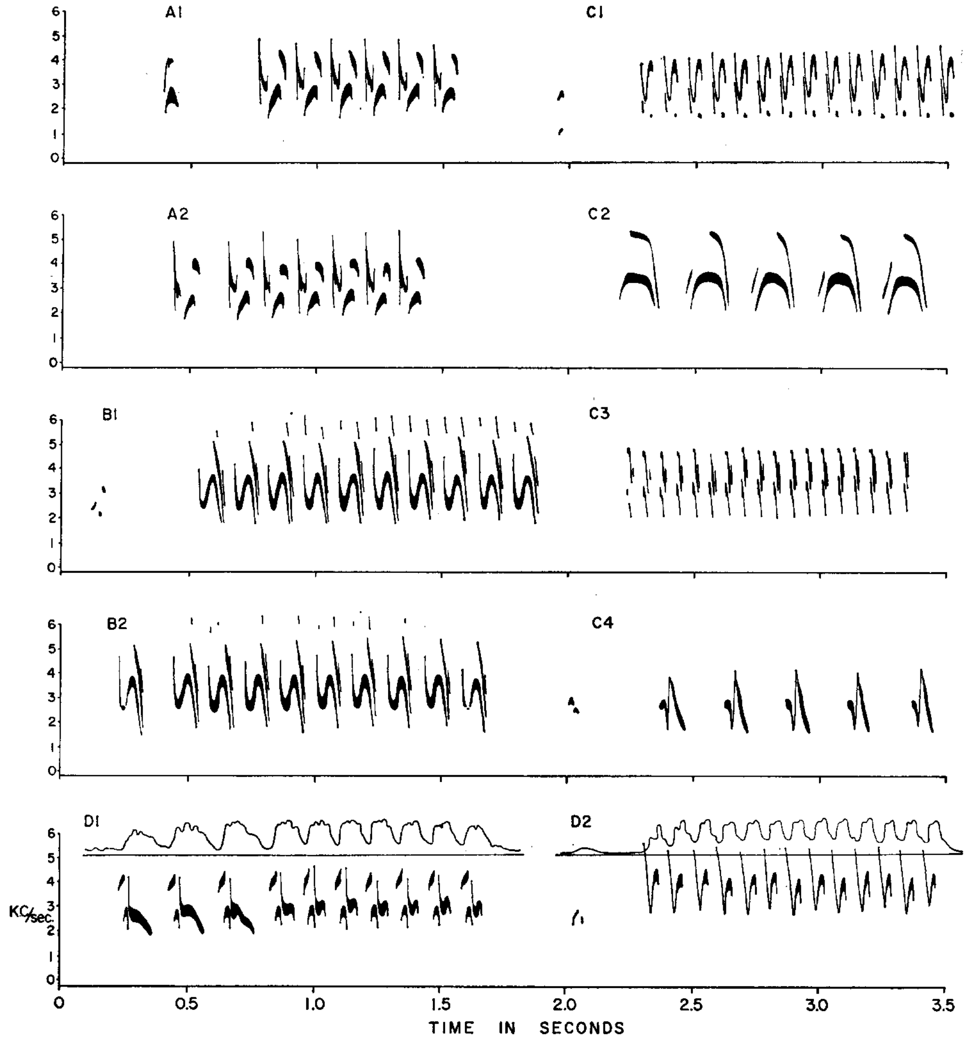

Fig. 1. Frequency/time sonagrams of ten songs of the Brown Towhee. These records can be read from left to right in much the same way as a musical score. A1 and A2, B1 and B2 illustrate the alternative methods of starting a song either with a special introductory note, or by one of the trill syllables which is displaced in front of the main part of the trill. C1 to C4 are songs from different individuals, emphasizing the variability in the number of trill syllables as compared with song duration. D1 and D2 also include some typical patterns of loudness or, more strictly, of amplitude modulation. Note how the soft introductory note in D2 is represented by a small deflection of the curve, while the trill syllables have a stronger effect.

cordings, it was found that four of the 21 had soft introductory syllables. Of the remaining 17, 10 had an alternative pattern. Instead of the introductory *chip* syllable, one of the trill syllables was displaced into the corresponding position. These two methods of achieving an introduction also occur in alternative renderings of the same theme (fig. 1, A,B).

In addition each bird possesses several distinct song types, identifiable by the different syllable structure. Figure 2 shows how five syllable types were used in 53 songs by Calvillo B24. Note how trills sometimes include two syllable types. This is particularly common when there is a change-over from one song type to another, the transitional song being half of one type and half of another (for example, song number 13 in fig. 2). Double trills apparently can also occur as distinct themes. Songs 26 to 47 in figure 2 all include both type C and D syllables. However, these double trills were rare in the general sample, accounting for only five of the 61 types recorded.

*The temporal pattern of singing.*—Brown Towhees in Aguascalientes normally select singing posts 20 to 30 feet above the ground and usually remain stationary while performing. In B24 the song duration was 1.49±0.19 seconds and the interval between songs was 11.6±5.4 seconds (fig. 3, A, B). Thus about 12 per cent of performance time was spent in song. Song duration in B24 was almost the same as in the general sample, the value for the latter being 1.52±0.31 seconds. Although song duration varies somewhat, variation in the number of syllables which make up the song is much more striking (fig. 3, C). The extremes of the general sample are 4 and 26, with an average and standard deviation of 10.4±4.5. For Calvillo B24 the corresponding values are 6 to 16 and 10.2±2.1.

The question then arises how variation in the number of syllables is related to song duration. Does a small number of syllables imply a short song? As can be seen from figure 4,A this is by no means necessarily the case. Although there is a trend for longer songs to have more syllables, a song with four or five syllables can be as long as one with 15. Thus the rate of syllable production varies widely, being 7.4±2.1 syllables/second in the general sample. This suggests the possibility that syllable duration may vary in an inverse fashion with the number of syllables per song. As figure 4,B shows, such a relationship does exist. In other words, a song may be made up of a few long syllables or of a large number of short syllables. The average syllable duration for the general sample is 101±57 milliseconds, and for B24, 116±25 milliseconds.

*Frequency characteristics.*—The variation in syllable structure, described later in more detail, results in wide variation in the pitch or frequency characteristics of the song (fig. 5). Among the 51 songs of B24 the maximum frequency ranges from 4.5 to 7.6 kilocycles per second, and varies even more widely in the general sample. Averages and standard deviations are 5.86±0.86 KC/sec. for the general sample and 6.50±0.71 KC/sec. for B24. Minimum frequencies vary somewhat less (1.84±0.35 KC/sec. for the general sample and 2.04±0.47 for B24). The frequency spread, however, differs remarkably from bird to bird, from as little as 2.0 KC/sec. to as much as 5.8 KC/sec. Once again the variation in B24 (4.47±0.73 KC/sec.) is only slightly less than that in the rest of the sample (4.01±0.92 KC/sec.).

Some of this variation in frequency is probably the result of amplitude variations, as has already been described for the Chipping Sparrow. In that species, syllable structure varies relatively little. In the Brown Towhee the greater degree of variation in syllable structure has a more dominant effect on frequency variation, and detailed measurements of amplitude characteristics have therefore not been made. A typical amplitude record is presented in figure 1,D, showing the weak introductory note and the approximately constant amplitude peaks of each syllable type in the trill.

*Syllable structure.*—The introductory syllable with which most songs begin is so soft that there are only a few good sonagrams. The best are shown as tracings in figure 6. All are considerably shorter than the trill syllables (42±17 msec. in B24, and 41±17 msec. in the general sample). The commonest pattern is a syllable with two or more frequency bands that first rise and then fall. Sometimes there are modulations on this

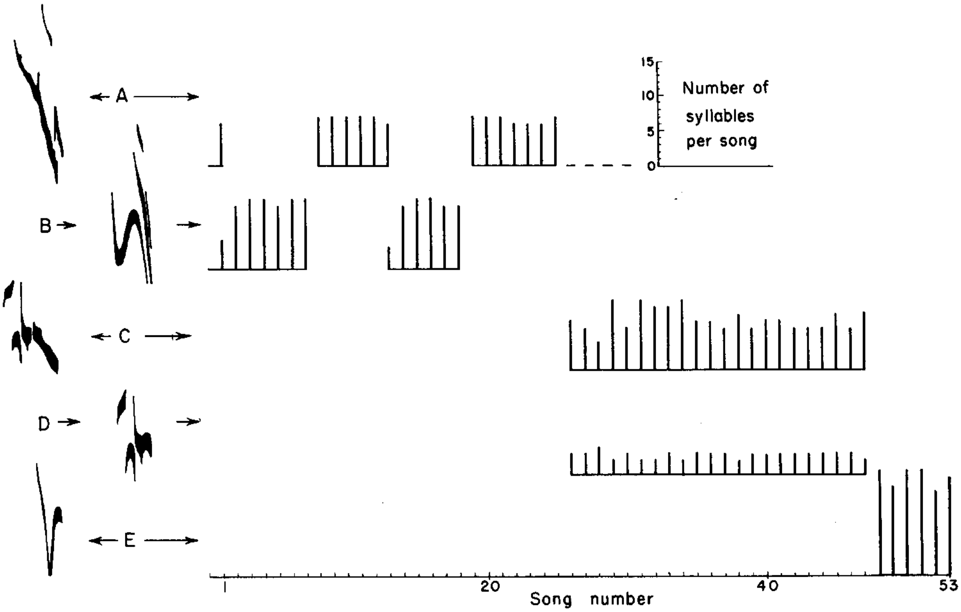

Fig. 2. A diagram of 53 consecutive songs of Calvillo bird 24. The syllable types are illustrated on the left. Their occurrence and number in a given song are indicated by a vertical line placed opposite the appropriate syllable and above the number of the song. Note how some songs include two syllable types and that types C and D always occur together. The number per song varies with different syllable types, being greater with short syllables, such as E, than with longer ones, such as B.

basic pattern, as in syllable E1 of figure 6. A bird may use an introductory syllable of a different structure with each different trill type (as in syllables J1–J3 of figure 6). Usually there is no apparent similarity between the structure of the introductory syllable and of the trill syllables with which it is used, but occasionally some resemblance is evident. Syllables C1 and J3 of figure 6 are reminiscent of their corresponding trill syllables (fig. 7:part I—syllable J1, and part II—syllable H3, respectively). The most striking case is figure 6: syllable N1, which is a miniature and slightly distorted version of the trill syllable (fig. 7: part IV—syllable E1). However, these resemblances are sufficiently uncommon that they may be a result of chance. As noted earlier the place of the introductory note is sometimes taken by one of the trill syllables which, apart from its spacing, differs in no way from those used in the trill.

A prime concern of this paper is the remarkable diversity of syllable types which make up the trill. Tracings of each of the syllable types found are shown in figure 7. They are arranged in four groups. Each of the first three include a sample of birds found so close together that we can assume they could hear each other. The diversity within a group is no less striking than that between groups. In many instances birds were actually recorded while countersinging. Yet no case was found of the sharing of a distinctive syllable type by two adjacent birds. The lowest line in figure 7 represents songs of birds from a number of areas. These are not obviously more diverse than those in the rest of the sample.

We may also note the variability in different syllable types of the same individual. The types used by B24 are shown in figure 2. Two of these syllables (C and D) are variations on the same pattern, but the rest are quite distinct from each other. The differences between syllable types are rigidly maintained, with no transitions between them.

Similarly in the general sample we find examples from the same individual of syllable types which are different but related (see fig. 7: part I—syllables I1 and I2; part II—syllables B1, B2, and B3; part III—syllables D1, D2, F1, F2, and F3; and part IV—syllables B1, B3, C1, and C3). We also find syllable types in the same individual which are distinctly different (fig. 7: part I—syllables A1, A2, H1, H2, and H3; part III—syllables B1, B2, C1, and C2; part IV—syllables B2 and B3). At first sight it appears that some members of a group may share certain characteristics. Note, for example, the close resemblance of syllables C2 and H3 and of syllables D2 and E1 in part I. However, comparable syllable types occur in different groups (see fig. 7: part II —syllable C1 and part IV—syllable K1; and also part III—syllable D2 and part IV—syllable F1). We must not overlook the possibility that comparison with a sample from a different area might bring out some subtle characteristics shared only by the members of this population. At the moment such shared characteristics of detailed syllable structure are not discernible.

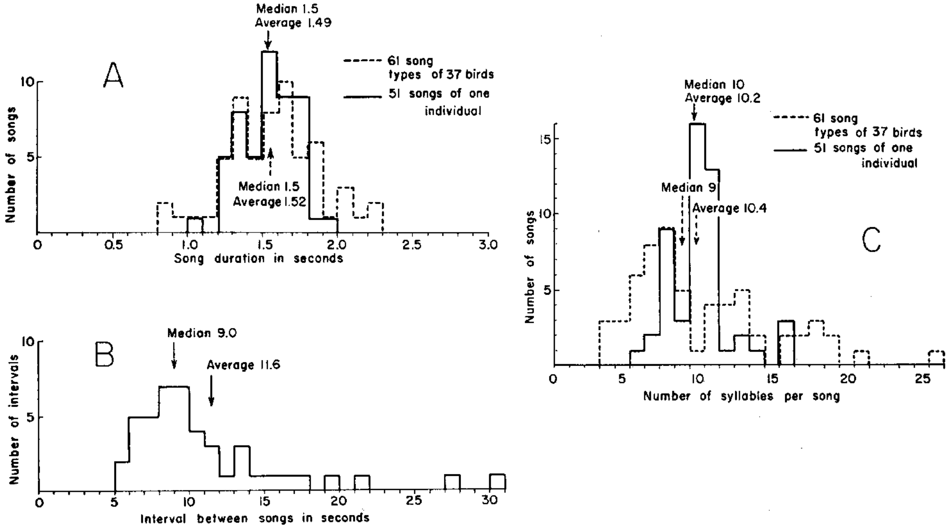

Fig. 3. Frequency distributions of (A) song duration in B24 and in the general sample, (B) intervals between songs in a bout of singing by B24, and (C) the number of syllables per song in B24 and in the general sample.

## DISCUSSION

*The problem of describing song variation.*—A description of the songs of a bird in a given area should include information on the characteristics both of individual repertoires and also of the song of the whole population. In the latter case it is clear that a large sample is necessary, but this need is not so obvious in describing the behavior of individuals. Where the song of the individual varies little, as in the Chipping Sparrow (Marler and Isaac, *op. cit.*) it is true that a small sample is adequate, but this simple condition is probably rare. The Brown Towhee is fairly conservative, in comparison with some of the more versatile songsters, yet a sample of 53 songs from one bird was hardly sufficient to define its repertoire. The histograms illustrating variation of song duration, frequency and number of syllables (figs. 3 and 5) in one individual are surprisingly similar to those for the whole population. This may mean that the sample of songs from the population as a whole should have been larger for a truly adequate description. We are thus confronted with a difficult and time-consuming problem in describing variation in bird song, even with a species as conservative as the Brown Towhee. How much more serious this becomes with the more versatile songsters, such as the Song Sparrow, *Melospiza melodia* (Nice, 1943; Mulligan, MS) or, in Europe, the Robin (*Erithacus rubecula*), and the Mistle Thrush (*Turdus viscivorus*). One individual Song Thrush (*Turdus ericetorum*) gave 143 different songs in a series of 203, and the repertoire was still not exhausted (Marler, 1959). Characterization of the song of a population of such species is a major project, not to be undertaken lightly.

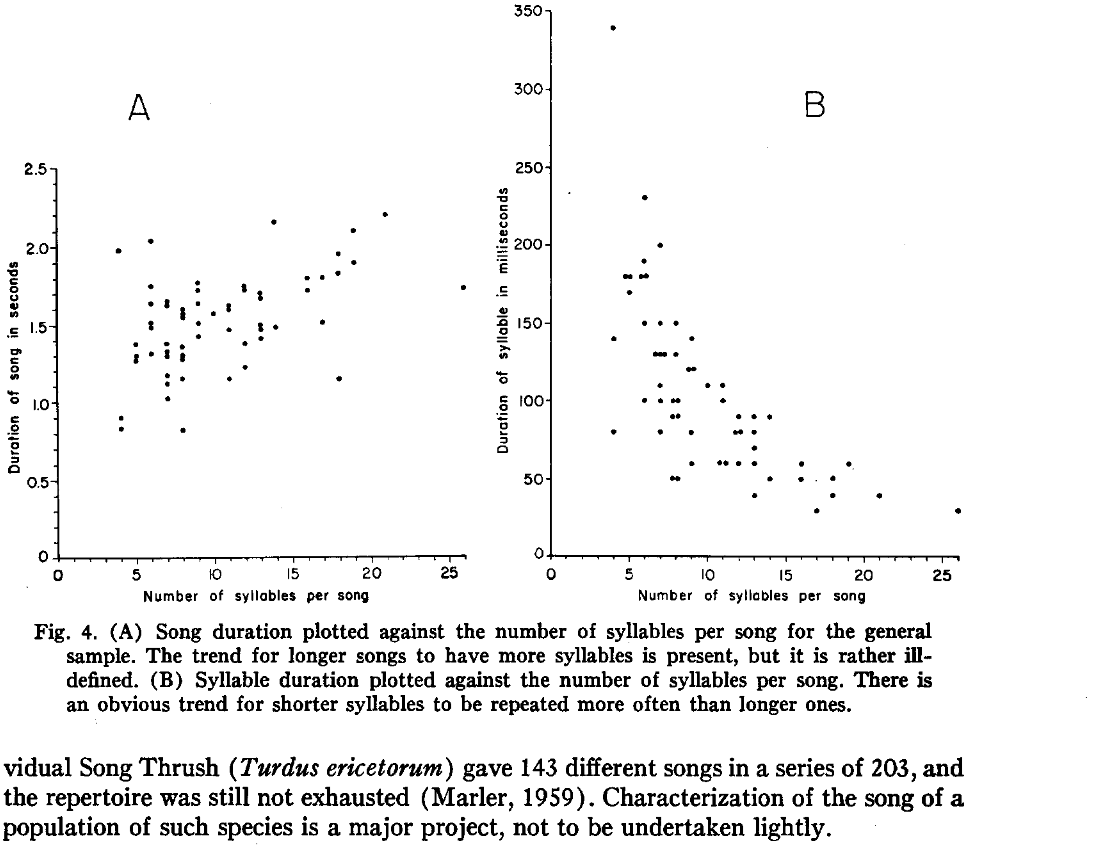

Fig. 4. (A) Song duration plotted against the number of syllables per song for the general sample. The trend for longer songs to have more syllables is present, but it is rather ill-defined. (B) Syllable duration plotted against the number of syllables per song. There is an obvious trend for shorter syllables to be repeated more often than longer ones.

*Song variation and continuity.*—Hartshorne (1956) has suggested that variability in song is correlated with the continuity of singing, so that discontinuous singers are usually the least versatile. He cites many examples of a principle that holds in an appreciable number of cases. It remains to be shown whether this principle holds within a given family. Thus the Chipping Sparrow, which is a non-versatile singer, just qualifies as a discontinuous performer (by Hartshorne's criterion) with about 30 per cent of the performance period spent in song (Marler and Isaac, 1960). Brown Towhees are more versatile than Chipping Sparrows, yet one bird spent only 12 per cent of its performance period in song. Similarly, in the Rufous-sided Towhee (*Pipilo erythrophthalmus*), another variable singer, Davis (1958) finds that singing occupies only 9.1 per cent of the performance period. These may be extreme examples, but it seems that the concept of continuity will need to be re-examined when more data are available.

*Song variation and recognition.*—It has been argued elsewhere that the high degree

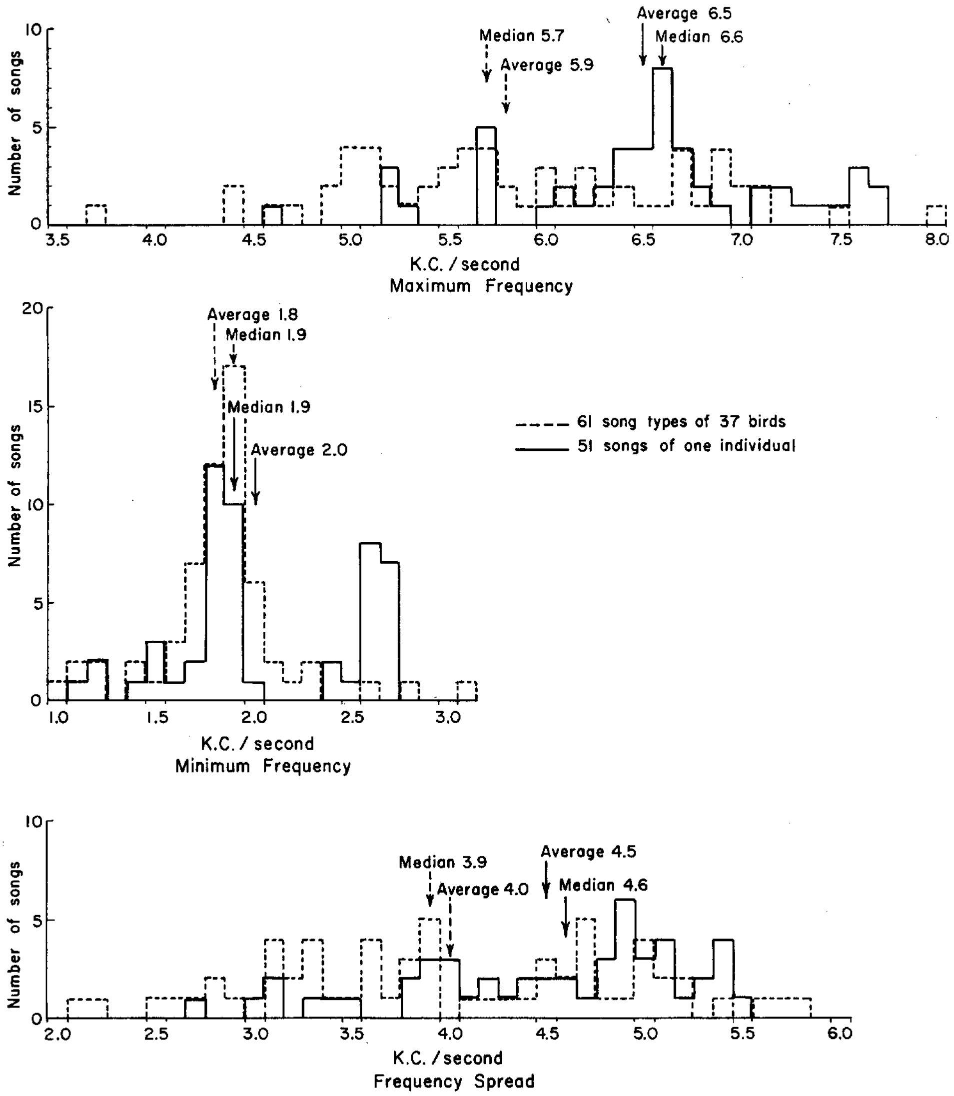

Fig. 5. Distributions of the frequency characteristics of the songs of B24 and of the general sample. Note the remarkable similarity in the two samples.

of variability which we find in the songs of certain birds is unlikely to be accidental (Marler, *in press*). There is evidence that some species use song both for species recognition and for individual recognition. These two functions are likely to encourage different evolutionary trends. To be effective for recognition purposes, a song needs to be distinctly different from other sounds likely to be heard at the same time and place. The most probable source of confusion in the sound background is the song of other birds. We would expect that the degree and kind of distinctiveness of the song of a given species should in some measure be related to the need for recognition.

The function of species recognition would seem to be best served by species-specific song which is stereotyped within a given population. On the other hand, the function of individual recognition would require consistent individual differences in the songs of the members of a population. If both of these needs were present, natural selection would be encouraged to proceed in conflicting directions, favoring stereotypy on the one hand and variability on the other. There is reason to think that this conflict does in fact arise and is resolved in some cases by relegating the two functions to different variables of the song (Marler, *in press*). This hypothesis needs to be tested experimentally; but meanwhile, we can apply it to the songs of the Brown Towhee, to see which variables could serve the postulated functions of individual and species recognition.

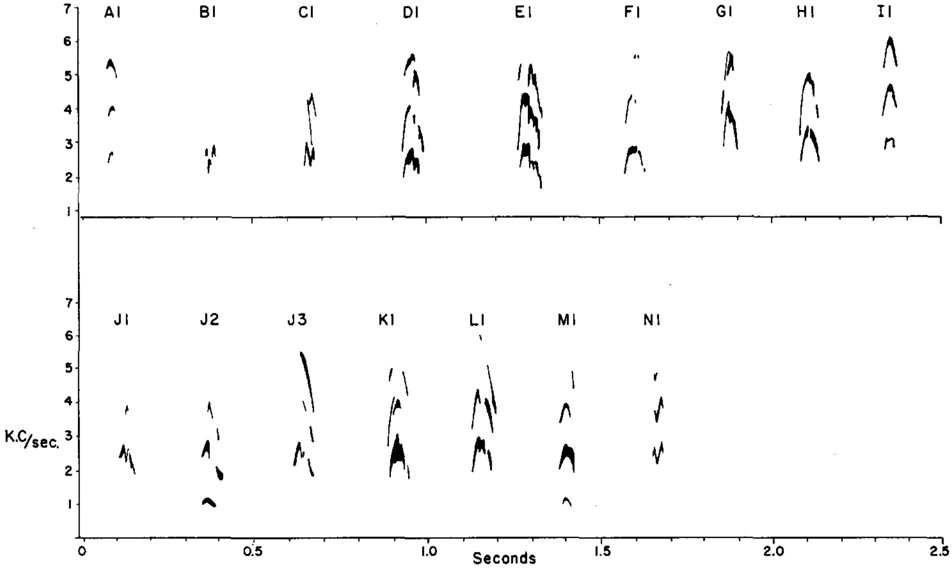

Fig. 6. Tracings from frequency/time sonagrams of some of the introductory notes of the songs of Brown Towhees.

The possible variables of songs of the Brown Towhees of Aguascalientes which we have described are: duration, temporal pattern, frequency pattern, syllable duration, rate of syllable production, and syllable frequency/time structure. Of these, the first two have relatively small variability and in particular the overall temporal pattern is strikingly consistent. Although more than one syllable type occasionally occurs in the trill, most songs consist of an introductory syllable followed by a trill of one syllable type. These characters might be used in species recognition. In contrast, the syllable characteristics are quite variable, especially frequency/time structure which is consistent in each syllable type of each individual and different between individuals, even when they are close neighbors. These could provide a suitable basis for individual recognition.

*A comparison with the songs of the Rufous-sided Towhee.*—The Brown Towhee ranges from southern Oregon in the United States to Oaxaca, México. The associated species assemblages and consequently the sound background vary considerably from one end of this range to the other. While songs of any species could influence the evolution of song characters, close relatives are particularly worthy of attention, where such relatives are sympatric. Confusion could exist because of similarities in vocalizations, general behavior, ecology and anatomy. Also the possibility of dysgenic hybridization may place a particularly high premium upon specific distinctiveness of characters involved in reproductive isolation (Marler, 1957; Sibley, 1950). Information on songs of species similar to the Brown Towhee is sparse, but enough is available to speculate on the possibility of such interaction between the Brown and Rufous-sided towhees.

The range of the Rufous-sided Towhee includes most of that of the less widely distributed Brown Towhee. Recent studies suggest that these species may not be congeneric, *P. fuscus* being probably closer to the genus *Melozone* (Davis, 1951, *in litt.*; Sibley, 1955; Parkes, 1957). Thus it is probable that sterility barriers are well established between the two species, although it must be admitted that we do not know if hybrids can be produced in captivity. However, it is not necessary for them to be sibling species, in order to affect the evolution of each other's song. As long as they live together and are grossly similar in size and structure there is a chance that they may tend to produce similar sounds. If these sounds function in reproductive isolation a problem in achieving specific distinctiveness may thus arise.

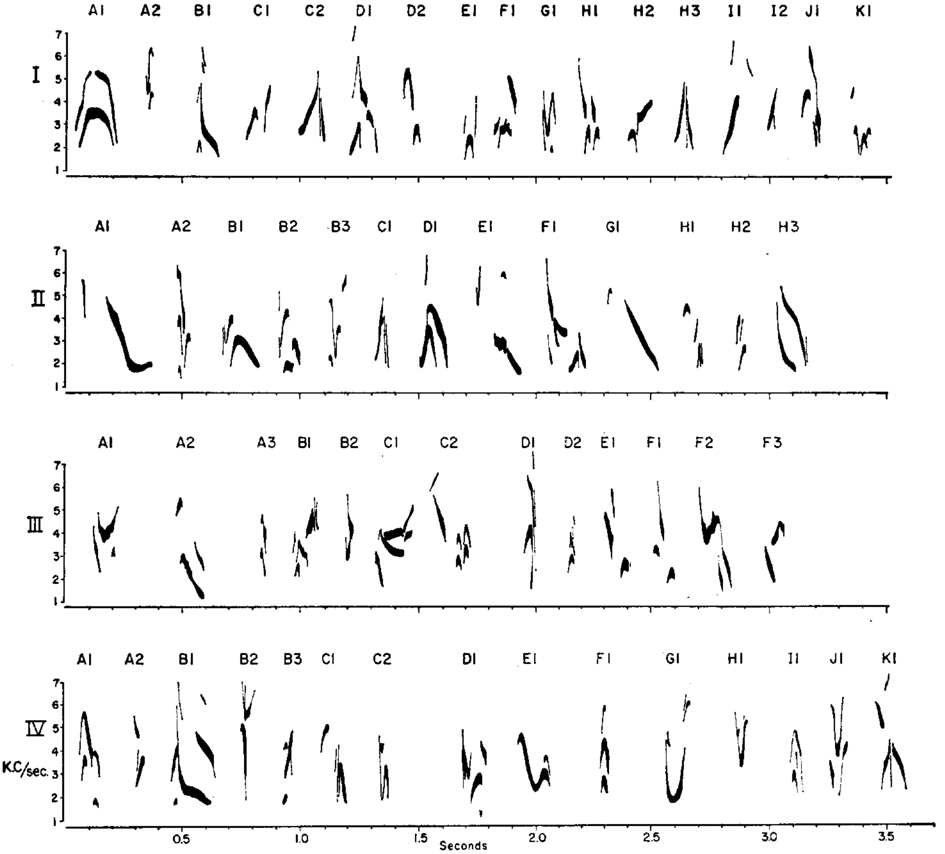

Fig. 7. Tracings from frequency/time sonagrams of 58 syllable types from the songs of 37 Brown Towhees. The three upper rows each represent a sample from a rather restricted area. The bottom row is a mixed sample from several locations. Alternative syllable types from the same individual are indicated by numbers, such as A1 or A2.

The Brown and Rufous-sided towhees occupy different habitats in parts of their range, especially in México, but they cohabit closely in certain areas, occurring in the same habitats in California, where they make frequent interspecific contacts (Miller, 1951; Davis, 1957). We may also note considerable resemblance between the structure of trill syllables in the Brown Towhee and the syllables in the terminal part of the songs of the Rufous-sided Towhee described from the eastern United States by Borror (1959), although the latter are somewhat shorter and are repeated fewer times, at a more rapid rate than in the Mexican Brown Towhees. The total duration of the songs of eastern *erythrophthalmus* and Mexican *fuscus* is also similar (about 1.3–1.5 seconds). It seems reasonable, therefore, to speculate on possible interaction between them in the evolution of their songs.

Comparison of the songs and singing habits of the two towhees in different parts of their range is hindered by the sparsity of information, but some attempt is possible. In the east, where *fuscus* is absent, *erythrophthalmus* has a considerably longer and more elaborate song than in California. There is a relatively long, complex and variable introduction, followed by a repetitive trill (Borror, 1959). In California there is a simple short trill, sometimes preceded by a single introductory syllable (Davis, 1957), and the trill seems to correspond with the terminal part of the eastern bird's song. The nature of the songs of *erythrophthalmus* in México is more difficult to ascertain, but they are probably closer to the eastern birds than to those in California (cf. Sibley, 1950). One bird recorded in Chihuahua used five basic song types among 24 songs. These consisted of a trill introduced by one or several syllables of various types, reminiscent of those described by Borror. The total duration (average, 1.4 seconds) was longer than that in California (0.4–0.6 seconds, Davis, 1957) and similar to that in the eastern states (1.3 seconds, estimated from some of Borror's data). We may also note from all populations of this species a striking degree of individual variation, involving more variables of the song than we have found in *fuscus*.

The songs of *fuscus* in México are probably not very different from those in California except that the latter have a change in tempo in the middle. A *chip* note is repeated three or four times, and then given in a rapid trill (Quaintance, 1938). Probably the same syllable type is used in both parts, thus corresponding with the alternative method of achieving an introduction used by the Mexican birds (cf. fig. 1) but with several repetitions of the introductory syllable. Double trills, with a change of syllable type partway through the song, evidently occur both in California and in México (Quaintance, *op. cit.*). There is, however, a radical difference in the seasonal pattern of singing in the two areas. In California, where the Brown Towhee is resident throughout the year and apparently mates for life, song is almost restricted to unmated males and as a result is seldom heard (Quaintance, 1938; Davis, 1957). In Aguascalientes there was persistent singing throughout the day from birds which were mated and breeding in July.

We can summarize the points which emerge from this comparison as follows:

1. In México, where *fuscus* and *erythrophthalmus* are sympatric but occupy different habitats, the song of the latter is similar to that of birds in the eastern United States, where *fuscus* is absent.
2. In California, where the two species are in closest contact, the song of *fuscus* is basically similar to that in México, but it is rarely heard except from unmated males. In California the song of *erythrophthalmus* is much simpler than in México and in the eastern United States.
3. In México the total song duration of both species is similar to that of *erythrophthalmus* from eastern United States, and about twice as long as that of *erythrophthalmus* from California.

The problem is to decide whether or not the trends in song and singing habits of the two species in California, where they are in closest contact, are closely related. As Davis has indicated, information about the song of related genera, especially *Atlapetes* and *Melozone* is almost certain to throw light on the situation. Meanwhile, it is tempting to speculate that the close contact between the two towhees in California has resulted in interaction between them. If song duration is a critical factor in their species recognition, the shortening of the song of *erythrophthalmus* in California might be a necessary change to avoid confusion with *fuscus,* when females were selecting mates. This possibility is complicated by the rarity of song in *fuscus* in California, which seems to be associated with the maintenance of the territory and the pair bond throughout the year. The Rufous-sided Towhees on the other hand, do not maintain their territories through the winter and probably re-establish pair bonds each year (Davis, *in litt.*). Persistent singing may thus serve a real function here, and we can also see how individual variation, which is particularly marked in this species might have value in facilitating individual recognition. Whether this free use of song has in any way been responsible for the rarity of singing in *fuscus* in California we cannot at present decide, but there is clearly an intriguing problem here, which may be solved when we have more information.

## SUMMARY

Variation in the songs of a single population of Brown Towhees (*Pipilo fuscus*) has been studied in Aguascalientes, México. An extended sample from one bird was also analyzed. The typical song pattern is a soft introductory *chip,* then a pause, and then a louder trill of 4–26 syllables, usually all of the same type, occasionally of two types. Song duration varies relatively little, being 1.52±0.31 seconds. Syllable duration bears an inverse relationship with the number of syllables per song, so that a song may comprise few long syllables or many short ones. Song frequency varies widely in different birds, and in the same bird at different times. Each individual uses several types of introductory and trill syllables. The latter are particularly diverse in different individuals, even if they hold adjacent territories.

The standard deviation of song characteristics in the sample from a single bird is almost as great as that of the sample from the whole population. Thus a larger sample than the one used is probably necessary to define the song characteristics of the population adequately. For more versatile singers a much greater sample will be required.

The temporal pattern of singing does not conform to expectations from Hartshorne's "continuity hypothesis." To facilitate the function of species recognition, the duration and overall temporal pattern of the song would be most suitable. For individual recognition the syllable characteristics and particularly their frequency/time structure would be most appropriate points of reference. A resemblance between syllable structure in songs of the Brown and Rufous-sided towhees is indicated and the possibility of interference between these two species in California, where they come into close contact, is discussed.

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