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SONG CHARACTERISTICS OF THE YELLOW WARBLER

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The Yellow Warbler (*Dendroica petechia*) is one of the most widespread species of Parulidae; its breeding range extends from north-central Alaska to central Georgia, and from Newfoundland to northern Baja California (Bent 1953). In this paper we describe the general organization of Yellow Warbler song, variation in song form within a single individual and among different individuals, and some geographic variation in song characteristics.

METHODS

Bankwitz recorded the songs of 45 male Yellow Warblers in 2 widely separated areas of southern Michigan. The first of these was in Dearborn, a suburb of Detroit, in southeastern Michigan. A second, much larger area, included 6 different recording sites in Kalamazoo County, ca. 170 km west of Dearborn.

Recording techniques.—From 21 May through 2 June 1974, and on 28 May 1975, Bankwitz recorded with a Uher 4000 Report S tape recorder, an Electrovoice microphone, and a 50-cm aluminum parabolic reflector. From 19 June through 12 July 1974, and 6–10 July 1975, he used a Uher 4000 Report 1 C tape recorder. In 1974 and on 28 May 1975, recordings were made at 19 cm per sec; the remaining 1975 recordings were made at 9.5 cm per sec.

To facilitate accurate and complete notes, the date, time, weather conditions, location, and number of the male were spoken into the microphone before recording each individual. At least 20 songs of each territorial male were recorded whenever possible. Some individuals were recorded more than once during the day, between 04:00 and 21:00 EST, and on different days. One male was observed all day.

Because rain and strong winds tended to reduce the amount of singing, and because wind also distorted the recordings, recording was avoided during these conditions. Usually, undisturbed, territorial males were recorded. In a few instances Bankwitz recorded territorial disputes between males. He also recorded the response of males to the playback of tape recordings of their own or another male's song.

From a sample of 45 individuals, Bankwitz recorded 1328 songs of which 745 were analyzed using a Kay Electric Company Sona-Graph (model 661B) at the high shape and wide band settings. All song patterns from short song series were analyzed. When long sequences were composed of the same song pattern, as detected by ear, only a few songs from the beginning, middle, and end of the series were used. If the sequence contained different song patterns, each pattern distinguishable by ear was analyzed spectrographically. Song length and frequency range were measured on the sound spectrograms with the aid of a grid scratched on plexiglass. Song figures found in songs from southern Michigan were compared with figures from Yellow Warbler songs recorded in other parts of the United States and published on commercial phonograph records.

RESULTS

Analysis of song figures.—The smallest unit of the Yellow Warbler's song is the song figure. Shiovitz (1975) defines a song figure as "a sound

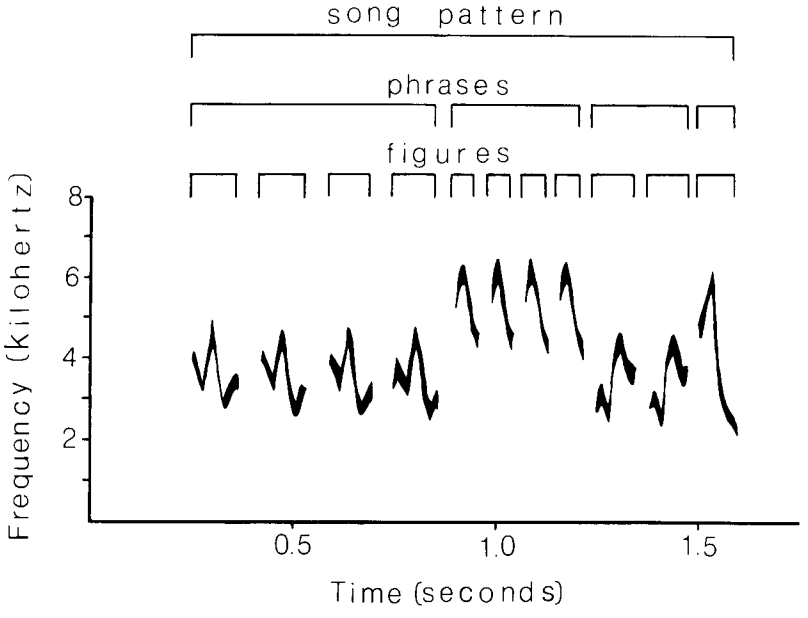

FIG. 1. Terminology applied to a typical Yellow Warbler song.

which produces a single, complete, and distinct impression uninterrupted by silences greater than two centiseconds." A song phrase is 1 or a series of identical figures comprising a group. Borror (1967) defined a "phrase" as a group of "notes" (=figures) repeated 1 or more times. A particular sequence of song phrases is a song pattern. All songs having the same arrangement and kinds of figures are said to have the same pattern. Fig. 1 illustrates the application of these terms to a spectrographic representation of a typical Yellow Warbler song.

Each different figure found in the songs was traced, transferred to drawing paper, and inked. These figures were then grouped according to frequency characteristics and similarity of shape to form a catalog (Fig. 2). From the 1974 and 1975 recordings we obtained 40 distinct figures.

Some figures occur only within 1 song pattern, while others are found in several. Similar figures are grouped in a song phrase within a given pattern. They vary slightly within a single song, and more in similar patterns sung by different individuals. However, the figures are sufficiently stable in form for us to designate them as the same. Some rather different figures, although clearly related, are connected within the population by a series of intermediates that grade almost imperceptibly from one extreme form to another. Fig. 3 shows variation in the form of figures sung by a

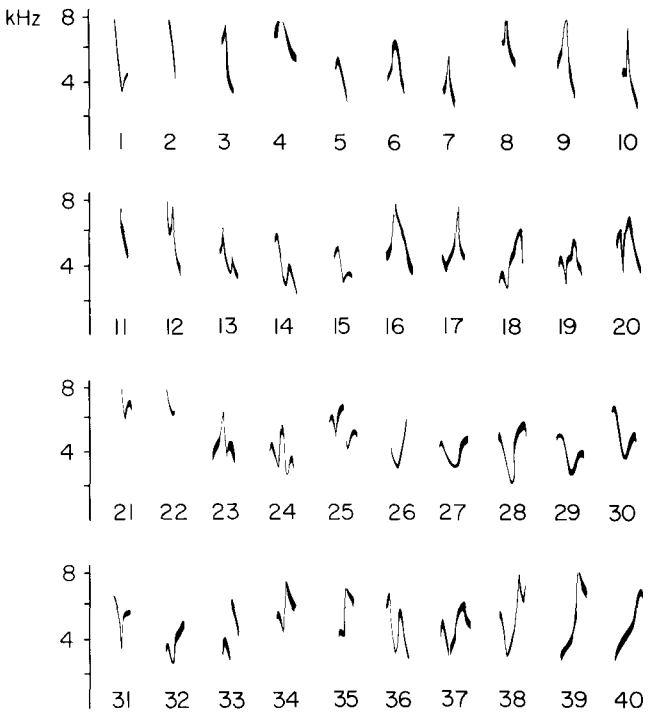

FIG. 2. Figure catalog of Yellow Warbler songs.

single bird, and by different individuals in the population. Figures that were similar, but showed consistently different form and no intermediates, were given different catalog numbers.

In Fig. 4 we have plotted the cumulative number of figures sung by a single male Yellow Warbler during a continuous series of 100 songs. The levelling off at 16 figures rather early suggests that this number represents the complete repertoire of this individual. The total figure repertoire recorded for individual males ranged from 2–27, with a mean of 8.82 ($\pm$6.10, N = 45). Almost certainly those with very small repertoires were not recorded long enough to sample all their song patterns and figures. The actual average for all individuals is therefore very likely larger than 8.82.

A cumulative plot of new song figures in all the Michigan populations with increasing numbers of consecutive individuals sampled is also shown in Fig. 4. The asymptote seems to be approached at 40 figures and 42 birds.

Fig. 5 illustrates the sharing of the various song figures among the 45 male Yellow Warblers recorded in 1974 and 1975. Some figures were

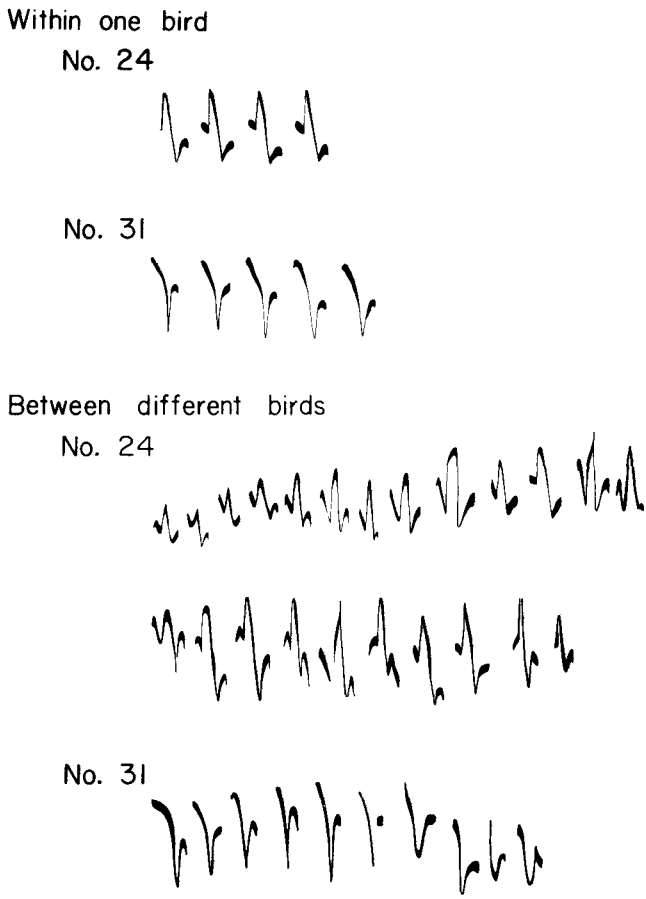

FIG. 3. Variation within song figures.

widely distributed throughout the population, but a few were sung by only 1 individual.

There was a high degree of continuity in the use of the same figures from year to year. Thirty-nine figures were recorded in 1974, while 33 were found in 1975. Of the 745 songs analyzed during the 2 years, about 60% were recorded in 1974.

Analysis of song types and song patterns.—Previous studies (Ficken and Ficken 1962, 1965, 1970; Morse 1966) have shown that the Yellow Warbler, along with some other wood warblers, has 2 principal song types. One ends with a prominent, ascending figure, e.g., 39 and 40 in Fig. 2, (Accented Ending or AE Song, Fig. 6A), while the other lacks an emphasized

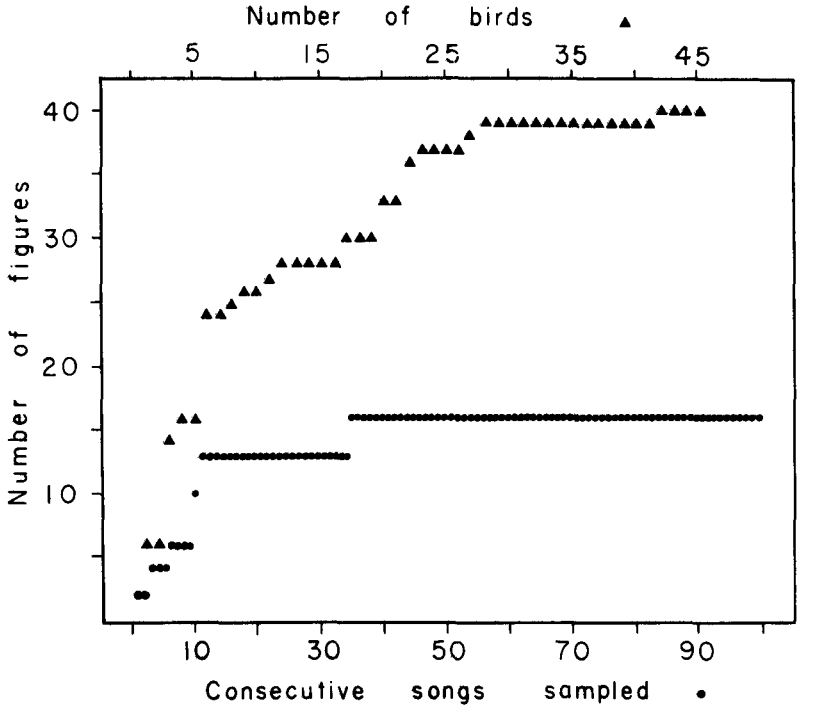

FIG. 4. Cumulative plots of the number of song figures with increase in number of birds sampled, and of the number of song figures sung during a consecutive series of songs of one individual.

ending (Unaccented Ending or UE Song, Fig. 6C,D). Morse (1966) described an additional song type sung by the Yellow Warbler, the Intermediate Ending Song. It is sung when birds change from one song type to another, and appears intermediate in motivation. Morse (1966) stated that "This song type usually has a weak upslurred accented ending, but is of an overall lackluster quality when compared to the Accented Ending Song." We did not find any songs clearly fitting this description in our recorded samples. Ficken and Ficken (1962, 1965, 1970) and Morse (1966) refer to "muted songs," either Accented Ending or Unaccented Ending song types sung at low volume in moments of extreme aggression. We found no clear examples of this in birds we observed.

In 30 Yellow Warbler songs we found a variation of the AE Song type, the Incomplete Accented Ending (IAE) Song. The IAE Song shown in Fig. 6B, had the same arrangement and kind of figures as one of the AE Songs, Fig. 6A, but lacked the ascending terminal figure. We assume that the

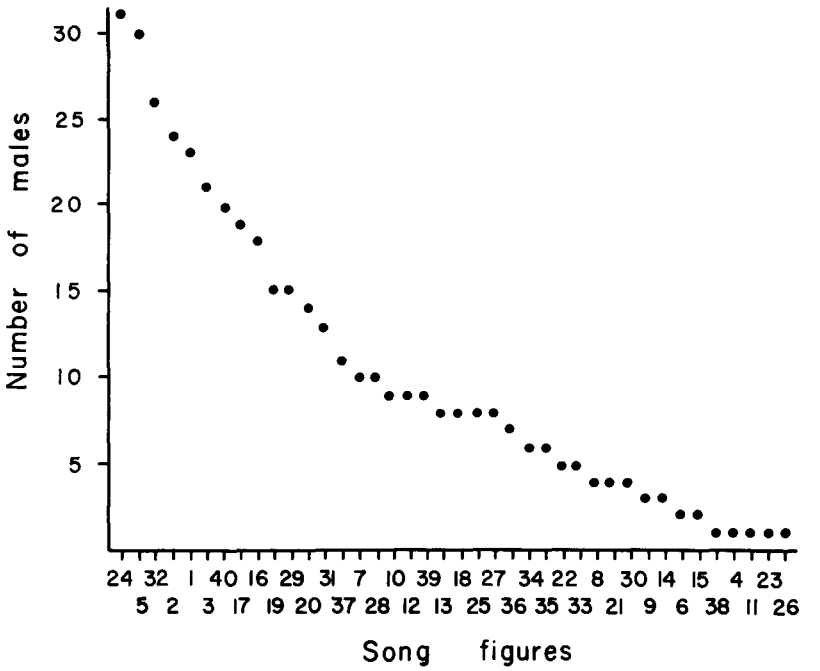

FIG. 5. The sharing of the various song figures by 45 males in 1974 and 1975.

IAE Songs represent the same song pattern as the AE, but perhaps because of lower motivation the full pattern is not sung. Singing of incomplete patterns is common, e.g., in the Indigo Bunting (*Passerina cyanea*) (Thompson 1972). The 8 males which sang these sang a similar AE Song at the same locality, general time, and date. The IAE Songs were generally interspersed among similar AE Songs, but in some cases UE Songs, of different figure composition, were also sung in the same bout. The contexts in which these similar IAE and AE songs were sung were not noted.

We distinguished 60 Unaccented Ending Song patterns and 4 AE patterns. Each of these 64 patterns had at least 1 song phrase composed of a different kind of song figure, or had the phrases arranged in a different sequence.

Song variation.—The songs of an individual differ in the arrangement, kind, and number of figures within the song. Changing the number of figures results in variation in (1) the presence or absence of certain phrases, (2) phrase length, and (3) the song ending. An individual may also alter the relative loudness of particular figures, phrases, or song patterns.

A given male sings a variety of song patterns. Male 38, recorded for 223

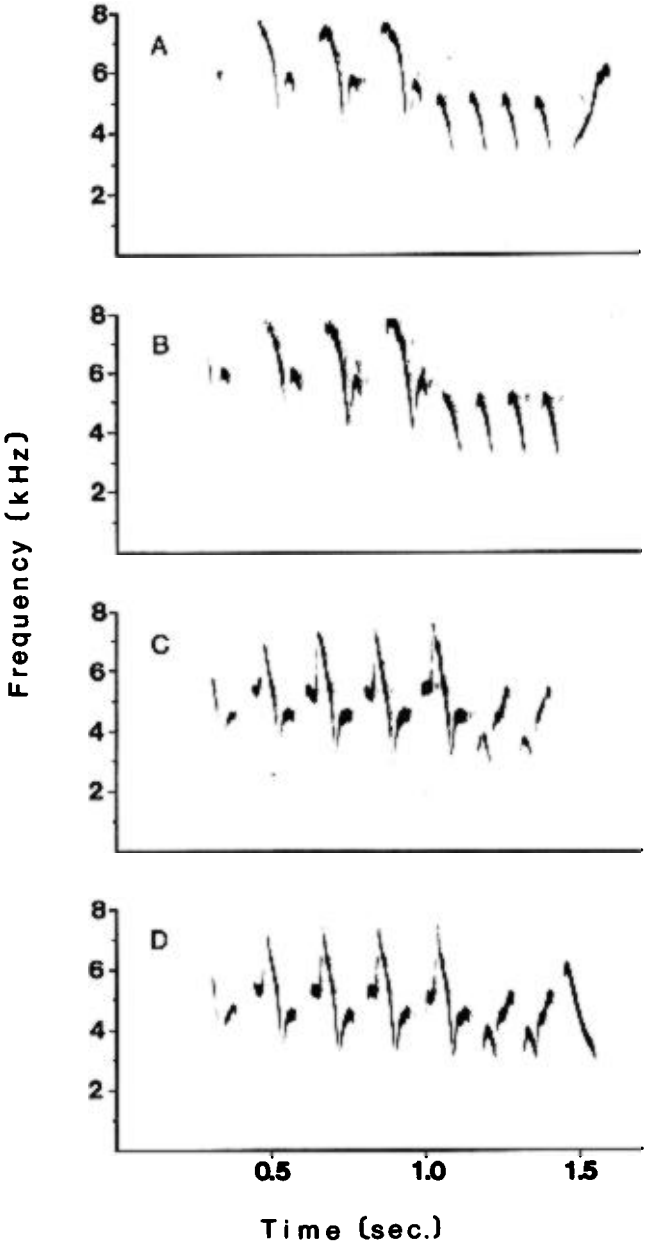

FIG. 6. Sound spectrograms of 4 typical Yellow Warbler songs.

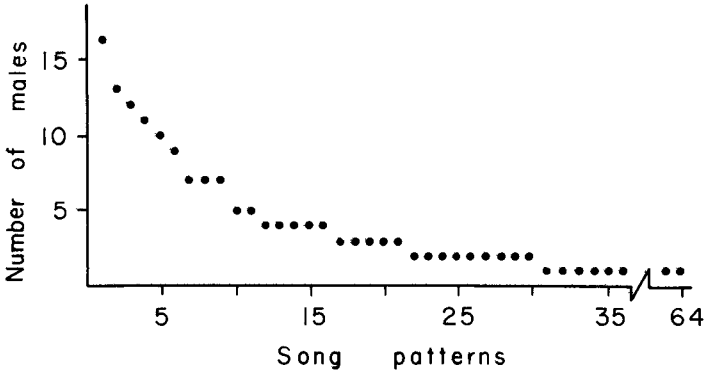

FIG. 7. The sharing of song patterns by 45 males in 1974 and 1975.

min during 4 days in July 1975 at Fort Custer, Kalamazoo Co., sang 17 different song patterns composed of 27 different figures. The number of different song patterns sung by an individual ranged from 1–16 (mean = 4.27 ± 3.36, N = 45).

There was extensive sharing of song patterns among different individuals (Fig. 7). The number of individuals singing a single pattern in the 2 years combined ranged from 1–17, with averages of 7.75 for AE and 2.65 for UAE patterns (overall mean = 2.96 ± 3.38, N = 64). Several song figures were used in different song patterns. Some figures were interchanged between AE and UAE patterns. The mean number of song patterns containing a given figure is 4.98 ± 4.46 (N = 40, range = 1–18).

An individual singing a large number of songs of a given pattern varied within that pattern. Male 17, recorded on 22 June 1974, at Coldbrook Park, Kalamazoo Co., sang a particular UE Song pattern 5 times within 5 min. During this time he sang 2 variations (see Fig. 6C,D). Song C is like song D, but lacks the descending terminal figure found in D. An individual may also vary the number of song figures per phrase. Male 3, recorded in Dearborn, sang a particular AE Song pattern 71 times on 2 June 1974. This pattern is composed of introductory, middle, and terminal phrases. The introductory phrase generally contained 5 repeated figures, but the number ranged from 3–6. Likewise, the middle phrase was usually composed of 4 repeated figures, but the number ranged from 1–4. This AE Song pattern has 1 ascending figure in the terminal phrase. The same bird altered the pattern further by omitting both the middle and terminal phrases, or just the terminal phrase.

Repetition index.—A measure of figure repetition in songs is given by the repetition index, calculated by dividing the total number of figures by

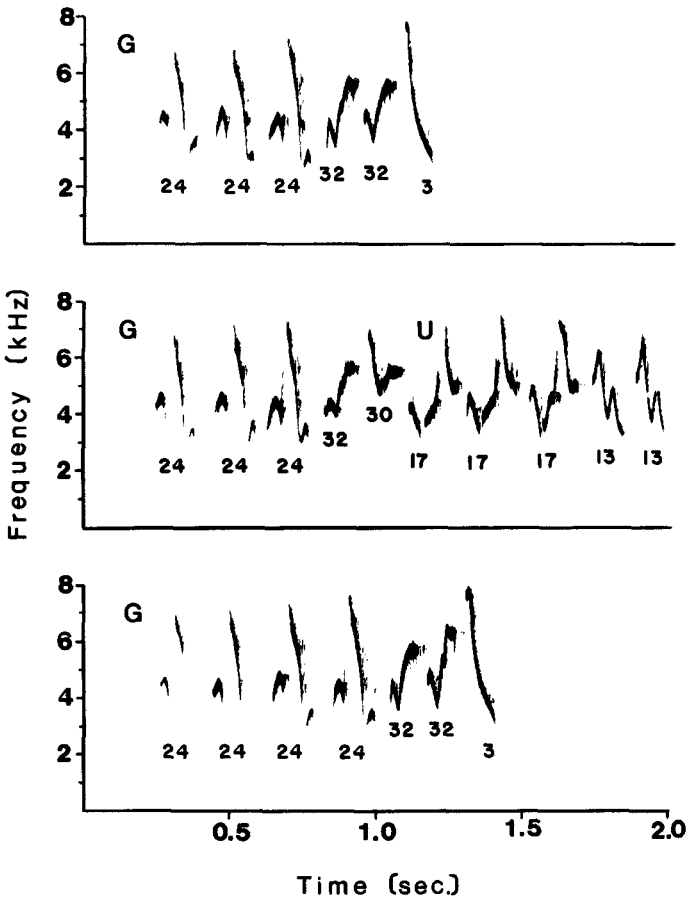

FIG. 8. Run-on song G-U with song G sung immediately before and after.

the number of kinds of figures. Repetition indices for the Dearborn population are higher than those for the XY Marsh population, in Kalamazoo County. This may be because, as already mentioned, many of the songs sung in the beginning of the breeding season when the Dearborn males were recorded are AE Songs, while many of those sung toward the end of the breeding season at XY Marsh are UE Songs. The mean repetition index for all AE Songs is 2.63, while that of UE Songs is 2.39. For both years and both types of songs together the mean number of figures per song was 6.99 ± 1.71 (N = 204), the mean number of kinds of figures per song 2.88 ± 0.92 (N = 204), and the average repetition index 2.42.

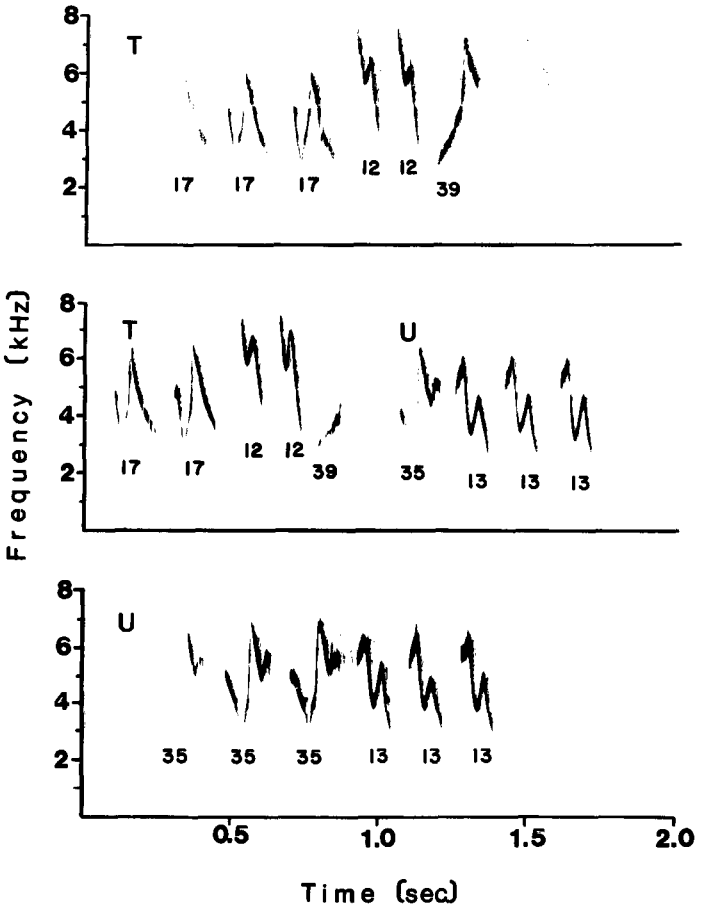

FIG. 9. Run-on song T-U with song T sung immediately before and song U after.

Run-on songs.—Six males from 4 localities sang 16 run-on songs. Thompson (1972) defined a run-on song as "a series of complete song patterns sung without break." Usually, if a bird was singing several different song patterns in a bout it simply connected any 2 to form a run-on song. However, twice new patterns not found elsewhere in the bout were used in the run-on song. Fourteen of the 16 run-on songs in our sample were composed of Unaccented Ending Songs, with no 2 UE Song patterns grouped together more than 3 times. In every case where 2 patterns were run together the second was a UE Song.

Figs. 8 and 9 show 2 sequences of run-on songs. In Fig. 8 the UE pattern

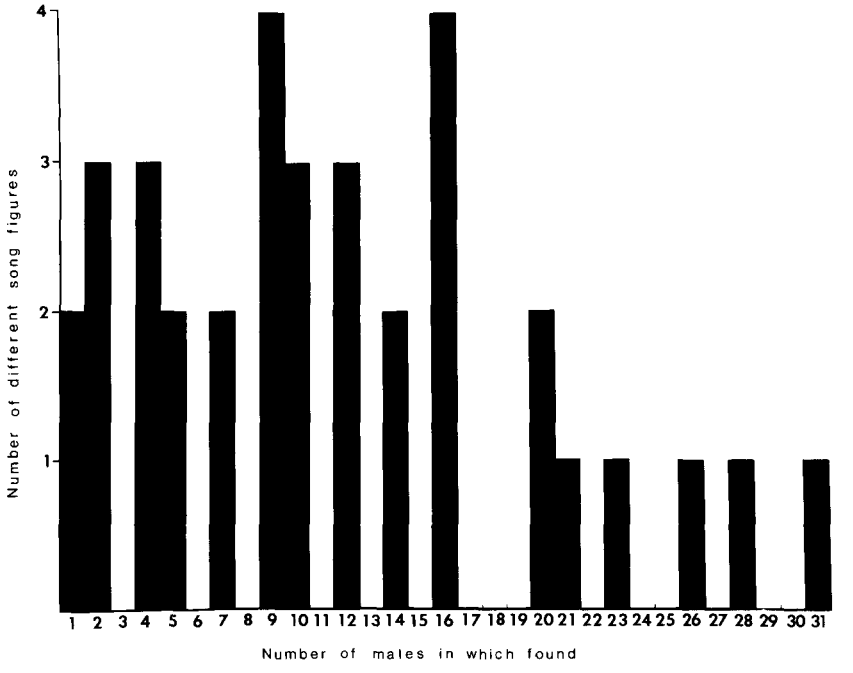

FIG. 10. Cumulative plot of the number of song patterns with increase in the number of songs sung.

G both precedes and follows the run-on song G-U. The spacing between song figures 30 and 17 that connect the 2 different UE patterns in the run-on song is no greater than the spacing between consecutive figures in either of the normal patterns. Song figure 3 found in song pattern G is omitted in the run-on song, and replaced by song figure 30. Although 30 does not appear in the other songs of this male, it appears as a terminal figure in the regular songs of 16 other individuals, and so cannot be considered peculiar to run-on songs. In contrast, the spacing between song patterns that make up AE-UE run-on songs is greater than the spacing between consecutive figures in the normal patterns. Fig. 9 shows a run-on song composed of the AE Song pattern T and the UE Song pattern U. The space between song figures 39 and 35 that connect song patterns T and U is 0.16 sec in comparison with the 0.04 sec space between song figures 30 and 17 in the run-on song of Fig. 8. Song figure 39, a terminal, ascending figure in song pattern T, is in the run-on song pattern T-U. Song figure 35 is repeated 3 times in the usual song pattern U, but appears only once in the run-on song pattern T-U.

It is possible that run-on songs are a form of individual variation associated with territorial defense. Thompson (1972) suggests than run-on songs are sung by the Indigo Bunting if a conspecific male intruder does not leave at once the resident's territory when challenged. The geographic distribution of Yellow Warbler run-on songs tends to support this hypothesis. Three of them were sung at Coldbrook Park, 4 at 44th Street, 2 at Fort Custer, and 7 at XY Marsh, all in Kalamazoo County. At each of these localities Yellow Warbler territories were small and situated in wet areas covered with heavy underbrush. Due to close proximity there would likely have been a higher incidence of intrusions, resulting in an increased number of run-on songs associated with unusually high aggressive motivation.

Geographic distribution and frequency of song-patterns.—The males inhabiting mideastern and northeastern Kalamazoo County sang approximately 5 times as many different song patterns per min as did the males recorded in Dearborn, and 3 times as many different patterns per min as did the males recorded at XY Marsh. There are 2 likely reasons why this was so. First, the Dearborn males were recorded early in the breeding season when they were singing primarily AE Song patterns. Since there are only 4 different AE Song patterns, there would not be much variety in the Dearborn males' songs. Second, the males at XY Marsh, which were recorded on a single, windy day late in the breeding season when singing was at a minimum, sang fewer songs than any of the other populations.

Although the Dearborn males sang the highest percentages of AE Song patterns, at least 1 kind of AE Song pattern was recorded in each locality sampled in southern Michigan. Between 21 May and 2 June 1974, males recorded in Dearborn sang 37.5% AE Songs and 62.5% UE Song patterns. In contrast, 3 males recorded on 7 July 1975, at XY Marsh sang for the same amount of time as did the Dearborn males, but sang only 7.7% AE Song patterns.

Fig. 10 shows a cumulative plot of the number of song patterns against the total number of songs sung. At first, the curve rises sharply, but as more songs are sampled, and increasingly larger numbers of song patterns reappear, the cumulative number of new song patterns approaches an asymptote.

The males inhabiting the marshy areas of the Fort Custer Recreation Area during the summer of 1974 sang the greatest variety of song figures. This population also shared the largest number of figures and song patterns with the other populations in southern Michigan. This could be due to the greater number of songs recorded at Fort Custer. However, the total number of songs sung by the Dearborn population in 1974 is nearly equal to

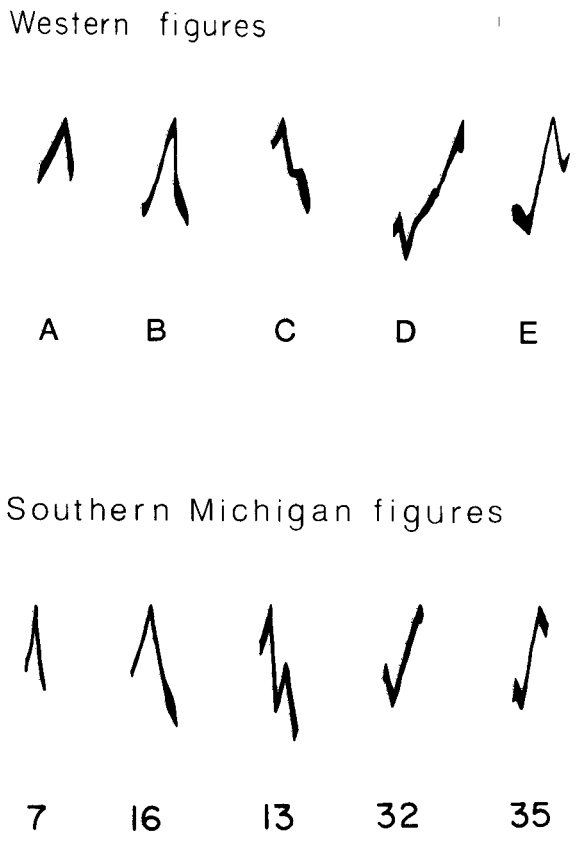

FIG. 11. Different Yellow Warbler figures sung in Nevada and California and comparable figures from southern Michigan.

the number sung by the Fort Custer population in the same year, suggesting that other factors may be important in determining the variety of song figures and song patterns. A calculation of the "overlap" of each study population with the Fort Custer figures is used to give an estimate of figure distribution. Overlap as used here is the percentage of figures found in other southern Michigan populations that are also represented in the Fort Custer-1974 population. Mideast Kalamazoo County, where Fort Custer is located, has the highest overlap (95.24%), followed by northeast Kalamazoo County (87.5%). The smallest overlap is found with the southwest Kalamazoo population (84.0%) and Dearborn (84.2%) which are farthest from Fort Custer. Nevertheless, the high overlap values found in each of the 4 main study areas, indicate a wide distribution and common

TABLE 1
FIGURE COMPOSITION OF YELLOW WARBLER SONGS

	Dearborn	Northeast Kalamazoo Co.	Mideast Kalamazoo Co.	Southwest Kalamazoo Co.
	1974–75	1974	1974–75	1975
Ave. no. of figures/song	8.18	7.15	7.02	6.00
Ave. no. of figure-types/song	3.05	2.79	2.89	2.74
Ave. repetition index	2.69	2.56	2.43	2.19

	All locations 1974	All locations 1975	Total all locations 1974–75
Ave. no. of figures/song	7.32	6.98	7.2
Ave. no. of figure-types/song	2.88	2.86	2.87
Ave. repetition index	2.54	2.43	2.5

occurrence of many figures. It is interesting that Dearborn, 170 km from Fort Custer and southwest Kalamazoo County, 34 km from Fort Custer have such similar overlap values. That may relate to the small sample size for both localities.

Songs from several individuals in the Upper Peninsula of Michigan (Boyes and Boyes 1969), New England (Kilham 1963), Nevada, and California (Gunn and Kellogg 1963) were taken from phonograph records. Figures found in both northern Michigan and New England are also found in southern Michigan. Six of 11 figures sung in Nevada and California are also sung in Michigan. Although 5 of the 11 differ from those found in northern Michigan, they are similar to certain figures in our catalog and may merely represent individual variation (see Fig. 11). There were also 5 new song patterns in these recordings. Merely changing the arrangement of figures found in southern Michigan produced the different AE Song pattern found in the New England recordings. The California recordings yielded 2 new UE Song patterns, and 2 additional AE Song patterns came from the Nevada recordings. The addition of new figures to arrangements previously recorded produced 2 of these patterns, while the other 2 resulted from rearranging figures that are found in the southern Michigan catalog and adding new ones.

Song length in terms of the average number of figures per song varied slightly among the 4 major study areas (see Table 1). Data for 1974 and 1975 reveal that the Dearborn population, recorded earliest in the season, has the highest average number of figures per song, while the XY Marsh population, recorded last, has the lowest. Data on the average number of kinds of figures per song show a similar pattern.

DISCUSSION

The song figures of the Yellow Warbler seem to maintain stability of form over time and over considerable geographic distances. The high overlap values among the song figures obtained from Fort Custer in 1974 and the other areas within Kalamazoo County, southeastern Michigan and other areas of the United States, confirm the extent of this stability. Borror (1967) found that in the Common Yellowthroat (*Geothlypis trichas*) a particular "phrase type" has a range of between 200 and 460 km. Similarly, Shiovitz and Thompson (1970), Emlen (1971), and Forsythe (1974) noted extensive geographic distribution of song figures in the Indigo Bunting.

The Yellow Warbler used various combinations of 40 figures to produce 64 different song patterns. In comparison, Shiovitz and Thompson (1970) found that the Indigo Bunting has about 118 figures, and Borror (1967) found that the Common Yellowthroat has 83 "notes" (figures). Shiovitz and Thompson (1970) calculated that even with a song length of 5 figures, a limited repertoire of 100 figures, and no repetition, a total of over 9 billion different song patterns is theoretically possible. Substituting the corresponding values for the Yellow Warbler (an average of 2.87 figure types per song and a total repertoire of 40 figures) results in a theoretical total of over 59,000 different song patterns. In actuality, the number of possible song patterns is more limited, because certain figures tend to appear either at the beginning or end of the song.

Probably a combination of several interrelated factors results in the Yellow Warbler's having so many UE (60) and so few AE (4) songs. We found, as did Morse (1966), that the AE Song patterns are sung mostly prior to and during pair formation, while the UE Songs are sung toward the end of the breeding season, following pair formation, and along territorial boundaries. Morse (1966) states that the "Accented Ending Songs were almost always given in the presence of female Yellow Warblers." According to Ficken and Ficken (1965) "the Accented Ending Song is more attractive to conspecific females than the" Unaccented Ending Song. The less variable AE Song would permit fast recognition by a female of the same species. Ficken and Ficken (1962) found that the AE Songs of the Yellow Warbler were strikingly different from AE Songs sung by other species of warblers belonging to the same genus, while the UE Songs of the Yellow Warbler were quite similar to those of the Chestnut-sided Warbler (*Dendroica pensylvanica*), Magnolia Warbler (*Dendroica magnolia*), and American Redstart (*Setophaga ruticilla*). Ficken and Ficken (1965) found that the AE Songs, in at least 2 species of *Dendroica*, seemingly functioned in maintaining reproductive isolation. Morse (1966) thought AE Songs of male Yellow Warblers both attracted conspecific females and discouraged intrusion of males of other species. We are uncertain why

songs unlike their own should discourage males of other species from intruding. It would seem more logical for UE Songs, resembling the songs of other species, to serve this function. Ficken and Ficken (1965) also associate AE Songs with success in territorial defense, and UE Songs with escape tendencies. Lein (1972), in a dissenting view, concluded that AE Songs in the Black-throated Green Warbler (*D. virens*) are sung under the influence of a high androgen level, in the breeding habitat, and in the absence of conflicting external inputs. He found that males sing UE Songs in the presence of another male, when on insecure ground, or at low light levels. Our data are not sufficient to resolve these differences of opinion.

If species identification is a prime function of AE Songs, then this function would be served by the small number of patterns we find, making identification simpler. In contrast to the small number of AE Songs, the 60 different UE Song patterns represent a much greater variability. After pair formation, the stability of song patterns that facilitates species recognition and mating seems to become less important than song variation which allows the Yellow Warbler to be recognized as an individual. The UE Song patterns are sung predominantly along territorial boundaries to male conspecifics (Ficken and Ficken 1965, Morse 1966, Lein 1972). The variety of UE Song patterns would allow the territorial male to differentiate between the songs of a territorial neighbor and a stranger. From an ecological point of view, once territorial boundaries are established, a bird can conserve energy by not responding to a neighbor's song (Falls 1969).

The only other parulid that regularly occupied Yellow Warbler habitat in this study was the Common Yellowthroat. The temporal arrangement of the Common Yellowthroat's song is clearly different from the Yellow Warbler's UE Song. The average song length and repetition index of the Common Yellowthroat song in various Michigan localities was 1.75 and 3.33 sec, respectively, and its rhythmic characteristics are quite different. Borror (1967) found that the frequency range of most Common Yellowthroat songs that he recorded was 4.00 kHz. This is much different from the Yellow Warbler's UE Song, which on the average is shorter (1.30 sec), has a lower repetition index (2.50), and a higher frequency (5.10 kHz). In addition, the "notes" (=figures) of the Common Yellowthroat, as described by Borror (1967), consisted of simple slurred elements, having no rapid frequency modulation. The Yellow Warbler figures are generally short in duration (narrow) and have a rapid frequency modulation. The songs of the 2 species thus serve as clearly distinctive epigamic and intrasexual displays.

SUMMARY

During May, June, and July 1974 and 1975, 47 male Yellow Warblers (*Dendroica petechia*) from 9 localities in southern Michigan were observed and 1328 songs from these populations

recorded. Spectrographic analysis of 745 songs yielded 40 different types of figures arranged in various combinations to form 4 Accented (AE) and 60 Unaccented Ending (UE) song patterns.

Song variation in individual males resulted from variation in the number, arrangement, and kind of figures, deletion or addition of phrases, or change in arrangement of phrases within the song pattern. Twelve of the 14 song patterns that were combined to form 16 run-on songs were UE Song patterns.

The average number of kinds of figures per song was 2.87. A greater percentage of AE Songs was sung toward the earlier part of the breeding season, while more UE Songs were sung toward the end. Differences in the repetition indices between localities seemed to be based on this difference in seasonal behavior. Thirty-nine of the 40 different figures were recorded in 1974 and 33 in 1975. The mean number of song patterns containing a given figure was 4.98. High overlap values (84.0%–95.2%) for figure composition of songs were found in all the southern Michigan populations studied.

Furthermore, 19 of the 24 figures found in songs recorded in 3 separate areas in the U.S. were the same as those found in southern Michigan. This suggests that the figures sung by the Yellow Warbler are limited in number and maintain great stability of form.

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NEW LIFE MEMBER

Mrs. Betty Darling Cottrille is an avid photographer/ornithologist, who has recently become a Life Member of The Wilson Ornithological Society. For many years she and her husband have been studying North American Warblers, flycatchers and vireos on their breeding grounds, and have on occasion contributed to the literature. Mrs. Cottrille has also published on the distribution of the Piping Plover (*Charadrius melódus*) in Michigan, and has co-authored a study on the Great Blue Heron (*Ardea heródias* L.). In keeping with her interests as a photographer Mrs. Cottrille has also presented slide programs of her work. Besides being a member of a number of ornithological/naturalist societies Mrs. Cottrille is, by avocation, a pianist.