STRUCTURE IN PRIMARY SONG OF THE MOCKINGBIRD (*MIMUS POLYGLOTTOS*)

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MOST of what has been written about the song of the Mockingbird has been concerned with interspecific mimicry (Whittle, 1922; Visscher, 1928; Mayfield, 1934; Bent, 1948; Bedichek, 1947) or with various aspects of the song in relation to ontogenetic and behavioral phenomena in addition to mimicry (Laskey, 1935, 1944; Michener and Michener, 1935). The present study presents a quantitative description of certain aspects of primary or advertising song of male Mockingbirds on territory in spring and early summer. Tentative suggestions concerning the significance and function of various parameters of the song are included.

METHODS AND MATERIALS

The present study is based primarily on tape-recorded samples of the songs of a Kansas bird (Kansas bird no. 1) and a Florida bird (Florida bird no. 1); some data were taken from samples of the song of one additional bird in each locality (Kansas bird no. 2 and Florida bird no. 2). The Florida samples were recorded at Richmond Air Force Base by B. J. and P. P. Kellogg in March and May of 1950 on a Presto PT-900 recorder using a WE 633A microphone and a 40-inch parabola. I recorded the Kansas samples on the campus of The University of Kansas, in June and July of 1962, in part on a Magnemite W 610 E recorder using an Electrovoice Model 666 microphone and in part on a Grundig Niki SKL/E recorder using a 23-inch parabola. Audiospectrographs were made with a Kay Electric Company Vibralyzer using a Magnecord recorder operating at 15 inches per second. Wide band pass and high shape settings were used with a frequency range coverage of 44 to 4,400 cycles per second. A stopwatch was used to obtain gross temporal data and fine measurements were taken from audiospectrographs by converting linear measurements to equivalent duration and sound frequency.

TERMINOLOGY AND GENERAL DESCRIPTION

Most of the terminology used in this study was developed to refer to basic structural elements of primary song of Mockingbirds and may not be applicable to songs of other species. The terms *syllable* and perhaps *syllable-pattern* (see below) are exceptions.

It is necessary to divide Mockingbird song into units in order to describe the structure of the song quantitatively and to establish a basis for comparison of songs of individuals. Units are defined according to three characteristics. As will be seen below, actual units determined by these characteristics coincide for a considerable portion of the song.

Structural units based on the gross temporal aspect of the song.—The song is composed ultimately of fundamental units (sounds) of continuous duration in which the frequency may remain the same or vary through

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time. Such sounds, here termed *syllables,* would be expressed in musical notation either as single notes or as series of notes as in a *glissando. Syllable* is preferable to note, since a single note defines both a specific temporal unit and a specific frequency, and few syllables in bird vocalizations remain at one frequency (Thorpe, 1961: 61).

Syllables may occur singly, but more commonly they are repeated to form units called *syllable-clusters.* Syllable-clusters also may occur singly but most often are rendered in series, here called *groups.* Groups are the gross temporal divisions and are marked by the fact that often a transition from one to another is accompanied by a transition from one pattern to another. It is important to note, however, that groups are defined solely on the basis of their temporal character. That is, the silent intervals between the syllables or syllable-clusters of the group are shorter than those separating the groups. The absolute duration of the silent intervals separating the syllables or syllable-clusters within a group or separating the groups varies with the rate of singing. No instances were found here, but theoretically an inter-syllable silent interval in a sample of lesser rate could be greater than an inter-group silent interval in a sample of greater rate. Groups, then, are defined by the relative duration of silent intervals within one period of singing at a given rate and not on absolute duration of silent intervals.

Structural units based on changes of pattern.—The most prominent aspect of the Mockingbird's song is the rendition of like syllables, syllable-clusters, or groups to form series of varying lengths. Syllables, syllable-clusters, or groups that are of like configuration are considered to be of the same *syllable-pattern.* Thus, when syllable-pattern no. 1 is referred to, all units are included that show the particular configuration so numbered. Renditions of a given syllable-pattern, unlike the temporal units defined above, are similar not only as to total duration but also as to duration, frequency configuration, and arrangement of the constituent syllables.

A syllable-pattern is defined as the smallest configuration of syllables or syllable-clusters that is rendered essentially identically each time it appears in the course of the song. This, of course, may even be a single syllable. In units consisting of rapid repetitions of syllables of the same configuration, as in a trill or a buzz, and in which it is impractical to separate the smallest like units, the next largest unit is considered to be a syllable-pattern. The temporal equivalent of a syllable-pattern may be a single syllable, one or more syllable-clusters or, less often, a group.

Series comprised of renditions of the same syllable-pattern are called *phrases.* Present also in the song are a few series in which the constituent syllables or syllable-clusters are not of the same syllable-pattern. These units are temporally comparable to the units called phrases. Both phrases

TABLE 1

DURATION[1] OF SYLLABLE-PATTERNS AND SILENT INTERVALS ASSOCIATED WITH SYLLABLE-PATTERNS, PHRASES, AND GROUPS

Samples	*Kansas bird no. 1*	*Kansas bird no. 2*	*Florida bird no. 1*	*Florida bird no. 2*
Syllable-patterns				
Mean	0.019 (557)[2]	0.019 (218)	0.018 (890)	—
Range	0.002–0.085	0.002–0.051	0.005–0.077	—
Intersyllable-pattern intervals				
Mean	0.020 (376)	0.013 (152)	0.010 (604)	—
Range	0.0007–0.158	0.001–0.067	0.0007–0.085	—
Interphrase intervals				
Mean	0.70 (345)	0.30 (93)	1.30 (205)	0.90 (118)
Range	0.1–11.0	0.2–2.2	0.1–11.2	0.1–18.1
Intergroup intervals				
Mean	1.07 (367)	0.62 (89)	1.23 (257)	1.28 (93)
Range	0.1–14.0	0.2–2.2	0.1–10.2	0.1–18.1

[1] In seconds.
[2] Sample size in parentheses.

and these units with pattern variety can be considered "sense units" in that their elements are related to one another not only temporally but as parts of a larger pattern. These integrated units could conceivably be considered large syllable-patterns but I prefer to consider them phrases since they are more similar to phrases than to ordinary syllable-patterns in duration.

It should be noted here that there is nothing inherent in the structure of these units as physical entities that imparts "sense" to them. It is the human mind that recognizes that certain sound patterns exemplify good continuation, completion, and closure, and other principles of pattern perception as applied to sound patterns by Meyer (1956, Chapters II and III; see also Erickson, 1955: 13–69). It would be difficult to prove that birds also recognize and prefer structural organizations that adhere to these principles, but circumstantial evidence that they do is considerable (Craig, 1943; Thorpe, 1961: 6; Hall-Craggs, 1962: 295; Hartshorne, 1958b: 53). In this regard it is of interest to consider that while man surely did not influence the structure of sound patterns used by birds, exposure to bird vocalizations may well have influenced man in his choice of structural patterns that he considers to be of aesthetic significance.

Structural units based on the numerical aspect of the song.—X-units are defined as those units of the song that are most comparable on the basis of the number of syllable-patterns per unit. The justification for describing a unit such as this will be discussed more fully below, in the section on numerical characteristics of the song.

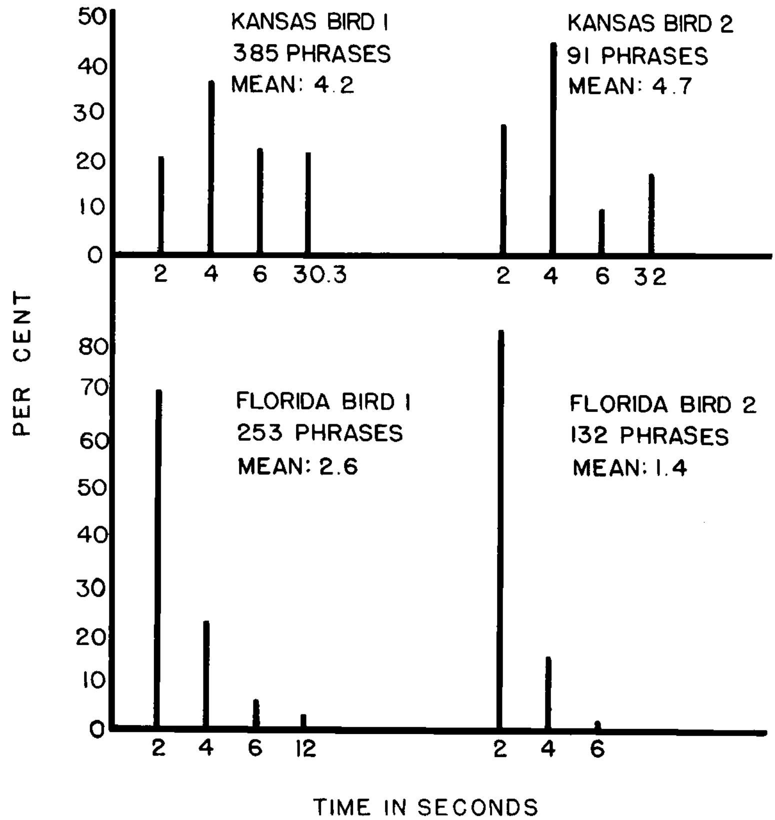


Figure 1. Frequency distributions showing duration of phrases for the Kansas and Florida samples.

Analysis of Structure

Temporal Characteristics of the Song

Duration of units and silent intervals.—Average values for duration of phrases, groups, x-units, syllable-patterns, and associated silent intervals are shown in Table 1 and Figures 1, 2, and 3. The values in every case are based on measurements of consecutive units. If a sample of song were available in which all syllable-patterns were represented at least 10 times, it would be possible to find the average length of phrases comprised of a given syllable-pattern. The length of the present sample does not permit this since the greatest number of times any syllable-pattern is represented is seven and most occurred only twice. I think, however, that the measurements presented here give a good indication of the general temporal aspect of the song.

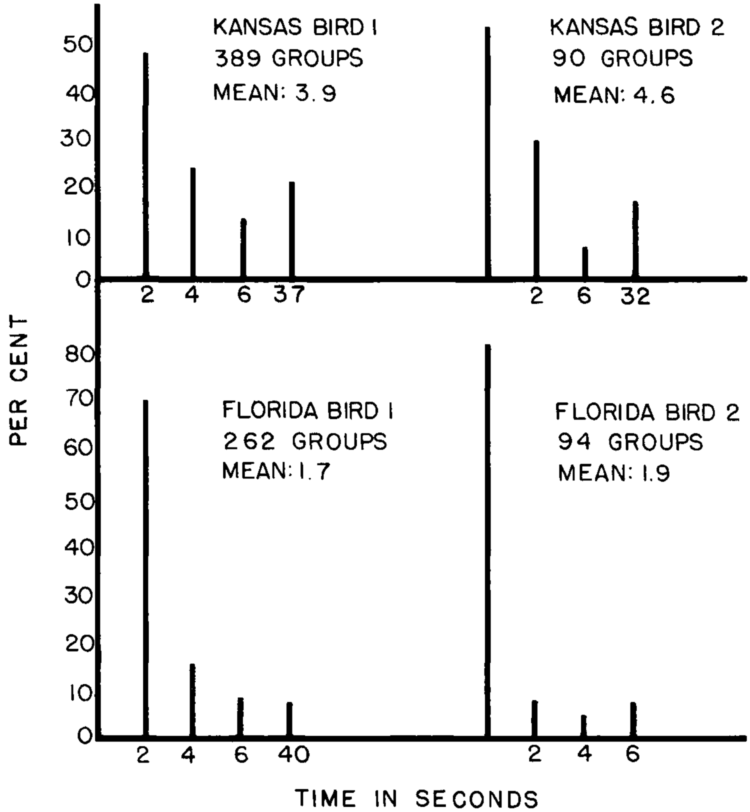


Figure 2. Frequency distributions showing duration of groups for the Kansas and Florida samples.

The average duration of syllable-patterns is based on several samples of each separate syllable-pattern. The average durations of syllable-patterns of the three birds for which this was calculated are almost identical; average values for inter-syllable-pattern silent intervals are more variable.

The average duration of phrases, groups, and x-units are greater for the Kansas than for the Florida samples; this is to be expected since the average values for number of syllable-patterns per unit are larger for the Kansas than for the Florida samples (Figures 4, 5, and 6). Modal values and pattern of distribution for phrases are different between the two areas (Figure 1), but are similar for groups and x-units in all four birds (Figures 2 and 3).

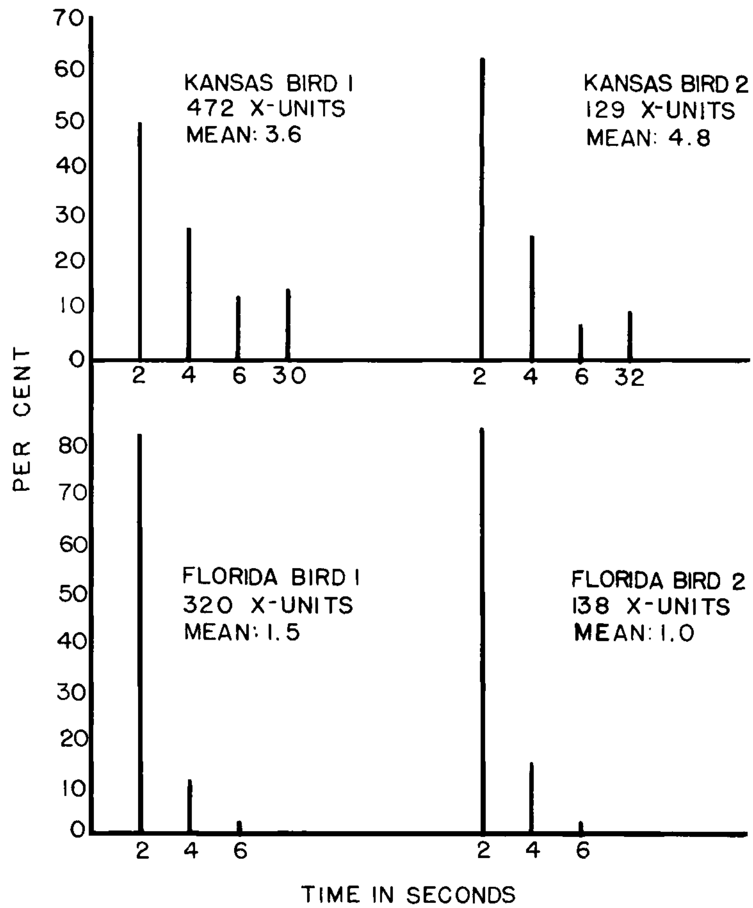


Figure 3. Frequency distributions showing duration of x-units for the Kansas and Florida samples.

Continuity.—Hartshorne (1956: 177) wrote:

> Continuity concerns the extent to which singing is free from interruption, during a normal "performance period" of a minute or more, by "substantial pauses," silences longer than those separating notes within songs or phrases. There is no wholly sharp line between such pauses and musical "rests," such as those separating the phrases in songs of some thrushes of the genus *Hylocichla*, which are integral to the musical pattern; but if a bird habitually sings several or many notes a second for two or three seconds, and then is silent for eight or more seconds, this is highly discontinuous singing. With such a singer there is much more silence than song for any period longer than a few seconds.

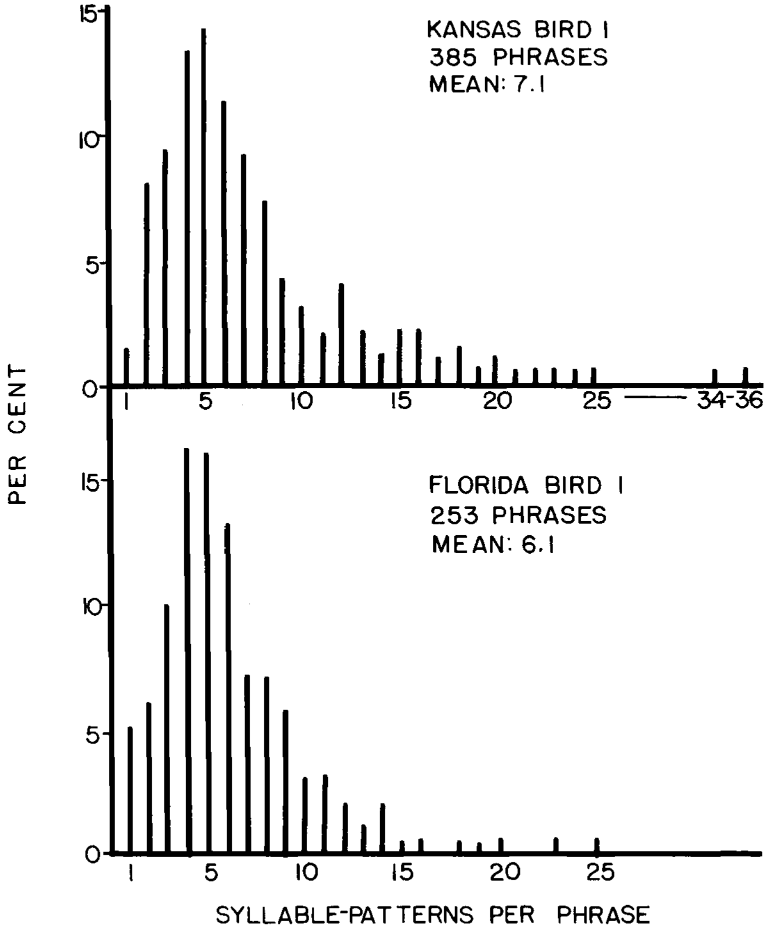


Figure 4. Frequency distributions showing number of syllable-patterns per phrase for Kansas bird no. 1 and Florida bird no. 1.

Hartshorne recognized three categories of continuity: continuous, semicontinuous, and discontinuous. According to him the rendition of song patterns comprises more than 50 per cent of the performance time in the first, between 30 and 50 per cent in the second, and less than 30 per cent in the third.

In determining the percentage of the time spent in performance (hereafter called *per cent performance time*), Hartshorne apparently measured the duration of units corresponding to the groups or phrases of the present study, and thus he included silent periods between syllables and syllable

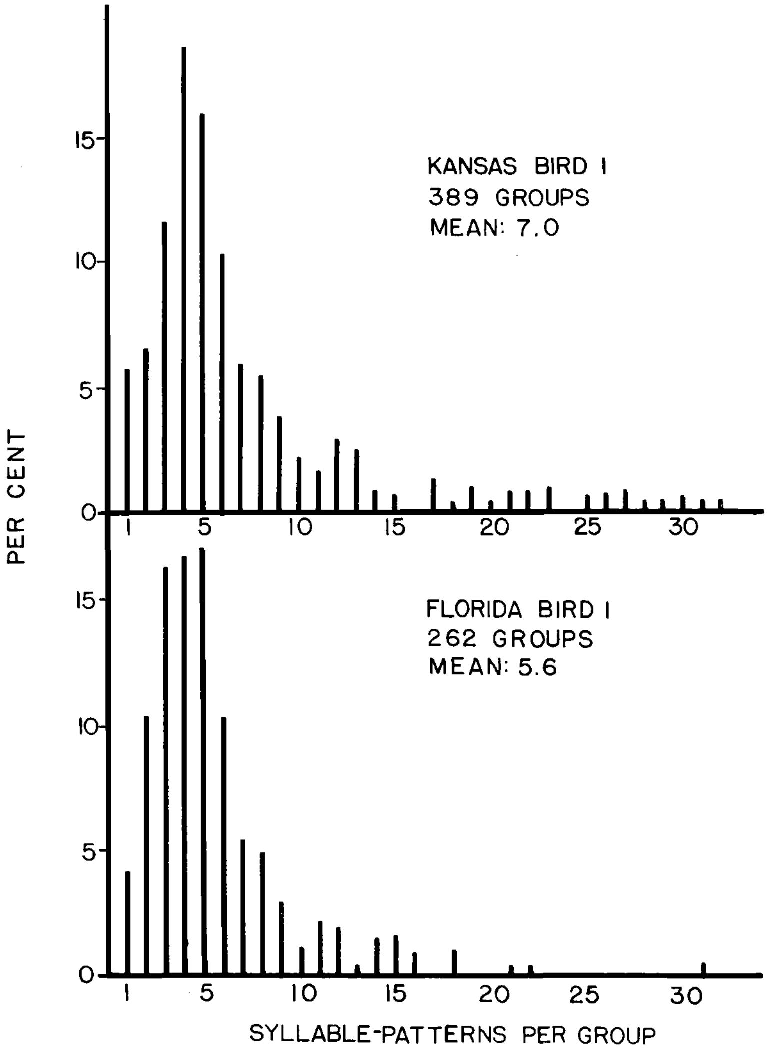


Figure 5. Frequency distributions showing number of syllable-patterns per group for Kansas bird no. 1 and Florida bird no. 1.

clusters in the performance time. When inter-syllable-pattern silent intervals were not included in the performance time, I found the per cent performance time for the Florida sample to be approximately 30. On this basis, the Mockingbird would rate at best as semicontinuous. Table 2 shows the per cent performance time for the four Mockingbirds studied, based on measurements of groups. Groups were chosen rather than phrases

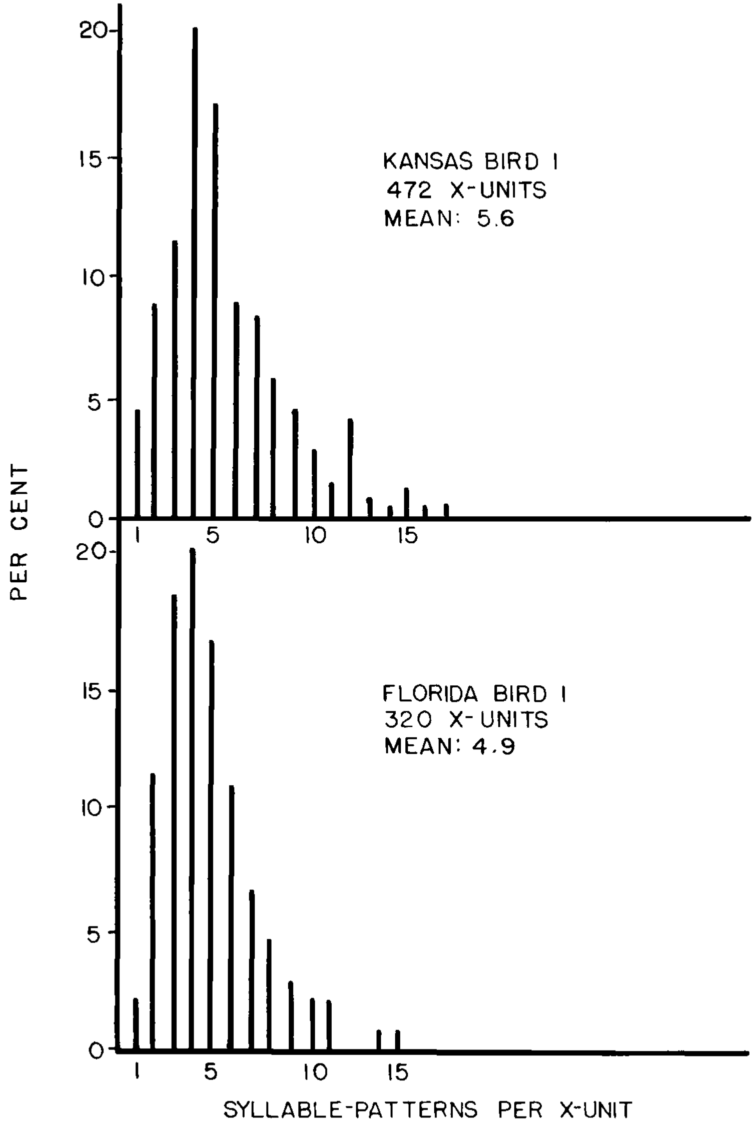


Figure 6. Frequency distribution showing number of syllable-patterns per x-unit for Kansas bird no. 1 and Florida bird no. 1.

because continuity is a function of the temporal, not the pattern, aspect of the song.

In the sample for Florida bird no. 2 (Reel 7 Cut 3), the first part of the cut is an example of rapid song delivered while the bird was engaged

TABLE 2

CONTINUITY OF SONG[1] COMPARED WITH VALUES FOR AVERAGE GROUP DURATION MINUS AVERAGE INTERGROUP SILENT INTERVAL DURATION

Samples	*Per cent performance time*	*Difference in seconds between duration of unit and duration of interval*
Kansas bird no. 1:		
Reel 0 cut 0	66	2.17
Reel 1 cut 1	78	3.48
Reel 2 cut 2	79	3.53
Kansas bird no. 2:		
Reel 3 cut 3	83	3.98
Florida bird no. 1:		
Reel 6 cut 1	50	0.49
Reel 6 and 7 cut 2	52	0.45
Florida bird no. 2:		
Reel 7 cut 3		
Part 1	72	1.53
Part 2	37	1.10

[1] Expressed as per cent performance time.

in "acrobatics," flying up from its perch, somersaulting, and catching insects while singing continuously. The second part is more leisurely. Per cent performance time is twice as great in the first as in the second part. Per cent performance time, then, may vary as much or more between different portions of the song of one individual as between individuals, or between the norms for separate species (Hartshorne, 1956: 177–192). However, the general tendency for high continuity in Mockingbird song is unmistakable.

Per cent performance time is a function of the ratio of average duration of unit to average duration of interval. Thus the same value could represent either a relatively short unit duration associated with a short interval duration, or a relatively long unit duration associated with a long interval duration. Obviously, the greater the positive value for average unit duration minus the average interval duration for any one sample, the greater the per cent performance time (Table 2).

PATTERN CHARACTERISTICS OF THE SONG

Syllable-patterns.—The syllable-pattern is the basic pattern unit of the song. A given syllable-pattern is used again and again by a bird at various intervals; some syllable-patterns occur more often than others. Variation among renditions of the same syllable-pattern by one individual is limited; illustrations of the degree of variation are shown further on, in Figure 9. The samples in Figure 9, A, B, and C are exceptional; few syllable-patterns show this much variation.

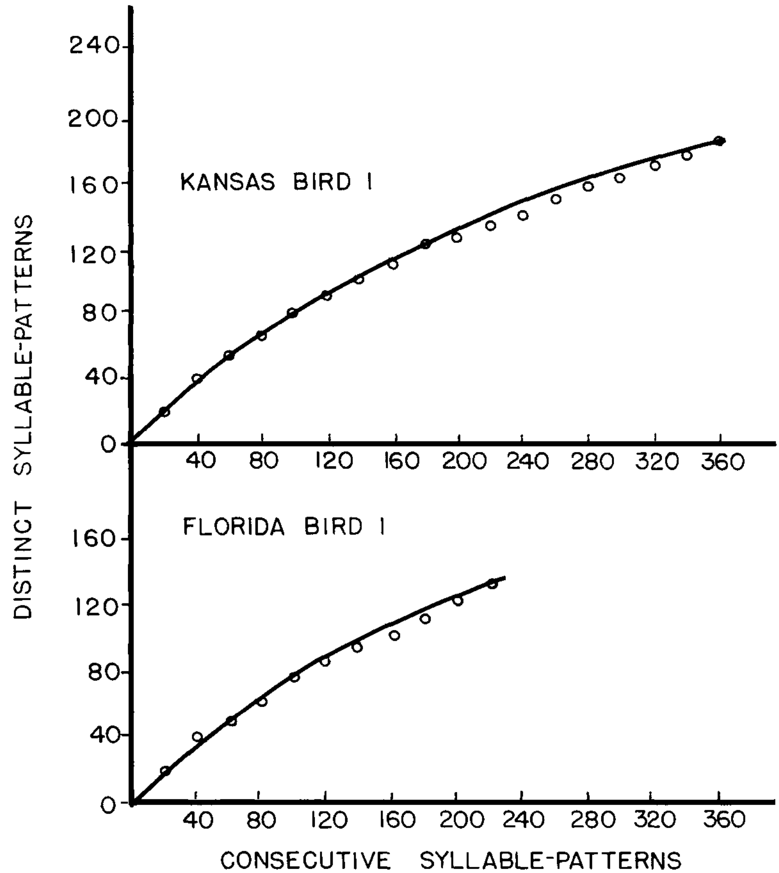


Figure 7. Repertory and mode of introduction of distinct syllable-patterns for Florida bird no. 1 and Kansas bird no. 1. Observed data are represented by small circles; exponential curves are represented by continuous lines.

Repertory.—One of the most striking characteristics of Mockingbird song is the large number of syllable-patterns constituting the repertory of each individual. Figure 7 shows repertories of two Mockingbirds. This figure shows that the number of distinct syllable-patterns used in a given singing effort increases as the song progresses, and that the rate of introduction of distinct syllable-patterns falls off steadily as the bird approaches the probable limit of its repertory. Similar data obtained for two Mockingbirds in Texas by Selander and Hunter (MS) are wholly consistent with this interpretation.

TABLE 3

REPERTORIES FOR FOUR MOCKINGBIRDS ESTIMATED ON BASIS OF EXPONENTIAL CURVE EXTENSION

Sample	*Kansas bird no. 1*	*Kansas bird no. 2*	*Texas bird no. 1*[1]	*Texas bird no. 2*[1]
Known number of syllable-patterns	194	134	66	91
Estimated number of syllable-patterns	244	213	66	96
Per cent of total repertory represented	79.5	63.0	100.0	95.0
Total consecutive changes of syllable-pattern	380	220	260	300

[1] Values determined from data of Selander and Hunter (MS).

Obviously, the slopes of the curves would reach the horizontal if the total repertory were plotted. In instances where data sufficient to reach this level are lacking, as was the case in the present study, I devised a method for estimating the total repertory. I found that when the data were plotted as in Figure 7, the curves obtained approximate exponential curves adjusted to pass through the last point of the actual data. This indicates that successive syllable-patterns are given at random (see below). Hence, the exponential curves may be extended to provide an estimate of minimum total repertory. Estimated repertories of four Mockingbirds are shown in Table 3.

None of the birds has an estimated repertory identical in size to that of any other. Both the Kansas and Florida birds have probable repertories considerably larger than the Texas birds. I first thought that some of the differences between the Kansas and Florida and the Texas samples was due to differences of approach by the investigators. After a discussion of criteria for distinguishing syllable-patterns, and after Dr. Selander viewed audiospectrographs of the samples, it was clear that the differences noted were not a result of technique.

Laskey (1944: 218), writing of the repertory development of a four-year-old, hand-raised Mockingbird, stated: "His repertory was gradually enlarged, but some songs were only temporary acquisitions while others were used intermittently." If the total repertory in fact increases as a function of time (days to years), the slopes of the curves would not become permanently horizontal, as would the slopes of exponential curves. Hence the estimates of total repertory based on exponential curves represent estimates of the minimum total repertory, and this only for the period under consideration.

Mode of occurrence of syllable-patterns.—The introduction of new syllable-patterns as a function of the total number of consecutive syllable-patterns given in the course of a period of singing was shown above in

Figure 7. The experimental curves are closely approximated by exponential curves of the form,

$$n = N\ (1 - e^{-T/N})$$

where n is the number of distinct syllable-patterns in the sample, T is the total number of syllable-patterns in the sample, and N is the total number of distinct syllable-patterns in the repertory.

The fits of the curves to the observed data are made by adjusting N so that the curves pass through the last points of data. The N thus chosen is the predicted size of the repertory. To determine the sample size necessary to obtain a number, X, of distinct syllable-patterns which is a given number, M, less than the predicted total, N, we set $Ne^{-T/N}$ equal to M and solve for T from mathematical tables.

The best explanation for this functional dependence is that the probability of occurrence of a new syllable-pattern is proportional to the number of unused syllable-patterns remaining in the repertory of the Mockingbird. The underlying assumptions of this theory are that a bird has an essentially constant repertory (for the duration of the trial) and that the syllable-patterns are selected randomly from this collection of syllable-patterns.

The assumption that syllable-patterns occur at random appears to be valid for any sample of large size. Some syllable-patterns tend to occur in short series of up to four that recur in the same or in slightly rearranged order, although many of the syllable-patterns in these series occur in other contexts. These short series, however, would not be expected to affect the shapes of the curves.

Versatility.—Craig (1943) and Hartshorne (1956) noted a relationship between the number of distinct patterns in the song of a given species (versatility) and the amount of time the species spends in the actual performance of its song phrases (continuity). Versatile species on the whole tend to spend a greater amount of time in performance than do semi-versatile or nonversatile species. According to Hartshorne, such relationship is evidence that birds tend to avoid producing sounds in such a way that they become monotonous to the listening individuals, and thus fail to fulfill their biological functions. Hartshorne (1958a: 45) classified as versatile all members of the family Mimidae. The present data fit his concepts as they concern Mockingbirds.

Individual variation of syllable-patterns.—By means of audiospectrographs, repertories of the Kansas birds were compared with one another and the entire Kansas sample was compared with the sample for Florida bird no. 1. Examples of similar syllable-patterns were selected by ear from the sample for Florida bird no. 2, audiospectrographed, and compared with the sample for Florida bird no. 1.

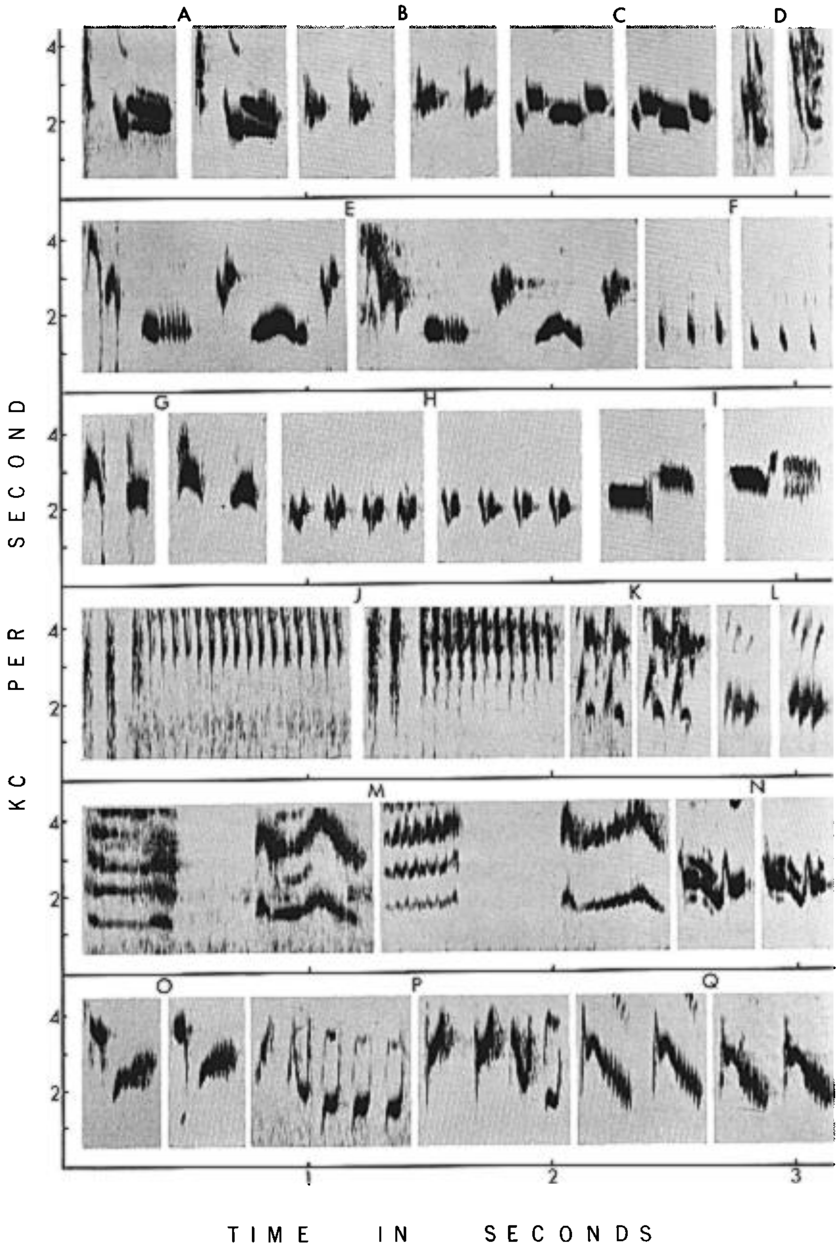


Figure 8. Audiospectrographs illustrating identical syllable-patterns used by Kansas birds no. 1 and no. 2. The lettered pairs A–Q in each case show the vocalizations of Kansas bird no. 1 on the left and of Kansas bird no. 2 on the right.

Of the 86 distinct syllable-patterns of Kansas bird no. 2 and the 194 distinct syllable-patterns of Kansas bird no. 1, 18 were similar enough to be considered renditions of the same syllable-patterns, that is, probably derived one from the other or both from the same model. These 18 instances of similarity are illustrated in Figure 8. A few examples of separate renditions of syllable-patterns within a sample for one bird are also shown to illustrate the basis of comparison (Figure 8, B, F, H, and Q). There is also an instance in which the sequence, as well as the syllable-pattern, is the same (Figure 8, M). The Kansas birds were within hearing distance of one another.

Two instances of renditions of the same syllable-pattern in the Florida samples are shown in Figure 9 (A and B, N and O). The degree of similarity is as great here as between the two Kansas birds.

When the Kansas sample (262 distinct syllable-patterns) as a whole was compared with that of Florida bird no. 1 (134 distinct syllable-patterns), three instances were found that can be considered renditions of the same syllable-pattern (Figure 9, A, B, and C; D and E; F and G). In three other cases individual syllables in the syllable-pattern, but not the entire syllable-pattern, are similar (Figure 9, K and L; M, N, and O; P and Q). Three instances were found in which there is a structural similarity but the renditions are not of the same syllable-pattern (Figure 9, H, I, and J; R and S; T and U). Many syllable-patterns among the repertories of the individuals were found to resemble one another to lesser extents.

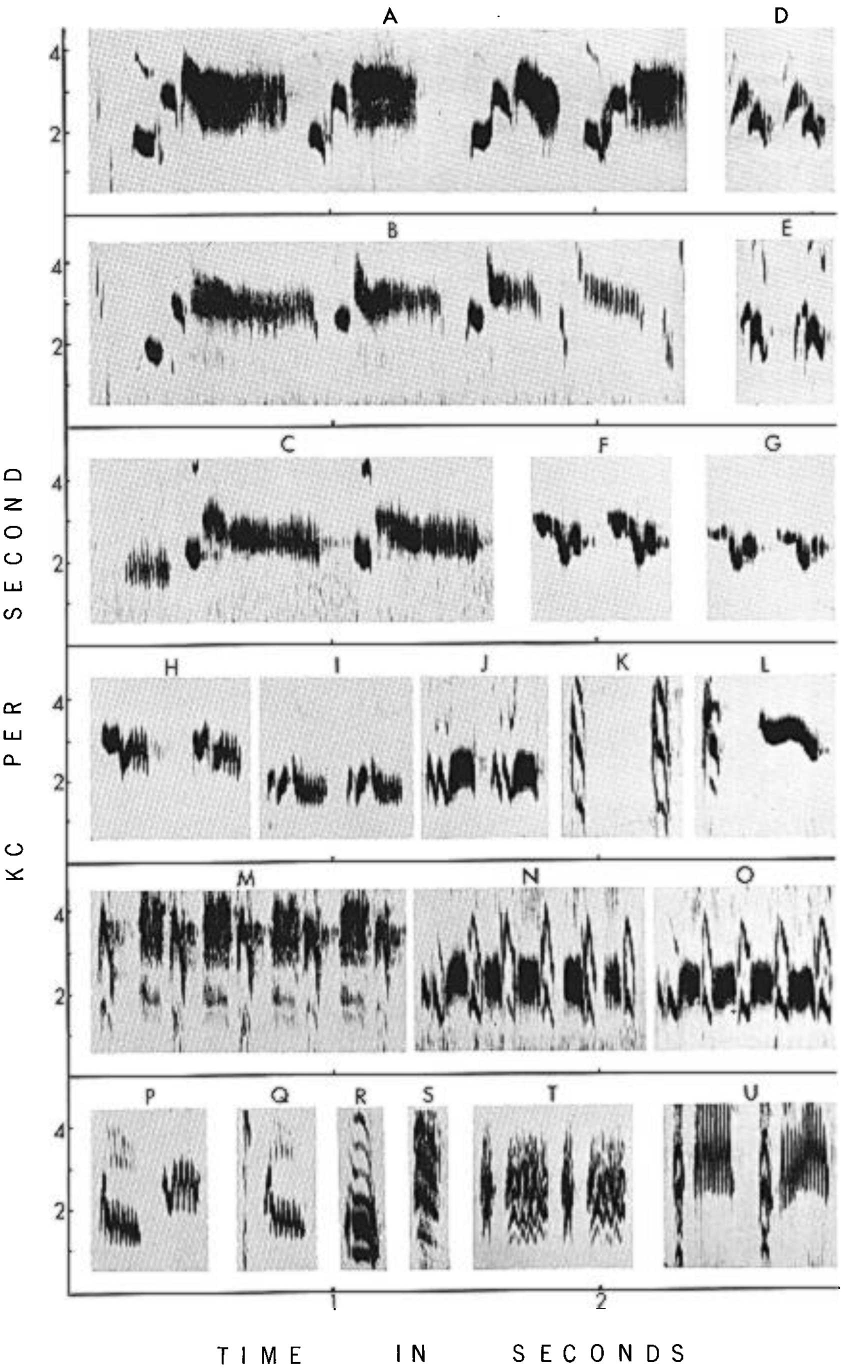
On the whole, the Florida birds used syllable-patterns that are more compact, that is, extremes of frequency vary less than syllable-patterns used by the Kansas birds (Table 4). As Thorpe (1961: 73) put it, the frequency "envelope" of the Florida song is smaller; also the averages for highest, lowest, and most prominent frequencies are lower for the Florida than the Kansas samples. The lowest frequency varies less than the highest. Marler and Isaac (1960) also found this to be true of songs of the Chipping Sparrow, *Spizella passerina*. Representative syllable-patterns in the Kansas samples show a greater variety of styles than those of the Florida samples (compare Figures 8 and 9).

Classification of phrases.—Phrases are classed into three types, according to constituent syllable-patterns, as follows:

Type I. Phrases consisting of successive renditions of the same syllable-pattern.

Type II. Phrases consisting of renditions each of a different syllable-pattern.

Type III. Phrases consisting of renditions of more than one syllable-pattern, any one of which may be rendered more than once.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KC PER SECOND
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TIME IN SECONDS

TABLE 4

SUMMARY OF FREQUENCY CHARACTERISTICS OF SYLLABLE-PATTERNS

Samples	*Kansas bird no. 1*	*Kansas bird no. 2*	*Florida bird no. 1*
Highest frequency			
Mean	3917[1] (425)[2]	4046 (136)	3834 (505)
Range	1864–7050	2591–7050	1045–5000
Lowest frequency			
Mean	2136 (515)	2045 (198)	1500 (664)
Range	455–4136	1227–3500	542–2591
Most prominent frequency			
Mean	3500 (162)	3228 (72)	2773 (89)
Range	1909–4455	1955–4545	1875–4136

[1] Frequency in cycles per second.
[2] Sample size in parentheses.

Table 5 shows the distribution of phrases for each cut and bird, according to the three types. The distribution in each instance is similar and constant; note especially the relatively small samples in Cut 4 (Kansas bird no. 1) and Cut 1 (Florida bird no. 1).

Phrases may also be categorized according to the number of groups composing them and whether they are part of single or multi-phrase groups (Tables 6 and 7, in which the distribution of phrase-types I, II, and III is included). In songs of each of the four birds represented, approximately half the phrases of all types are composed of one group. Two-phrase groups show a relatively high frequency of occurrence in Florida bird no. 1, but not in the other birds. The distribution of phrase-types I, II, and III for each class is much the same as it is for all phrases (compare Tables 5, 6, and 7).

NUMERICAL CHARACTERISTICS OF THE SONG

Number of syllable-patterns per phrase.—The number of syllable-patterns per phrase for two birds is shown in Figure 4. The range of variation in number of syllable-patterns is greater for Kansas bird no. 1 than for Florida bird no. 1 (Figure 4). This is reflected in the slightly higher averages for the Kansas samples. In both, however, phrases with four and five syllable-patterns predominate.

←

Figure 9. Audiospectrographs illustrating similarities in syllable-patterns between Florida birds no. 1 and 2 and between the entire Florida and Kansas samples. Florida bird no. 1, B, D, F, K, M, P, H, I, R, and T. Florida bird no. 2, A and N. Kansas sample, C, E, G, L, O, Q, J, S, and U.

TABLE 5

PERCENTAGE DISTRIBUTION OF PHRASES AS CLASSIFIED ACCORDING TO TYPES I, II AND III

Samples	*Total number of phrases*	*Type I*	*Type II*	*Type III*
Kansas bird no. 1	438	83 %	2 %	15 %
Cut 0	180	83	0	17
Cut 1	107	87	2	11
Cut 2	100	75	1	24
Cut 4	51	78	8	14
Kansas bird no. 2 Cut 3	95	76	1	23
Florida bird no. 1	247	81	4	14
Cut 1	39	82	0	18
Cut 2	208	81	4	14
Florida bird no. 2 Cut 3	129	81	3	16

Saunders (*in* Bent, 1948: 310) realized that Mockingbirds tend to render patterns four or five times and stated that this is one of the characteristics of Mockingbird song that distinguishes it from that of the Catbird (*Dumetella carolinensis*) and of the Brown Thrasher (*Toxostoma rufum*). Modal values of four and five are probably characteristic of the song of most Mockingbirds. It is of interest to note that 36 is the greatest number of times (1 is the least) in the present data that a bird was found to render a given syllable-pattern in one phrase.

Number of syllable-patterns per group.—Modal values for number of syllable-patterns per group (Figure 5) are close to those for number of

TABLE 6

DISTRIBUTION OF PHRASES FOR KANSAS BIRD NO. 1 INTO GROUPS AND DISTRIBUTION OF TYPES I, II, AND III FOR EACH CLASS[1]

Classes	*All types*	*Type I*[2]		*Type II*[2]		*Type III*[2]	
Number of groups per phrase							
1	55 (215)[3]	84	56	1	25	15	49
2	8 (32)	78	8	0	0	22	0
3	5 (19)	95	6	0	0	5	2
4	1 (5)	100	2	0	0	0	0
5	1 (3)	100	1	0	0	0	0
Number of phrases per group							
2	7 (26)	81	7	4	25	15	6
3	6 (25)	64	5	0	0	36	13
4	8 (33)	79	8	3	25	36	13
5	4 (16)	75	4	6	25	19	4
6	2 (6)	83	2	0	0	17	2
13	3 (12)	75	3	0	0	25	5

[1] All values are expressed as percentages.

[2] Read left-hand column horizontally and right-hand column vertically for each type.

[3] Sample size in parentheses.

TABLE 7

DISTRIBUTION OF PHRASES FOR FLORIDA BIRD NO. 1 INTO GROUPS AND DISTRIBUTION OF TYPES I, II, AND III FOR EACH CLASS[1]

Classes	*All types*	*Type I*[2]		*Type II*[2]		*Type III*[2]	
Number of groups per phrase							
1	49 (121)[3]	77	47	5	67	17	58
2	9 (23)	100	11	0	0	0	0
3	3 (8)	100	4	0	0	0	0
4	3 (7)	100	3	0	0	0	0
5	1 (2)	100	1	0	0	0	0
6	1 (1)	100	1	0	0	0	0
Number of phrases per group							
2	21 (52)	79	20	0	0	21	31
3	6 (14)	86	6	7	11	7	3
4	5 (13)	62	4	15	22	23	8
5	2 (6)	100	3	0	0	0	0

1 All values are expressed as percentages.
2 Read left-hand column horizontally and right-hand column vertically for each type.
3 Sample size in parentheses.

syllable-patterns per phrase, as would be expected since approximately 50 per cent of the units designated "phrases" are also "groups" (Tables 6 and 7). The average number of syllable-patterns per group is similar to the average per phrase; the range of variation is greater for groups in both samples. The greatest number of times units not all of the same syllable-pattern were found to be rendered without pause was 63 (not illustrated), the least being 1.

Number of syllable-patterns per x-unit.—If the number of syllable-patterns per unit is plotted as per group in multi-group phrases and as per phrase in multi-phrase groups, the range of variation in the number of syllable-patterns per unit decreases, that is, the variation is less than that observed for phrases or groups separately (Figure 6). Units so defined are called *x-units.* The average number of syllable-patterns per x-unit is smaller than that per phrase for all samples. The modal values are similar to those for number of syllable-patterns per phrase and group.

The duration of x-units also shows less variation than for phrases or groups (compare Figures 1, 2, and 3). The justification for recognizing x-units at all, then, is based on both numerical and temporal characteristics. X-units are the units of the song that are most comparable one to another, that is, that show the least variation for these characteristics.

Because of the constancy of x-units in number and duration, they strike the listener as being natural divisions of the song. This impression is enhanced by the fact that most often—in approximately 80 per cent of recorded instances (see Table 5)—each x-unit is comprised of renditions of the same syllable-pattern. Either periodic silent intervals or periodic changes of pattern equally impress the listener that discrete units are being distinguished. Hartshorne (1956) has noted that either silent intervals or changes of pattern may function in the avoidance of monotony. These kinds of interruptions serve generally as a means by which the producer or observer may organize the stream of stimuli into units of emphasis that are more easily remembered than would be an uninterrupted, and hence less organized, output. The thing to be emphasized concerning x-units is that the use of either kind of interruption may result in the definition of comparable units.

Number of syllables per syllable-pattern.—A comparison of the two Kansas birds with one another and with Florida bird no. 1 for number of syllables per syllable-pattern is shown in Figure 10. The distribution of syllable-patterns is closely similar between Kansas bird no. 1 and Florida bird no. 1; the range of variation is greater for the Kansas sample. The sample for Kansas bird no. 2 is small and may not be representative.

The relationship between number of syllable-patterns in successive x-units.—It is of interest to determine whether or not the number of syllable-patterns in a given x-unit has any influence on the number of syllable-patterns in the succeeding x-unit.

Assuming that x-units containing different numbers of syllable-patterns occur randomly, the probability that an x-unit of N syllable-patterns is succeeded by an x-unit of M syllable-patterns is equal to the probability of occurrence in the total sample of an x-unit of N syllable-patterns multiplied by the probability of occurrence in the total sample of an x-unit of M syllable-patterns. To find the predicted occurrences in which the syllable-patterns per x-unit change by P syllable-patterns, $N - M$ is set equal to P and the various probabilities are summed for all values of N. This gives the probabilities of successive x-units differing in number of syllable-patterns by P syllable-patterns based on the assumption that the x-units are randomly selected from the weighted total sample.

When the expected random distribution of these instances is compared (Figure 11) with the observed distributions for instances of like and unlike pattern separately, it is seen that the distribution of observed instances is approximately the same as the random distribution, except for instances of like pattern. A greater percentage of instances of like pattern show no difference in number than would be expected from chance.

Selander and Hunter (MS) have evidence that phrases comprised of renditions of the same syllable-pattern tend to contain the same number of syllable-patterns. The number of renditions of phrases of like pattern is too small in the present data to warrant comparison. However, the data in

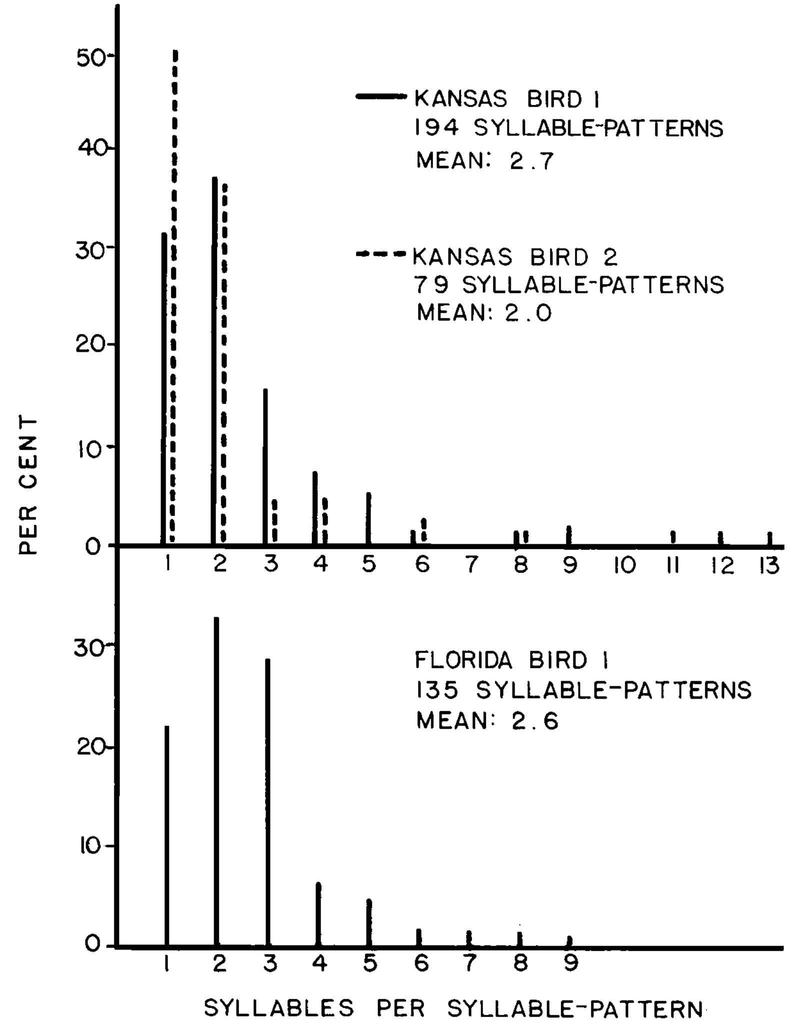

Figure 10. Frequency distributions showing number of syllables per syllable-pattern for Kansas birds no. 1 and 2 and Florida bird no. 1.

Figure 11 show that a similar condition is found for x-units. The close approximation of pattern and number in the two samples is indicated both from the point of view of the proportion of instances of units containing the same number of syllable-patterns that are also of the same pattern and from the point of view of the proportion of units of like pattern that contain equivalent numbers of syllable-patterns.

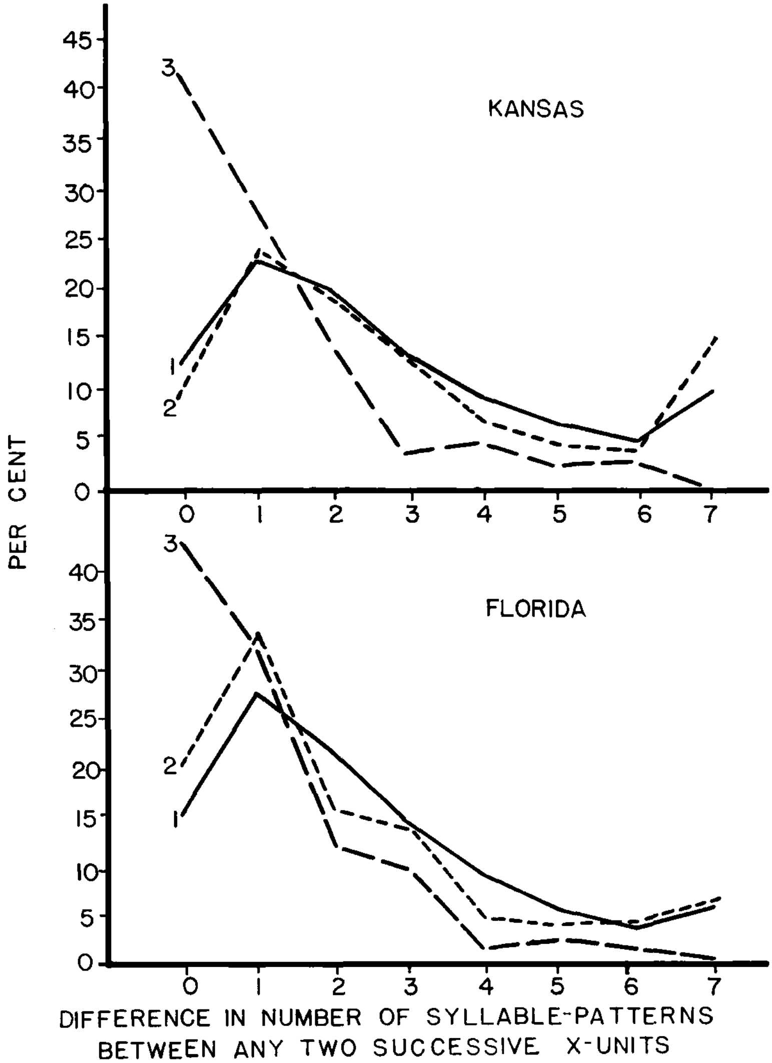

Figure 11. Comparison of observed and predicted values for number of syllable-patterns per successive x-units. Curve no. 1 is based on random distribution of x-units. Curve no. 2 represents instances of unlike patterns. Curve no. 3 represents instances of like patterns.

Discussion

Functions of Primary Song in the Mockingbird

General characteristics of primary song.—In order to fulfill its advertising function, primary song must necessarily possess a number of qualities. Besides being readily heard and located, it must have some property or properties that are relatively constant throughout the species. Nevertheless, in addition to constant characteristics, one could expect to find some variable aspects of primary song that would facilitate individual recognition. Individual recognition is important between members of a potentially mated or mated pair and between birds in adjacent territories. The relative complexity of primary song, as well as secondary song, as opposed to call notes would seem to render it potentially effective for this function, although call notes have been reported as being operative in individual recognition (Thorpe, 1961: 47).

Primary song, then, may serve multiple functions. Marler (1960: 361) and Thorpe (1961: 58) suggested that the relegation of these functions to different parameters of the song alleviates the problem of conflicting selection pressures toward both stereotypy and variability. Data obtained for Mockingbirds in the present study suggest that different aspects of the song could serve different functions.

The significance of individual variation.—Little variation between the Kansas and Florida samples is seen for the characteristics of duration of units, number of syllable-patterns per unit, and for the patterns of distribution of phrases, when classified according to two sets of criteria. The samples from one area were more similar in these respects than the samples from different areas. Measurements of frequency showed some variation between the two areas, whereas the Kansas samples were quite similar in frequency. In spite of the large number of different syllable-patterns found (388 in all), the average duration of syllable-patterns and number of syllables per syllable-pattern for Kansas birds nos. 1 and 2 and Florida bird no. 1 were very similar. Syllable-pattern variation is mostly a function of characteristics other than number of syllables per syllable-pattern and duration.

Relatively large variation was seen in the syllable-patterns comprising the repertories of birds in the two areas. Birds within each area not only shared more syllable-patterns but also the degree of similarity was greater for the shared syllable-patterns.

The temporal, numerical, and to some extent, the frequency characteristics, which taken together describe the general mode or style of singing, could be those constant aspects of Mockingbird song that function in species recognition. It is possible that these characteristics also describe the genetically determined aspects of the song, although this cannot be established until Mockingbirds have been raised in auditory isolation. The great variation of syllable-patterns suggests that individual differences could function in individual recognition. The similarities that *are* observed among syllable-patterns are due (1) to the restriction imposed by the structure as expressed by the temporal, numerical, and frequency characteristics and (2) to the similarity of pattern models available throughout the range of the species.

Thorpe (1961: 58) stated that: "The features of songs which most often confer specific distinctiveness are those of total duration, the occurrence of characteristic phrases, motifs or progressions and the acoustic quality of the notes." Only the first appears to be primarily operative for this function in Mockingbird song. Borror and Reese (1956) stated that:

> The principal difference between the Mockingbird's imitations of Carolina Wren songs and the songs of the wrens themselves lies in the Mockingbird's singing style. The wren generally sings the same song for a while, and averages about ten songs a minute, while the Mockingbird seldom sings more than a few wrenlike songs before uttering notes that are quite unlike those of the wren, and its wrenlike songs are sung at a much faster rate (averaging 27 a minute) and successive songs are quite often different.

The use of mode of delivery as a character of the species is especially suggested by the fact noted by Saunders and mentioned above that the only striking difference between the song of the Brown Thrasher and song of the Mockingbird is that the Brown Thrasher renders syllable-patterns only twice on the average whereas the Mockingbird characteristically gives four or five renditions. Also, for example, I am unable to tell whether Kansas bird no. 1 or a Blue Jay (*Cyanocitta cristata*) is giving a typical Blue Jay call until sufficient time has elapsed that either the Mockingbird has changed pattern, that is, established its characteristic style or, if it is a Blue Jay, it continues to give the call without changing. The jay's rendition is somewhat louder. It appears likely that the acoustic quality of the sounds functions little, if at all, in species recognition.

The possible use of syllable-pattern variation in individual recognition is indicated by the fact that I am able to distinguish between Kansas birds nos. 1 and 2 after hearing a sample of sufficient duration to be aware of particular syllable-patterns used more often by one bird than the other, or of syllable-patterns used only by a given bird. In a species such as the Mockingbird, which possesses a very distinctive mode of singing and which is capable of using a large variety of patterns, the selection pressure toward syllable-pattern uniformity as a character of the species would be relaxed. Syllable-pattern variety could then be developed in response to selection pressure toward better individual recognition. The distinctive mode of singing and the versatility would, of course, have been developed simultaneously.

Thorpe (1961: 87) stated that "physiological synchronization might be better effected by variation than by stereotypy." Singing by a male

Mockingbird immediately preceding copulation has been observed (B. H. Wildenthal, pers. comm.). It is possible that versatility, functioning as an individual mark, may play a direct part in stimulating and coordinating sexual behavior between members of a mated pair. Tinbergen (1951: 21) suggested that sexual social releasers function not only to stimulate and direct particular behavioral sequences but, concurrently, to inhibit aggressive and fleeing tendencies. Obviously, aggressive and fleeing tendencies must be repressed for successful pair formation and sexual and parental behavior. A continuous flow of song delivered by a male known by its mate partly by the distinctive collection of syllable-patterns of its song would appear to be efficient as an inhibitor of these tendencies, particularly in a species such as the Mockingbird, which is noted for its generally aggressive behavior.

On the other hand, the considerable number and close similarity of syllable-patterns held in common by adjacent birds suggests that some advantage may be had from using the same patterns. Thorpe (1961: 86–87) suggested that sharing patterns may enhance the territorial function of primary song. The use of certain common patterns as well as distinctive ones may contribute to easier individual recognition. If individuals holding adjacent territories are known to each other, they need not expend energy in investigation whenever one or the other sings.

As noted above, selection in Mockingbird song apparently acts to circumscribe temporal and numerical characteristics of syllable-patterns used but not the particular syllable-pattern configuration. Hence, the expression of geographic variation of syllable-patterns observed here is probably fortuitous. It is best considered the result of variation in the sound environment, that is, in the available models in the range of the species. There is no evidence that the specific syllable-patterns used convey discrete items of information or that syllable-patterns learned from other species play any part in interspecific communication.

The adaptive significance of continuity.—It is possible, then, that a song with high versatility could serve multiple functions. It is of interest to consider possible functions of continuity as such, other than that of being an effective means of achieving a distinctive mode of delivery of syllable-patterns.

Hartshorne (1958a: 46) suggested that there may be a competitive advantage to an individual, for maintenance of territory or mate attraction, in keeping up a steady stream of sound. Logically, of course, this would lead to selection for greater continuity and, consequently, to higher versatility, if one accepts Hartshorne's assertion that high continuity is incompatible with low versatility. With this in mind, high continuity could not be considered advantageous of itself but could only be considered as one of the complex of attributes that renders the song effective. A relatively high degree of continuity is necessary, of course, if versatility is to achieve expression in a reasonably short period of time.

Marshall (1950) noted that most Australian species that are highly imitative (hence versatile) are species that sing in habitats affording limited visibility. With visual releasers able to play a minor role only in communication, sound signals are emphasized accordingly; Marshall thus asserted that production of more sound (greater continuity) is of advantage in habitats affording low visibility. Thorpe (1961: 89) argued that more sound *per se* cannot be advantageous unless "the vocal quality is such that the species is recognizable *whatever* song-pattern it utters." Since it has been shown in the present study that the mode of singing, rather than the quality or pattern content, probably renders Mockingbird song distinguishable whatever patterns are used, the high continuity of Mockingbird song could contribute to its effectiveness in territorial delimitation and defense.

The Mockingbird is noted for its conspicuousness but many other mimids prefer dense, brushy habitats affording low visibility. Mockingbirds characteristically choose well-hidden nest sites. Songs of most members of the family share to varying degrees the high continuity and versatility characteristic of Mockingbird song. With these considerations in mind, it seems likely that the song of the Mockingbird may have developed as it did as a result of the species having its early evolutionary history associated with habitats of low visibility. This is, of course, assuming that characteristics held generally throughout a family probably represent the primitive condition of members of the various species composing the family.

Although the Mockingbird is now a conspicuous species, its song may continue to carry a heavy functional load in relation to that carried by visual social releasers of the species. This is especially suggested by the lack of sexual dimorphism characteristic of the Mockingbird and other members of the family as well.

The role of mimicry.—Hartshorne (1958a: 46) stated that, "A corollary is that highly imitative birds, which of course are versatile, tend to be continuous singers." The Mockingbird is among the species on which Hartshorne's "corollary" is based. Interspecific mimicry of sound patterns may logically be considered the easiest, that is, the most probable, method by which versatility may be attained and, as suggested by Thorpe (1961: 89–90), the most probable way "of increasing the individual character of a bird's song, since no two birds are likely to copy the same model in the same way or sequence."

COMPARISON OF UNITS OF MOCKINGBIRD SONG WITH THOSE OF OTHER SPECIES

It is of interest to consider the validity of equating certain units—phrases, groups, x-units, and syllable-patterns—of Mockingbird song with various units of songs of other species. The concept of syllable-pattern appears widely applicable to pattern units of call notes, as well as primary and secondary song of most, if not all, species. The songs of species such as the Chipping Sparrow (*Spizella passerina*) (Marler and Isaac, 1960) and the Carolina Wren (*Thryothorus ludovicianus*) (Borror, 1956; Borror and Reese, 1956) are made up of song phrases that can be considered analogous to Type I one-group phrases (Tables 6 and 7) in Mockingbird song. One pattern is rendered a number of times in each song phrase; each temporal grouping contains syllable-patterns of one configuration, although different syllable-patterns are used in different phrases. Songs of various species of wrens, orioles, warblers, and finches could be considered comparable with phrases of Types II and III.

It is clear that a unit that could be said to be comparable with a unit in Mockingbird song could probably be found in the songs of most species. The predominant style of phrase in Mockingbird song (Type I, one-group) is comparable with the least complex of songs used by birds. The complexity of Mockingbird song is more a function of the high continuity and large repertory than intricate structure of individual units.

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SUMMARY

The primary song of the Mockingbird can be divided into units based on the temporal disposition of elements, units based on change of pattern, and units that are comparable with one another on the basis of number of basic pattern units (syllable-patterns) per unit. A *syllable*, the basic unit, is a sound of continuous duration in which the frequency may remain the same or vary through time. A *syllable-cluster* is a unit of temporally associated syllables of any configuration and a *group* consists of a temporally associated series of syllables or syllable-clusters. The basic pattern unit of the song, the *syllable-pattern*, consists of a configuration of syllables, syllable-

clusters, or of a group and is rendered essentially identically each time it occurs. A series of renditions of syllable-patterns is called a *phrase*. Units defined by both change of pattern and temporal separation and which are similar as to duration and number of syllable-patterns per unit are called *x-units*.

Duration and number of syllable-patterns per unit are given for syllable-patterns, phrases, groups, and x-units. Also, duration of silent intervals associated with these is given. These characteristics that, taken together, describe the characteristic mode of singing are considered to represent that aspect of the song that functions in species recognition.

Repertories of 66, 91, 134, and 194 syllable-patterns for four birds are presented. The curve representing number of distinct syllable-patterns, plotted against total consecutive syllable-patterns, fits an exponential curve based on the last data point. This means that, on the whole, syllable-patterns are introduced at random in the course of singing. It is thus valid to extend the exponential curve to arrive at an estimate of the probable total repertory for the period of time under consideration. Estimated repertories for the four birds are 66, 96, 213, and 244 syllable-patterns.

Each bird uses a characteristic set of syllable-patterns. A number of syllable-patterns were shared between the two Kansas birds; few were shared between the Kansas and Florida birds. Both individual variation in syllable-patterns and sharing of syllable-patterns may function in individual recognition.

Hartshorne's (1958a: 45) designation of the Mockingbird as a versatile, continuous singer is substantiated. Fifty to 83 per cent of characteristic performance periods are spent in actual production of the units called groups. There is evidence that primary song in Mockingbirds functions to stimulate and perhaps coordinate activities of members of a mated or potentially mated pair. The continuity and versatility observed in the song may enhance this function.

Approximately 80 per cent of phrases consist of renditions of the same syllable-pattern, approximately 3 per cent consist of renditions of syllable-patterns each of which is different, and approximately 17 per cent are made up of renditions of syllable-patterns any one of which may be rendered more than once.

It is shown that successive x-units comprised of the same syllable-pattern tend to contain the same number of renditions of syllable-patterns more often than would be expected from chance.

Various units of Mockingbird primary song are compared with units of songs of other species. The style of singing in the Mockingbird, while distinctive, is essentially a continuous flow of units similar to the simplest songs known for birds.

Three appendices available with the original thesis on file at the University of Kansas, Lawrence, Kansas, contain a list of species whose calls and songs are thought to be imitated by the Mockingbirds studied, a discussion of general considerations concerning terminology, and the derivation of the formula for the exponential curves.

LITERATURE CITED

BEDICHEK, R. 1947. Adventures with a Texas naturalist. Garden City, New York, Doubleday and Co., Inc.

BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U. S. Natl. Mus., Bull. 195.

BORROR, D. J. 1956. Variation in Carolina Wren songs. Auk, **73:** 211–229.

BORROR, D. J., AND C. R. REESE. 1956. Mockingbird imitations of Carolina Wren. Bull. Massachusetts Audubon Soc., **40:** 245–250.

CRAIG, W. 1943. The song of the Wood Pewee, *Myiochanes virens* (L.): a study of bird music. New York State Mus. Bull., no. 334.

ERICKSON, R. 1955. The structure of music. New York, The Noonday Press.

HALL-CRAGGS, J. 1962. The development of song in the Blackbird, *Turdus merula*. Ibis, **104:** 277–300.

HARTSHORNE, C. 1956. The monotony-threshold in singing birds. Auk, **73:** 176–192.

HARTSHORNE, C. 1958a. Some biological principles applicable to song-behavior. Wilson Bull., **70:** 41–56.

HARTSHORNE, C. 1958b. The relation of bird song to music. Ibis, **100:** 421–445.

LASKEY, A. R. 1935. Mockingbird life history studies. Auk, **52:** 370–381.

LASKEY, A. R. 1944. A Mockingbird acquires his song repertory. Auk, **61:** 211–219.

MARLER, P. 1960. Bird songs and mate selection. Pp. 348–367 *in* Animal sounds and communication (W. E. Lanyon, W. N. Tavolga, eds.). Washington, AIBS Publ. no. 7.

MARLER, P., AND D. ISAAC. 1960. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. Condor, **62:** 124–135.

MARSHALL, A. J. 1950. The function of vocal mimicry in birds. Emu, **50:** 5–16.

MAYFIELD, G. R. 1934. The Mockingbird's imitation of other birds. Migrant, **5:** 17–19.

MEYER, L. B. 1956. Emotion and meaning in music. Chicago, Univ. of Chicago Press.

MICHENER, H., AND J. R. MICHENER. 1935. Mockingbirds, their territories and individualities. Condor, **37:** 97–140.

THORPE, W. H. 1961. Bird-song. Cambridge, Cambridge Univ. Press.

TINBERGEN, N. 1951. The study of instinct. London, Oxford Univ. Press.

VISSCHER, J. P. 1928. Notes on the nesting habits and songs of the Mockingbird. Wilson Bull., **40:** 209–216.

WHITTLE, C. L. 1922. Additional data regarding the famous Arnold Arboretum Mockingbird. Auk, **39:** 496–506.

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