STRUCTURE IN PRIMARY SONG
OF THE MOCKINGBIRD, *MIMUS POLYGLOTTOS*

by

Joyce L. Wildenthal
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INTRODUCTION

Vocalizations of birds have been the subject of considerable ornithological interest in the past, partly because of their use as taxonomic and field characters and partly because they are of aesthetic interest. More recently, studies have been carried out mainly by investigators interested in the behavior, ontogeny, ecology or systematics of birds. Since audiospectrographic analysis has come into general use, many studies include as a basis a physical analysis or quantitative description of the elements of the vocalizations. Recent studies in which audiospectrographs were used include Borror (1956, 1959a, 1959b), Borror and Reese (1954, 1956b), Marler (1952), Marler and Isaac (1960a, 1960b, 1960c, 1961), Lanyon (1957), Lanyon and Fish (1958) and Thorpe (1958a).

The present study presents a quantitative description of certain aspects of the song of the Mockingbird, *Mimus polyglottos*. Tentative suggestions concerning the significance and function of various parameters of the song are included. Especial attention was paid to developing economical means of obtaining certain kinds of data using a sample size large enough for purposes of a general comparative study. The considerable complexity of song in Mockingbirds has impeded taking quantitative data in the past. Marler (1960b: 277) referred to this problem as it concerned other species with similarly complex song.

The study is limited to a description of primary song as defined by Lister (1953a) and described more fully by Thorpe (1961). Primary or advertising song, defined functionally, is that sound used by male birds for delimitation and defense of territory and for mate attraction. Territorial song has been reported in banded female mockingbirds in the fall (Laskey, 1936). The recorded samples of song used in the present study are of advertising song delivered by males on territory in early summer.

Most of what has been written about the song of the Mockingbird has been concerned with interspecific mimicry, for which the species is noted (Dickey, 1922; Whittle, 1922; Early, 1921; Wright, 1922; Townsend, 1924; Visscher, 1928; Mayfield, 1934; Miller, 1938; Richardson, 1906; Bent, 1948; Bedichek, 1947). Laskey (1933, 1935, 1936, 1944) and Michener and Michener (1935), all of whom worked without benefit of tape recordings, discussed certain aspects of the song in relation to ontogenetic, behavioral and life-history phenomena, in addition to mimicry. The present study includes only a brief discussion of the mimetic aspect of the song; a list of species presumed to be imitated by the birds studied is given in Appendix III.

Methods and Materials

The present study is based primarily on tape-recorded samples of the song of one bird in Kansas (Kansas Bird No. 1) and one bird in Florida (Florida Bird No. 1). Some data were taken from smaller additional samples from each locality. The samples for Florida Bird No. 1 are represented entirely on audiospectrographs, excluding only the longer silent intervals; examples of renditions of each song pattern in the Kansas samples are represented on audiospectrographs. Specific locality, duration, equipment used and other data concerning each cut are summarized in Table 1. A cut represents a single recording period; not all gross temporal characteristics may be represented, since some recordings were interrupted at intervals.

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. Unless special conditions required one-half tape speed, audiospectrographs were made at full tape speed covering a frequency range of 44 to 4400 cycles per second. Duration of audiospectrographs is 2.2 seconds at this frequency range.

A stop watch was used to obtain gross temporal data. Fine measurements were taken from audiospectrographs by converting linear measurements to equivalent duration and frequency.

Each cut was first diagrammed by a method similar to that used by Saunders (1951); diagrams were corrected after audiospectrographs were made. Diagramming in this manner gives ready and exact access to any particular point on the tape.

Terminology and General Description

It is necessary to divide Mockingbird song into units in order to describe structure of the song quantitatively and in order to establish a basis by which songs of individuals may be compared. Units are defined according to three characteristics. The first of these is gross temporal pattern. The second is fine temporal pattern, which, in conjunction with frequency characteristics of syllables, will be considered in this study under the heading of Pattern Characteristics of the Song. The third basis for establishing units concerns the number of elements in units defined by the first two bases--temporal and pattern characteristics. As will be seen below, actual units determined by these characteristics coincide for a considerable portion of the song.

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. General considerations on which choice of terms is based are discussed in Appendix I.

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 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 preferred 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). _Syllable_ is used in this study in the same sense as that adopted at the Paris Colloquium on Acoustics of Orthoptera (Busnel, 1954).

Syllables do occur singly, but most commonly form units called _syllable-clusters_. Syllables or syllable-clusters in turn may occur singly but most often are rendered in series, here called _groups_. These are the gross temporal divisions emphasized by the fact that often a transition from one to another is marked by a transition from one pattern to another. However, it is important to note that units called groups are defined solely on the basis of their temporal character, that is, the silent intervals between syllables or syllable-clusters comprising the group are shorter than those separating groups from one another. The actual duration of silent intervals separating syllables or syllable-clusters within a group or of intervals separating groups varies as the rate of singing. Although no instances were found in the present study, theoretically an inter-syllable or syllable-cluster silent interval in a sample of slow rate could be greater than an inter-group silent interval in a sample of fast rate. Groups, then, are defined on the relative duration of silent intervals within one period of singing of 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. The syllables, syllable-clusters or groups that are of like pattern 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 that is rendered essentially identically each time it appears in the course of the song. 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 and these units with pattern variety can be considered "sense units" in that the elements are related to one another not only temporally but as parts of a larger pattern, just as the elements of the song phrases of wrens or cardinals, for example, are related. These intergrated units could be considered large syllable-patterns but I prefer to consider them phrases since they are more similar to phrases than 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, 1961: 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 units. The justification for describing a unit such as this will be discussed more fully below in the section on numerical characteristics of the song.

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 2 and Figures 1, 2 and 3. The values for phrases, groups, x-units and associated silent intervals are based on measurements of consecutive units. If a sample of song were available such that each syllable-pattern were represented enough (at least 10 times) that a characteristic duration of separate phrases of one syllable-pattern could be determined, it would be desirable to express the overall average duration of phrases as the average of the modal values for each separate group of phrases of a given syllable-pattern. This would be necessary since some syllable-patterns occur more often than others. Even taking these considerations into account, the present data give a good indication of the general temporal aspect of the song because 1) a large proportion of the probable total repertory is represented, 2) different syllable-patterns tend to recur only twice on the average and 3) there is much overlap of ranges of variation for duration of units made up of different syllable-patterns.

Average duration of syllable-patterns is based on several samples of each separate syllable-pattern. The average duration of all syllable-patterns for all samples is almost the same; average values for inter-syllable-pattern silent intervals are more variable.

The average duration of phrases, groups and x-units are longer 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 8 to 13). Modal values and pattern of distribution for phrases are different between the two areas and consistent between samples within each area

(Figure 1). Modal values and patterns of distribution of groups and x-units are similar for all samples (Figures 2 and 3).

Continuity.--Hartshorne (1956: 177) stated, "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." Hartshorne recognized three categories of continuity. They are continuous, semi-continuous and discontinuous; 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 his determination of the percentage of the time spent in performance (called per cent performance time hereafter), Hartshorne apparently measured the duration of units corresponding to groups or phrases of the present study, rather than units corresponding to syllable-clusters or syllables. If inter-syllable-pattern silent intervals are taken into account in determining the values for per cent performance time, the value for the Florida sample is approximately 30. On this basis, the Mockingbird would be classified at best as semi-continuous. Table 3 shows the per cent performance time for the Florida sample just mentioned and for three other mockingbirds based on measurements of groups. Groups were chosen, rather than phrases, since 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 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 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. Characteristically, however, the general tendency for high continuity in average samples of Mockingbird song is unmistakable.

The values for per cent performance time are a function of the ratio of average duration of unit to average duration of interval. The same value could be found either when relatively short unit duration is associated with short interval duration or when relatively long unit duration is associated with long interval duration. Generally, the greater the positive value for average unit duration minus average interval duration for any one sample, the greater the value for per cent performance time (Table 3).

Pattern Characteristics of the Song

Syllable-patterns.--The syllable-pattern represents 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 in Figure 7. Figure 7, A, B and C are exceptional; few syllable-patterns show this much variation.

Repertory.--One of the most striking characteristics of Mockingbird song is the large number of syllable-patterns constituting the repertory of each individual. Figure 4 shows repertories for two mockingbirds. This figure shows that the number of distinct syllable-patterns used in a given singing effort increases as the song progresses, but that the rate of increase in distinct syllable-patterns falls off 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 consistant with this interpretation.

Obviously, the slopes of the curves would reach zero if the total repertory were plotted. In instances lacking sufficient data to show this, a method for estimating the total repertory was devised. It was found that curves obtained when the data were plotted in this way closely approximate exponential curves based on the last point of the data. This fact indicates that successive syllable-patterns are given at random (see below). Presumably, additional data would follow the same pattern; hence, the exponential curves may be extended to provide an estimate of minimum total repertory. Estimated repertories for four mockingbirds are shown in Table 4.

None of the birds has a repertory identical in size to that of any other. Both the Kansas and Florida birds have repertories considerably larger than the Texas birds. It was first thought that a portion of the difference between the Kansas and Florida and the Texas samples was due to difference 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.

It is important to note that the values for total repertory given here are based on a single period of singing for the Texas and Florida birds and on three periods within one week for the Kansas bird. 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 zero, as would the slopes of exponential curves. Hence the importance of recognizing that 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 syllable-patterns given in the course of a period of singing is shown in Figure 4. 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 derivation of the formula is given in Appendix II.

The fits of the curves to the observed data are made by adjusting the parameter N so that the curves pass through the last points of data. The N thus chosen is the predicted size of the repertory. The total number of syllable-patterns needed to obtain N - M of the distinct syllable-patterns is found by setting $Ne^{-T/N}$ equal to M and solving T from mathematical tables.

The best theoretical 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. Selander and Hunter (MS) also have evidence that there is a tendency for some syllable-patterns to be associated with certain other syllable-patterns more often than would be expected from chance assortment. However, these short series 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 non-versatile species. According to

Hartshorne, such relationship is evidence that birds tend to avoid producing sound in such a way that they become monotonous to the listening individuals, and thus fail to fulfill their biological functions.

Species in which each normal individual has a repertory of four or more distinct patterns are termed versatile by Hartshorne. The phrases of semi-versatile species show internal variation, but each phrase is practically identical to the others. Non-versatile species are those whose phrases are lacking in internal variety and each phrase may vary only in the number of renditions of the syllable-pattern. Hartshorne (1958a: 45) classified as versatile all members of the family Mimidae. The present data fit his concepts as they concern Mockingbirds.

Stability of repertory.--The quotation from Laskey cited above suggests that the repertory constantly grows. Hall-Craggs (1962) showed that in one song season (March to June) the pattern composition of the repertory of a single blackbird (*Turdus merula*) underwent considerable change. New patterns were added and others were dropped. New patterns were developed by the modification of existing patterns. "Basic" patterns were then used less or not at all.

In addition, a second process involved the rearrangement of existing patterns in complex phrases, which became characteristic of the developed form of the song. Hall-Craggs (1962: 292) noted that after periods of temporary cessation of song, when singing was resumed, the transition from the "basic" to the "developed" form of the song was repeated to some extent.

There is circumstantial evidence of a similar change in the pattern composition of repertory in Mockingbirds. Many syllable-patterns may be grouped on the basis of similarity of general configuration. It is conceivable that all syllable-patterns within such a group have been derived from a single, basic syllable-pattern. Also, a number of instances of apparent transition from one syllable-pattern to another are found in the samples studied. Hypothetical steps, illustrated by audiospectrographs (Figure 5), by which a new syllable-pattern might be derived from an existing syllable-pattern can be listed as follows:

1. The basic syllable-pattern is slightly modified (Figure 5, A and B).

2. Modification of the basic syllable-pattern is more pronounced, but modification is associated temporally with the basic syllable-pattern (Figure 5, C, D, E and F).

3. Temporal association of the basic syllable-pattern and the modification is decreased, but they are adjacent.

4. The modification, now termed a distinct syllable-pattern, and the basic syllable-pattern occur largely at random.

Units called multiphrase groups (see classification of phrases below) are characteristic of the samples studied. These are similar to the compound phrases described by Hall-Craggs. Demonstration that these processes of pattern and structural change are characteristic of Mockingbird song would require recording the song of a given bird throughout a song season or preferably for an entire year or more. Samples of song used in this study were made in June and would, presumably, by representative of a "developed" form, if such exists in Mockingbird song.

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.

Of the 86 distinct syllable-patterns of Kansas Bird No. 2 and 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 6. 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 6, B, F, H and Q). There is also an instance in which the sequence, as well as the syllable-pattern, is the same (Figure 6, 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 illustrated (Figure 7, 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 to 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 7, A, B and C; D and E; F and G). In three instances individual syllables in the syllable-pattern, and not the entire syllable-pattern, are similar (Figure 7, 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 7, H, I and J; R and S; T and U). A large number of 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 5). 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 (1960a) also found this to be true of songs of the Chipping Sparrow, Spizella passerina. Syllable-patterns in the Kansas samples show a greater variety of styles than those of the Florida samples. A comparison of Figures 6 and 7 will enable the reader to appreciate this; the syllable-patterns shown are representative.

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.

Table 6 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, 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 7 and 8). 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 6, 7 and 8).

Mimicry.--Ornithologists agree that Mockingbirds engage in interspecific vocal mimicry. However, it is difficult to determine whether a given syllable-pattern is learned from another mockingbird or from members of the species that characteristically use it. Laskey (1944) cited instances of apparent direct, interspecific mimicry by a hand-raised bird. Borror and Reese (1956b) found 102 patterns in Mockingbird song that were close enough to patterns used by Carolina Wrens (*Thryothorus ludovicianus*) to be termed interspecific mimicry. They state that two of these patterns were identical to patterns used by Carolina Wrens within a half-mile from the mockingbirds. I have observed a number of instances in which the Kansas birds rendered what, to my ears, were exact imitations immediately after hearing songs and calls given by Robins (<u>Turdus migratorius</u>), Yellow-shafted Flickers (<u>Colaptes auratus</u>) and Common Grackles (<u>Quisculus quiscula</u>). From these observations, it seems clear that the Mockingbird not only uses sound patterns of other species but is aware of and responsive to these patterns when rendered by members of other species. Laskey also mentioned an instance in which the mockingbird she raised gave flicker calls when flickers came into view but had not made a sound. It is possible that Mockingbirds associate sounds with the appropriate species as well as attend to the patterns themselves.

Whether the original source of such patterns is direct or indirect, it seems clear that the Mockingbird does ultimately derive many of its syllable-patterns from the calls and songs of other birds. Coincidence, which is the only alternative explanation for such occurrence seems to be reasonably out of the question (Borror and Reese, 1956b). Avian species, songs and calls of which are thought to be imitated by the birds studied, are listed in Appendix III.

Numerical Characteristics of the Song

<u>Number of syllable-patterns per phrase</u>.--The number of syllable-patterns per phrase for four birds are shown in Figures 8 and 9. The range of variation in number of syllable-patterns is greater for Kansas Bird No. 1 than for Florida Bird No. 1 (Figure 8). This is reflected in the

slightly higher averages for the Kansas samples. In both, however, phrases with four and five syllable-patterns predominate.

Kansas Bird No. 2 and Florida Bird No. 2 (Figure 9) are represented by samples inadequate for close comparison of the characteristic under consideration, but the data derived from them indicate that individual variation of the modal value is probably relatively slight. The modal value for Kansas Bird No. 2 is six, which is only one step removed from those of the other samples. Overall, the samples show a considerable constancy for this characteristic.

The number of syllable-patterns per phrase is mentioned in the literature by Goodpasture (1908) and by Saunders (Bent, 1948: 310). Data presented by Goodpasture (1908: 204) is summarized in Table 9. He definitely stated that the values are for units based on change of pattern (phrases). Comparison with the present data shows that while the values given by Goodpasture are not widely disparate from the present data, they are lower both as to average and range. It is impossible to determine, of course, if comparable entities are being counted. The larger the units considered to be syllable-patterns, the lower the average number per phrase. When working by ear alone there is a tendency to recognize larger units as syllable-patterns than seem logical when recordings and audiospectrographs are used. Also, it is easier to count fewer elements. Experiment demonstrated that little accuracy was achieved by me in counting syllable-patterns per phrase in a continuously playing sample when more than eight or nine elements per phrase were involved. Under these circumstances the differences between the two sets of data may not be considered significant; the relative similarity is, however, worthy of mention.

Saunders (Bent, 1948: 310) recognized 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 in the present data that a bird was found to render a given syllable-pattern in one phrase; one is the least number of renditions observed.

Number of syllable-patterns per group.--Modal values for number of syllable-patterns per group (Figures 10 and 11) are close to those for number of syllable-patterns per phrase, as would be expected since approximately 50 per cent of the units designated "phrases" are also "groups" (Tables 7 and 8). The average number of syllable-patterns per group is similar to the average per phrase; the range of variation is greater for groups, in all samples. The greatest number of times units not all of the same syllable-pattern were found to be rendered without pause was 63; the least number of times was 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 of number of syllable-patterns per unit decreases, that is, the variation is less than that observed for phrases or groups along (Figures 12 and 13). 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 the same (four and five) as for number of syllable-patterns per phrase and group except for Florida Bird No. 2 for which the mode falls clearly at five.

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 numerical and duration constancy of x-units, they strike the listener as being natural divisions of the song. This impression is enhanced by the fact that most often--approximately 80 per cent of 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 emphasis concerning x-units is that the intermingling of both kinds of interruptions 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 14. 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 15) 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 15 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.

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 between areas. Frequency measurements showed some variation between the two areas whereas the Kansas samples were quite similar in this characteristic. In spite of the large number of different syllable-patterns found (388 in all), the average duration 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 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 to 1) the restriction imposed by the structure as expressed by the temporal, numerical and frequency characteristics and 2) 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 (1956b) 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 bluejay is giving a typical Bluejay call until sufficient time has elapsed that either the mockingbird has changed pattern, that is, established its characteristic style, or if it is a bluejay, 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 does not function 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. com.). 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 (1954: 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: 86-7) 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 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 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.

<u>The adaptive significance of continuity</u>.--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 social 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 of song, 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."

Summary.--A song combining a distinctive mode of delivery and a great variety of syllable-patterns could function in species recognition, individual recognition, stimulation of activities of a mated pair, and, in addition, allow the use of some of the same syllable-patterns by adjacent birds, which would enhance territorial delimitation and defense. Interspecific mimicry is best explained as a probable means by which a large repertory of syllable-patterns may be acquired. The distinctive mode of singing in the Mockingbird precludes the possibility that the use of these syllable-patterns might interfere with intraspecific communication by members of the imitated species.

A species whose progenitor was capable of learning many patterns might well have an auditory releaser such as primary song develop to serve to a large extent functions handled by visual releasers in other species. An emphasis on auditory releasers would be especially advantageous to a species whose evolutionary development took place in a habitat affording low visibility, as seems likely concerning all species of the family Mimidae.

In order to broaden the functional capacity of the song, a complex structure is necessary. The primary song of the Mockingbird is a simple modification of the typical song structure of many species which involves temporally separated phrases consisting of successive renditions of syllable-patterns. The Mockingbird essentially produces a continuous stream of such phrases, each successive phrase consisting of renditions of a different syllable-pattern.

Suggestion of Geographic Trends

The number of individuals used in this study was limited by the amount of time required to extract and analyze data for a song as lengthy and complex as that of the Mockingbird. The kinds of variation described may not be representative of general geographic trends, although critical listening to recordings from a number of localities indicates that they are. For example, syllable-patterns used by Texas birds sound much more similar to those used by Kansas birds than are those used by birds in Ohio, Massachusetts or Florida. Also, the Florida and Texas samples, although differing greatly as to syllable-patterns used, are similar in that they both have a regular, machine-like style when compared to the other samples mentioned. This indicates that the Texas samples share the relatively limited variation of various units described for the Florida samples.

These suggestions of general trends are of interest in connection with the observation of several workers (P. P. Kellogg, pers. com.) that mockingbirds on the northern periphery of the range, such as in Massachusetts, Ohio and Kansas, engage in inter-specific mimicry to a greater extent than more southerly populations. Observations indicate that these peripheral populations also have a more variable mode of delivery and larger repertories.

The possible existence of "song dialects" as discussed by Marler (1952) is worth investigation on the basis of the large number of syllable-patterns held in common in one area and the great similarities between birds within hearing distance of one another.

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 to various units of songs of other species. The concept of syllable-pattern appears widely comparable to pattern units of call notes as well as primary and secondary song in most, if not all, species. The songs of species such as the Chipping Sparrow, Spizella Passerina, (Marler and Isaac, 1960a) and the Carolina Wren, Thryothorus ludovicianus, (Borror, 1956; Borror and Reese, 1956b) 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 to phrases of Types II and III.

It is clear that a unit that could be said to be comparable to 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 to 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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GENERAL SUMMARY

This report concerns studies in structure of primary song of the Mockingbird, Mimus polyglottos. The song can be divided into units based on the temporal disposition of elements, units based on change of pattern and units that are comparable to one another on the basis of number of basic patterns 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 for 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.

Continuity and versatility observed in the song may enhance this function.

Observations (Laskey, 1944: 218) have indicated that the repertory of Mockingbirds undergoes change as a function of time. Evidence is presented that new syllable-patterns may arise as modifications of existing syllable-patterns.

Approximately 80 per cent of phrases consist of renditions of the 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.

A summary of evidence for interspecific mimicry of syllable-patterns is presented. It seems likely that Mockingbirds are aware of certain syllable-patterns when sung by members of other species and may also associate syllable-patterns with the appropriate species even when the latter are silent. Interspecific mimicry is best explained as the most probable way of acquiring a large repertory of syllable-patterns.

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.

Suggestion of geographic trends are discussed. Samples of song of birds on the northern periphery of the range are more variable and contain more interspecific mimicry than song of birds from more central portions of the range.

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.

In Appendix I, general considerations concerning terminology are discussed. Appendix III contains a list of species whose calls and songs are thought to be imitated by the mockingbirds studied.

APPENDIX I

General Considerations Concerning Terminology

The terminology used in bioacoustics has been drawn from the fields of music, phonetics and physical acoustics or a combination of these depending upon the background of the investigator, the nature of the sounds he is studying, and the aspect of the sounds that he wishes to emphasize. Bioacoustics is a behavioral science; hence, terminology emphasizing only physical aspects of sounds and their production would be inadequate. Much work of phoneticians is pertinent to study of animal sounds, but the terminology of phonetics has been developed to describe particular elements--human speech sounds--and thus is not entirely applicable to animal sounds.

Considerable controversy centers around the use of musical terminology in describing the songs and calls of birds. Those who oppose this usage fear that it implicitly suggests that birds are exercising artistic creativity. This implication need not accompany the use of the terms, since musicians themselves recognize an approach to music other than artistic--the study of the elements of music as acoustic entities as practiced by musicologists.

Drawing an analogy between music and bird vocalizations is by no means without basis. Biologists (Craig, 1943; Hartshorne, 1958b) and musicians (Herzog, 1941; Szoke, 1962) alike have recognized that all the essential elements of music can be found in bird vocalizations. The differences are of a quantitative nature, there being greater complexity and duration of the musical units and much more extensive use of polyphony in much music.

The artistic approach to music emphasizes the relationship of certain sound patterns to largely culturally determined psychic phenomena--intellectual and emotional--in man. Obviously, bird vocalizations did not evolve in relation to psychic phenomena in man, so in this way they cannot be considered artistic. Yet, man does consider certain sounds produced by birds as being aesthetically significant.

Such consideration is evidence of a notable instance of biological paralleliam between mammals (especially man) and birds, based on the physical properties of sound and the similar mechanisms by which the two groups have made use of sound. Specifically, the syrinx of birds and the larynx of mammals are biological analogues in that the trachea and bronchii (trachea only in mammals) have been variously modified in the derivation of the organs. The oral cavities (resonating chambers) are homologues, however, and therefore the sound producing systems as wholes can be considered as partly analogous and partly homologous.

Considering the sound receiving organs, Pumphrey (1961) stated, "Although there is a certain similarity in the disposition of the homologous parts, the differences between the mammalian and avian ears are evidently substantial and deserve detailed consideration." Here, again, the organs are partly homologous and partly analogous. The physical differences are reflected in different functional capacities although not all the physical bases of functional differences are known.

Lorenz (1957), writing of the comparative studies of behavior of Whitman and Heinroth, stated, "Neither Whitman nor Heinroth ever use the term 'homology.' Yet both their studies are based on the assumption that this concept, so sidely used in morphology, applies to innate, genetically determined motor patterns as it does to organic characters." Marler and Isaac (1961) call attention to the similarity of the study of vocalizations to classical comparative anatomy. The concept of homologous characters can be used to describe the relationship of the use of sounds for communication in mammals and birds. While the physical means with which sound is employed are only partly homologous, the fact of the use of the sounds may be thought of an instance of functional homology. The sounds themselves may then be treated as homologous entities. From this point of view, there seems to be no reason to avoid the application of the same terms to comparable elements. Where a close correspondence between elements can be shown, the use of pre-existing terms such as those used in musical notation or language study might well serve to promote clarity of description and facilitate communication between investigators better than would neologisms.

Although Thorpe (1961: 1) preferred the term vocalization for scientific usage, he used song often presumably because it is more concise. So entrenched in the language is the term song in reference to bird vocalizations that part of the first definition for the word given by the Oxford Universal Dictionary (1955) is, "b. The musical utterance of birds..." As stated in the definition, the usage has tended to center on those vocalizations that are "musical" or "pleasant" to the ear. From this tendency grew the widespread habit of ornithologists of using the term to distinguish primary song and secondary song from call notes. It would be best to use song only in a general sense and attach qualifiers such as primary or secondary for other purposes.

When used in avian bioacoustics, song should mean only the product of the vocal apparatus as opposed to art forms such as poems, or musical settings for poems and ballads, etc. These distinctions are clearly made in the definitions for song given in both the Oxford Universal Dictionary (1955) and Webster's Collegiate Dictionary (1948).

APPENDIX II

Derivation of Formula for Exponential Curves

Expressed mathematically, the rate of introduction of new syllable-patterns, that is,

$$\frac{-d(N - n)}{dT}$$

is proportional to the remaining unsung syllable-patterns, $(N - n)$. The solution of this differential equation,

$$\frac{d(N - n)}{dT} = -K(N - n)$$

is

$$\ln(N - n) = -KT + C_1$$

where K and C_1 are constants to be evaluated from the initial conditions. The above solution is equivalent to

$$(N - n) = e^{(-KT + C_1)} = C_2e^{-KT}$$

Hence,

$$n = N - C_2e^{-KT}$$

Evaluating the constants, we see that for $T = 0$, we must obviously have $n = 0$. Hence,

$$N - C_2e^0 = N - C_2 = 0, \quad C_2 = N, \quad n = N(1-e^{-KT})$$

When $T = 0$,

$$\frac{dn}{dT} = 1$$

that is, the first syllable-pattern of the sample must be an unsung pattern. Hence,

$$1 = NKe^{0} = NK, \quad K = \frac{1}{N}$$

This yields the final form of the formula,

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

APPENDIX III

Avian Species Thought to be Imitated by the Mockingbirds Studied

Five persons with field knowledge of avian calls and songs listened independently to the samples and indicated instances of similarity between syllable-patterns used by the birds in the present study and various other species. Counting only those cases in which two or more persons agreed on the possible source of a given syllable-pattern, it was found that 18.5 per cent of the entire Kansas sample and 5 per cent of the entire Florida sample consisted of instances of presumed interspecific mimicry.

The genera and species named for the Kansas samples follow in order of frequency of occurrence starting with the most frequent: Cardinal (*Richmondena cardinalis*), Bluejay (*Cyanocitta cristata*), Purple Martin (*Progne subis*), Killdeer (*Charadrius vociferus*), Sparrowhawk (*Falco sparverius*), Tufted Titmouse (*Parus bicolor*), phoebes (*Sayornis*), flickers (*Colaptes*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), Catbird (*Dumetella carolinensis*), Carolina Wren (*Thryothorus ludovicianus*), Bobwhite (*Colinus virginianus*), Eastern Bluebird (*Sialia sialis*) and Robin (*Turdus migratorius*). On the basis of my own observations, I would add House Wren (*Troglodytes aedon*), thrushes (*Hylocichla*), Common Grackle (*Quisculus quiscula*), Red-winged Blackbird (*Agelaius phoeniceus*), meadowlarks (Sturnella) and House Sparrow (Passer domesticus).

Those named for the Florida sample were Cardinal (Richmondena cardinalis), Tufted Titmouse (Parus bicolor), Bluejay (Cyanocitta cristata), flickers (Colaptes), Sparrowhawk (Falco sparverius), Catbird (Dumetella carolinensis), Carolina Wren (Thryothorus ludovicianus), Red-winged Blackbird (Agelaius phoeniceus), House Sparrow (Passer domesticus), Robin (Turdus migratorius) and the House Wren (Troglodytes aedon).

These allocations undoubtedly represent only a minimal number of the actual instances of similarity. Only striking, unmistakable cases are included here. The species most frequently imitated are also those whose calls and songs are most apparent in the area in which the recordings were made. For the Kansas sample, members of many species and genera listed were seen regularly within the territorial boundaries of Kansas Birds Nos. 1 and 2 and others were seen well within hearing distance. Although this may have some bearing on frequency of imitation, it is of less interest as far as the learning of the patterns at all. Laskey (1944) warned that it should not be assumed that individual mockingbirds have occupied certain areas since birth. Patterns could be learned over the entire area of dispersal either by direct contact with the imitated species or by way of another mockingbird or other imitating species.

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TABLE 1

Localities and Specifications of Recordings Used in the Present Study

Locality	Reel and Cut	Date of Recording	Time Length	Time of Day	Recorded By	Recorder Used	Micro-phone	Para-bola	Tape Speed
Richmond Air Base Florida	6 Cut 1	3 May 1950	2:06	after-noon	B.J., P.P. Kellogg	Presto PT-900	WE 633A	40 inch	7.5 in. per sec.
"	6 & 7 Cut 2	"	12:09	"	"	"	"	"	"
"	7 Cut 3	12 March 1950	5:26	"	"	"	"	"	"
Univ. of Kansas, Lawrence, Kansas	0 Cut 0	10 June 1962	17:55.2	mid-night	J.L. Wil-denthal	Grundig Niki SKL/E	Grundig GM 1	23 inch	1.75 in. per sec.
"	1 Cut 1	12 June 1962	8:17.4	"	"	Magne-mite W 610 E	Electro-voice Model 666	"	15 in. per. sec.
"	2 Cut 2	"	7:48.4	"	"	"	"	"	"
"	3 Cut 3	13 June 1962	8:21.3	"	"	"	"	"	"
"	4 Cut 4	25 July 1962	4:00	6:30 AM	"	"	"	"	"

TABLE 2

Duration in Seconds of Syllable-patterns and Silent Intervals Associated with Syllable-patterns, Phrases and Groups

Samples	Kansas Bird #1	Kansas Bird #2	Florida Bird #1	Florida Bird #2
Syllable-patterns				
Mean	0.019 (557)[1]	0.019 (218)	0.018 (890)	---
Range	.002-.085	.002-.051	.005-.077	
Inter-syllable-pattern Intervals				
Mean	0.020 (376)	0.013 (152)	0.010 (604)	---
Range	.0007-.158	.001-.067	.0007-.085	
Inter-Phrase 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
Inter-group 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]Sample size in parentheses.

TABLE 3

Continuity Expressed as Per Cent Performance Time
Compared with Values for Average Group Duration
Minus Average Inter-group Silent Interval Duration

Samples	Per Cent Performance Time	Difference in Seconds Between Duration of Unit and Duration of Interval
Kansas Bird #1:		
Reel 0 Cut 0	66	2.17
Reel 1 Cut 1	78	3.48
Reel 2 Cut 2	79	3.53
Kansas Bird #2:		
Reel 3 Cut 3	83	3.98
Florida Bird #1:		
Reel 6 Cut 1	50	0.49
Reel 6&7 Cut 2	52	0.45
Florida Bird #2:		
Reel 7 Cut 3 Part 1	72	1.53
Part 2	37	1.10

TABLE 4

Repertories for Four Mockingbirds Estimated on Basis of Exponential Curve Extension

Sample	Kansas Bird #1	Kansas Bird #2	Texas Bird #1[1]	Texas Bird #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).

TABLE 5

Summary of Frequency Characteristics of Syllable-patterns

Samples	Kansas Bird #1	Kansas Bird #2	Florida Bird #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 Prominant 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 6

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 #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 #2	95	76	1	23
Cut 3				
Florida Bird #1	247	81	4	14
Cut 1	39	82	0	18
Cut 2	208	81	4	14
Florida Bird #2	129	81	3	16
Cut 3				

TABLE 7

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 8

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.

TABLE 9

Summary of Temporal and Numerical Characteristics of Mockingbird Song Taken From Goodpasture (1908)

Duration of sample	Number of Patterns	Average Number of Renditions of Each	Range
10 minutes	46	3.41	1-9
3 "	28	4.00	1-9
1 "	13	6.30	1-9
10 "	137	3.18	1-12

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

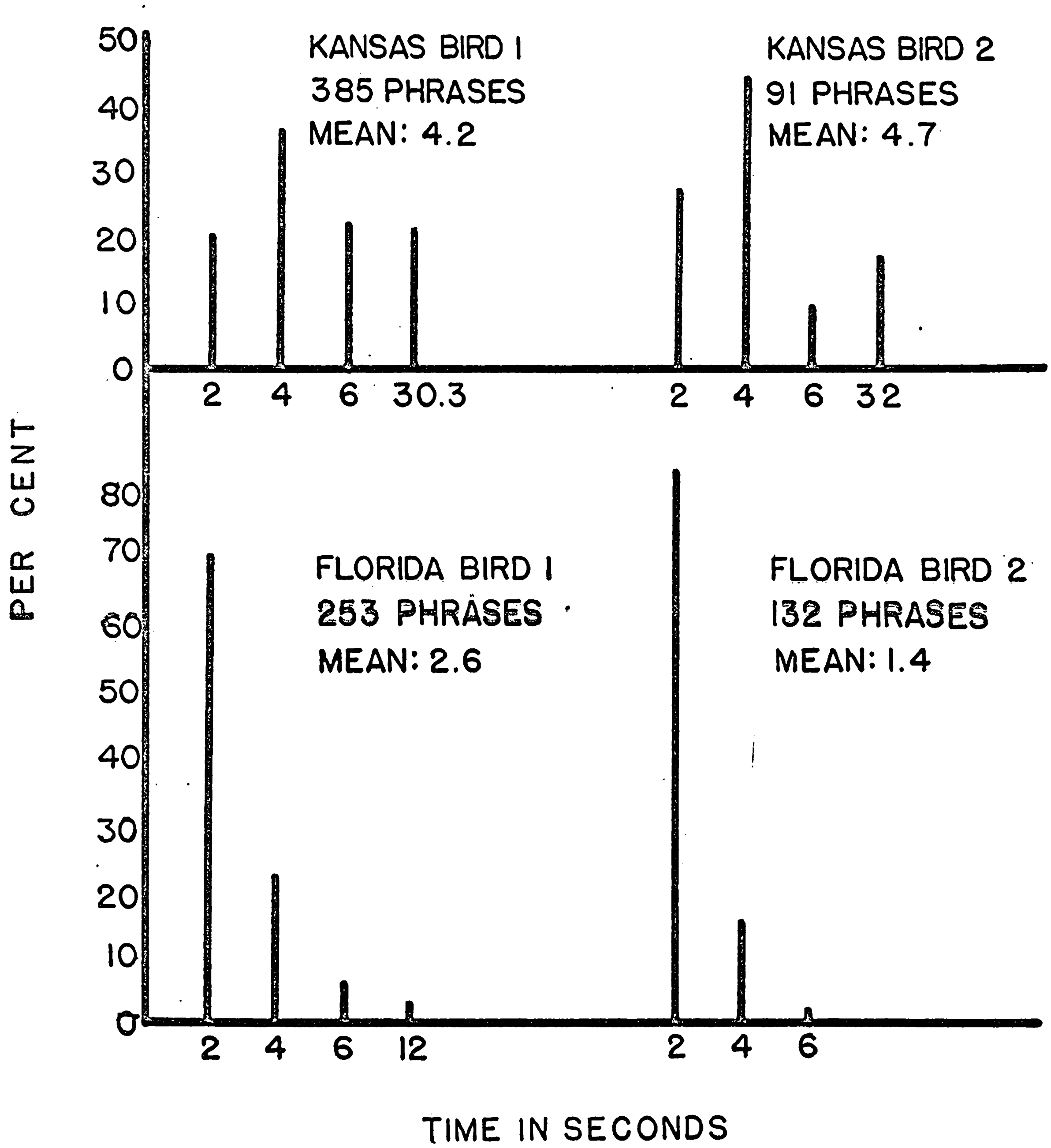

KANSAS BIRD I
385 PHRASES
MEAN: 4.2
KANSAS BIRD 2
91 PHRASES
MEAN: 4.7
FLORIDA BIRD I
253 PHRASES
MEAN: 2.6
FLORIDA BIRD 2
132 PHRASES
MEAN: 1.4
PER CENT
0
10
20
30
40
50
60
70
80
2
4
6
30.3
32
12
TIME IN SECONDS

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

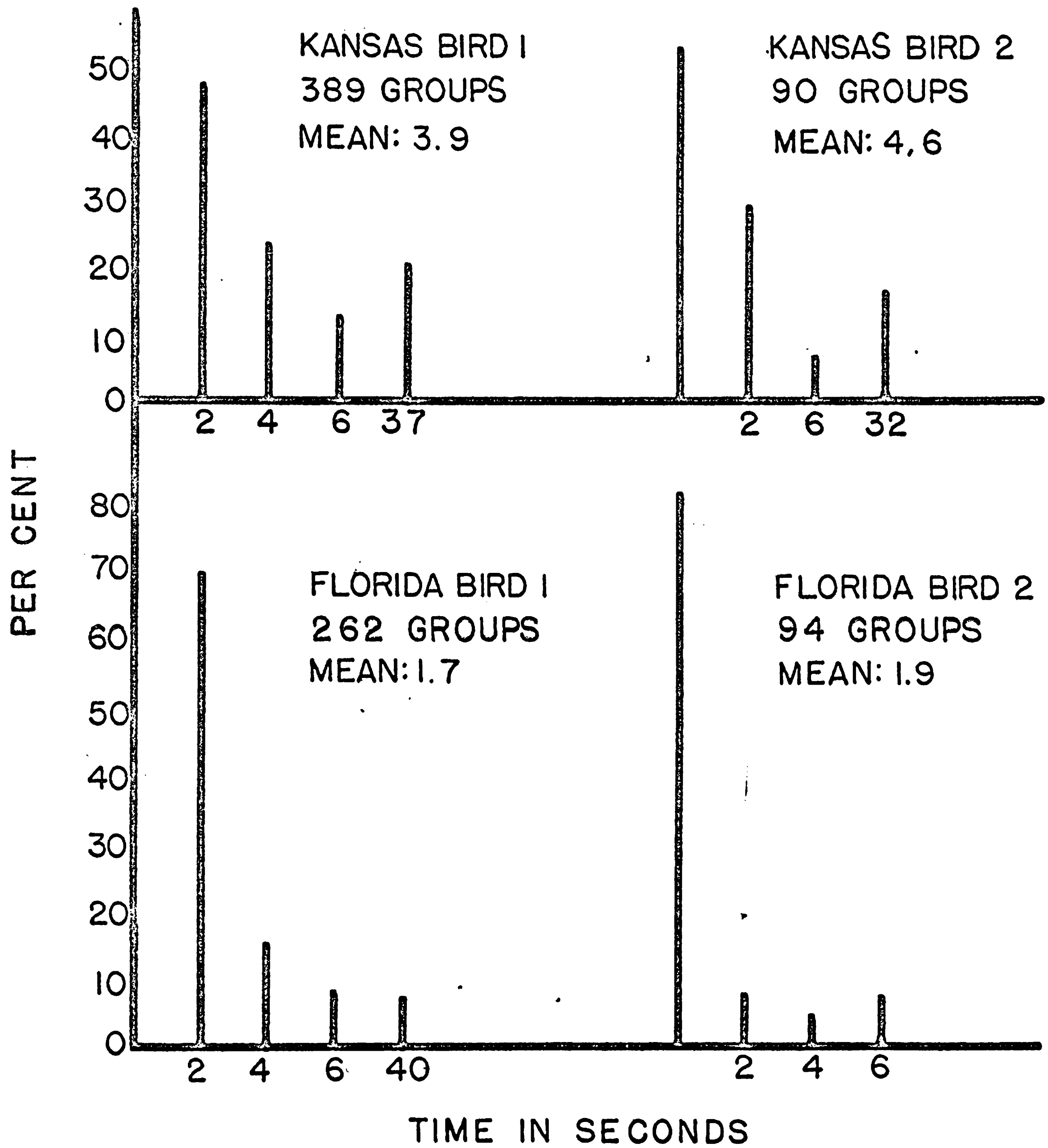

KANSAS BIRD I
389 GROUPS
MEAN: 3.9
KANSAS BIRD 2
90 GROUPS
MEAN: 4,6
FLORIDA BIRD I
262 GROUPS
MEAN: 1.7
FLORIDA BIRD 2
94 GROUPS
MEAN: 1.9
PER CENT
0
10
20
30
40
50
0
10
20
30
40
50
60
70
80
2 4 6 37
2 6 32
2 4 6 40
2 4 6
TIME IN SECONDS

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

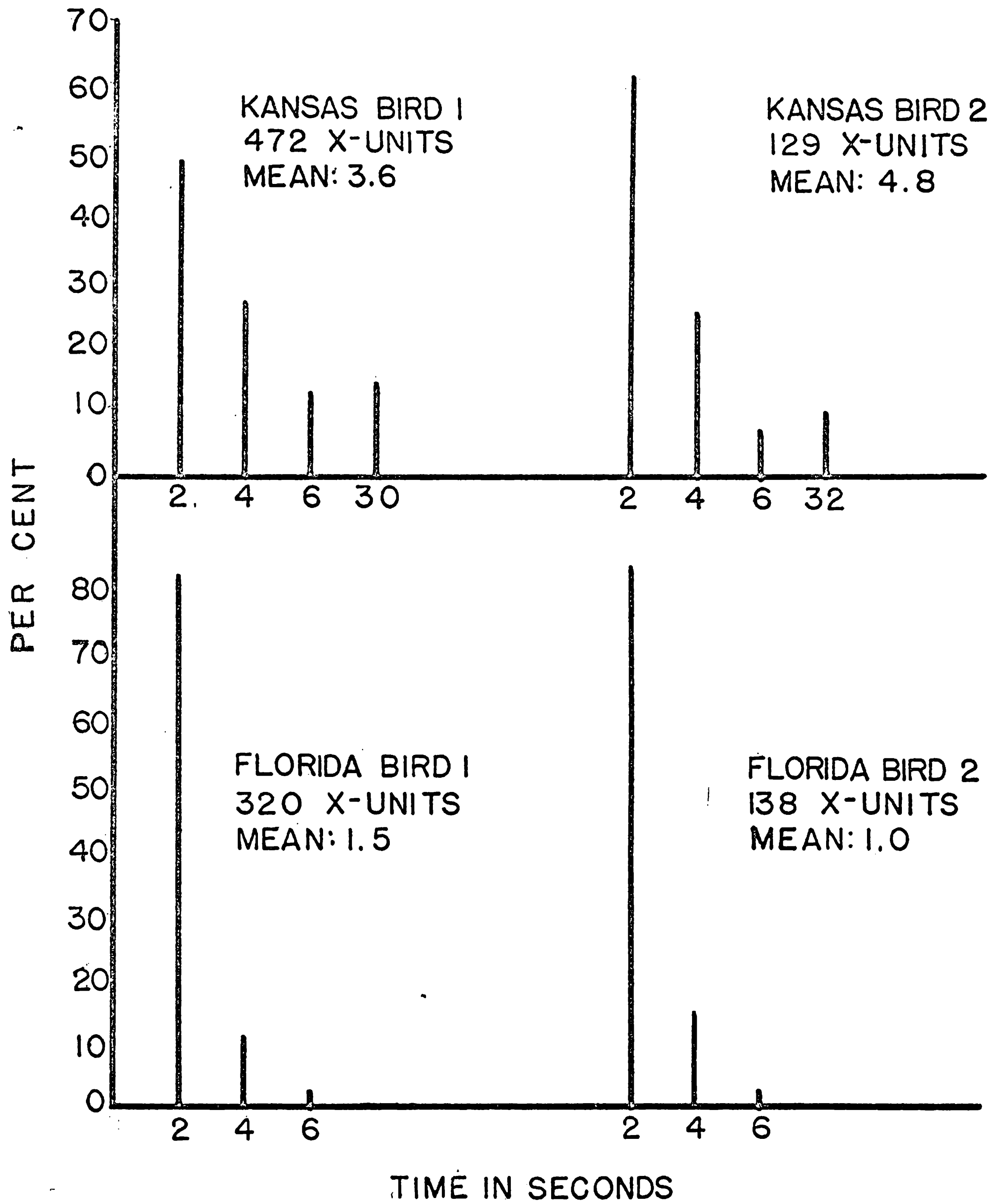

KANSAS BIRD I
472 X-UNITS
MEAN: 3.6
KANSAS BIRD 2
129 X-UNITS
MEAN: 4.8
FLORIDA BIRD I
320 X-UNITS
MEAN: 1.5
FLORIDA BIRD 2
138 X-UNITS
MEAN: 1.0
PER CENT
TIME IN SECONDS
0
10
20
30
40
50
60
70
80
2
4
6
30
32

Figure 4. 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.

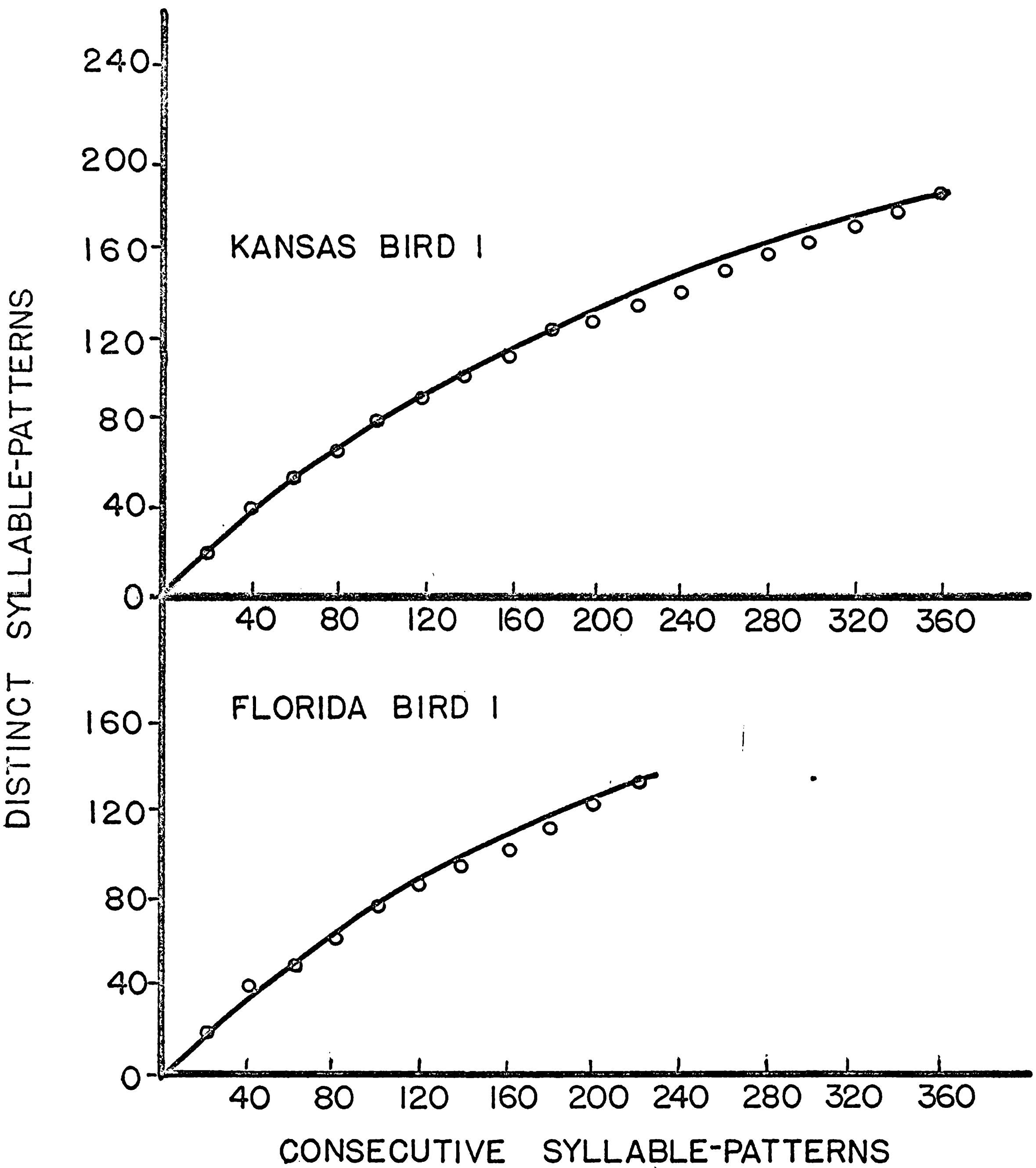

DISTINCT SYLLABLE-PATTERNS
240
200
160
120
80
40
0
KANSAS BIRD I
40 80 120 160 200 240 280 320 360
FLORIDA BIRD I
160
120
80
40
0
40 80 120 160 200 240 280 320 360
CONSECUTIVE SYLLABLE-PATTERNS

Figure 5. Audiospectrographs illustrating examples suggesting the derivation of new syllable-patterns from existing ones. Figure 5, A and B, illustrates hypothetical Step No. 1; Figure 5, C, D, E and F, illustrates hypothetical Step No. 2.

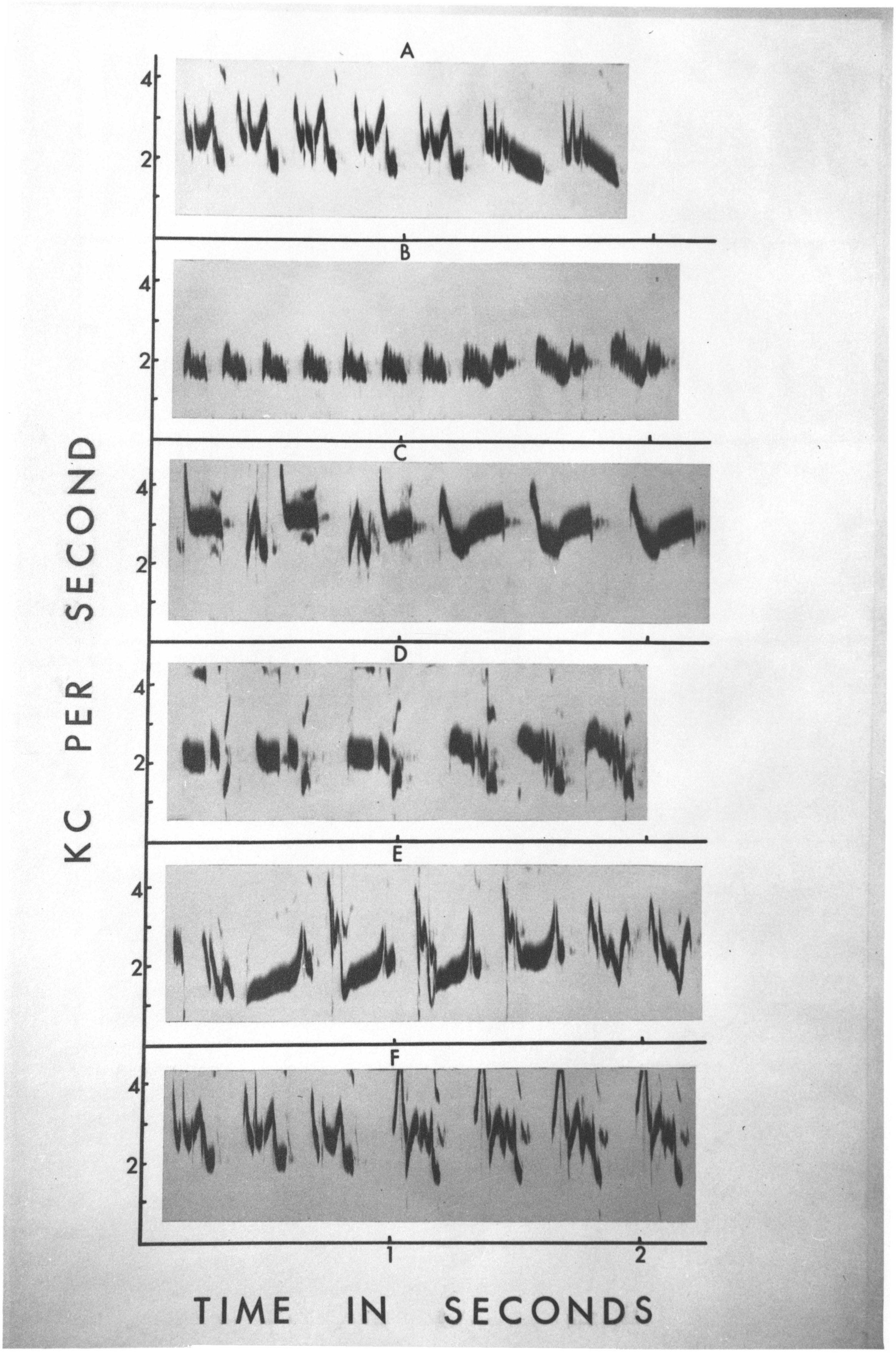

A
B
C
D
E
F
4
2
KC PER SECOND
1
2
TIME IN SECONDS

Figure 6. Audiospectrographs illustrating identical syllable-patterns used by Kansas Birds Nos. 1 and 2. Syllable-patterns of Kansas Bird No. 1 are on the left and those of Kansas Bird No. 2 are on the right.

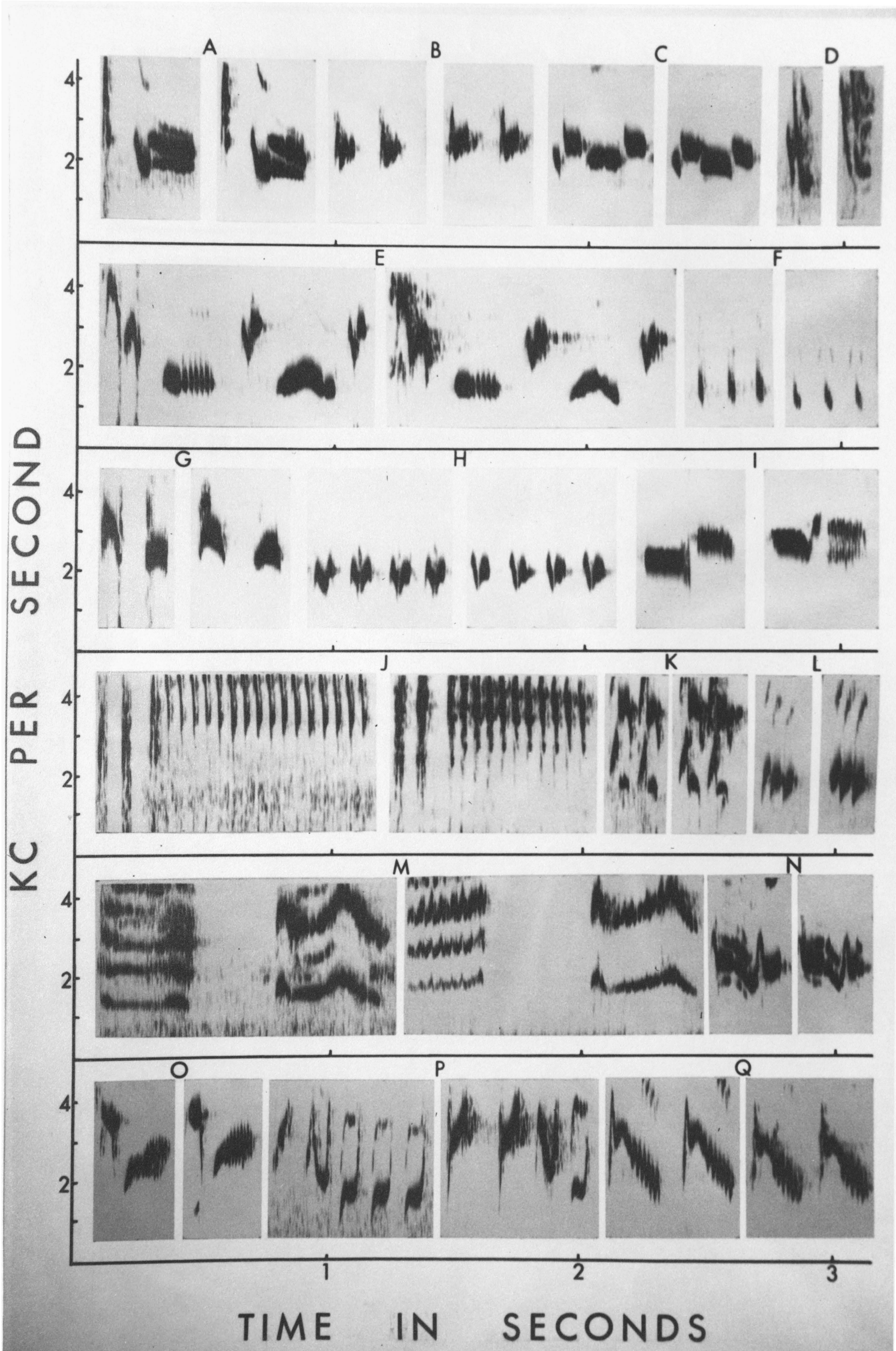

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
4
2
KC PER SECOND
1
2
3
TIME IN SECONDS

Figure 7. Audiospectrographs illustrating similarities in syllable-patterns between Florida Birds Nos. 1 and 2 and between the entire Florida and Kansas samples. Figure 7, C, E, G, L, O, Q, J, S and U shows syllable-patterns from the Kansas sample. Figure 7, B, D, F, K, M, P, H, I, R and T shows syllable-Patterns from the sample for Florida Bird No. 1. Figure 7, A and N shows syllable-patterns from the sample for Florida Bird No. 2.

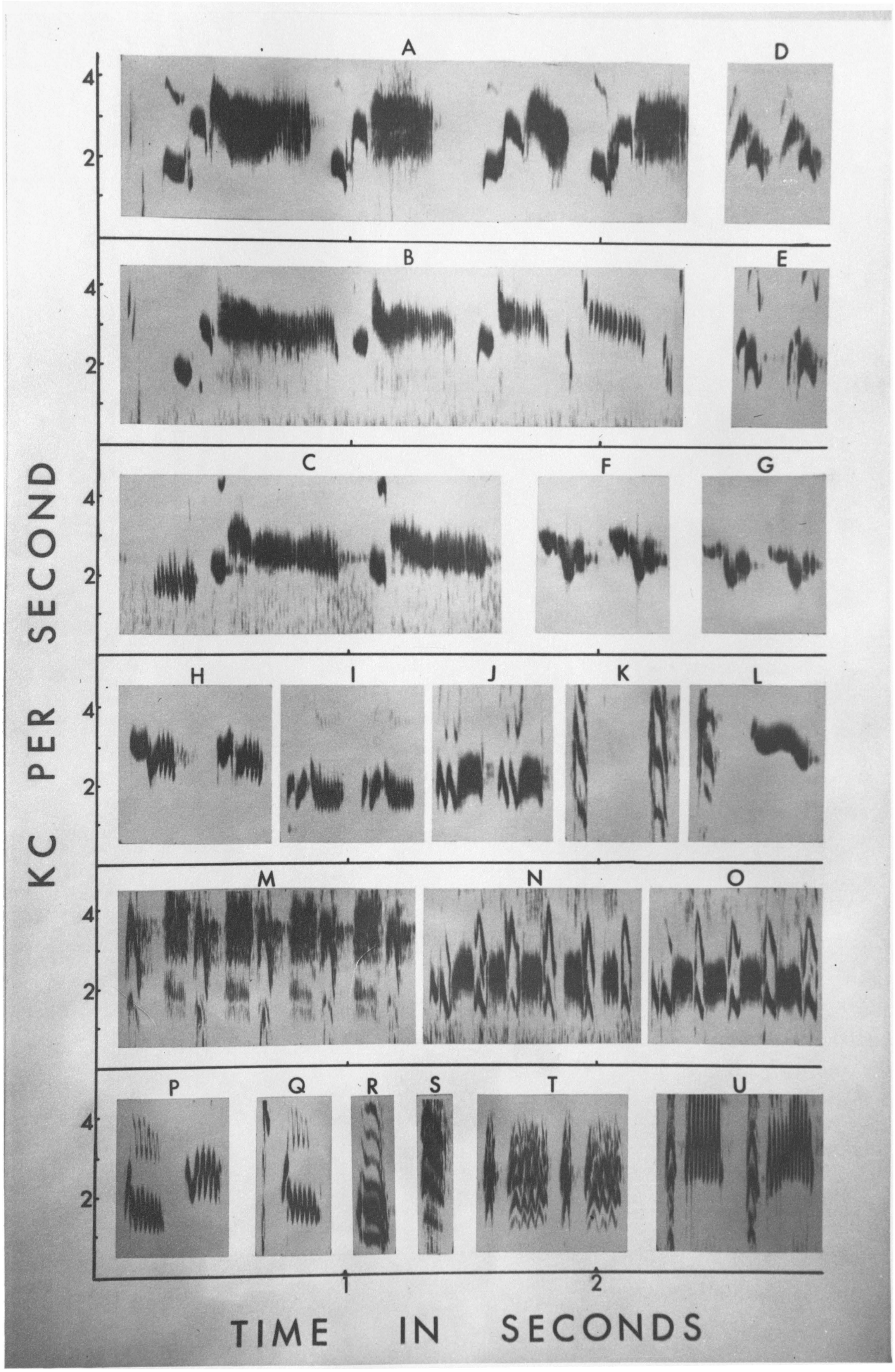

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
KC PER SECOND
TIME IN SECONDS
4
2
1
2

Figure 8. Frequency distributions showing number of syllable-patterns per phrase for Kansas Bird No. 1 and Florida Bird No. 1.

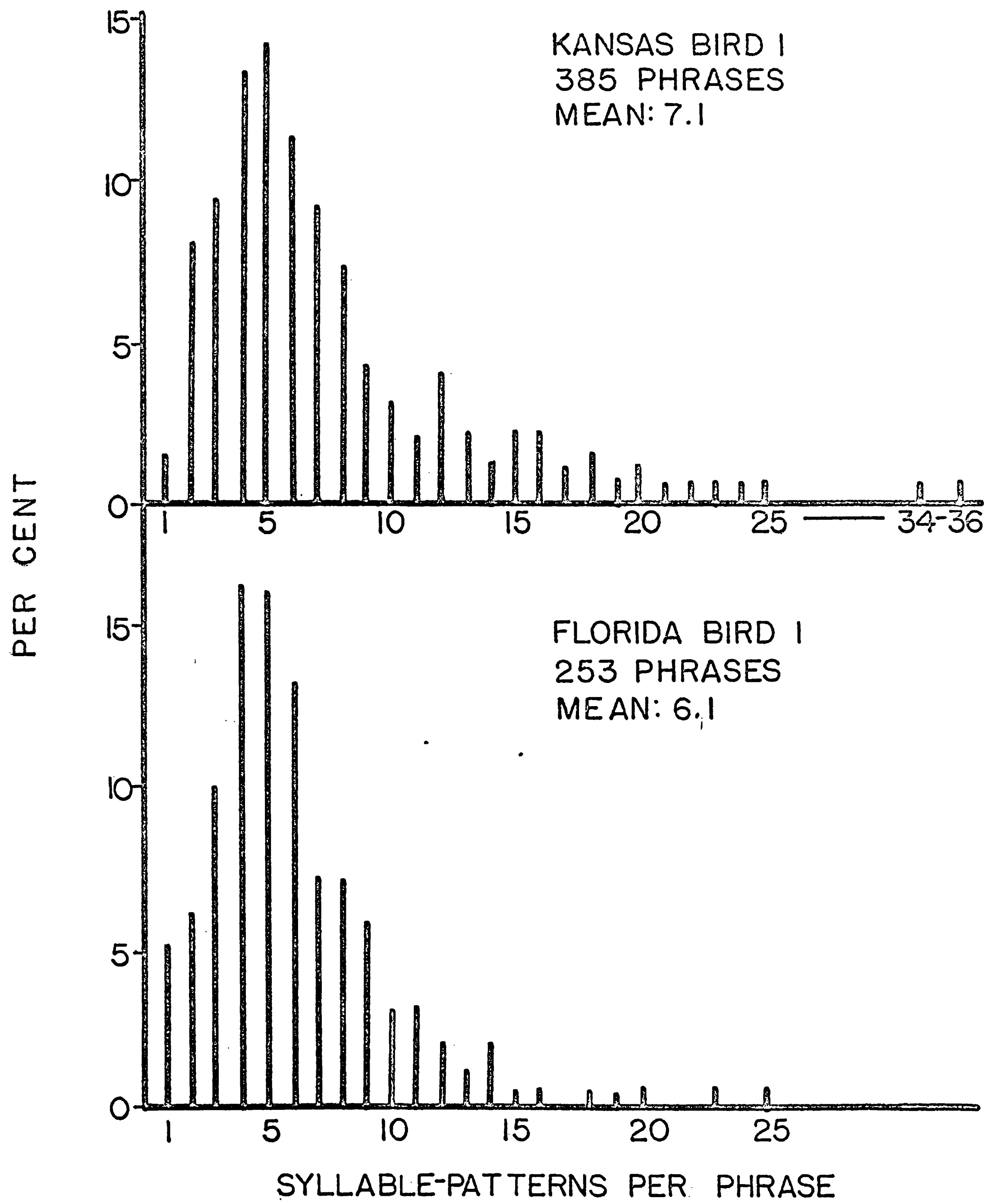

KANSAS BIRD I
385 PHRASES
MEAN: 7.1
FLORIDA BIRD I
253 PHRASES
MEAN: 6.1
PER CENT
0
5
10
15
1
5
10
15
20
25
34-36
SYLLABLE-PATTERNS PER PHRASE

Figure 9. Frequency distributions showing number of syllable-patterns per phrase for Kansas Bird No. 2 and Florida Bird No. 2.

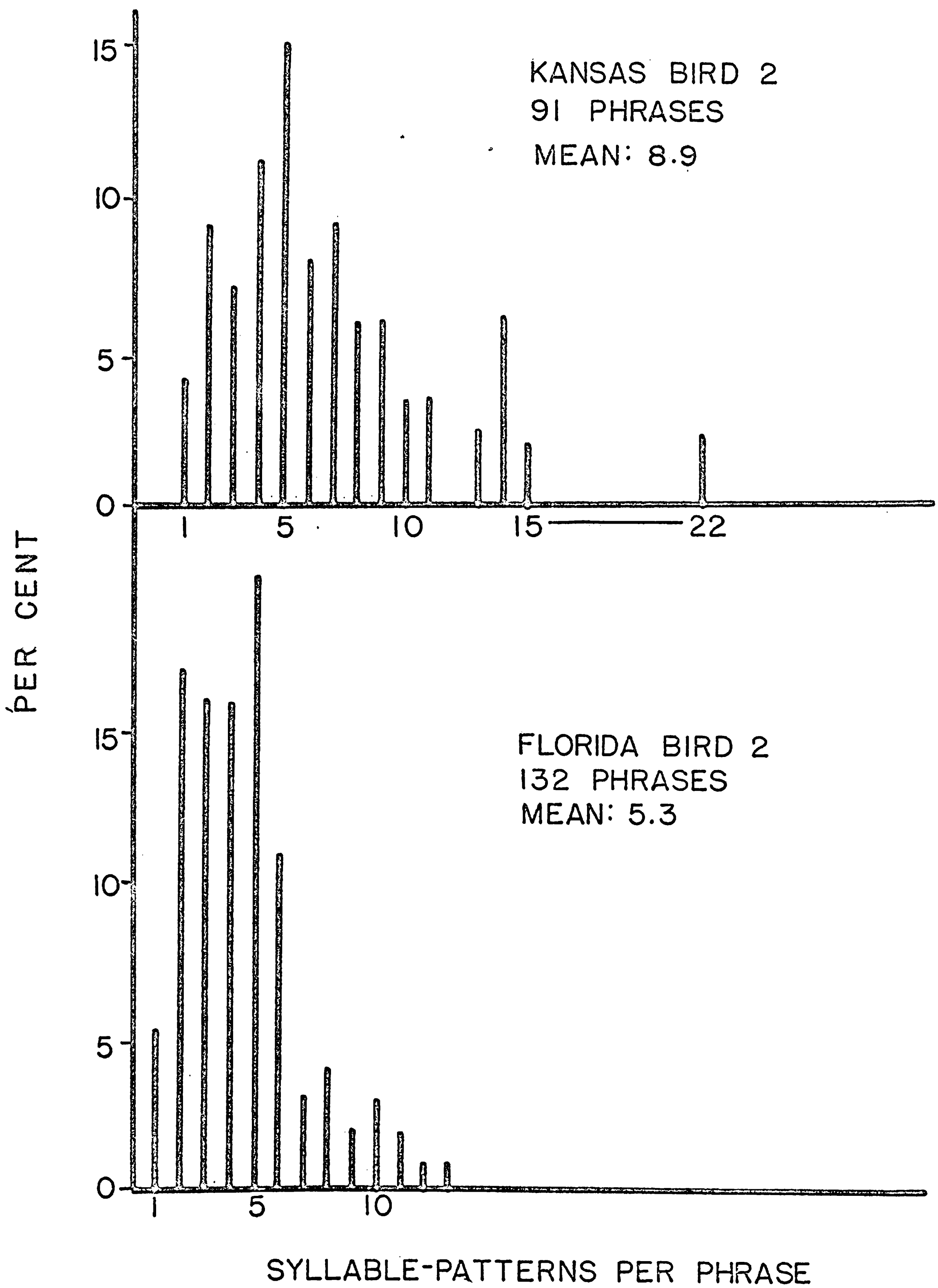

KANSAS BIRD 2
91 PHRASES
MEAN: 8.9
FLORIDA BIRD 2
132 PHRASES
MEAN: 5.3
PER CENT
0
5
10
15
1
5
10
15
22
SYLLABLE-PATTERNS PER PHRASE

Figure 10. Frequency distributions showing number of syllable-patterns per group for Kansas Bird No. 1 and Florida Bird No. 1.

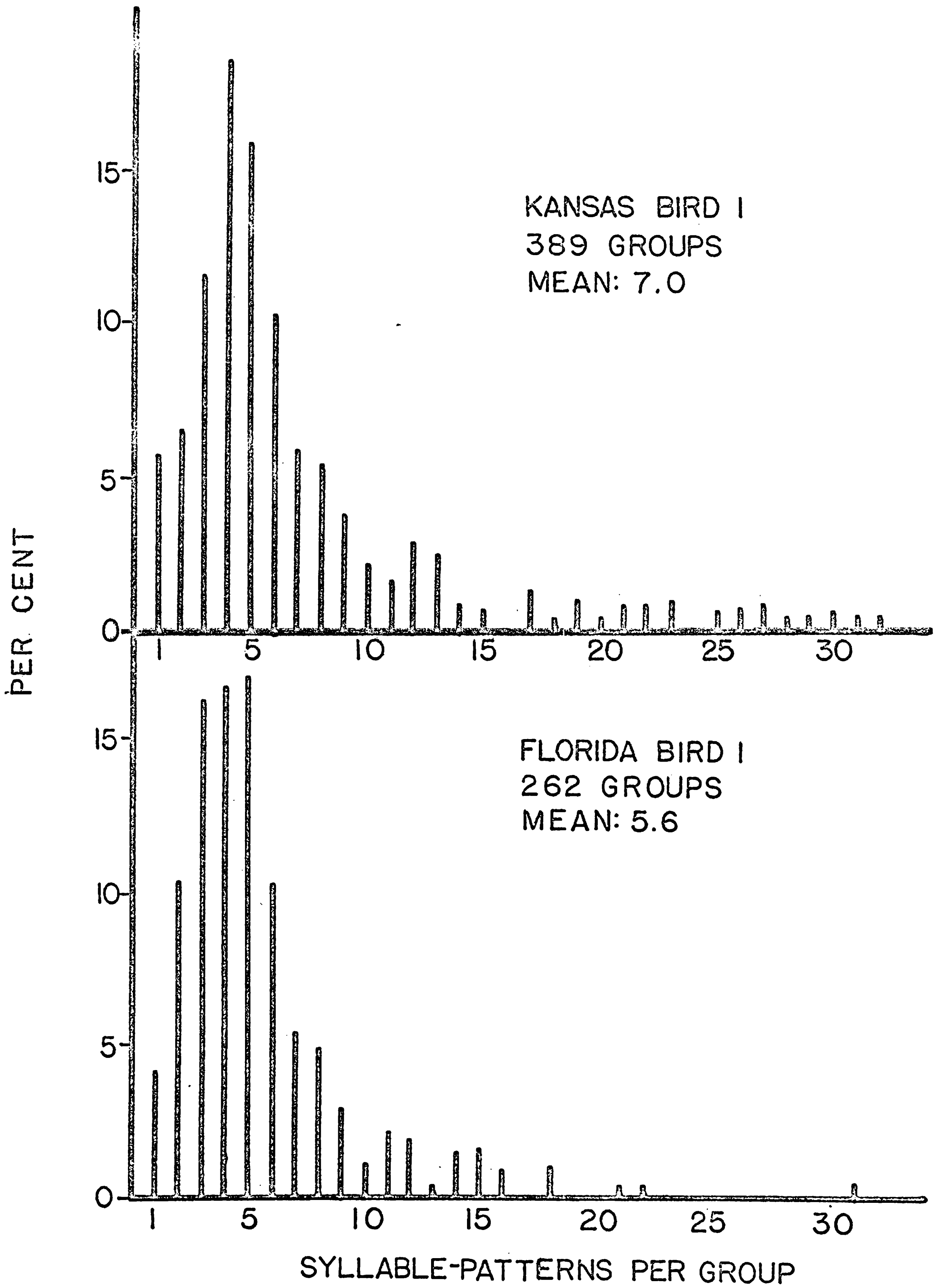

KANSAS BIRD I
389 GROUPS
MEAN: 7.0
FLORIDA BIRD I
262 GROUPS
MEAN: 5.6
PER CENT
0
5
10
15
1
5
10
15
20
25
30
SYLLABLE-PATTERNS PER GROUP

Figure 11. Frequency distributions showing number of syllable-patterns per group for Kansas Bird No. 2 and Florida Bird No. 2.

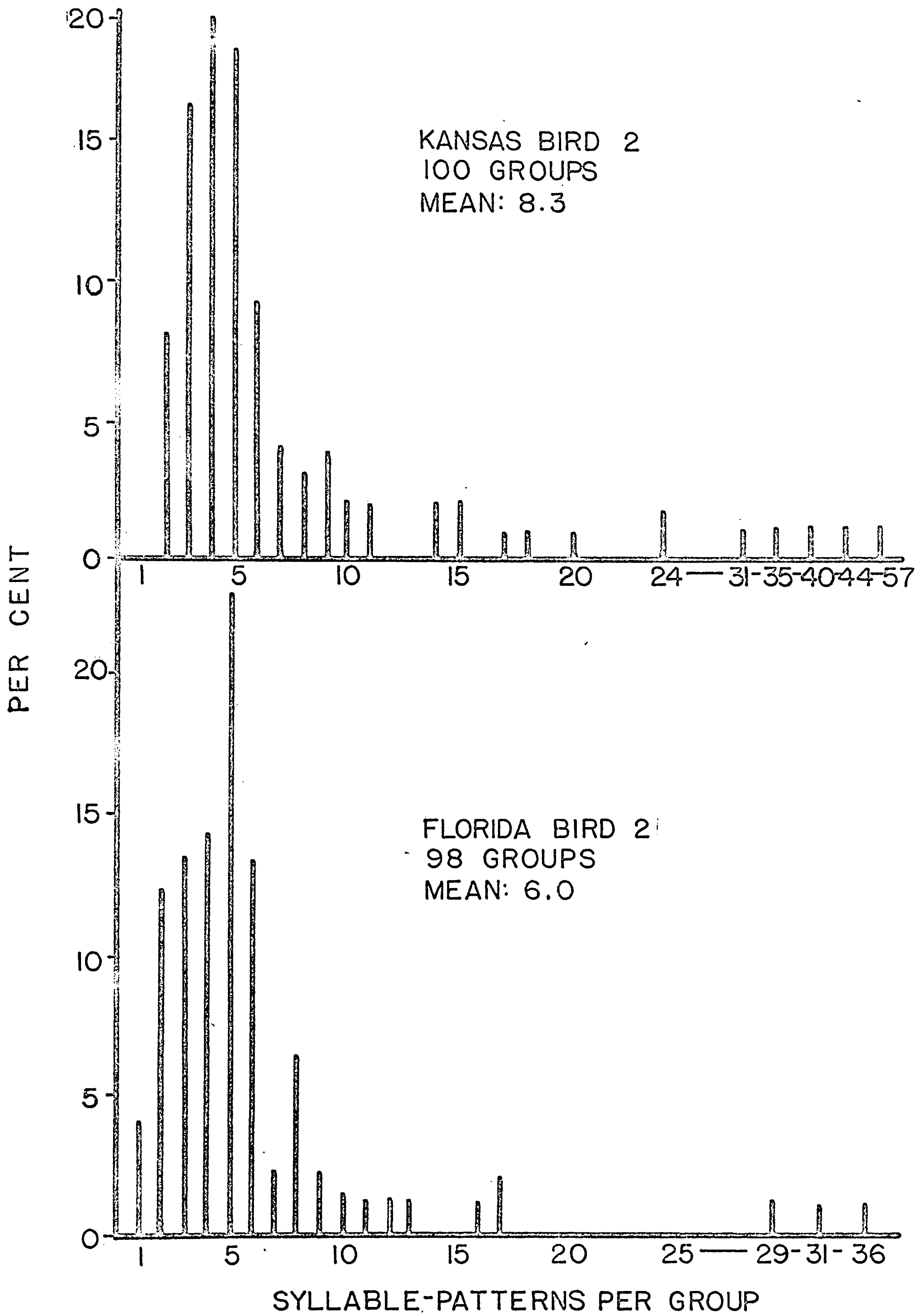
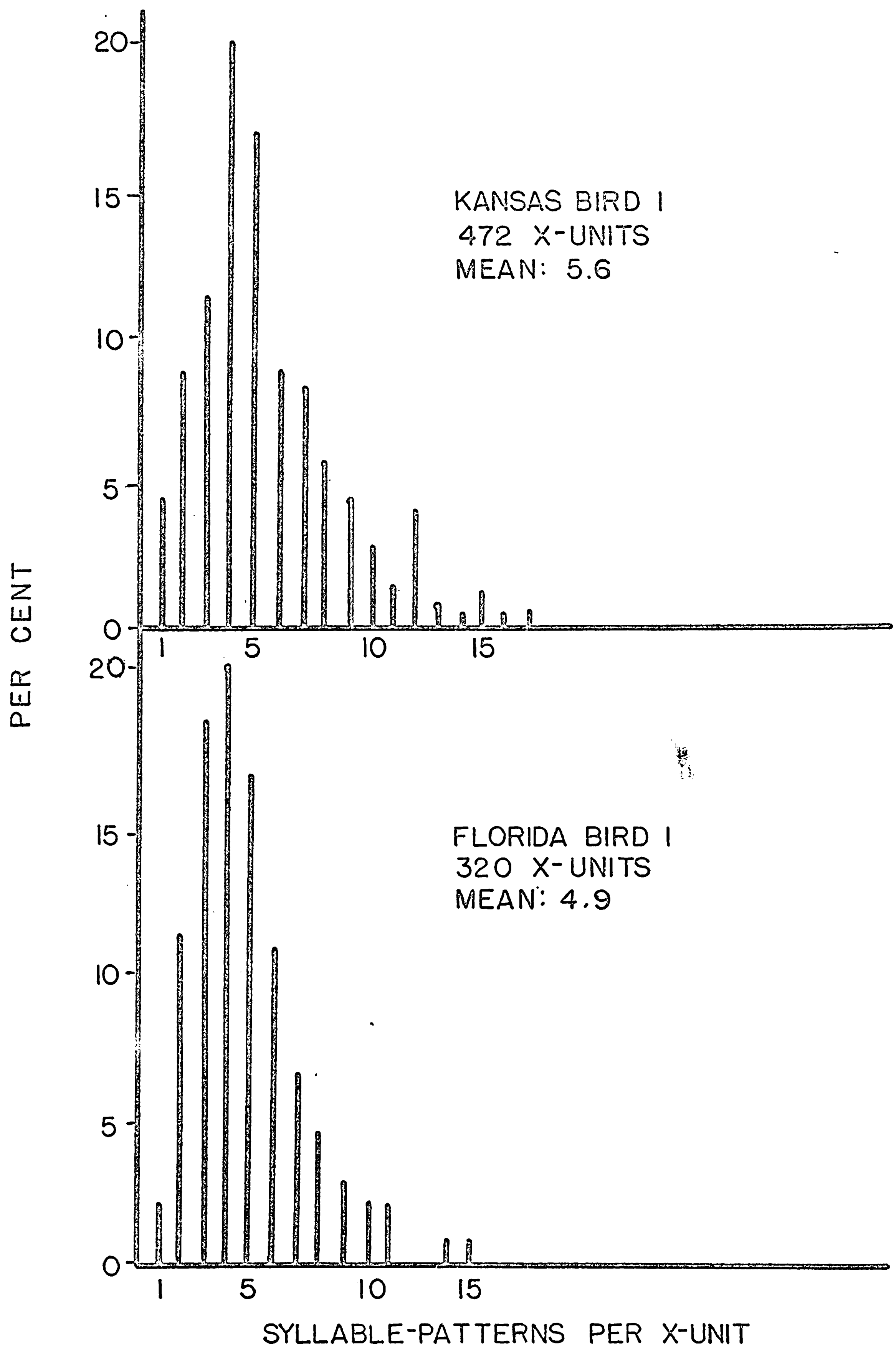

KANSAS BIRD 2
100 GROUPS
MEAN: 8.3
FLORIDA BIRD 2
98 GROUPS
MEAN: 6.0
PER CENT
0
5
10
15
20
1
5
10
15
20
24 — 31-35-40-44-57
25 — 29-31-36
SYLLABLE-PATTERNS PER GROUP

Figure 12. Frequency distribution showing number of syllable-patterns per x-unit for Kansas Bird No. 1 and Florida Bird No. 1.



20
15
10
5
0
KANSAS BIRD I
472 X-UNITS
MEAN: 5.6
1
5
10
15
PER CENT
20
15
10
5
0
FLORIDA BIRD I
320 X-UNITS
MEAN: 4.9
1
5
10
15
SYLLABLE-PATTERNS PER X-UNIT

Figure 13. Frequency distributions showing number of syllable-patterns per x-unit for Kansas Bird No. 2 and Florida Bird No. 2.

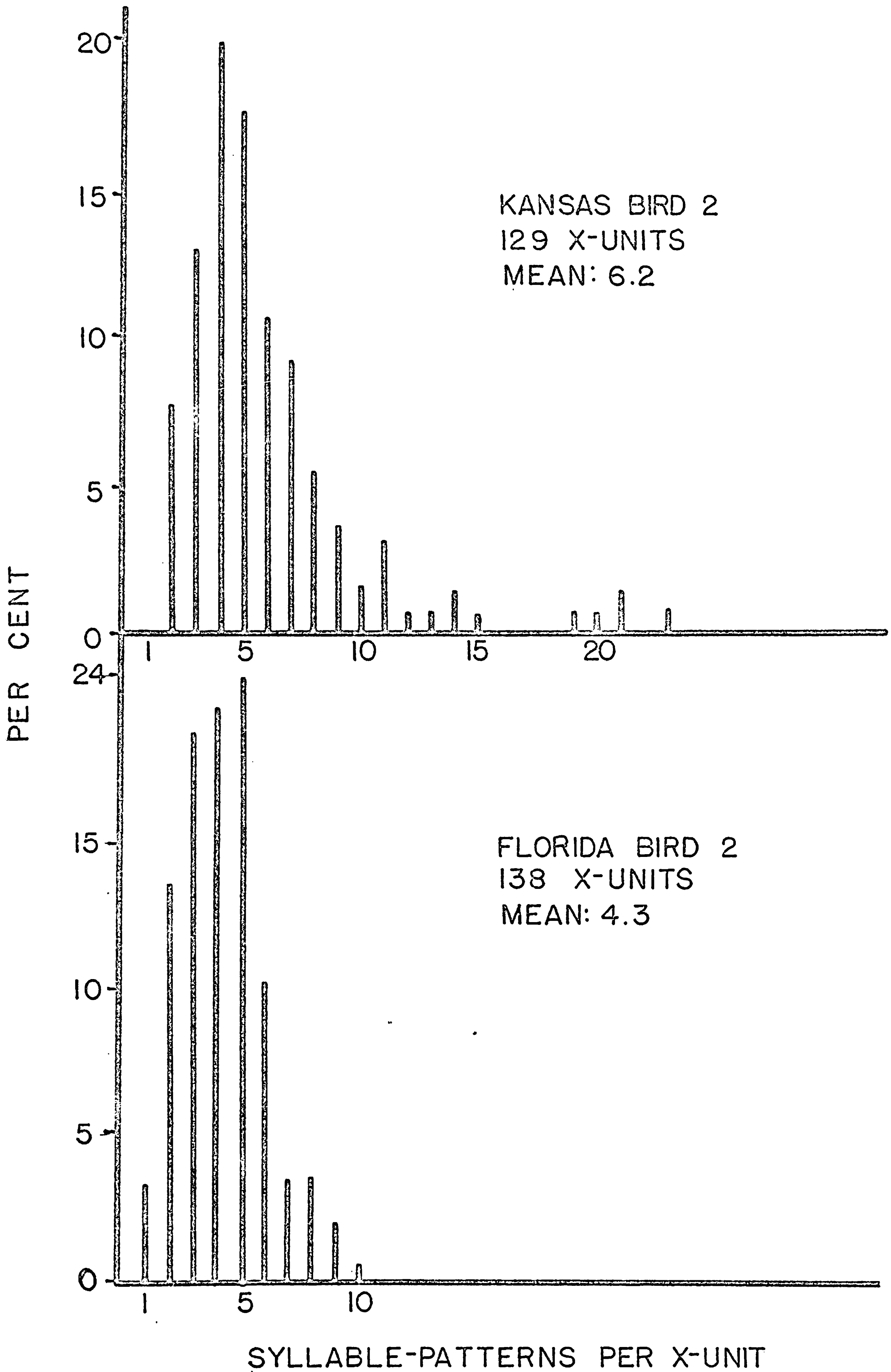

KANSAS BIRD 2
129 X-UNITS
MEAN: 6.2
FLORIDA BIRD 2
138 X-UNITS
MEAN: 4.3
PER CENT
20
15
10
5
0
1
5
10
15
20
24
15
10
5
0
1
5
10
SYLLABLE-PATTERNS PER X-UNIT

Figure 14. Frequency distributions showing number of syllables per syllable-pattern for Kansas Birds Nos. 1 and 2 and Florida Bird No. 1.

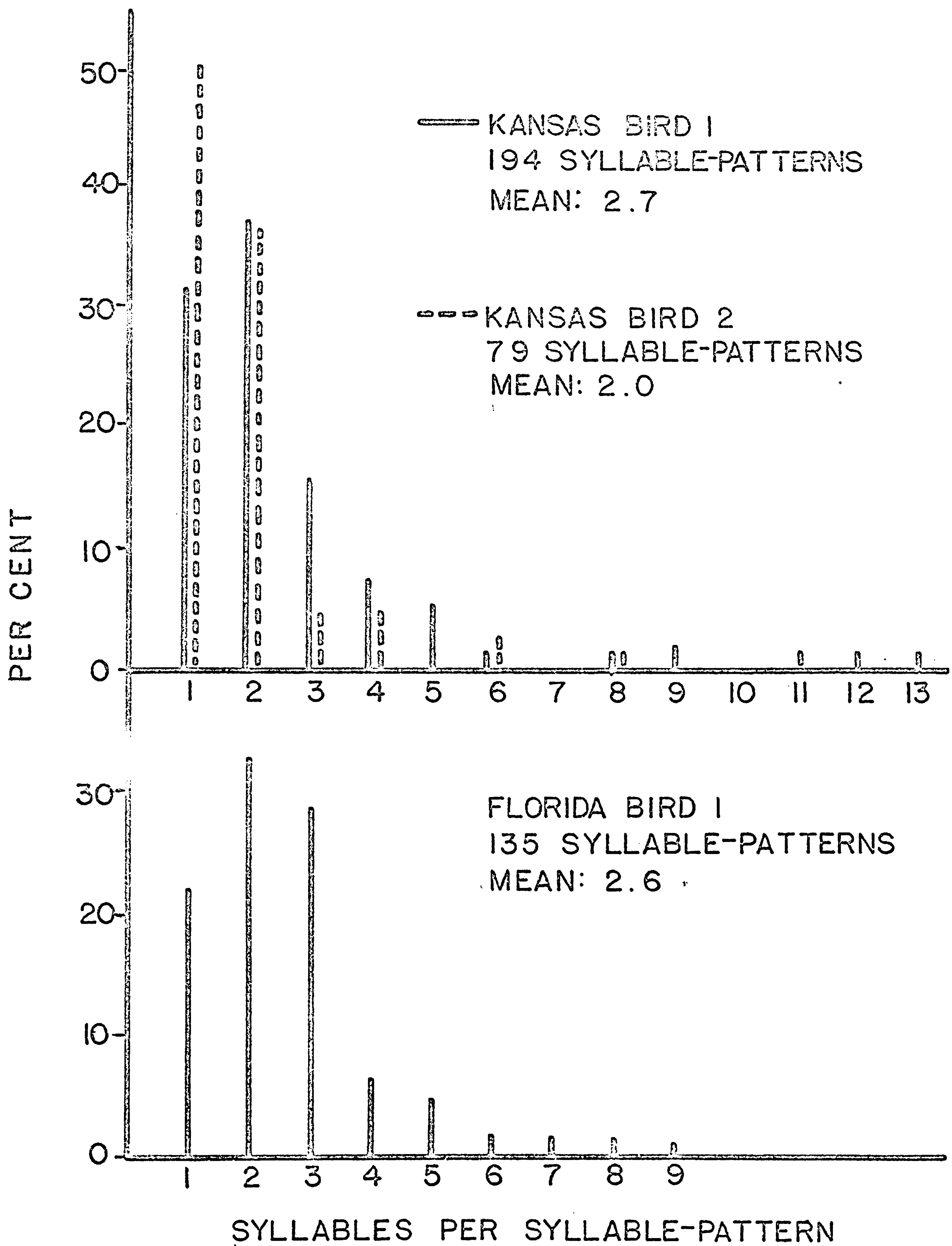
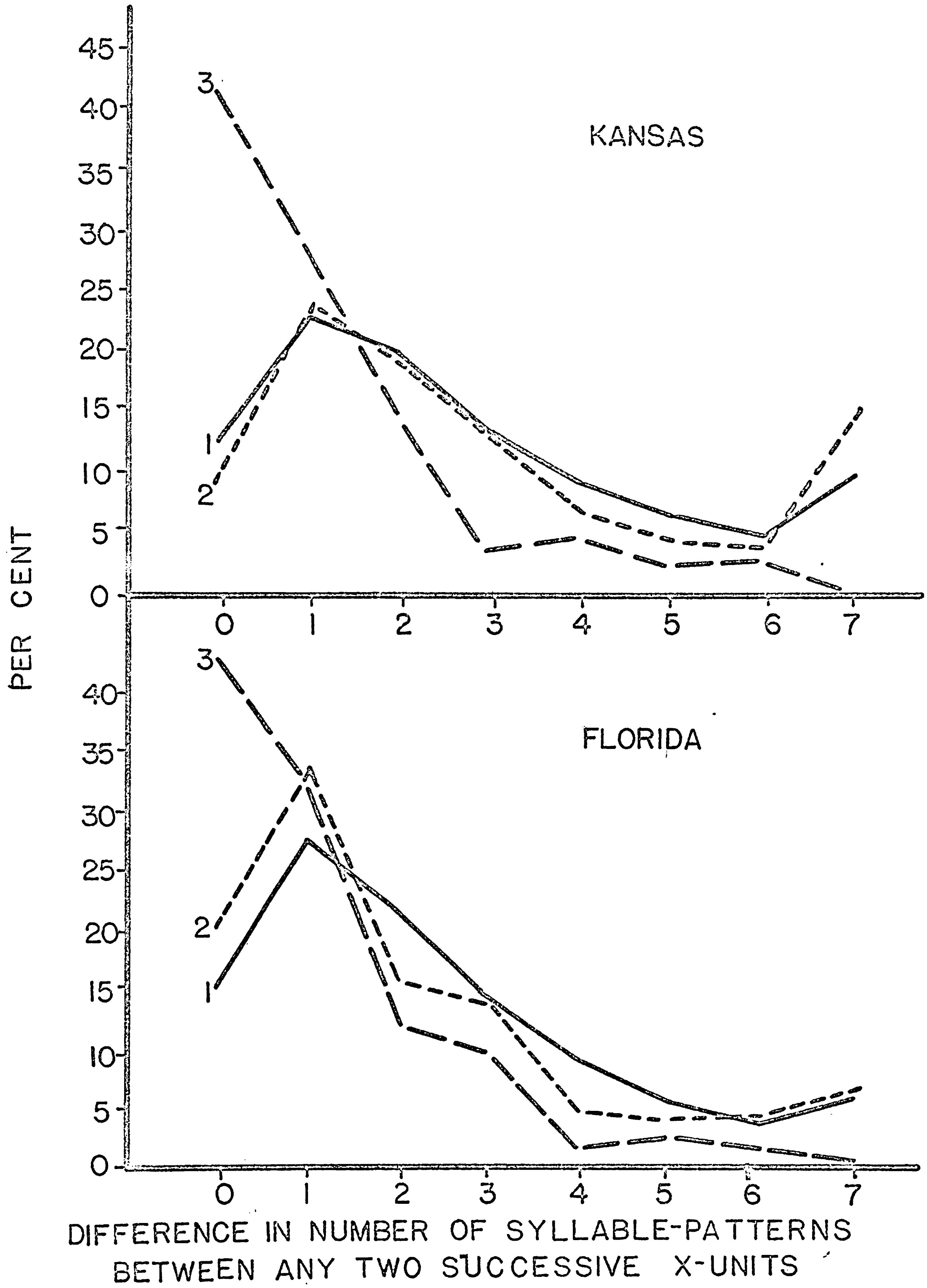

50
40
30
20
10
0
PER CENT
KANSAS BIRD 1
194 SYLLABLE-PATTERNS
MEAN: 2.7
KANSAS BIRD 2
79 SYLLABLE-PATTERNS
MEAN: 2.0
1
2
3
4
5
6
7
8
9
10
11
12
13
30
20
10
0
FLORIDA BIRD 1
135 SYLLABLE-PATTERNS
MEAN: 2.6
1
2
3
4
5
6
7
8
9
SYLLABLES PER SYLLABLE-PATTERN

Figure 15. 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 pattern. Curve No. 3 represents instances of like pattern.



DIFFERENCE IN NUMBER OF SYLLABLE-PATTERNS
BETWEEN ANY TWO SUCCESSIVE X-UNITS