

## ANALYSIS OF SYLLABLE STRUCTURE IN SONGS OF THE BROWN TOWHEE

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THE new methods of analysis developed in recent years have resulted in a rapid increase in our knowledge of the physical structure of bird songs. The numerous descriptive studies now being conducted already provide us with extensive information about the ways in which songs are constructed. For the most part these studies are focused on the pattern of notes in time, and rightly so, since this provides their most effective characterization to our ears, and perhaps to the birds themselves. There is another property, detectable to our ears, but less easy to analyze physically, namely the tonal quality of the notes that comprise the song. Several authors (*e.g.*, Borror and Reese, 1956; Thorpe, 1958; Marler and Isaac, 1960a) have drawn attention to this as an important characteristic of the songs of some birds, and we must concede the possibility that a species-specific tonal quality could be important in song recognition.

With this in mind, we have made a study of the detailed physical structure of single syllables from the songs of a number of Brown Towhees (*Pipilo fuscus*), living together in the same population. Previous study (Marler and Isaac, 1960b) has shown a high degree of variability in such characters as the number of syllables per song, syllable duration, frequency, and over-all pattern in time. In the search for more consistent characteristics, we decided to examine the overtone structure and the detailed temporal pattern of the syllables.

### METHODS

As described in a previous paper (Marler and Isaac, 1960b), the recordings were made in Aguascalientes, Mexico, in July 1958, from a single population of Brown Towhees. This analysis is based on syllables selected from five different songs from one bird (B24) and from 17 songs selected from the general sample of other birds in the same area. In each case a single, typical syllable was analyzed from each song.

The selected syllables were sectioned serially by means of a slightly modified Kay Electric Company Sonagraph (Marler and Isaac, 1960), using narrow band-pass filters. The sections appear as histograms of amplitude versus frequency at intervals of 5.0 milliseconds from the beginning to the end of a syllable. As can be seen in Figure 1, a syl-

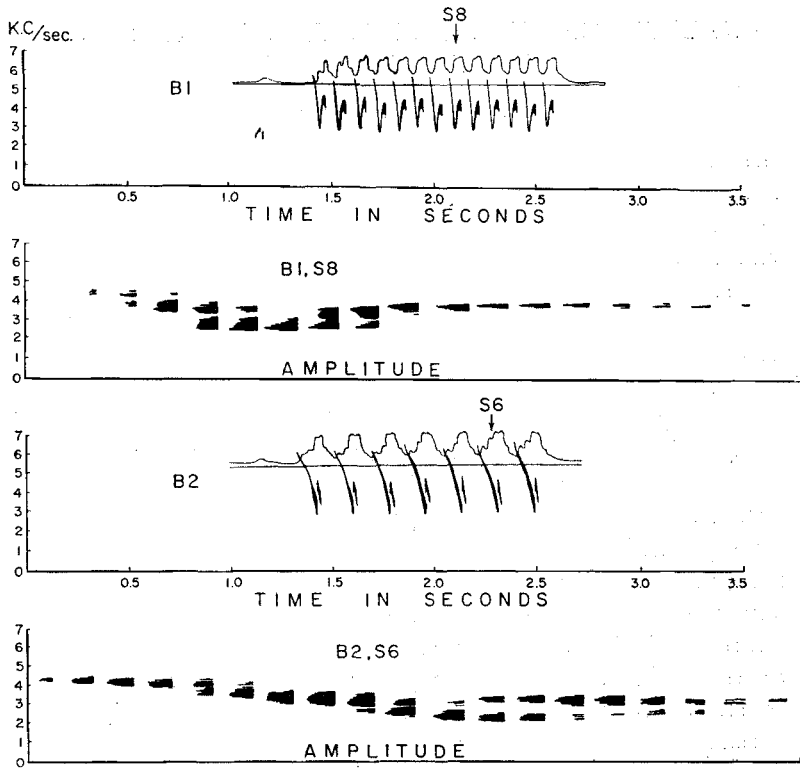


Figure 1. Two examples of the methods of analysis used in this study. Time/frequency analyses of two songs shown in B1 and B2, with a curve of maximum amplitude superimposed in each case. Introductory notes are very soft, while trill syllables all have about the same intensity, although the first one or two are a little weaker than the rest. A single syllable was selected from each song, syllable 8 in B1 and syllable 6 in B2. The series of frequency/amplitude sections from the beginning to the end of these chosen syllables are shown below in each case.

lable may be broken down into 20 or more sections. These reveal both the amplitude of the different frequencies represented at chosen moments in the syllable, and also the ways in which both frequency and amplitude change with time, in more detail than can be obtained either from the usual time/frequency analyses or from the amplitude displays. Frequency is expressed in kilocycles per second, the individual "bars" of the histograms (*i.e.*, the lines produced by the stylus of the Sonagraph) representing about 0.02 kc/sec. Amplitude is given on a decibel scale; however, since actual amplitude depends on several unknown variables, the measurements are relative and arbitrary. For

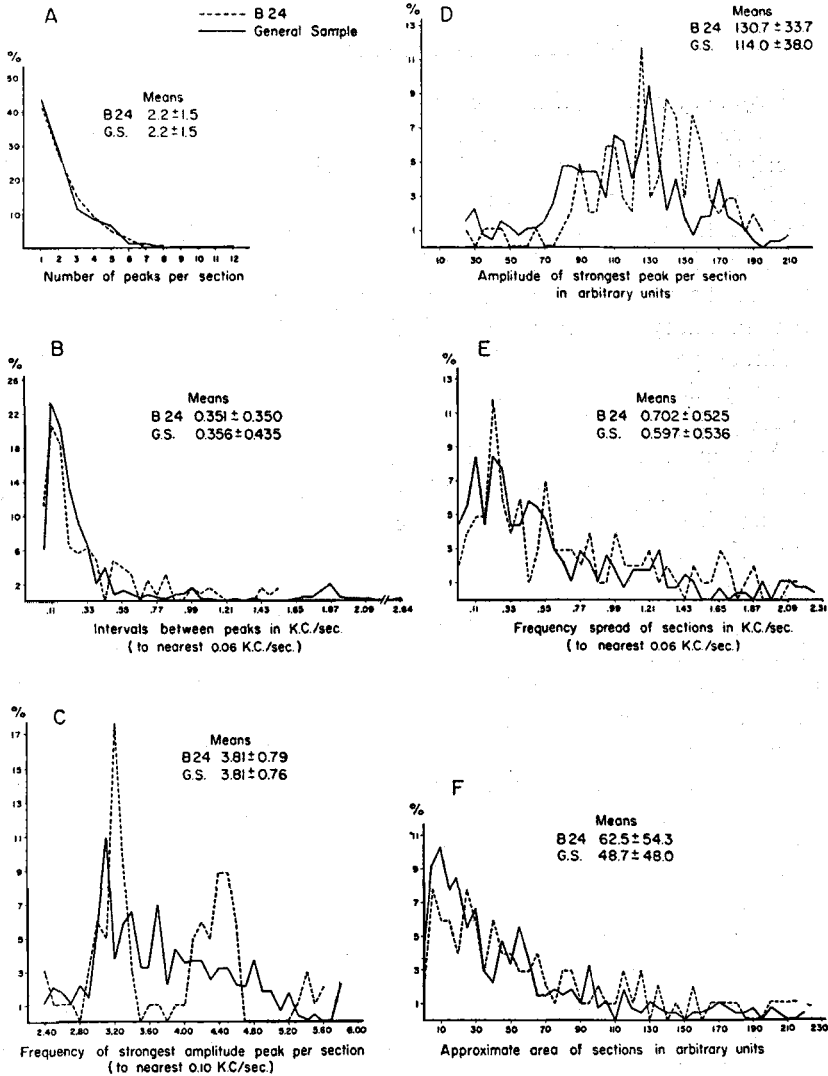
this reason amplitude values were simply measured in arbitrary units, on the linear time scale used in the frequency/time analyses.

#### DESCRIPTION OF SYLLABLE STRUCTURE

*Frequency and amplitude characteristics.* Each section has frequency as its base line, with amplitude as the other axis. For purposes of description, we have quantified the following parameters: First, it is possible to count the number of peaks in each section. All peaks that are bounded by troughs penetrating more than one third of the way to the base line are included in this estimate. Second, the frequency intervals between the highest point of adjacent peaks have been measured, in kilocycles per second. Third, the frequency of the highest amplitude peak in each section is noted. Fourth, the amplitude of the highest peak in each section has been noted, in arbitrary units. Fifth, the frequency spread of each section has been measured, this being the range from the lowest to the highest frequency in kilocycles per second. Finally, the approximate areas of all sections have been calculated by treating them either as triangles or as trapezoids and applying the appropriate formula.

In Figure 2, the total values of these characteristics for all sections of all syllables from bird 24 are compared with similar totals for all other birds together, the results being given as percentages of the totals in each case. The first point emerging is that, for the most part, the values for B24 and the general sample correspond closely. This is all the more striking when we recall the smaller size of the sample from B24 (102 sections, as compared with 273 for the general sample). If we calculate the means and standard deviations of these distributions, the essential correspondence between the single bird and the general sample is again apparent (see Figure 2). The only marked discrepancy between the two distributions is seen in the frequency of the strongest amplitude peak, which forms a fairly smooth curve for the whole sample but has two peaks in B24 at 3.2 and 4.5 kilocycles. Since B24 had only five syllable types, some of which were rather similar (see Marler and Isaac, 1960b, Figure 2), we might expect a discontinuous distribution. It is interesting to surmise in this connection that such strongly selected distribution of frequency usage could be used as information for individual identity. However, the present material is insufficient to test this idea. In spite of this difference in distribution, the mean values are identical, and the over-all variability is nearly the same.

What do the figures represented in Figure 2 tell us about the proper-



**Figure 2.** Distribution on a percentage basis of measurements from the sections of syllables from the songs of B24 and from syllables from 17 song types selected from the other birds. The means and standard deviations of each of the measures are also given.

ties of the syllables in Brown Towhee songs? It can be seen from Figure 2A that a large number of the sections—about 40 per cent—have only one peak, implying that in this case there are no overtones. Twenty-five per cent have two peaks, and those with more peaks become less frequent. Sections seldom have more than five peaks, the mean value being 2.2. The remainder of the graphs are concerned with that 60 per cent of the sections that have more than one peak. Figure 2B shows the interval between these peaks in kilocycles per second. The curves for both B24 and the general sample peak sharply at about 0.15 to 0.20 kc/sec. Values between 0.10 and 0.35 kc/sec. account for about three quarters of the whole sample. Thus there is a possibility of characterizing the typical overtone pattern in these syllables in a rather definite way.

However, a problem of interpretation arises, since two kinds of intervals are included in these data. In addition to true overtones, there are occasions when syllables include two distinct notes that overlap in time. If the notes have widely different frequencies, then very large intervals result. Unfortunately, it is impossible to separate these two types of intervals consistently, and for this reason the data have been lumped together. We have, however, examined the effects of eliminating all obvious cases of note overlap in the general sample.

The mean in frequency interval between amplitude peaks calculated from these revised figures for the general sample is  $0.211 \pm 0.131$  kc/sec. as compared with  $0.356 \pm 0.453$  kc/sec. for the original figures. There is thus a marked reduction in variability in the new estimate, suggesting a rather typical interval between overtones of about 200 cycles.

The plot of the frequency of the strongest amplitude peak (Figure 2C) has already been commented upon. While a given syllable may have a single dominant frequency, the range for the sample as a whole is very wide indeed. This is consistent with findings in other species, where absolute frequency is one of the most variable parameters. The amplitude of the highest peak is similarly variable, as we might expect, and the same is true of section area (Figure 2D and F). The distribution of the frequency spread of the sections is worthy of closer attention (Figure 2E); the tail end of the curve is affected by the overlap in time of two notes, with different frequencies, in the same way as discussed above for the interval between peaks. Thus, by elimination of obvious cases of note overlap, the frequency spread of  $0.597 \pm 0.536$  kc/sec. is reduced to  $0.469 \pm 0.344$  kc/sec. It is interesting to compare this with the figure for frequency spread of the entire songs obtained in a previous analysis— $4.01 \pm 0.92$  kc/sec.

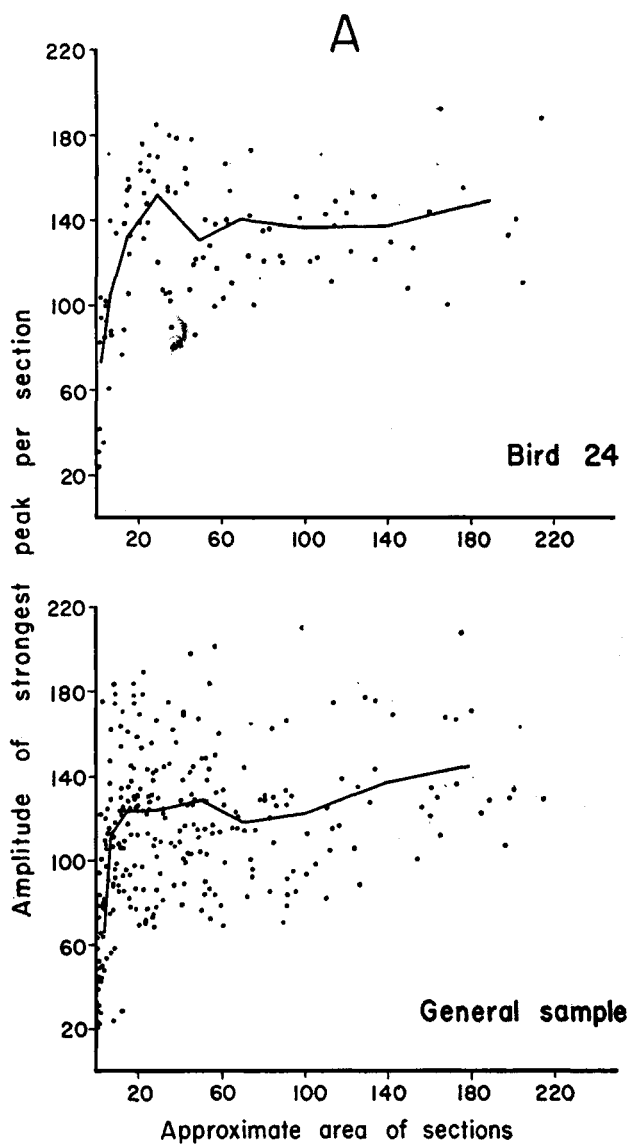


Figure 3A. Graph of the correlations between the total energy in a section, as revealed in section area, and the amplitude of the strongest peak.

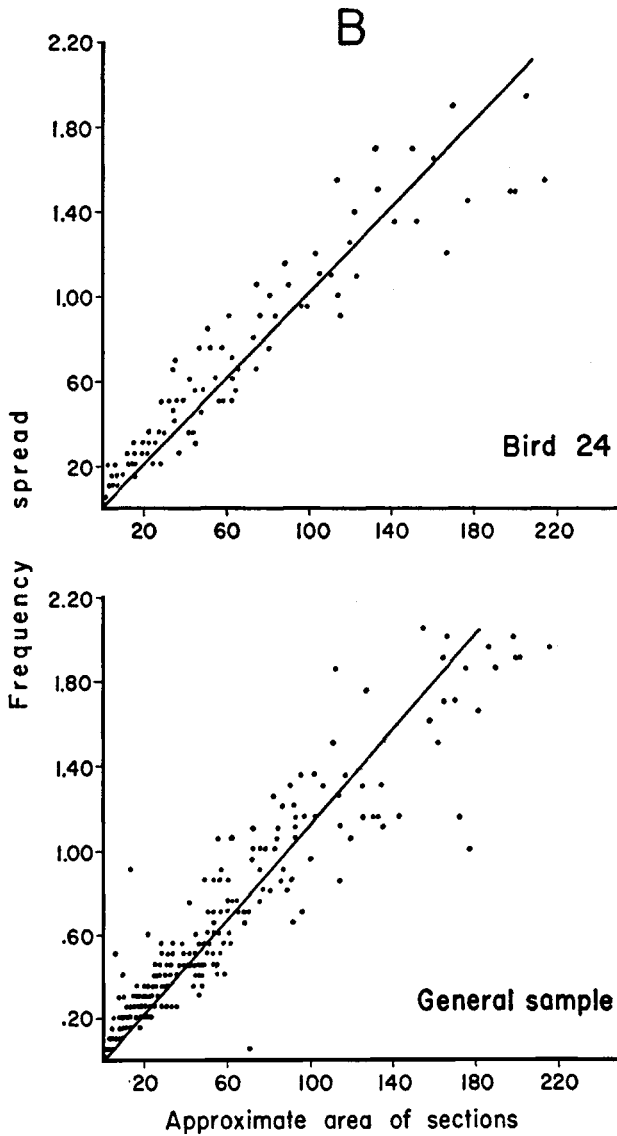


Figure 3B. Graph of the correlations between the total energy in a section, as revealed in section area, and the frequency spread.

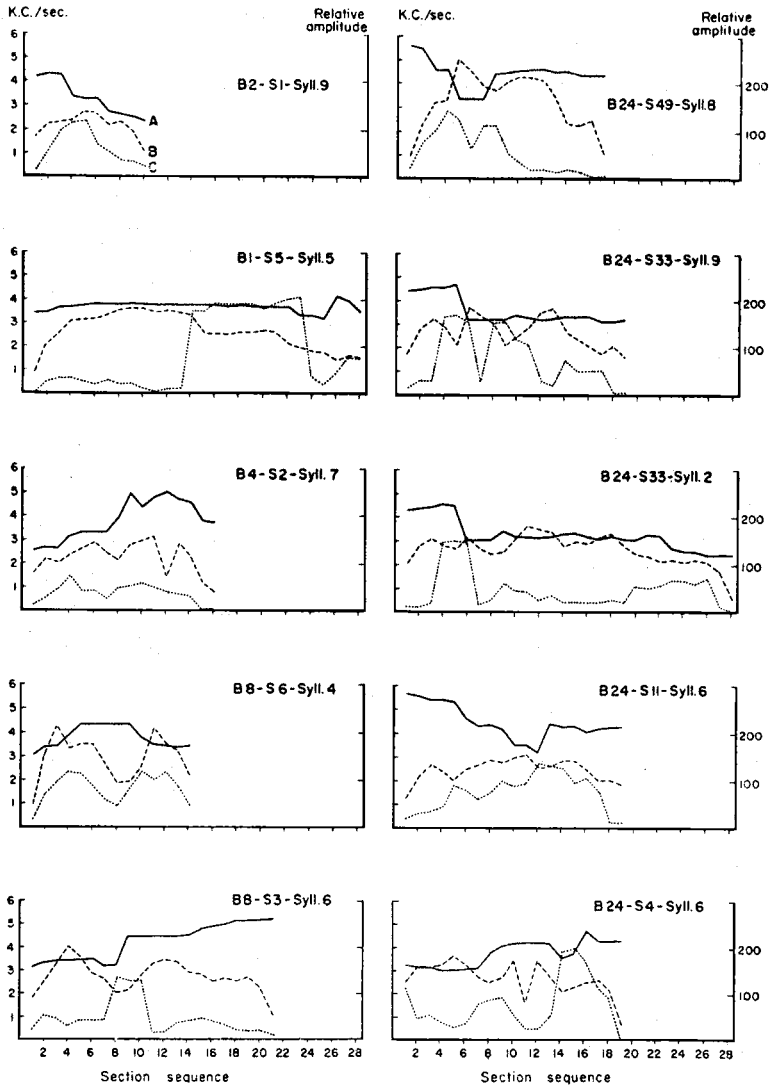
(Marler and Isaac, 1960b). Even allowing for the fact that the latter are based on wide-band filter settings, the difference is still striking. As we shall see more clearly later, the wider range of a complete syllable is achieved by variation of the frequency of its constituent notes in time.

*Correlations between different measurements.* The area of the sections was taken as an approximate measure of the total sound energy being produced. It is of some interest from the point of view of the mechanism of sound production to know whether variations in area are a result of changes in amplitude of the highest peak or of changes in the frequency spread. The graphs in Figure 3 give a clear answer to these questions. Only when the area is small (below 7 per cent of the maximum) is there any correlation with the amplitude of the strongest peak (Figure 3A). With larger areas the curves form a plateau. Even if we make allowance for the fact that the decibel scale from which the amplitude measures are derived has a logarithmic basis, the same relationship appears. The alternative explanation for increasing section area is a correlation with frequency spread, and as shown in Figure 3B, they have a linear relationship. Thus, for the most part, variations in the total sound energy in Brown Towhee syllables are associated more with differences in the breadth of frequencies encompassed than with differences in amplitude of the constituent frequencies. Nevertheless, both factors must be taken into account, especially when we consider the pattern of the syllable in time, such as at the start and finish of the syllable, when the amplitude of the frequency peaks may be low.

*Temporal patterns within the syllable.* Up to now, we have been considering all sections together, irrespective of their arrangement within the syllable. In order to analyze the pattern in time, we have selected three measures for detailed treatment. Figure 4 plots their course through 10 syllables selected to illustrate certain points. The variables are: A. the frequency of the strongest peak; B. the amplitude of the strongest peak; and C. frequency spread. Section area and the number of peaks per section as stated above are closely correlated with frequency spread and therefore follow the same time course.

The right side of Figure 4 shows the five syllables of B24. It is clear that the same bird can produce quite different patterns. The frequency may be deflected in various ways. The same applies to frequency spread. Only with amplitude of the strongest peak do we see any sign of consistent trend for lower values at the start and finish of the song—a trend also visible in the syllables of other birds. Examination of the detailed patterns reveals a close correspondence between syllables 2 and 9 of song 33, a song that included two syllable types





**Figure 4.** Diagrams of the changes taking place during the time course of 10 selected syllables: A. the frequency of the strongest peak (solid line); B. the amplitude of the strongest peak (dashed line); C. the frequency spread (dotted line).

(see Marler and Isaac, 1960b, Figure 1). It had already been deduced from the time/frequency analyses that these two syllable types were basically similar. The second one has the last part drawn out, and the present analyses bear this out. The other syllable types of B24 have no such detailed resemblance.

It is clear from Figure 4 that the three measures can vary to some extent independently of each other. Sometimes frequency spread and the amplitude of the strongest peak seem to march together, as in B8, S6, syll. 4. In other cases they have a reciprocal relationship, as in S3, syll. 6, of the same bird, and sometimes one varies while the other remains more or less steady, as in B1, S5, syll. 6, or B24, S33, syll. 2. Similarly, the frequency of the strongest peak seems to be a free variable, unhampered by any detailed correlation with the other measures.

#### DISCUSSION

Analyses of bird songs have already revealed an impressive degree of variability in the structure of the syllables from which songs are built up. Although a given individual bird may only use a limited number of syllable types, which are repeated in identical form, other individuals may have quite different syllable types, even though they may live in adjacent territories (*e.g.*, the Chipping Sparrow, Marler and Isaac, 1960a; the Mexican Junco, Marler and Isaac, in press; and the Brown Towhee, Marler and Isaac, 1960b). The present study helps us to understand how this variability can come about. The Brown Towhee evidently has sufficient versatility in its sound-producing mechanism to manipulate at least four variables somewhat independently: the dominant frequency, the amplitude of the peaks, the pattern of overtones, and the frequency spread. These can be varied both in their pattern at one instant, and in the way in which they change with time. With regard to the structure at one instant, we have seen how the syllables of a single individual give much the same distribution as those of the whole population. It is probable then that all members of this population were using syllables with a similar basic structure. In contrast with this consistency in the basic structure is the striking variability in the way in which the pattern of the syllable changes with time, giving each song type a degree of individuality.

One of our concerns in this study was the possibility of a species-specific tonal quality in Brown Towhee songs. Tonal quality is controlled by these variables we have been measuring, and most particularly by the pattern of simultaneous overtones. We have seen a rather striking consistency in the interval between overtones in these songs—

about 200 cycles per second—which could provide a basis for specific recognition. However, species-specificity can only be discussed against the background of sounds of other species living in the same area. At present we do not have the information necessary for this comparison. Because of the limited number of possible combinations that are available, it is not easy to imagine a number of sympatric species relying heavily for specific distinctiveness of their songs upon different patterns of overtones. When we add to this the demonstrated variability of the frequency characteristics of many bird songs and the effects of differential rates of attenuation of high and low frequencies, the chance of tonal quality alone providing a reliable basis for specific recognition seems rather remote. This is not to say that its role may not be an important one in some species, the Brown Towhee included, but in general we may expect other factors to be involved as well.

Our attention naturally turns to the pattern in time. However, we have seen that the pattern in time of the internal structure of the syllables shows great individual variation, which is hardly consistent with a prime function of specific recognition—although suitable as a basis for individual recognition, as we have suggested elsewhere. It is rather the over-all time pattern of the whole song that is likely to provide a means of specific recognition, and this does in fact have some consistent characteristics in Brown Towhee song (Marler and Isaac, 1960b).

How these different aspects of the song develop in the course of ontogeny we do not know. It seems conceivable that the overtone pattern is a direct result of the nature of the sound-producing structures, which in turn may have species-specific properties. The individual nature of the temporal pattern within the syllable could be a result of chance or random processes during the course of development. The species-specific nature of the over-all time pattern calls for some more-elaborate means of neuromuscular control, either through a genetic mechanism or by learning of a song tradition from other members of the same species.

#### SUMMARY

As a method of analyzing the physical basis of tonal quality, frequency/amplitude serial sections were made at five-millisecond intervals through the individual syllables of 22 Brown Towhee songs. These sections reveal an overtone structure with the interval between overtones ranging around 200 cycles per second. This overtone structure provides a possible basis for a distinctive tonal quality. Other charac-

teristics of the sections, such as number of peaks per section, frequency and amplitude of the strongest peak, frequency spread, and section area, are more variable. A search for correlations between different measures suggests that variations in total sound energy are associated more with the breadth of frequencies encompassed than with the amplitude of the constituent frequencies. Analysis of the temporal pattern within the syllables shows that frequency and amplitude of the strongest peaks and frequency spread can vary to some extent independently of each other, so providing the basis for the individual characteristics in Brown Towhee songs.

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