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Spectrographic Analysis of Variation in the Songs of a Population of Blue-winged Warblers (Vermivora pinus)

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Recent interest in the variation of avian vocalizations is due to (1) an increasing awareness of the significance of such variation in our understanding of the social and systematic relationships among individuals, populations, and species, and to (2) technological advancements in recording and analytical procedures (Borror, 1960; Kellogg, 1960). Apart from its intrinsic value, as a basis for comparison with the variation that has been demonstrated in other species, a spectrographic analysis of the songs of the Blue-winged Warbler (Vermivora pinus) is of special interest because of the potential importance of song in the relationships between this species and the Golden-winged Warbler (V. chrysoptera). We have demonstrated through the use of playback techniques that song has an important role in effecting species discrimination in some Blue-winged Warblers (Gill and Lanyon, in press). But, where their ranges overlap, these forms are known to hybridize, and there are numerous field observations of individuals singing "aberrant" patterns and having bivalent repertoires of songs characteristic of both forms (Eisenmann, 1946; Short, 1962). A thorough analysis of variation in song within an area where both species occur on a common breeding ground has not yet

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been made. Preliminary to such a study we felt it desirable to ascertain, through spectrographic analysis, the limits of individual and intrapopulational variation in the songs recorded from Blue-winged Warblers in a locality where Golden-winged Warblers do not breed. This constituted the objective of a study conducted at the Kalbsleisch Field Research Station of the American Museum of Natural History while Gill was a National Science Foundation Undergraduate Research Fellow in 1961 and a recipient of a Frank M. Chapman Award in 1962 and 1963.

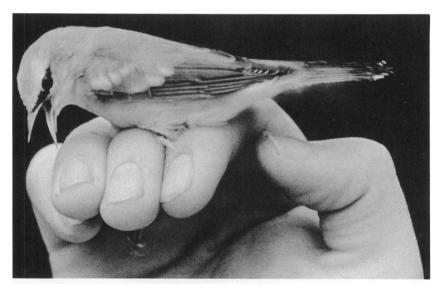


Fig. 1. This male Blue-winged Warbler was mist-netted at the Kalbfleisch Station and color-banded to facilitate individual recognition after release.

METHODS

Our study population consisted of Blue-winged Warblers that breed at the Kalbfleisch Field Research Station, Huntington, Long Island, New York. The Golden-winged Warbler is rarely found as a breeding bird on Long Island and has not bred at the Kalbfleisch Station since the latter was established in 1958. During the summers of 1961, 1962, and 1963, from 12 to 14 pairs of Blue-winged Warblers bred on the 94 acres of the Station, arriving in early May and departing by mid-August. Most of these birds were mist-netted and color-banded to facilitate individual recognition (fig. 1) and exhibited little, if any, evidence of intro-

gression with *V. chrysoptera*. The recordings analyzed here were made from five color-banded males in 1962 and 11 color-banded males in 1963.

In 1962 we used a Transmagnemite tape recorder that operated at a speed of 15 inches per second. In 1963, a Uher 4000 tape recorder that operated at a speed of 7½ inches per second was used. In both years the recordings were made with an Altec 660B microphone mounted in a parabolic reflector 24 inches in diameter, and a preamplifier. Analyses of all recordings were made with a Kay Electric Company Sonagraph, with the use of the "high-shape" setting. Since the songs of Blue-winged Warblers contain fundamental frequencies above 8 kilocycles, the upper limit of the frequency scale normally registered by our Sonagraph, it was necessary for us to analyze them at one-half of the normal speed. This procedure effectively doubled the frequency scale (16 kilocycles instead of 8 kilocycles) and halved the time scale (1.2 seconds instead of 2.4 seconds) normally associated with a sound spectrogram. The decreased duration of each graph necessitated splicing together two graphs to complete the analysis of most songs. The graph that resulted from this type of analysis, when compared with a graph made from a song played back at normal speed, will appear to be compressed vertically (with a concomitant loss in frequency-resolution) and extended horizontally with a corresponding improvement in time-resolution). We further improved the resolution in time by using the wide band-pass filter. A comparison of graphs made with this filter and the narrow band-pass filter is shown in figure 2.

Though the term "song" may offend some readers as being too ambiguous, we feel strongly that more specific terms implying function or connoting motivation should be avoided until more is known of the behavioral significance of these vocalizations. The term "song" is used here in reference to those vocal patterns that are commonly rendered by territorial males and that are more complex in character and of longer duration and greater intensity than other elements within the male's vocal repertoire (call notes, twitters, and so on). There is no "flight song" in this species that is in any way distinct from the vocalizations that we have included here under the general category of "song."

BASIC STRUCTURE OF SONGS

Four basic components have been recognized in the songs recorded from 16 males in this population, each of which is structurally distinct when viewed spectrographically and audibly distinct when heard separately by the human ear. The first of these we have designated component A (fig. 2A). At normal speed this is heard as a continuous, rasping type

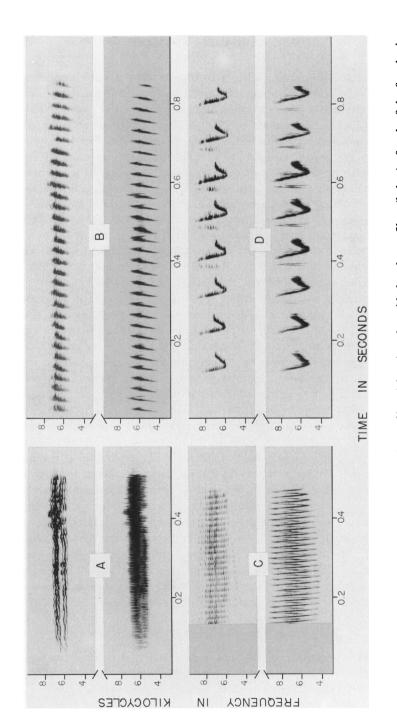
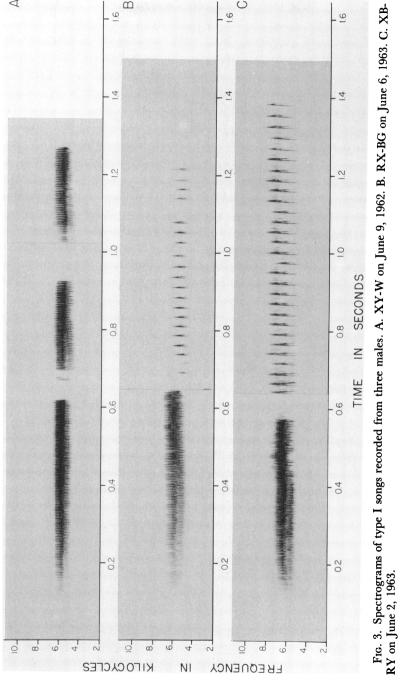


Fig. 2. Spectrograms made with a narrow band-pass filter (above) and a wide band-pass filter (below) of each of the four basic components in the songs recorded from 16 males.

of note, composed of energy distributed over nearly 2 kilocycles but centering roughly upon 6 kilocycles. The narrow filter of the sound spectrograph provides us with a graph of this component that represents the sound much as the human ear perceives it—a continuous, nonpulsating note. But the wide filter, with its greater resolution in the time dimension, clearly indicates that this component actually consists of one or more oscillating elements. These oscillations occur at a rate of more than 200 per second, and cannot be heard by the human ear until the component is slowed down to one-sixteenth of the normal speed. Variation in component A within the repertoire of a single male appears to be limited to subtle variations in the duration and configuration of the note which are not perceptible to the human ear (fig. 6). Variation from male to male within the population is more pronounced. The duration of the component in our recordings varies from brief bursts of 0.05 second to longer series up to 0.80 second, though most renditions are just under 0.5 second in length. An unusually long component A appears in figure 4C, while a short burst appears in figure 4B and at the beginning of the terminal portion of each song pattern in figure 7. The most noticeable variation among males is whether or not the average frequency of the longer renditions remains constant throughout the duration of the component. Eight males rendered component A's which did not change perceptibly in average frequency, as in figure 2A and in all the graphs in figures 3 and 4. But seven males habitually rendered component A's that were noticeably down-slurred, in some instances by as much as 3 kilocycles. Examples of this variation are shown in the three graphs in figure 5.

Component B consists of a series of discontinuous elements, delivered at a rate of about 40 per second (varying from 36 to 42 in our series) and is illustrated in figure 2B. Each individual element within this component appears as an inverted V when graphed with the wide filter, with the ascending portion often being longer and of greater intensity. The graphic configuration of the elements in component B is remarkably constant within the individual (fig. 6) but varies considerably from one male to another (as in the terminal portion of those song patterns in figs. 3 to 5 in which component B is represented). When heard at normal speed, the only perceptible variation in the component B's rendered by the various males is in the duration of the component—from 0.25 to 0.95 second in our series.

Component C is heard by the human ear as a buzzy trill. The wide filter indicates that it consists of a continuously oscillating element, with energy concentrated on the descending portion of each oscillation (fig. 2C). The rate of these oscillations varies from 60 to 100 per second. The

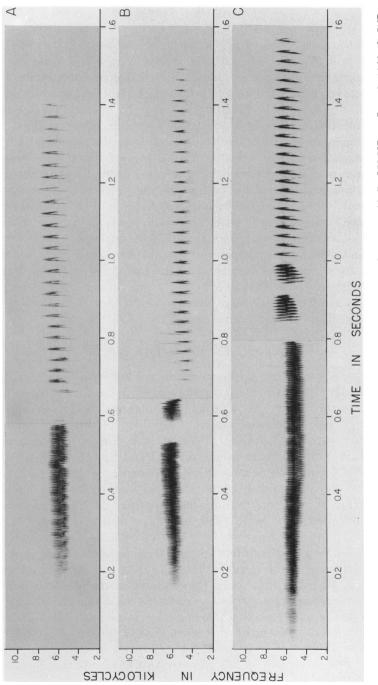


component may be expressed in brief bursts, lasting less than 0.05 second (as in the central portion of each song pattern in fig. 5 and in the introductory portion of each pattern in fig. 7), or in longer renditions of up to 0.50 second (as in the terminal portion of each song pattern in figs. 7 and 8).

Component D consists of a series of discrete elements, rendered at constant intervals one from another. According to the wide-band filter, these elements are of two types (fig. 2D). One is related to the element that appears as a continuously oscillating note in component C, though in this instance only one-half of each oscillation (usually the upper half) is registered by the sound spectrograph, and this at very low intensity. Its presence in component D is not discernible by the human ear. Alternating with this low-intensity element is a more prominent note which is not found in any other component. Variation in component D among males consisted chiefly of differences in the configuration of this high-intensity element (note differences in figs. 7 and 8) and in the delivery rate of this same element—from seven to 12 per second in our series. Duration of this component varied from 0.25 to 1.00 second.

VARIATION IN SONG PATTERNS

Variation in the songs of this population is achieved as a result of change in the sequences and combinations of these four basic components. Our analysis of this variation has confirmed field observations (Saunders, 1951; Ficken and Ficken, 1962) that, in this species as in many wood warblers (Parulidae), there are two distinct types of song. We have arbitrarily designated these as type I and type II. Though their structural differentiation is now clearly understood, we are unable at this time to differentiate them on functional grounds. Both types of song can be heard throughout the three-month period during which these warblers are present at the Kalbfleisch Station, though song type II is heard more prominently during the month that follows the cessation of nesting. We have heard both types of song from territorial males, before and after encounters with intruding birds. In the course of playback experiments in June, the initial vocal response of a territorial male was invariably a rendition of song type I, even in the event that the playback recording was of song type II. Following the cessation of a playback recording, however, a territorial male often gave a number of renditions of song type II, later to be followed by resumption of song type I. We frequently took advantage of this in our efforts to obtain recordings of type II patterns.



Fro. 4. Spectrograms of type I songs recorded from three males. A. RX-BW on June 6, 1963. B. GY-XR on June 5, 1963. C. WR-YX on June 6, 1963.

Type I songs in our population consisted of various combinations of components A, B, and C, with component A being given consistently as the introductory phase of each variant pattern. In our series of recordings of type I songs from 15 males, there are only four different combinations of basic components (intrapopulational variation). The distribution of males according to these four combinations is presented in table 1. This intrapopulational variation in song type I is illustrated by the spectrograms in figures 3 through 5.

The songs that we have classified as type I are generally described by the field observer as being weak, non-musical, and consisting of two or

	DASIC COMPONENTS	OMPONENTS USED IN SONG TYPE I	
Component A	Components A+B	Components A+C+B	Components A+C
XY-W (fig. 3A)	RX-BG (fig. 3B) XB-RY (fig. 3C)	WR-YX (fig. 4C) BW-XR (fig. 5A)	GW-XR (fig. 5C)
	RX-BW (fig. 4A)	XR-R (fig. 5B)	
	GY-XR (fig. 4B)	XW-YG	
	BG-XY	RW-YX	
	CX-	G-RX	
		XR-	

TABLE 1

DISTRIBUTION OF MALES^a According to the Combinations of

RASIC COMPONENTS LIGHT IN SONG TYPE I

more insect-like, buzzing notes (Saunders, 1951). Possibly the only consistent distinction that is made in the field between the variant patterns of song type I illustrated here is the subjective impression of whether the terminal portion of the song rises or falls in pitch (frequency) with respect to the introductory component A. For example, in those songs in which the down-slurred variation of component A is used (fig. 5), the terminal phase generally sounds higher-pitched by way of contrast.

No male within our population was known to render more than one of the variant patterns of type I illustrated in figures 3 through 5. Variation within the many renditions of song type I of a particular male (individual variation) was limited to differences in the length of the continuous components, A and C, and to differences in the number of elements included in a series of the discontinuous component B. Individual variation did not include alteration of the combination and sequence of the basic components. This limited variability within an in-

^a Identified by symbols representing color-band combinations.

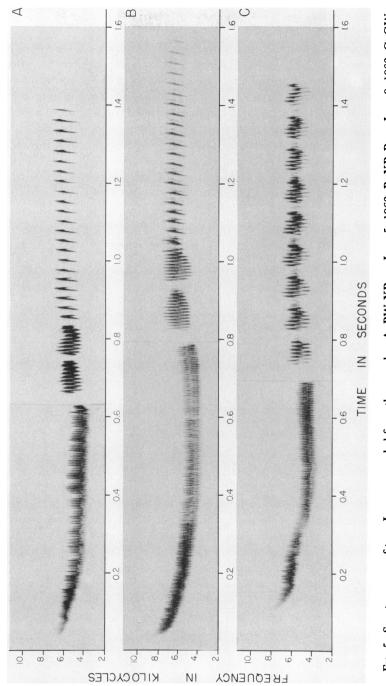


Fig. 5. Spectrograms of type I songs recorded from three males. A. BW-XR on June 5, 1963. B. XR-R on June 9, 1963. C. GW-XR on June 2, 1963.

dividual's renditions of its song type I is illustrated by the series of recordings that we have for male GY-XR. The type I song of this male was unique in that it included a brief burst of component A between the longer components A and B (fig. 4B). Twenty-two renditions of this song were recorded on June 2, 1963, and nine more renditions were recorded on June 5, 1963. The extremes in variation found within this series of recordings from one individual are illustrated in figure 6. The individuality of the song was maintained by the inclusion of the short burst of component A as an intermediate phase in all 31 renditions, whereas variation was limited to alterations in the duration of the components

TABLE 2
Distribution of Males^a According to the Combination of Basic Components Used in Song Type II

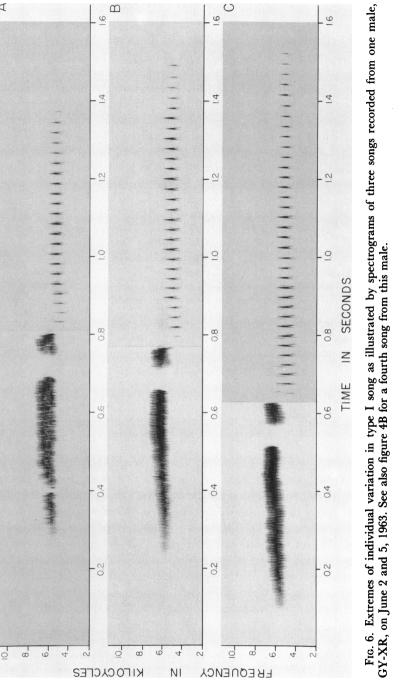
Components $C+D+A+C$	$\begin{array}{c} \text{Components} \\ \text{A} + \text{C} + \text{D} + \text{C} \end{array}$	$\begin{array}{c} \text{Components} \\ \text{D+A+C} \end{array}$
CX- (fig. 7A) XB-RY (fig. 7B) RW-YX (fig. 7C) G-RX (fig. 8A) WR-YX RX-BW	BG-XY (fig. 8B)	GY-XR (fig. 8C)
RX-BG XG-		

^a Identified by symbols representing color-band combinations.

and hence the entire song pattern. The 31 renditions varied from 1.12 to 1.53 seconds, and averaged 1.29 seconds in length. In one instance there was a brief interruption in the introductory component (fig. 6A).

Type II songs in our population consisted of various combinations of components A, C, and D. They were characterized by the presence of component D and the absence of component B. In our series of type II songs from 10 males, there are only three different combinations of basic components represented (intrapopulational variation). The distribution of males according to these three combinations is presented in table 2. This intrapopulational variation in song type II is illustrated in figures 7 and 8.

To the field observer song type II often sounds longer and more variable than song type I. In our series of recordings, however, type II patterns averaged only slightly longer than type I patterns for each of six males for which there were adequate samples (table 3). Intrapopulational



D

variation appears to be no greater in type II patterns than in type I patterns in our population. On the contrary, there was greater uniformity among males in the combination of basic components used in type II patterns than in type I patterns. This is evidenced by the fact that all but two of the type II patterns in our recordings consisted of the same combination and sequence of basic components (table 2), whereas two distinct combinations of components were prevalent in our recordings of type I patterns (table 1).

	Song Type I	Song Type II
GY-XR	1.29 (31) b	1.31 (12)
RX-BW	1.22 (9)	1.30 (10)
CX-	1.38 (10)	1.49 (7)
WR-YX	1.53 (10)	1.64 (5)
RX-BG	1.27 (6)	1.37 (9)
XB-RY	1.42 (6)	1.52 (4)

 $TABLE \ 3$ Average Duration (in Seconds) of Songs of Six Males a

Individual variation in type II patterns was limited to differences in the length of continuous components, A and C, and to differences in the number of elements included in a series of the discontinuous component D. As in the case of song type I, individual variation in type II patterns did not include alteration of the combination and sequence of the basic components. The graphs in figure 9 illustrate the extent to which variation occurs within a male's renditions of its type II patterns.

Each male Blue-winged Warbler in this population had a vocal repertoire that included one type I pattern and one type II pattern. The total size of an individual's repertoire of songs, then, consisted of but two distinct patterns. No male was found to have more than this number. With respect to size of individual repertoires of distinct song patterns, the Blue-winged Warbler would appear to be somewhat less restricted than the Chipping Sparrow (Spizella passerina) and White-crowned Sparrow (Zonotrichia leucophrys) in which each male is reported to have but one song pattern (Marler and Isaac, 1960; Marler and Tamura, 1962). Somewhat larger individual repertoires of from three to nine distinct song patterns have been documented spectrographically for the Great Tit, Parus major (Gompertz, 1961), thrushes of the genus Hylocichla (Borror,

^a Identified by symbols representing color-band combinations.

^b Number of songs analyzed.

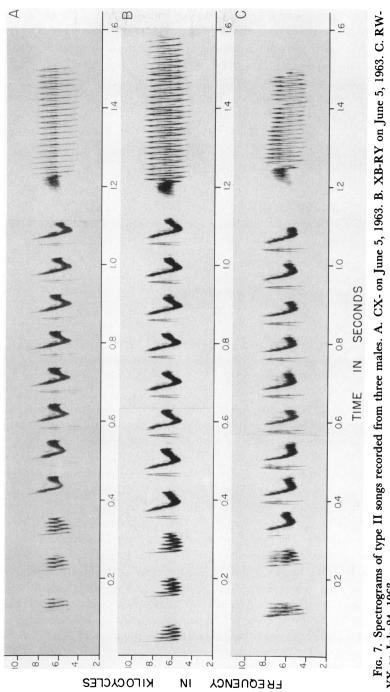
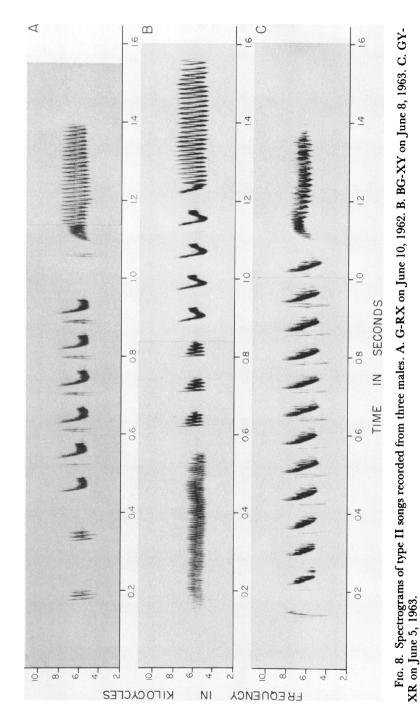
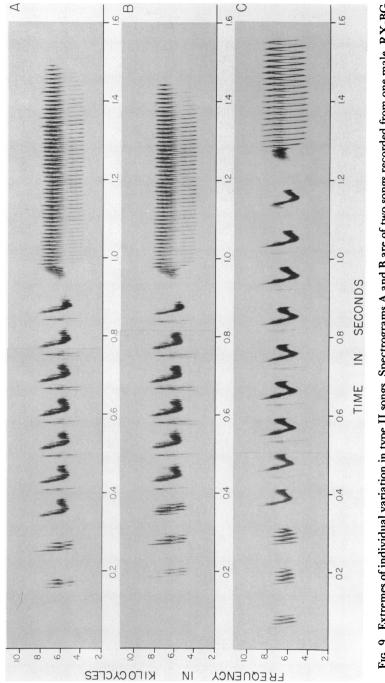


Fig. 7. Spectrograms of type II songs recorded from three males. A. CX- on June 5, 1963. B. XB-RY on June 5, 1963. C. RW-YX on July 24, 1963.





Fro. 9. Extremes of individual variation in type II songs. Spectrograms A and B are of two songs recorded from one male, RX-BG on June 6, 1963. C is of a song recorded from CX- on June 5, 1963 and can be compared with another song from this male (fig. 7A).

1961a), and the Western Meadowlark, Sturnella neglecta (Lanyon, 1957). Borror (1961b) provides additional data on intraspecific variation in other species.

In view of field observations of individual Blue-winged Warblers having bivalent repertoires of songs characteristic of both *V. pinus* and *V. chrysoptera*, in areas where these two species occur together, two points resulting from our study are of special interest and merit repetition here. (1) No male was found to have more than one type I pattern and one type II pattern in its repertoire of song. (2) There was no evidence that a male varies either of these two song patterns by altering the combination and sequence of the basic components. One immediately wonders what factors may be operating to increase this limited individual variability in at least some individuals in areas of sympatry. We have no data at present on the extent of geographical variation in the songs of the Blue-winged Warbler. Above all, detailed spectrographic studies are needed of recordings made from individuals suspected of having bivalent repertoires, as well as information concerning the ontogeny of song in this species.

SUMMARY

A spectrographic analysis of tape recordings of Blue-winged Warblers at one locality on Long Island, New York, revealed the limits of individual and intrapopulational variation in the song of that species in an area where the closely related Golden-winged Warbler does not breed. Intrapopulational variation consisted of different combinations and sequences of four basic components. Individual variation involved minor alterations in the duration and configuration of these components but did not include changes in their combination or sequence. Each male had a repertoire of only two distinct song patterns. The significance of these findings is discussed with reference to reports that some Blue-winged Warblers have a greater variability in song in areas where the Golden-winged Warbler also occurs.

BIBLIOGRAPHY

Borror, D. J.

1960. The analysis of animal sounds. In Lanyon, W. E., and W. N. Tavolga (eds.), Animal sounds and communication. Publ. Amer. Inst. Biol. Sci., no. 7.

1961a. Variation in thrush songs. Wheaton Club Bull., vol. 6, pp. 9-15.

1961b. Intraspecific variation in passerine bird songs. Wilson Bull., vol. 73, pp. 57-78.

EISENMANN, E.

1946. Interchange of song between the Blue-winged and Golden-winged Warblers. Proc. Linnaean Soc. New York, nos. 54–57, pp. 53–54.

FICKEN, M. S., AND R. W. FICKEN

1962. The comparative ethology of the wood warblers: a review. Living Bird, First Ann. Cornell Lab. Ornith., pp. 103–122.

GILL, F. B., AND W. E. LANYON

[In press.] Experiments on species discrimination in Blue-winged Warblers.

Auk.

Gompertz, T.

1961. The vocabulary of the Great Tit. Brit. Birds, vol. 54, pp. 369–394, 409–418.

Kellogg, P. P.

1960. Considerations and techniques in recording sound for bio-acoustics studies. In Lanyon, W. E., and W. N. Tavolga, (eds.), Animal sounds and communication. Publ. Amer. Inst. Biol. Sci., no. 7.

LANYON, W. E.

1957. The comparative biology of the meadowlarks (Sturnella) in Wisconsin. Publ. Nuttall Ornith. Club, no. 1, 67 pp.

MARLER, P., AND D. ISAAC

1960. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. Condor, vol. 62, pp. 124–135.

MARLER, P., AND M. TAMURA

1962. Song "dialects" in three populations of White-crowned Sparrows. Condor, vol. 64, pp. 368–377.

Saunders, A.

1951. A guide to bird songs. New York, Doubleday and Co., 307 pp.

SHORT, L.

1962. The Blue-winged Warbler and Golden-winged Warbler in central New York. Kingbird, vol. 12, pp. 59–67.