SONG VARIATION IN SYMPATRIC BLUE-WINGED AND GOLDEN-WINGED WARBLERS

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THIS paper presents a spectrographic analysis of individual variation in the songs of the Blue-winged and Golden-winged Warblers (*Vermivora pinus* and *V. chrysoptera*), two species that hybridize extensively in northeastern United States (Short, 1963). The songs of these birds function in stimulating territorial aggression between males, both intraspecific and interspecific, and may also function as premating isolating mechanisms, enabling a female to pair with a conspecific male. Therefore analysis of the structure and variation in songs is a prerequisite for understanding the nature of the behavioral relationships of these two hybridizing species. This report is part of a study of both species and their hybrids in southern Michigan (Gill and Murray, 1972). For comparison there is only Lanyon and Gill's (1964) analysis of Blue-winged Warbler songs from eastern Long Island, New York, where Golden-winged Warblers do not breed.

METHODS

We tape-recorded songs of 34 territorial *Vermivora* in May and June 1969 and 1970 in two study areas in southeastern Michigan: Island Lake Recreation Area, Livingston County, and Rose Lake Wildlife Experimental Station, Clinton County. We used a Uher 4000 Report L tape recorder with either a Uher M514 microphone and 24-inch parabolic reflector in 1969 or a semidirectional AKG D190E microphone and Uher 106 GA preamplifier in 1970. Recordings were made at a tape speed of 7.5 inches per second and analyzed at one-half speed on a Kay Electric Company Sonagraph using a wide bandpass filter (see Lanyon and Gill, 1964).

Shortly after they established territories in our study areas, birds were netted, color-banded, indexed according to the criteria of Short (1963) and released. With one exception (R-XG), color bands (Red, Green, Yellow, White, Blue) were always placed on a male warbler's left leg, and a federal numbered aluminum band (X) on the right leg. In the individual codes, such as B-RG, the first letter (B) refers to the plumage phenotype of the male (*B*lue-wing, *G*olden-wing, *Br*ewster's, or *L*awrence's), while the second two letters refer to the color bands. G-1365 was a male Golden-wing that we collected after recording his songs.

We have on tape a total of 970 renditions of song type I (terminology of Lanyon and Gill, 1964) from these males and 457 renditions of song type II (Table 1). We made spectrograms of 309 song type I renditions and 143 song type II renditions. Where possible we made spectrograms of every other rendition. After initial study of the extent of variation within some males' repertoires based on these larger samples, we reduced the number of renditions spectrogrammed to five or six. These were selected from throughout the entire sequence of songs recorded from each male. Spectrograms were also made of any song that sounded aberrant to the human ear. These procedures have insured inclusion of the extremes of variation in each male's

TABLE 1

SAMPLES AND PATTERNS OF THE SONGS OF BLUE-WINGED AND GOLDEN-WINGED WARBLERS IN MICHIGAN

Male	Plumage index[1]	Song type I			Song type II		
		Recorded	Analyzed	Pattern(s)	Recorded	Analyzed	Pattern(s)
Blue-wings							
B-BB	0	31	12	A-B	0	—	—
B-BW	3	8	8	A-B	18	11	D_x-D′-F
B-GB	1	0	—	—	1	1	D-F
B-GG	1	19	14	A-B	15	7	D′-F
B-GR	6	12	5	A-B	37	8	D_x-D-F
B-GW	2	18	5	A-B	0	—	—
B-GY	2	26	16	A-B	5	5	D′-F
B-RB	5	16	9	A-B	0	—	—
B-RG	1	71	5	A-B	85	11	D_x-D-F
B-RR	1	18	11	A-B	26	14	D-F
B-RW	1	43	22	A-A-A	0	—	—
B-WG	2	10	10	A-B-A	0	—	—
B-WW	2	75	20	A-B	0	—	—
B-YG	4	18	5	A-B-(A)	0	—	—
B-YR	1	23	10	A-B	20	10	D-F
B-YW	1	57	10	A-B	0	—	—
R-XG	1	10	5	A-BDB	0	—	—
Brewster's							
Br-RR	9	65	15	A-B-(A)	12	5	D_x-D-F
Br-YY	7.5	63	8	A-B	8	5	D-F
Lawrence's							
L-RR	5	30	5	A-B	42	9	DE-D-F

[1] The sum of values of five characters (nape, back, rump, underparts, and wing bars), each of which was graded from the *pinus* condition (0) to the *chrysoptera* condition (4, or 5 in the case of wing bars). See Short (1963) for details.

TABLE 1–Continued

Male	Plumage index[1]	Song type I			Song type II		
		Recorded	Analyzed	Pattern(s)	Recorded	Analyzed	Pattern(s)
Golden-wings							
G-BB	17	2	2	C-C-C[2]	0	—	—
G-GG	21	46	18	C-C-C	0	—	—
G-GR	21	71	10	C-C-C	63	11	E′-D_x-G
G-GW	19	32	5	C-C-C	5	3	E′-G
G-RB	17.5	15	6	C-C-C	0	—	—
G-RG	19	15	5	C′-C-C	8	8	E
G-RR	17	47	11	C-C-C	0	—	—
G-RW	21	8	5	C-C-C	0	—	—
G-RY	17	11	5	C-C-C	15	7	D_x-G
G-WR	14	33	11	A-B	15	8	E′-G
G-WW	20	15	15	C-C-C	0	—	—
G-YB	20	9	6	C-C-C	33	9	E′
G-YG	20	41	5	C′-C-C	12	7	E′-G
G-1365	20	12	10	C-C-C	47	4	E-G
TOTALS	34	970	309	—	457	143	—

[2] The number of component C's in each song varies as a function of motivational state.

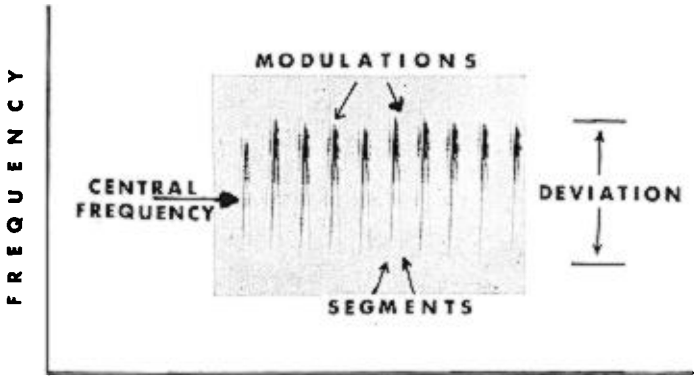

Figure 1. Sample spectrogram illustrating terminology and measurements used in this paper.

repertoire. The spectrograms and tapes used in these analyses are available for examination at the Academy of Natural Sciences of Philadelphia.

In our analyses we exclude variation in the length of individual components and in the length of the complete song. These are highly variable as a function of motivational state of the individual, as Ficken and Ficken (1967) have discussed and as quickly becomes evident during field study of these warblers. Detailed analysis of this complex aspect of variation in *Vermivora* songs is beyond the scope of the present study.

We use the terminology of Greenewalt (1968) to describe the acoustical properties of *Vermivora* songs, but we substitute the term "central frequency" for carrier frequency because of the difficulties in determining the latter due to asymmetry of the deviations from it. Central frequency is measured simply as the midpoint in the vertical distribution of energy shown on a spectrogram. "Amplitude" is used

TABLE 2
COMPONENTS OF BLUE-WINGED AND GOLDEN-WINGED WARBLER SONGS IN MICHIGAN

Components	Modulation rate (hz)	Phrase rate (No./sec.)	Frequency range (Khz) Total deviation	Frequency range (Khz) Limits of deviation from central frequency	Central frequency
A	210–260	—	2–2.5	4.5–7.5	5.8–6.5
B	40–50	—	3–6	3–9	5.5–7
C	90–180	—	2–3	4.5–9	6–8
D	120	10–13	4–4.5	4.5–9.5	6–7
E	80–90	8–9	2.5–3	4.5–8.5	5.8–6.5
F	50–65	—	2–3	3.5–8	5–6
G	40–65	—	2–3.5	3–7.5	4–5.8

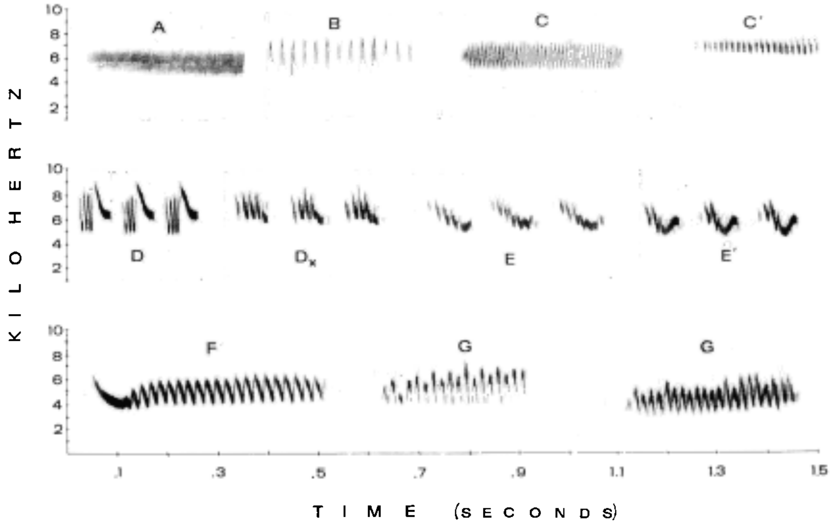

Figure 2. Song components of Michigan Blue-winged and Golden-winged Warblers. Component A, Blue-wing (B-RR) song type I; component B, Blue-wing (B-RR) song type I; component C, Golden-wing (G-GG) song type I; component C′, Golden-wing (G-RG) song type I; component D, Blue-wing (B-RR) song type II; component D_x, Golden-wing (G-RY) song type II; component E, Golden-wing (G-RG) song type II; component E′, Golden-wing (G-GR) song type II; component F, Blue-wing (B-RR) song type II; component G, extremes from songs of Golden-wing (G-RY).

only to refer to the intensity of energy (i.e. relative loudness) at a particular point in time. "Deviation about the central frequency" refers to the range of observed frequency changes during a modulation, i.e. the top and bottom points of vertical energy distribution on a spectrogram. A portion of a modulation is called a "segment." Discontinuous bursts of acoustical energy of defined structure are called "phrases." A sample spectrogram is illustrated in Figure 1.

Results

We recognize seven basic components in the songs of Michigan Blue-winged and Golden-winged Warblers (Figure 2, Table 2).

Component A.—This is a rapidly modulated signal centered on 6 kilohertz (Khz) with a total frequency deviation of 2 to 2.5 Khz and a modulation rate of 240 hertz (hz). Variation within individual male's song sequence usually consists of slight changes in modulation rate (up to 20 hz); several males (B-GY, B-RB, B-RG, R-XB) consistently had a modulation rate of 230 hz. Variation between males was evident in modulation rate, central frequency, and total deviation about the central frequency (Table 3). None of our Michigan males had a pronounced

TABLE 3
VARIATION IN TYPE I SONGS (A-B PATTERNS AND VARIANTS)

	Component A		Component B	
Male	Modulation rate (hz)	Limits of deviation from central frequency[1] (Khz)	Modulation rate (hz)	Limits of deviation from central frequency (Khz)
B-BB	220–240	5–7	45[2]	3–7.5
B-BW	230–250	5–7	40	4–9
B-GG	210–230	5–7	50	3–8.5
B-GR	230–240	5.5–7.5	45	5–8.5
B-GW	230–240	5.5–7.5	45[2]	5–9
B-GY	240	5–7	50[2]	3–8
B-RB	240	5–7	40	5–8.5
B-RG	240	5–7	45	4–8
B-RR	230–250	4.5–7	50[2]	3–9
B-RW[3]	220–230	5–7	—	—
B-WG	220–240	5–7	40	3–8
B-WW	220–240	5–7	45[2]	3–8
B-YG	230–250	5.5–7.5	40	4–8
B-YR	230–250	5–7	40	3–8
B-YW	240–260	5–7	40	4–8
R-XG	240	5–7	45–50[4]	4–8.5
Br-RR	240–260	5–7.5	40	3–8.5
Br-YY	230	5.5–7.5	45	4–8
L-RR	220–230	5–7	40	4.5–8
G-WR	210–230	5–7	40	5–8

[1] Central frequency as $\frac{\text{max-min}}{2}$.
[2] Skipped modulations.
[3] AAA pattern.
[4] Interrupted by D modulations.

downward slur in central frequency described by Lanyon and Gill (1964), although one male (B-YR) showed a slight tendency in this direction. Another male (B-GR, Figure 3) used a component A with an upward slur of about 0.5 kilohertz.

Component B.—Component B consists of a series of modulations, usually discontinuous and delivered at a rate of 40–50 per second. In some displays adjacent modulations are joined basally; this joint sometimes appears also as a (spurious) harmonic between adjacent apices. Energy tends to be concentrated on the upstroke of each modulation and at the apex, such that the descending segment is often lost on the spectrograms (see B-RB, Figure 3). Most modulations have a deviation of 4 Khz and some as much as 5.5 or 6 Khz; the central frequency of these modulations is usually at 6–7 Khz. The rate of delivery of B modulations is remarkably constant for any particular male warbler,

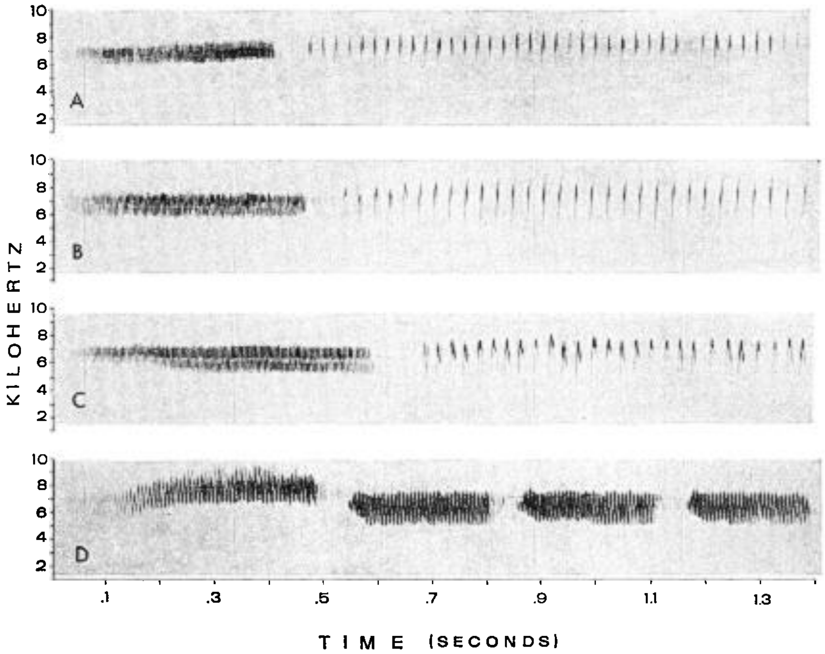

Figure 3. Type I songs of Michigan Blue-winged and Golden-winged Warblers. A, B-GR; B, B-RB; C, G-WR; D, G-RY.

and does not show the song-to-song variation evident in the rapidly modulated component A. The only variable delivery rate was evident in songs of R-XG, in which component B was interrupted by short bursts of continuous modulation (Figure 4). In addition to delivery rate, differences between the B components of different males are evident in the configuration of the modulations and in the occurrence of skipped modulations (Figure 4). The B modulations used by G-WR, the Golden-wing male that sang a Blue-wing song Type I, differ from other B modulations in being more widely spread with respect to time (Figure 3). This characteristic and the slight concentration of energy on the descending segment of the modulation tend toward the structure of component F.

Component C.—Component C is a continuously modulated tone that is distinguished by its intermediate modulation rate of 90–180 hz. The actual rate varies with position in the song as well as between individual males (Table 4). One male, G–1365, consistently rendered C's with rapid modulation rates of 160–180 hz. Energy is concentrated on the descending segment of each modulation; in some cases this is so pro-

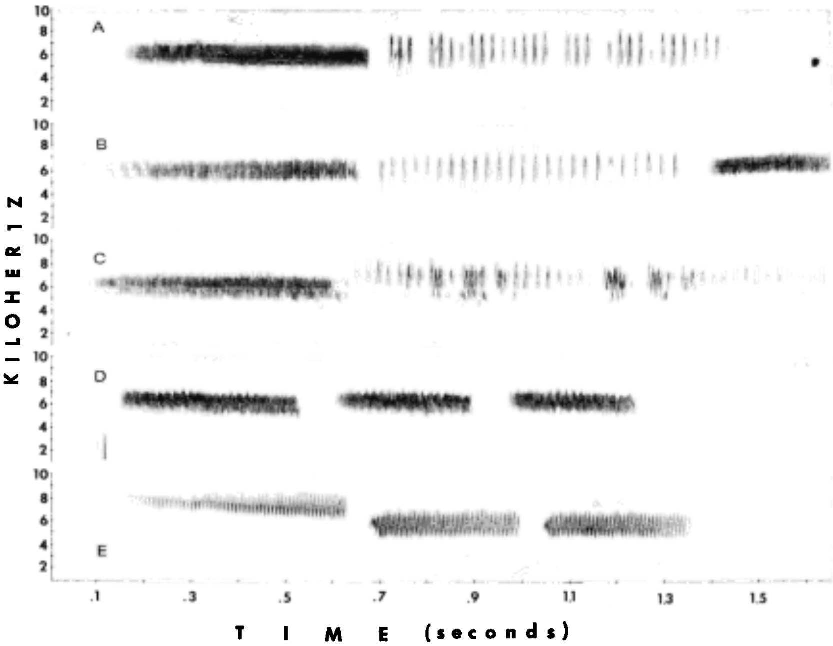

Figure 4. Type I songs of Michigan Blue-winged and Golden-winged Warblers. A, B-GY; B, B-WG; C, R-XG; D, B-RW; E, G-GG.

nounced that there is a tendency towards discontinuity of the modulations within the component (C′, Figure 1). The total frequency deviation of the modulation varies between males and also with respect to position in the song, but is normally 2–3 Khz (Table 4). Some males (e.g. G-RY, Figure 3) characteristically slurred an initial component C in their song type I.

Component D.—This component and the next (component E) are similar in that they consist of a series of discontinuous phrases that contain several (usually three) modulations and (in most cases) a terminal segment of great amplitude (intensity). In component D the phrase delivery rate is usually about 10 per second (occasionally as high as 13 per second), and the modulation rate within each phrase is 120 per second. The total frequency deviation of the modulations is 4 to 4.5 Khz centered on 6.5–7 Khz. The characteristic terminal segment of each phrase is an intense slur that descends continuously in central frequency from the highest frequency of the preceding modulation.

Variation within male repertoires consists primarily of changes in the number of modulations in each phrase, irregularities of energy dis-

TABLE 4
VARIATION IN TYPE I SONGS (C-C-C PATTERNS)

	Component C_1		Components C_{2-5}	
Male	Modulation rate (hz)	Limits of deviation from central frequency[1] (Khz)	Modulation rate (hz)	Limits of deviation from central frequency (Khz)
G-BB	140	7–9	150	5–7
G-GG	130–140	6–9	140–150	4.5–7
G-GR	130	6.5–8	140	5–7
G-GW	120	7–9	130–140	5–8
G-RB	130	7–9	140–150	5.5–8
G-RG	100[2]	8–9 to 6–8	120	5–8
G-RR	130–140	7.5–9.5	150	5.5–7.5
G-RW	130	6–9	130–140	7–9
G-RY	130	5.7 to 7–9	140–150	5–7.5
G-WW	110–120	7–9	130–140	5–7.5
G-YB	130–140	7–9	130–140	5–7.5
G-YG	90–100[2]	6.5–8.5	130	5–7.5
G-1365	160	7–9	170–180	5–7

[1] Central frequency equals $\frac{\text{max-min}}{2}$.

[2] Component C′.

tribution within the phrase, and in some individuals the occurrence of initial phrases that lack the differentiated terminal segment. Phrases representing intermediate stages of differentiation of the terminal segment appear at the beginnings of the component D's of some males (B-BW, B-RG, Br-RR and L-RR). They are the only phrases in the component D of one male Golden-wing (G-RY). A similar phrase, but with a more differentiated terminal segment, follows a rendition of component E in the song of another male (G-GR). Until more is known of the variation in these phrases we designate all except those of L-RR as component D_x. In the case of L-RR (Figure 5), there is a tendency towards the central frequency change of the modulations that is characteristic of component E; to stress their apparent intermediacy, a series of L-RR's phrases of this type are designated as component DE.

Variation between males consists of slight differences in phrase rates, in the total frequency deviation of the modulations, in the number of modulations, and in the vertical drop of the terminal segment's central frequency (Table 5). In most males the terminal segment is concentrated at frequencies equal to or higher than the central frequency of

TABLE 5
VARIATION IN TYPE II SONGS OF MICHIGAN BLUE-WINGED AND GOLDEN-WINGED WARBLERS

	Trill				Buzz	
Male	Phrase rate (No./sec)	Modulation rate (hz)	No. of modulations per phrase	Limits of deviation (Khz)	Modulation rate (hz)	Limits of deviation from central freq. (Khz)
B-BW	10	120	3	5–9	50–65	3.5–6.5
B-GB	11	120	3	4–8	55	4–7
B-GG	10	120	3	5–9.5	60	3.5–6.5
B-GR	11	120	3	5–9	55	4.5–8
B-GY	10	120	4	5–9	60	3.5–6.5
B-RG	10	120	4	4.5–8.5	60	4–7
B-RR	11.5	120	3	4.5–9	55	4–6
B-YR	10	120	3	—	50	4–7
Br-RR	10	120	3	4.5–8.5	50	4–6.5
Br-YY	13	90	2	4.5–8.5	50	4–7
L-RR	8[1], 11[2]	70[1], 120[2]	4[1], 3[2]	4.5–8.5	55	3.5–6.5
G-GR	8–9	90	2–3	4.5–7	40	4–6.5
G-GW	8	80	4	5–8	50	3–5
G-RG	8	80	4	5–8	—	—
G-RY	8	90	4	5–8	65	4–7.5
G-WR	8	80	4	4.5–8	50	3–5.5
G-YB	9	90	3	4.5–8	—	—
G-YG	9	90	4	4.5–7.5	50	3–5
G-1365	8	80	4–5	5–8	40	3–6

[1] DE components.
[2] D components.

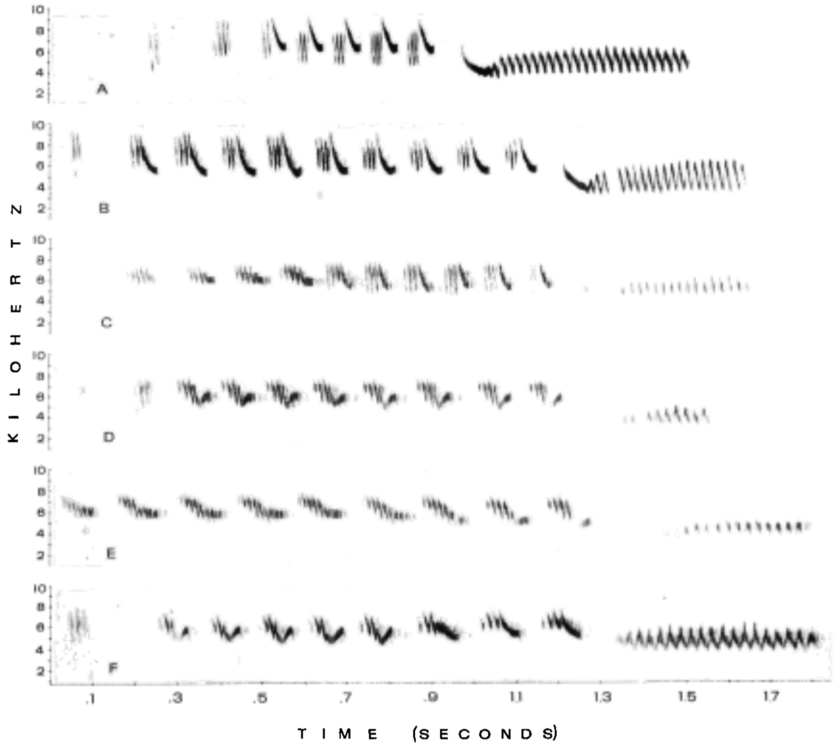

Figure 5. Type II songs of Michigan Blue-winged and Golden-winged Warblers. A, B-RR; B, B-GG; C, L-RR; D, G-YG; E, G-1365; F, G-GR.

the preceding modulation. In others (component D′) it extends to the lowest frequencies of the preceding modulation.

Component E.—This is apparently the Golden-wing homologue of component D, from which it differs in having a slower phrase rate (8 per second), a slower modulation rate (80–90 hz), a progressive decrease in the central frequency of each modulation, and a weakly differentiated terminal segment that originates from the lowest frequency of the preceding modulation (rather than the highest as in component D). With practice it can be distinguished by the human ear in the field as a slower and lower "trill."

Variation between males consists of differences in modulation rate, total frequency deviation of the modulations, and in the configuration (inflection) of the terminal segment. An inflected terminal segment distinguishes E′ from E (Figure 2). Variation within males consists of changes in the duration of the phrase, irregularities in the distribution of energy within the phrase, and in the differentiation of the terminal segment (Table 1 and Table 5).

Component F.—Component F is a modulated signal that is preceded by an initial segment of great amplitude and descending central frequency. It is distinguished by the combination of slow modulation rate (40–65 per second), limited total frequency deviation (2–3 Khz), the concentration of energy on the descending segment of each modulation, and the continuity or close approximation thereto of the adjacent modulations. In energy distribution this component resembles the more rapidly modulated component C, which shows a tendency (C′) towards concentration of energy on the descending segment of the modulation and discontinuity of the modulations. In certain males the energy in the descending segment of the modulations is barely resolved into rapid submodulations. This is exaggerated in the songs of G-GR, whose component F modulations consist entirely of resolvable rapid submodulations (Figure 5).

Component G.—This component can be distinguished from component F by the absence of the initial high intensity, slurred segment. No other consistent differences between component G and component F are apparent in our limited samples, except perhaps a greater tendency towards discontinuity of the modulations in component G.

INTERRELATIONSHIPS OF COMPONENTS

All seven components we have distinguished in the songs of Michigan *Vermivora* are primarily modulated signals. The rate of modulation is a distinguishing feature of each component and varies from a minimum of 40 hz (components B and F) to a maximum of 240 hz (component A). The deviation of modulations varies from two Khz (component A and C) to 4–5 Khz (component B, D). Most components consist of a series of modulations that are continuous or so closely juxtaposed as to appear nearly continuous, but component B is typically discontinuous, while components C′ and F tend towards discontinuity. The distribution of energy in the modulations may be uniform (components A, C), concentrated on the ascending segment (component B), or concentrated on the descending segment (C′ D, E, F, and G). Finally three components (D, E, and F) have a high intensity segment associated with the modulated tones.

Such differences in energy distribution and overt continuity probably reflect the interactions (phase relationships and relative importance) of amplitude versus frequency modulations of the acoustical signal (Greenewalt, 1968). For example component C seems to be primarily a frequency modulated signal, whereas the energy asymmetry and discontinuity of component C′ are probably the effect of superimposed amplitude modulations.

With few exceptions the components of songs recorded in Michigan are similar to those described by Lanyon and Gill (1964) for Blue-winged Warbler songs recorded in Long Island. Components A and B are the same in both places. Component D in Michigan is like that of Long Island songs in terminating with a high intensity segment but differs in including several continuous modulations of component C rather than a single modulation. The component C of Lanyon and Gill (1964) is not strictly comparable to any of our components. It appears in three contexts in the songs of Long Island Blue-wings: as short bursts in the terminal buzz of song type I, as short bursts in the "trill" of song type II, and as an extended component at the end ("buzz") of song type II. The first of these has a modulation rate of 100–120 hz and a total frequency deviation of 2–3 Khz. It resembles the longer, more rapidly modulated component C (usually 130–140 hz) that characterizes the song type I of Michigan Golden-wings. In the second situation it tends to involve slightly slower modulation rates (80–90 hz). In the last situation it is longer, has a modulation rate averaging 90–100 hz, and often has a greater total frequency deviation (3–4 Khz); it tends to be quite distinct from the component F of Michigan *Vermivora*, which is a more slowly modulated component of narrower frequency deviation. Rather it seems that the component C of Long Island Blue-wings are closest to the initial segment of the phrases of component D of Michigan Blue-wings. The component C that characterizes the song type I of Michigan Golden-wings seems distinct enough to prevent serious homological comparisons at the present time.

Song Type I

The familiar song of territorial male Blue-winged and Golden-winged Warblers has been referred to as territorial song, accented song, or song type I (Lanyon and Gill, 1964; Ficken and Ficken, 1967). The typical Blue-winged Warbler song type I consists of components A and B in sequence (Lanyon and Gill, 1964; Figures 3 and 4, this paper). Fifteen males in our study areas, including one Golden-winged Warbler (G-WR), one Brewster's Warbler (Br-YY) and one Lawrence's Warbler (L-RR), sang such a song type I (Table 1). Variation within and between these males consists of differences described previously for the components. Such song characteristics as modulation rate, total frequency deviation, and configuration of spectrograph patterns tend to be more stable within individual repertoires than between them. Component B of the Golden-winged Warbler (G-WR) was slightly aberrant and tended towards component F in structure.

Five males sang variations of the A-B song type I. Two Blue-winged Warblers (B-WG and B-YG) and a Brewster's (Br-RR) followed component B with a brief burst of component A. Only B-WG consistently sang this A-B-A pattern. Br-RR sang this variation only after strongly responding in playback experiments; the A-B-A pattern occurred briefly as muted song before resumption of normal (A-B) singing. B-YG sang this pattern once in a sequence of 18 songs. One male (R-XG) sang an apparently unique variation interrupting component B with bursts of a continuously modulated phrase like that found in component D. A last variation was sung by B-RW whose song consisted of 3 or 4 component A's of Blue-wing song type I in succession, resembling to the human ear a Golden-wing song type I, but of aberrant tonality and without the drop in frequency after the first component.

The typical song type I of Golden-winged Warblers in southern Michigan consists of a sequence of three to five renditions of component C, in which the first rendition averages 1.5–2 Khz higher in central frequency than the remaining renditions. Thirteen male *Vermivora,* all Golden-wings, used such a song type I. The number of renditions of component C in the song varies as a function of motivational state of the singing male; shortened songs are characteristic of disturbed and perhaps of mated males (Ficken and Ficken, 1967). In addition to central frequency, the first rendition of component C (C_1) in the sequence tends to differ from subsequent renditions in having a slightly slower modulation rate, and more limited total frequency deviation (Table 4). The C_1 renditions of two males (G-YG and G-RG) were of the modified C′ form, and of two other males (G-RB and G-RY) were noticeably slurred in central frequency.

In addition to our tape-recorded sample, we noted the song type I patterns of 44 different males that were collected, banded, or simply observed during our studies. Two patterns of song type I, A-B and C-C-C, clearly predominate in this total Michigan sample and correspond to the two sympatric species, the Blue-winged and Golden-winged Warblers respectively (Table 6). Of 49 Blue-winged Warblers heard in Michigan, 3 sang conspicuously aberrant patterns; 2 of these were A-B-A pattern and 1 the A-A-A pattern. Of 21 Golden-wings, only one sang an atypical song, a Blue-wing song type I (A-B). If one considers the A-A-A pattern a case of song interchange, then a maximum of 3 percent (2/70) of our Blue-winged and Golden-winged Warblers sang the song characteristic of the other species. Four Brewster's Warblers sang the typical song type I of one or the other species, and one

TABLE 6

TYPE I SONG PATTERNS OF MICHIGAN *Vermivora*

	Component sequence			
Male phenotype	A-B[1]	A-B-A	A-A-A	C-C-C
Blue-wings	46 (34)[2]	2	1	0
Brewster's	2 (1)	1	0	2 (2)
Lawrence's	1	0	0	0
Golden-wings	1	0	0	20 (7)
TOTALS	50	3	1	22 (grand total 76)

[1] A-BDB cannot be distinguished in field from A-B.

[2] Numbers in parentheses represent those males whose songs were not recorded and analyzed spectrographically.

sometimes sang the Blue-wing pattern A-B-A. The one Lawrence's Warbler sang the typical Blue-wing A-B pattern. These latter observations agree with previous observations of the songs of conspicuous hybrid phenotypes (Ficken and Ficken, 1967, 1968).

SONG TYPE II

The less familiar second song of the Blue-winged and Golden-winged Warblers has been referred to as the nesting song, trill buzz, unaccented song, and song type II (Lanyon and Gill, 1964; Ficken and Ficken, 1967). In Michigan the typical Blue-wing song type II consists of a series of D components (the "trill") followed by an extended F component (the "buzz") (Table 5). This song is usually introduced by a soft chip. Variation in the structure of the phrases within component D characterizes some males but not others. Three of eight male Blue-wings sang the D′ variant. The two Brewster's Warblers we recorded sang Blue-wing song type II, as did the one Lawrence's Warbler, except that the initial phrases of the Lawrence's "trill" were similar to component E. One Golden-wing male (G-RY) substituted component D phrases (actually D_x) for component E in his "trill," while another (G-GR) mixed both E and D_x components in his "trill."

Golden-wing song type II is only slightly different from Blue-wing song type II. The "trill" is component E rather than component D and the "buzz" is composed of component G rather than component F. Type II songs of two Golden-wings (G-RG and G-YB) consisted only of the "trill," component E; this may have been motivational (Ficken and Ficken, 1967). Except for the problematic D_x components, no Blue-wing male sang Golden-wing song type II or incorporated its components.

Thus two patterns of song type II, D-F and E-G, predominate in our Michigan samples and correspond to the two species of warblers. When distinguished in this manner by components F and G, we found no birds singing the song type II of the other species. Two Golden-wings, three Blue-wings, and a Brewster's included aberrant (D_x) components in their trill, but more information is needed to establish whether these are of hybrid origin. Intermediate components are distinguishable in the "trill" of the Lawrence's Warbler.

DISCUSSION

Studies on the variation in songs require spectrographic analysis of tape-recorded vocalizations of known individuals. Our results can be compared only with those of Lanyon and Gill's (1964) analyses of song variation in Long Island Blue-wings. In both Michigan and Long Island an individual male's repertoire is normally limited to one pattern each of song type I and song type II. In both populations of Blue-wings there are four patterns of song type I. On Long Island two patterns (A-B, A-C-B) are common, whereas in Michigan only one pattern (A-B) is common. Two Long Island Blue-wing patterns (A-C-B and A-C) seem to be absent in the Michigan populations, and two Michigan patterns (A-B-A and A-BDB) seem to be absent in Long Island. The aberrant A-A-A pattern is present in both populations.

The predominant D-F pattern of Michigan Blue-wing song type II is similar to the predominant C-D-A-C Long Island pattern in that most Michigan songs begin with one to several Long Island C components that grade into Michigan D components; our component D includes both of Lanyon and Gill's components C and D. Thus, rather than consisting of several distinct components, the "trill" of Michigan Blue-wings tends to be more homogeneous than on Long Island. While similar to the Long Island "buzz," the Michigan "buzz" has different modulation characteristics and is preceded by a high intensity slur rather than a brief burst of component A. A similar slur is evident in the type II song of BG-XY from Long Island (Lanyon and Gill, 1964, Figure 8). The differences in the components of type II songs in the two Blue-wing populations are more striking than is evident in a comparison of the components of song type I, indicating greater geographic flexibility (tendency towards dialect formation?) in the structure of song type II. We recorded no major pattern variants in our sample of type II songs comparable to the two Lanyon and Gill recorded.

The only published spectrogram of a Golden-wing song type II from a non-Michigan population is from Rockland County, New York (Gill and Lanyon, 1964, Figure 1). The "trill" of this song begins with phrases of component D like those used by Long Island Blue-wings, and ends with phrases of component D like those used by Michigan Blue-wings. The terminal "buzz" is a Golden-wing component G. Without additional information on song variation in Rockland County Golden-wings, we cannot be sure whether this type II song is representative or aberrant. If it is typical, it points to geographic variation in Golden-wing type II songs as well as Blue-wing type II songs, and perhaps to geographic interspecific exchange of song components.

Our data show some correlation between degree of introgression in plumage and aberration in songs (Table 1), in that those birds that sing either song type with some aberration tend to show some plumage introgression, but introgressed individuals don't necessarily sing aberrant songs. Our limited sample of recordings of both song types from individuals that showed some aberrancy in one song type indicates that both songs are not necessarily aberrant in the same individual.

Birds with two type I songs.—Some confusion exists in the literature regarding the singing of the song type I of both species by one *Vermivora.* There are numerous reports of a *Vermivora* male singing the song type I of the other species, such as our G-WR (e.g. Beebe, 1904; Eisenmann, 1946; Short, 1962; Ficken and Ficken, 1967). Beebe and Eisenmann, in particular, have been misquoted as having observed one bird sing both species' songs. In fact, Beebe only drew attention to the similarity of the first "syllable" of a Lawrence's Warbler song to the typical "syllable" of Golden-winged Warbler songs, and Eisenmann (1946) explicitly stated that he never observed a given individual singing more than one species' song.

The only concrete evidence of bivalent repertoires we are aware of are the observations of Bildersee (1904) who reports that a male Lawrence's Warbler sang both species' type I songs as well as a song type II, and the observations of Short (1962, 1963). Short (pers. comm.) is certain that at least one male Blue-wing sang both Blue-winged and Golden-winged songs interchangeably while under constant observation. Carter (1944) discusses a Lawrence's Warbler that "was heard to sing, besides the typical Blue-wing song, a more prolonged song approaching that of a Golden-winged Warbler." Unfortunately he does not describe the prolonged song in more detail. Inasmuch as the two recent intensive studies of *Vermivora* singing behavior in mixed colonies (e.g. Ficken and Ficken, 1967; present study) produced no similar observations, we must conclude that this is a rare phenomenon indeed. Further observations of bivalent repertoires will be of great interest, but they must be carefully documented. In particular, field observers working with unmarked birds or visiting an area only briefly must be cautioned against the possibility of error that can easily result from territorial overlap of sympatric Blue-wings and Golden-wings, as well as from the territorial relationships of adjacent males of the same species (Murray and Gill, MS).

Finally a point must be emphasized with regard to the relation between song variation and the size of an individual male's repertoire. Each male warbler in the Michigan and the Long Island populations had a repertoire that included one type I song pattern and one type II song pattern. Variation in the patterns designated is primarily an inter-individual phenomenon, but motivational song shortening can affect the pattern when a distinguishing component is dropped. This especially affects the A-B-A Blue-wing pattern, which is easily transformed into A-B. Dropping a terminal component of such a song pattern, as Ficken and Ficken (1967) described, is the same as reducing the number of component C's in a Golden-wing song. This in no way contradicts the earlier statement regarding the size of the individual repertoire, which is of interest for purposes of interspecific comparisons of song variability. The opposite phenomenon of motivational song lengthening, e.g. A-B to A-B-A, as we seem to have recorded for two males (Br-RR, B-YG) needs further study.

Our main conclusion is that the songs of Blue-winged Warblers in Michigan, which are sympatric with Golden-winged Warblers, are less variable (fewer predominant patterns) than are the songs of Blue-winged Warblers on Long Island, where the Golden-winged Warbler does not breed. The difference is most pronounced in type I songs. The small samples of song type II that have been analyzed tend in the same direction and, in addition, are structurally more different between the two populations than are type I songs.

Secondly there is less breakdown of species-specific vocal characters in this hybridizing population than there is of plumage color characteristics (Short, 1963; Gill and Murray, MS.). Some introgressed individuals have slightly aberrant songs, but the correlation is weak. The frequency of interspecific song interchange is less than 3 percent.

Third the lack of major variations within individual repertoires of modulation rates as well as of patterns of component arrangements suggest that differences between individuals in these two parameters of song variation function primarily in interindividual and interspecific recognition. Variation in modulation rates is the basis of much of the observed song variability in this complex and as such supports recent discussions about the importance of tonal quality in bird songs (Greenewalt, 1968; Marler, 1969). Motivational information is presumably contained in such features of song variability as song and component length, song type (I vs. II), context, and rate of song delivery (Ficken and Ficken, 1967; Falls, 1969).

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