

SONG FEATURES AS SPECIES DISCRIMINANTS IN
AMERICAN WARBLERS (PARULIDAE)

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SONG FEATURES AS SPECIES DISCRIMINANTS IN AMERICAN WARBLERS (PARULIDAE)

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ABSTRACT.—Using multivariate discriminant analysis, we examined 337 songs of 19 species of wood warblers sympatric in New Brunswick, Canada. We divided the warblers into five overlapping groups of species based on habits and songs. Our hypothesis was that song features would be the most reliable at high noise levels or under conditions of poor transmission. Hence, we predicted that within most of these groups the songs would segregate highly on the basis of song features alone, as opposed to features of individual sounds or phones. In four of the groups the analysis correctly classified 84 to 95% of the songs on the basis of song features alone. In Group 5 (Yellow, Chestnut-sided, Redstart, Magnolia warblers), only 68% were correctly classified on the same basis. The addition of phone features to discrimination for this group increased the correct classification to 85%. In some groups the frequency modulation patterns of the phones are so simple that they contribute little to improved discriminations. The relative contributions of phones may be functionally related to the importance of possible competitors, the distance of the communication and other noise factors, and to the relative development of repertoires.

An important function ascribed to bird song is the conveyance of information by which members of different species recognize their own kind. This role has been demonstrated in pairs, or, at most, small groups of species of wood warblers (Family Parulidae; Stein 1962, Ficken and Ficken 1967, 1969, Gill and Murray 1972) and other birds (Thielcke 1961, Stein 1963, Catchpole 1973, Becker 1976). In such studies the songs were compared either subjectively by visual analysis of sonograms or by measuring a limited number of variables.

Such comparisons are less satisfactory, however, when considering many species interacting in a natural environment. In that case, an objective method to compare quantifiable attributes of song is needed. In this paper, we examine relationships of songs among 19 sympatric species of warblers, using multiple discriminant analysis to objectively weigh differences among the songs. This multivariate technique is used both descriptively and to test an initial set of predictions on the structure of bird song necessary to achieve functional species recognition in species-rich habitats. To our knowledge, this approach has been used to only a limited extent (Sparling and Williams 1978, Brown and Lemon 1979).

Two general types of variables characterize the structure of bird song. Songs of most species are generated from a limited set of basic sounds, continuous in time, which we call "phones."

A song may be simply the clustered repetition of a single phone, or it may have combinations and sub-groupings of phones. We use these two levels of features—phone and song—to define variables that are useful in any comparison of songs.

Playback experiments on species recognition have shown that particular details of phones are sometimes essential to evoke a maximum degree of response (Falls 1963, Emlen 1972, Shiovitz 1975, Marler and Peters 1977, Shiovitz and Lemon 1980). Response to such detail is often limited even to members of the particular vocal community or dialect (Lemon 1969, Milligan and Verner 1971). Sounds are often distorted, however, through masking, attenuation and related phenomena, depending on the presence of other species' songs, distance, variable densities of air, etc. (Wiley and Richards 1978, Lemon et al. 1981, Richards 1981). Consequently, overall features of song, as opposed to precise details of phones, should be expected also to contribute strongly to species recognition in natural environments. For example, among certain warblers, the species differ by song characteristics such as range and mode of frequency, as well as by groupings of phones (Ficken and Ficken 1962, Lemon et al. 1981).

Because the problems of distortion should apply to details of phones more than to more general features of timing and sequence, we

TABLE 1. Summary of song types recorded per species and individual used in this study.

Species	Total no. of birds	Total no. of songs	Songs/individual
Black-and-white Warbler (<i>Mniotilta varia</i>)	8	9	2, 1*
Nashville Warbler (<i>Vermivora ruficapilla</i>)	15	15	1
Tennessee Warbler (<i>V. peregrina</i>)	17	17	1
Northern Parula (<i>Parula americana</i>)	13	14	2, 1
Cape May Warbler (<i>Dendroica tigrina</i>)	9	13	3, 1
Yellow Warbler (<i>D. petechia</i>)	9	36	14, 7, 3, 3, 3, 2, 2, 1
Yellow-rumped Warbler (<i>D. coronata</i>)	10	11	2, 1
Magnolia Warbler (<i>D. magnolia</i>)	28	29	2, 1
Chestnut-sided Warbler (<i>D. pensylvanica</i>)	22	28	3, 2, 2, 2, 2, 1
Bay-breasted Warbler (<i>D. castanea</i>)	20	20	1
Blackburnian Warbler (<i>D. fusca</i>)	14	14	1
Black-throated Green Warbler (<i>D. virens</i>)	11	12	2, 1
Ovenbird (<i>Seiurus aurocapillus</i>)	8	8	1
Northern Waterthrush (<i>S. noveboracensis</i>)	7	7	1
Mourning Warbler (<i>Oporornis philadelphia</i>)	7	7	1
Common Yellowthroat (<i>Geothlypis trichas</i>)	21	21	1
Wilson's Warbler (<i>Wilsonia pusilla</i>)	9	14	3, 2, 2, 2, 1
Canada Warbler (<i>W. canadensis</i>)	16	23	3, 2, 2, 2, 2, 2, 1
American Redstart (<i>Setophaga ruticilla</i>)	17	39	5, 5, 4, 4, 4, 3, 3, 2, 1
	<i>n</i> = 261	337	

* Two or more songs/individual always cited; otherwise only a single song is cited.

postulated a recognition hierarchy: that song features would be more reliable specific discriminators than phone features.

Therefore, in groups of species associated by habitat among our sympatric warblers, we predicted that most songs could be identified to species on song features alone. Where they could not be so separated, phone features should contribute the necessary additional information to discriminate the songs. We reasoned that if songs from within a subgroup could be successfully recognized in multiple discriminant analyses based on the selected song and phone features, then this provided objective, inferential support for the birds' abilities similarly to discriminate one species' song from another.

In order to test these predictions, we recorded and analyzed songs from most warbler species breeding in a 30 × 30-km block along the coast of southern New Brunswick, Canada. Probably 21 species occur in or near this area. So large a number of sympatric species in temperate North America is peculiar to the Parulidae (Cook 1969). The phenomenon appears to be associated with the high diversity of forest trees that occur in this coastal region (Loucks 1961). The floristic and faunistic diversity here provide an excellent opportunity to test the functional significance of song structure as a mechanism of species recognition in complex natural environments. In the analyses, the songs of these species were separated into functional subgroups on the basis of habitat preferences and similarity of song.

METHODS

Warblers were recorded during May and June in 1978–1979 in an area centered on St. George, Charlotte Co., New Brunswick. Recording sites near the Bay of Fundy were dominated by spruce-balsam fir (*Picea-Abies*); they have been placed in the Maritime Lowlands Ecoregion (Loucks 1961). Inland sites, north of St. George, were dominated by hardwoods such as maples (*Acer*) and birch (*Betula*), as well as by white pine (*Pinus strobus*); Loucks placed these sites in the Maguadavic Ecoregion. Species and numbers of songs recorded are listed in Table 1. Recordings were made on Uher Tape Recorders at 7½ and 3¾ ips, using a Dan Gibson parabolic microphone. Recordings were ana-

TABLE 2. Song and phone features used as variables for analysis.

SONG FEATURES	
SMAXFR	Maximum frequency of song as measured from any phone (kHz).
SMINFR	Minimum frequency of song as measured from any phone (kHz).
SMODFR	Modal frequency of song as determined from power spectrum (kHz).
SDUR	Song duration, from beginning of first phone in song to end of last (seconds).
PHONTYP	Total different types of phones per song, subjectively determined.
MANTYP	Maximum number of any one type of phone in a song.
DIVERS	Phone group diversity calculated by the Shannon-Wiener information index.
PHONE FEATURES	
First Measurable Phone (FP) and Last Phone (LP)	
DUR	Phone duration (seconds).
INFPTS	Inflection points, changes in direction of frequency sweep of at least 300 Hz as seen in standard sonogram.
UP	Proportion of total duration of phone spent in upward sweep in frequency (percent).

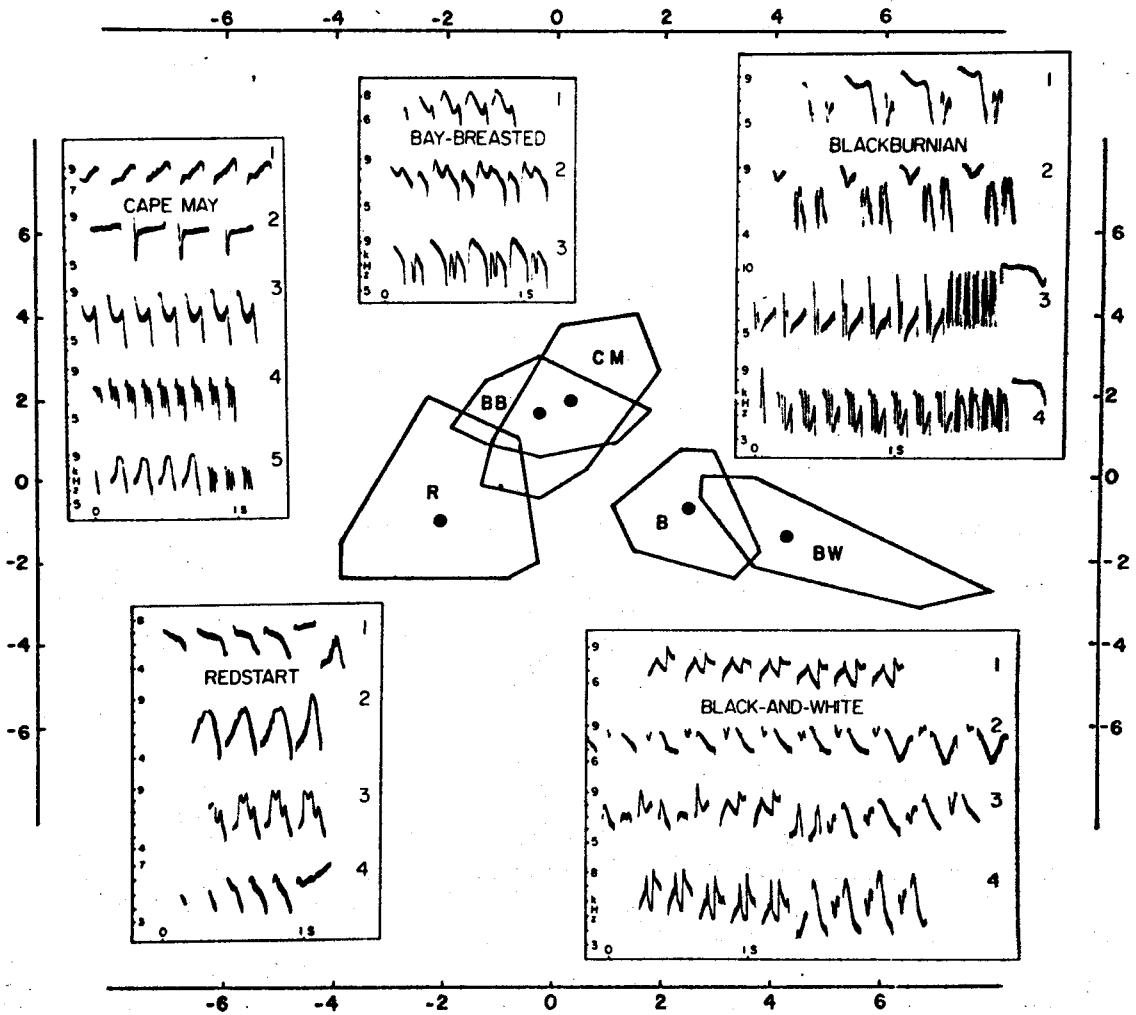


FIGURE 1. Discriminant analysis of the songs in Group 1, showing factors 1 (x-axis) and 2 (y-axis). Polygons enclose the largest area among the points of individual songs.

lyzed on a Kay Elemetrics Sonagraph for all measurements except the song modal frequency, which was obtained from a Ubiquitous Spectrum Analyzer.

Variables measured (Table 2) are of the whole song and of first and last phones in the song. A "phone" operationally is a continuous sound tracing in a sonogram, and therefore the term is equivalent to "note" or "figure" of other workers. For example, in Figure 1 the first song of the Cape May Warbler exhibits six phones while the fifth song exhibits eight phones. In the latter song, three phones at the end are of one type and five at the beginning are of another type, although the first of these five is incompletely expressed. We measured the first phone of good recording quality, since the initial phones in a song are often poorly recorded because of low amplitude. The variable "phone group diversity" (DIVERS) expresses the sequential diversity of subgroupings of phones within songs. Using letters to represent phone

types, three songs might be expressed as: 1) AAAA; 2) BCDBCBCD; 3) EFGHIJHIJKLKL. The first two songs have no diversity, whereas the third has considerable diversity. A series of unrepeated phones is designated as a separate group. For a whole song DIVERS is calculated as $H = -\sum P_i \log P_i$, based on the summation of all subgroups (Attneave 1959).

We initially used 35 variables to characterize the song—19 of them being song variables (including frequencies) and 8 for each of the first measured and last phones. First, we analyzed songs of all species in a single group. Although this approach yielded significant discriminations, the analysis was difficult to interpret because many functions were necessary. Much of this difficulty appeared to relate to the number of variables and their high intercorrelations (unpubl. data). Therefore, we reduced the number of variables by selecting those from the original set that were least cor-

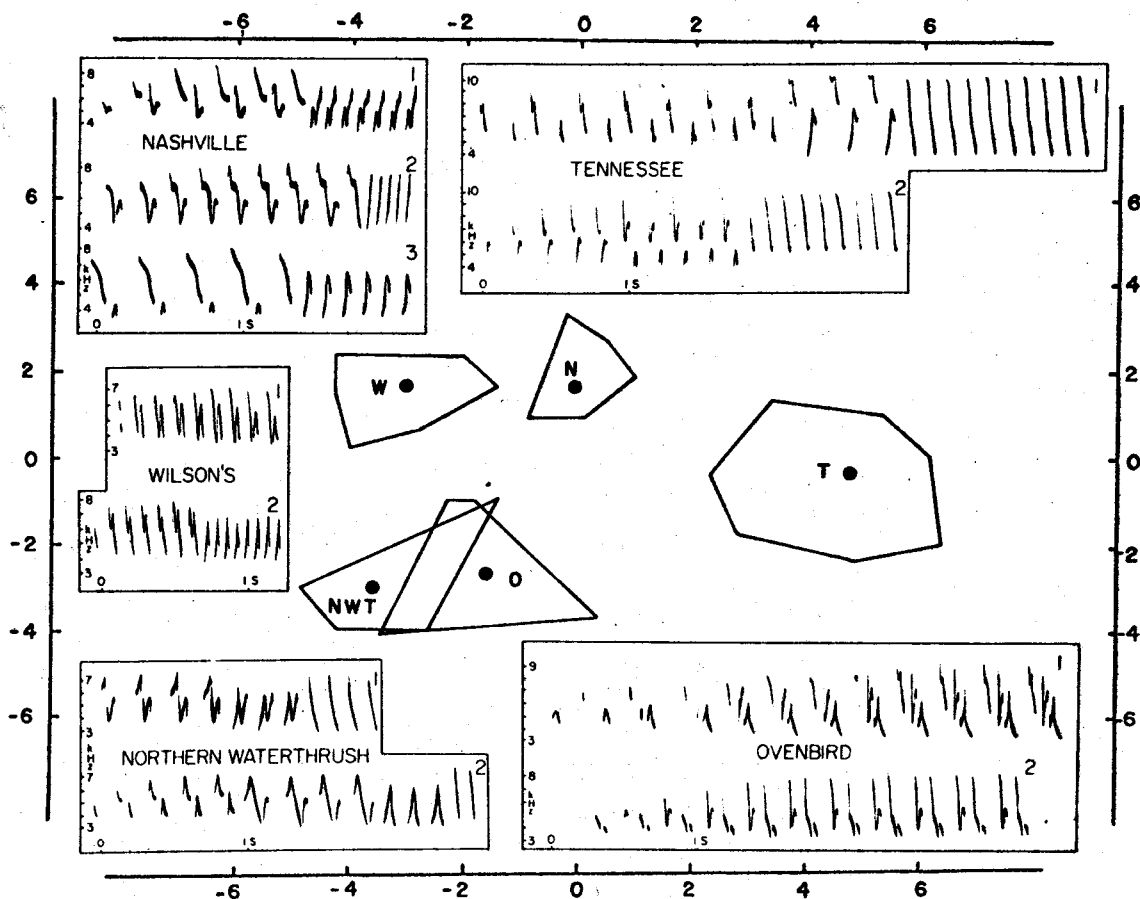


FIGURE 2. Discriminant analysis of songs in Group 2.

related statistically and biologically. Our goal was to define the smallest general set of objective variables to describe warbler song that would have biological meaning.

In all cases discussed here, the discriminant analyses were initially based on song features alone; if poor discrimination called for further analyses, six phone features were added. Tabulated results are confined to song features in four of the five cases. The multiple discriminant analysis is that of the SPSS package (Nie et al. 1975); a useful introduction to the application of this method was given by Gittins (1979). We used the unweighted direct method analysis.

RESULTS

We considered the 19 species in five groups, with some overlap across them (Figs. 1-5). These groups were defined by common habitat use and similarity of song. Our experience suggested that the species within these groups were most likely to interfere acoustically with, or respond to, one another's singing.

GROUP 1. HIGH FREQUENCY SONGS OF CONIFEROUS AND MIXED HABITAT

Bay-breasted. Blackburnian and Cape May warblers often live in conifers, especially spruce and fir. Consequently they may occur together, particularly at higher levels in the trees, often singing from the very tops. They feed in the foliage and along smaller branches but may separate by area within the tree crown (MacArthur 1958). Blackburnian and Cape May warblers nest high in the trees whereas Bay-breasted Warblers nest on the ground. Male Bay-breasted Warblers also sing often at mid-levels or even lower, and do so more than the other two. Bay-breasted and Cape May warblers may grow in numbers in response to local outbreaks of spruce budworm (Morris et al. 1958) and they have larger clutches than other warblers. The American Redstart also inhabits conifers, although it is less restricted to spruce-balsam. This warbler frequents white cedar (*Thuja occidentalis*) as well, and also deciduous shrubs or trees, often birch (*Betula*), alder (*Alnus*) or serviceberry (*Amelanchier*). It often feeds aerially and is not likely to feed

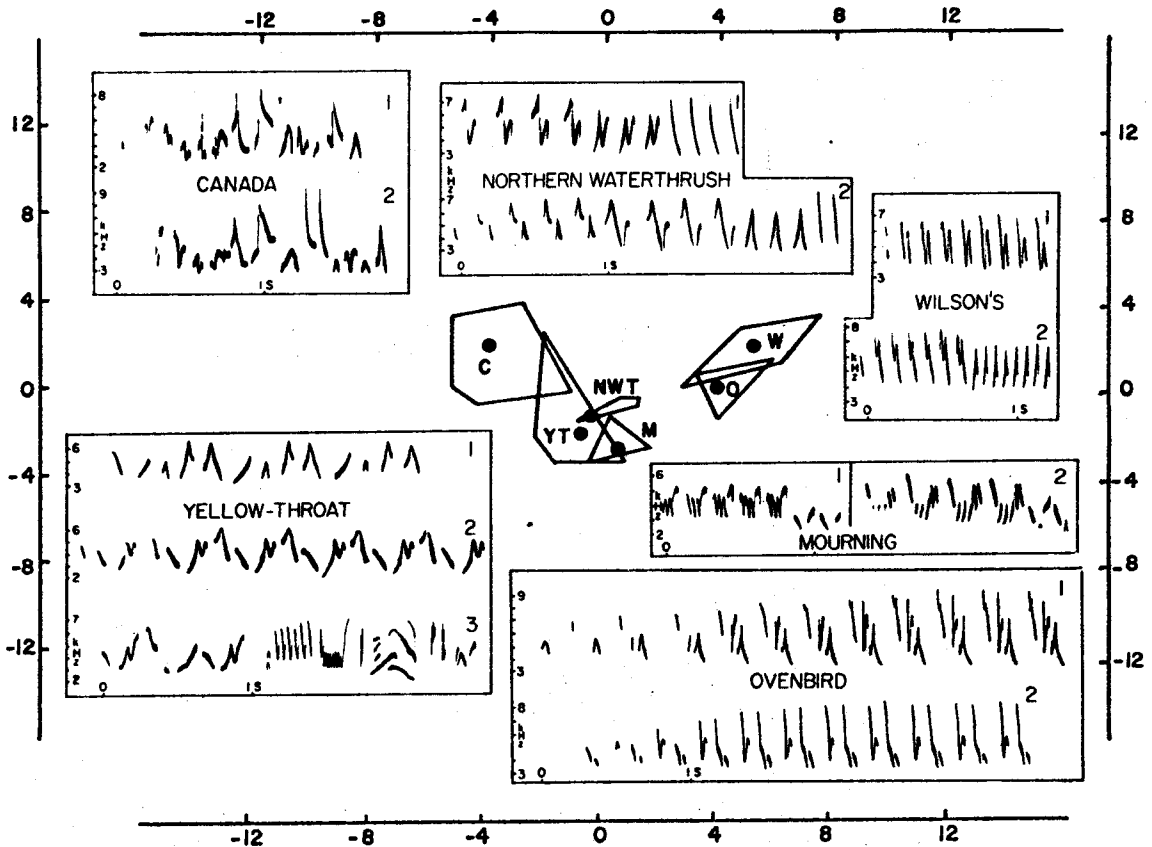


FIGURE 3. Discriminant analysis of songs in Group 3.

with the other members of the group. The Black-and-white Warbler, another characteristic species of coniferous habitat, feeds along main branches and trunks more than the other warblers in this group.

Songs of all of these species (Fig. 1) employ relatively high frequencies. Songs of American Redstarts, Cape May and Bay-breasted warblers are usually short, as also are some songs of Blackburnian Warblers, while those of Black-and-white Warblers and others of Blackburnian Warblers are much longer. We have heard some longer songs of Cape May Warblers since completing our analysis. All these species are complicated by the presence of repertoires of songs in each individual; within the group, repertoires are numerically largest in the redstart, with usually three to five songs per bird (Table 1).

The simplest songs to describe are perhaps the shorter ones. Those of the Cape May Warbler are usually repetitions of a single phone, although two phones may be used. The Bay-breasted Warbler either repeats a single phone or alternates two. The redstart also repeats a single phone or pair, and often "accents" the end of the song with one or a pair of unrepeated phones.

Some Blackburnian Warbler songs (Fig. 1, song 1) are similar to those of the Bay-breasted Warbler and as such are noticeably shorter than other Blackburnian songs which have two or three divisions, or phrases. All Blackburnian Warbler songs have phones with very rapid frequency sweeps. The longer songs often end with a high single (or "accenting") phone (Fig. 1, songs 3 and 4). The Black-and-white Warbler either repeats a phone or pair throughout the song, or may repeat groupings of different phones, using five or six types in the whole song. The songs of the Black-and-white and the more complex songs of Blackburnians are the longest of this group.

A discriminant analysis based on the seven song variables correctly separated most of the 95 songs to species (84%; Fig. 1). Separation on the first axis was mainly by song duration (Table 3), although other variables, such as modal frequency, were involved. Consequently, the songs of Black-and-white and Blackburnian warblers were easily separated from the remainder. Low internal diversity of pattern tended to act negatively on the first axis as well. On the second function, high values of minimum frequency and modal frequency tended to separate the Cape May and Bay-

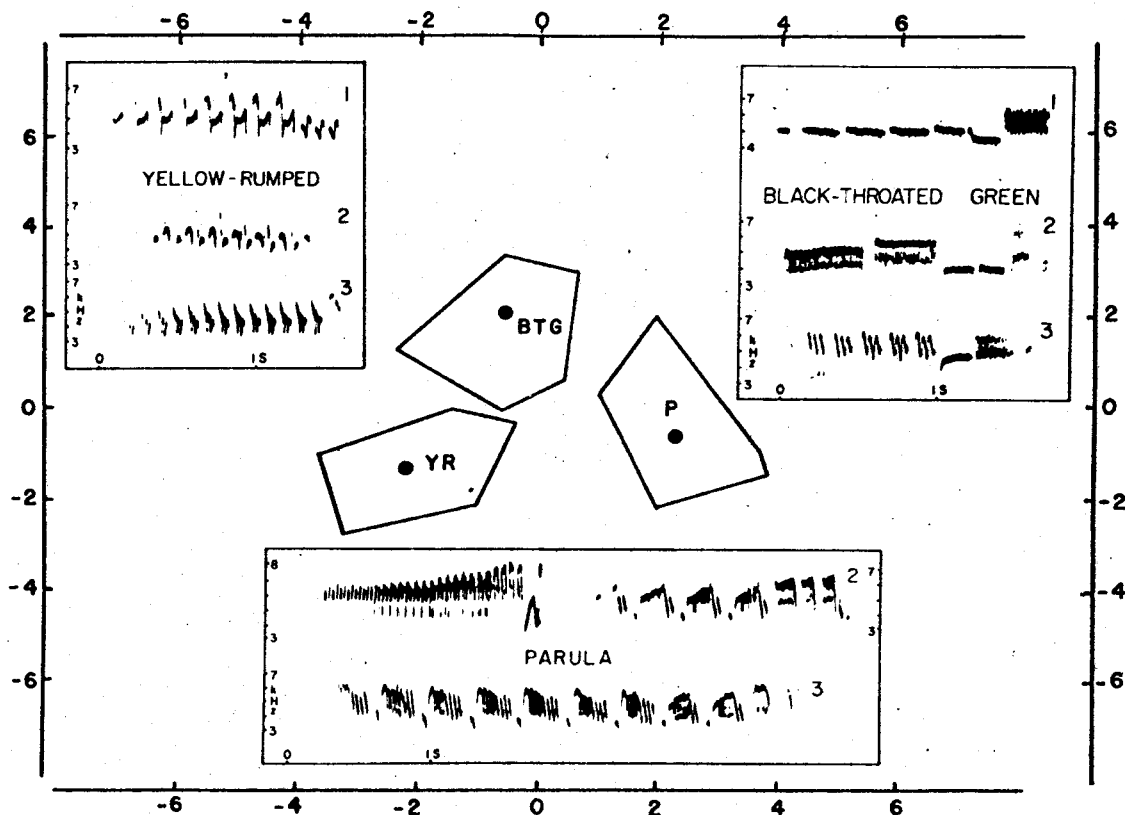


FIGURE 4. Discriminant analysis of songs in Group 4.

breasted songs from the others, with more internal diversity of pattern working in the opposite direction.

The polygons including the data points (Fig. 1) showed that Cape May and Bay-breasted warblers overlap considerably. In fact, only 54% (7 of 13) Cape May Warbler songs were correctly classified, three being classed as Bay-breasted Warbler. Similarly only 70% of the Bay-breasted songs were correctly classified, 6 of 20 being considered Cape May. Three of 39 redstart songs (8%) were classed as Bay-breasted Warbler. All songs of the other two species were correctly classified.

Close examination of the phones occasionally reveals similarities such as in American Redstart song 2, Cape May Warbler song 5 and Bay-breasted Warbler song 3 (Fig. 1). However, more phones tend to be distinctive to species. Therefore one should expect that phone information made available to an analysis should separate the songs more completely. When the six phone variables were included, a discriminant analysis raised the classification of all species from 84 to 89% correct, although six Bay-breasted Warbler songs (30%) were still classed as Cape May Warbler songs. Only two Cape May songs were misidentified, one as Bay-breasted and the

other as redstart. Two redstart songs were classed as Bay-breasted Warblers.

In summary, among the high-frequency singers, those with shorter songs (Cape May Warbler, Bay-Breasted Warbler and American Redstart) were separable to a great extent on song length and song frequency features alone, although details of phones also proved useful. The Black-and-white and Blackburnian warblers were usually separable from the others by longer songs and from each other on a number of song and phone features. Blackburnian short songs were easily separable from those of other species despite their similarities to certain songs of Bay-breasted Warblers.

GROUP 2. LOUD, REPETITIVE SINGERS OF MIXED WOODS

This group includes two pairs of congeners (Ovenbird and Northern Waterthrush [*Seiurus*], and Tennessee and Nashville warblers [*Vermivora*]) and the Wilson's Warbler. Tennessee and Nashville warblers sing from high to medium heights in mixed deciduous and conifer forests. The remaining three species sing closer to the ground: Northern Waterthrush especially along rivers and streams, Ovenbird in wood areas, and Wilson's Warbler in thickets and edges. Songs of these species

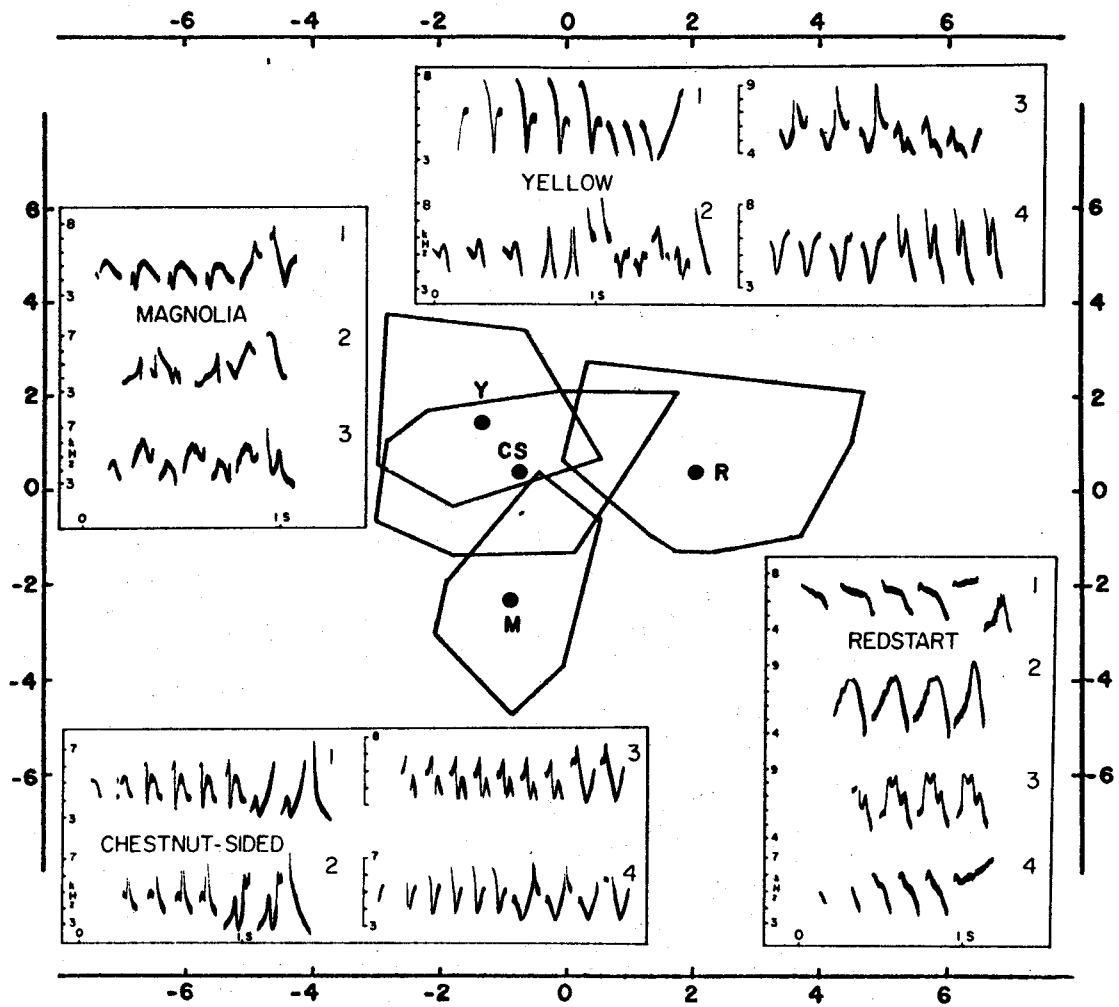


FIGURE 5. Discriminant analysis of songs in Group 5.

are considered similar because they are loud, repetitive and, except for that of the Wilson's Warbler, are often long.

All of these species sing repeated groups of phones, which in some cases change during the song (Fig. 2). Ovenbird and Northern Waterthrush songs are easy for naturalists to recognize. The waterthrush song has three parts, each with a single phone. The songs end in simple downward-sweeping phones, often three

in number. The Ovenbird song is not subdivided but instead repeats triplets of phones averaging in frequency from high to low. The songs of Tennessee and Nashville warblers can sometimes be confused. The former were usually the longest of any we recorded; commonly they had three noticeable parts as opposed to two in Nashville Warbler songs. The Wilson's Warbler song is loud and "chatterly" and although distinguishable from others, it resem-

TABLE 3. Standardized canonical discriminant coefficients and mean values of discrimination song variables for songs of warblers in Group 1. For variable means of American Redstart, see Table 7.

Variable	Discriminant coefficients		Species means of variables*			
	Function 1 (64%)**	Function 2 (25%)	Black-and-white Warbler	Cape May Warbler	Bay-breasted Warbler	Blackburnian Warbler
SMAXFR	+0.27	+0.11	9.42	9.62	9.21	10.00
SMINFR	+0.05	+0.57	4.83	5.89	5.52	3.49
SMODFR	+0.44	+0.53	6.87	7.82	7.62	7.14
SDUR	+0.88	-0.54	2.02	1.03	0.97	1.50
PHONTYP	+0.23	+0.41	3.67	1.23	2.00	3.21
MAXTYP	-0.01	+0.36	5.89	5.08	4.00	5.07
DIVERS	-0.26	-0.25	0.96	0.07	0.30	0.36

* Units in Table 2.
 ** Percent of total variance.

TABLE 4. Standardized canonical discriminant function coefficients and mean values of variables of songs from warblers in Group 2.

Variable	Discriminant coefficients		Species means of variables*				
	Function 1 (64.5%)**	Function 2 (23%)	Nashville Warbler	Tennessee Warbler	Ovenbird	N. Water- thrush	Wilson's Warbler
SMAXFR	+0.80	-0.09	8.51	10.38	8.35	7.87	7.53
SMINFR	+0.42	+0.61	3.18	2.99	2.60	1.90	3.14
SMODFR	+0.16	+0.45	5.44	5.48	4.33	4.46	4.87
SDUR	-0.44	-0.44	1.94	2.88	2.73	1.81	1.20
PHONTYP	+0.09	-0.39	2.73	4.59	3.00	3.86	2.00
MAXTYP	+0.21	+0.16	8.13	10.76	9.50	4.57	8.07
DIVERS	+0.27	+0.61	0.89	1.17	0.0	0.45	0.20

* Units in Table 2.

** Percent of total variance.

bles the Nashville Warbler's because of the two parts. In both parts, Wilson's Warblers repeat only a single phone whereas Nashville Warblers usually repeat two phones as a pair.

All of these species have single songs or, at most, repertoires of two or three. The Ovenbird and Northern Waterthrush use only one song type from their song perches but they will use a much more complex song in flight above the canopy (Ficken and Ficken 1962, Lein 1981). We have neither recorded any flight songs for this analysis nor heard flight songs from the other species in this group. We recorded only one song per bird from Tennessee and Nashville warblers and as many as three from Wilson's Warblers.

A discriminant analysis on song features alone correctly classified 93% of the 64 songs considered here. The only errors were two songs of Ovenbirds classed with the Northern Waterthrush and also one of the latter with the former. These songs seem very different to our ears and their misclassifications probably reflect large variances in the data in these two species with the smallest samples (Table 1).

Function 1 (Fig. 2, Table 4) clearly separated Tennessee Warbler songs from the others by several variables, chiefly song maximum frequency (SMAXFR). In addition, this species had the highest mean values for five of the other six variables listed. Wilson's Warbler, Northern Waterthrush, and Ovenbird tended to have the lowest values in these functions.

Function 2 of the analysis separated Wilson's and Nashville warblers on the positive side and Northern Waterthrush and Ovenbird on the negative. Several variables again contributed. Song minimum frequency was the most notable, being highest in Wilson's and Nashville warblers. The remaining features were less clear.

Most of the songs in this group of species consist of phones with few inflection points but with rapid frequency sweeps. Consequently, phones show strong similarities across the species: Northern Waterthrush and Tennessee

Warbler terminal phones are similar, although with different maximum frequencies; Wilson's Warbler phones are similar to some of Northern Waterthrush song 2, and so on. Despite these similarities, our analysis had little difficulty in specifically identifying the songs on the basis of song features alone. We therefore assume that the birds would usually do the same. Possibly the simplicity of the phones is readily interpreted in terms of amplitude modulation or rhythm as much as frequency modulation. In summary, although these five species had simple and often similar phones, we found them generally separable by song features, especially song frequencies, duration and internal organization.

GROUP 3. LOW-LEVEL SINGERS OF VARIOUS HABITATS

Warblers in this group often sing fairly close to the ground, although not exclusively so. Three of them are also included in group 2, described above. Mourning Warblers occurred very locally, usually in roadside thickets with immediate neighbors of the same species. Canada Warblers occurred commonly in moist woodland thickets. Common Yellowthroats were among the most common warblers in the study areas, occurring mainly in openings, sometimes near water but also in newly cleared areas with thick cover of emerging conifers.

The Common Yellowthroat's song is familiar to many naturalists as a kind of "witchety-witchety-witchety," which is based on repeated series of three to five phones (Fig. 3). The Mourning Warbler's song is highly repetitive like the yellowthroat's: "churry-churry-churry-pup-pup." but the "churry" is usually a continuously modulated phone. In contrast, the Canada Warbler utters a bubbly song with hardly any repetition except for very brief examples.

A discriminant analysis based on seven song features correctly classified 88% of the 80 songs in this group. Figure 3 nevertheless shows that certain species were particularly close when

TABLE 5. Standardized canonical coefficients and mean values of discriminating variables for songs of warblers in Group 3. For variable means of Ovenbird, Northern Waterthrush and Wilson's Warbler, see Table 4.

Variable	Discriminant coefficients			Species means of variables*		
	Function 1 (62.9%)**	Function 2 (18.4%)	Function 3 (13.7%)	Mourning Warbler	Yellow- throat	Canada Warbler
SMAXFR	+0.08	+0.45	+0.60	6.34	6.54	7.93
SMINFR	+0.27	+0.32	-0.05	2.13	2.42	2.58
SMODFR	+0.06	+0.23	-0.07	3.94	4.25	4.66
SDUR	-0.33	-0.45	+1.03	1.25	1.86	1.51
PHONTYP	-0.49	+0.63	-0.25	2.43	4.95	12.17
MAXTYP	+1.02	+0.33	-0.23	4.29	3.76	1.70
DIVERS	+0.20	-0.37	-0.18	0.79	0.59	0.26

* Units in Table 2.

** Percent of total variance.

examined on the first two functions. Function 1 (62% total variance) polarized the Ovenbird and Wilson's Warbler against the Canada Warbler and Common Yellowthroat. The first two species both had high maximum repetitions per phone type (MAXTYP) while Canada Warbler and Common Yellowthroat had the lowest scores for this feature (Table 5). These last two gained also on the negative axis with large scores of phone types. Function 2, with only 18% variance, partially separated the Mourning Warbler, Common Yellowthroat and Northern Waterthrush from the Canada and Wilson's warblers. Canada Warbler's high phone types and a number of other features, roughly equal in importance, were involved on the positive side; on the negative side were song duration and diversity. This second axis was particularly difficult to interpret. Function 3, with 13% of the variance, almost as much as function 2, separated Wilson's Warbler and Ovenbird, mainly by song duration. The same applied to Mourning Warbler versus Northern Waterthrush and yellowthroat.

Eight of 21 yellowthroat songs (38%) were misclassified, four to Northern Waterthrush, three to Mourning Warbler and one to Canada Warbler. Canada Warbler and Northern Waterthrush each had one song misclassified while the Ovenbird, Northern Waterthrush and Wilson's Warbler were correctly classified. In group 2, these last two species were confused in three cases. Again, the members of this group, tended to use simple phones with little frequency modulation extended over time. Yellowthroat songs statistically overlapped those of other species, yet they were generally distinctive to our ears. We have nevertheless included a yellowthroat flight song (Fig. 3, song 3), which resembles the Canada Warbler song in having an unusually low degree of phone repetition and consequently a high number of phone types. Adding the six phone features to the discrimination improved the classification to species by only 1%. Therefore song features

again seem to be especially important as functional discriminators.

GROUP 4. EARLY ARRIVALS

Black-throated Green, Northern Parula and Yellow-rumped warblers are the earliest migrants to Charlotte Co. All of these species may occur together in much the same area while feeding and singing at moderate heights usually in evergreens. Competitive interactions have been noted among them (Morse 1976). Perhaps because the birds have similar habits, their songs are similar in some respects. All three rapidly and repeatedly modulate some of their phones (Fig. 4). Consequently some of the songs of the Northern Parula and Yellow-rumped Warbler may sound similar, although the remaining songs may be quite distinct. Parula songs frequently end with a definite "accent." Songs of the Black-throated Green Warbler are more easily separated, often combining pure sustained whistles with buzzes. All these species have small song repertoires.

A discriminant analysis on seven song features yielded almost perfect separation of 33 songs, one Parula Warbler song being classified as Yellow-rumped Warbler (Table 6). Function 1 separated the parula songs, mainly on the basis of song duration, maximum frequency, and diversity of phone groups. On the negative side was the Yellow-rumped Warbler with low minimum frequency. The second function separated the Black-throated Green Warbler and some Northern Parula songs with high scores of diversity and song minimum frequency. Other variables were also involved.

In a discriminant analysis with the seven song variables plus six phone variables, the percentage of correct classification dropped by 5% as the songs of Northern Parulas and Yellow-rumped Warblers fell closer together. Black-throated Green Warbler songs presented a persistent problem in our analyses because of the very high scores of inflection points in the first and last phones when these

TABLE 6. Standardized canonical coefficients and mean values of discriminating variables for songs of warblers in Group 4.

Variable	Discriminant coefficients		Species means of variables*		
	Function 1 (64.5%)**	Function 2 (35.5%)	Northern Parula	Yellow-rumped Warbler	Black-throated Green Warbler
SMAXFR	+0.77	+0.33	8.20	6.68	7.28
SMINFR	-0.42	+1.08	3.01	2.90	3.78
SMODFR	+0.57	-0.54	5.55	4.42	5.13
SDUR	+0.79	+0.47	1.55	1.49	1.53
PHONTYP	+0.03	-0.22	2.79	1.91	2.42
MAXTYP	+0.27	-0.49	16.36	9.73	4.83
DIVERS	+0.71	+0.73	0.95	0.27	0.87

* Units in Table 2.

** Percent of total variance.

variables were included. These scores always dominated the first function, regardless of the number of species present. Although rates of inflection points were highest in this species' songs, in one case (Fig. 4, Black-throated Green, song 3), the first phones closely resembled those of the Yellow-rumped Warblers in their slower rate of up-down modulation.

In conclusion, the songs of these three species generally separate easily on the basis of song features, but they share the tendency to impose regular and repeated modulations on their phones. The terminal phones may be more evident than those earlier in the song, especially in the Northern Parula and Black-throated Green Warbler; such accenting, however, does not apply to all their songs.

GROUP 5. SPECIES WITH LARGE REPERTOIRES

This group includes species that tend to separate by habitat although they sometimes co-exist. Yellow Warblers prefer edge adjacent to water, Chestnut-sided Warblers favor drier uplands, otherwise similar to Yellow Warbler habitat, Magnolia Warblers prefer more heavily wooded areas, and American Redstarts inhabit conifers and deciduous vegetation as described above.

Our own aural discriminations of these species' songs ranged from easy to difficult. The Yellow and Chestnut-sided warblers have the largest song repertoires of all the species considered in this paper, and the redstart the next largest. Magnolia Warblers often associate with redstarts and Chestnut-sided Warblers and sometimes their song can be confused with those of the Chestnut-sided Warbler.

The songs of Yellow and Chestnut-sided warblers are particularly similar (Fig. 5), yet they can often be distinguished by their rhythm. They utter one or two introductory phrases of repeated phones that end characteristically with an accent: "wee-wee-o" for the Chestnut-sided Warbler (songs 1 and 2) or a faster "tee-

tee-wee" for the Yellow Warbler (song 1). The repertoires of these birds include songs which are not accented and are more difficult to separate. Some songs of Magnolia Warblers are accented and resemble certain songs of Chestnut-sided Warblers.

American Redstarts usually have a song that is easily recognized by its "accent" with a lower frequency terminal phone (song 1). The remainder of its three or more songs per bird often lack an accenting phone, although some may have a high frequency accent (song 4). To human ears, these latter songs may be confused with those of Yellow or Chestnut-sided warblers. Repertoires of neighboring redstarts may share essentially identical songs.

A discriminant analysis of 132 songs based on only seven song features yielded the lowest correct classification (68%) of the five analyses done. Yellow Warblers were recognized in only 39% of the cases (14 of 36) and Chestnut-sided Warblers had 46% correct (13 of 28). In contrast, Magnolia Warblers were judged correctly in 90% of the cases and redstarts in 95%. Adding six more phone variables raised the percentage of correct classifications to 85% (Fig. 5, Table 7). Yellow Warblers now had 79%, Chestnut-sided Warblers 82%, and Magnolia Warblers and redstarts both 90%. The polygons overlap widely for all four species except the Magnolia Warbler and American Redstart (Fig. 5). Function 1 separated redstart songs from the rest, especially on features of maximum number of phone types and high song minimum frequencies. The other species were distinguished by longer song durations and maximum phone types. Although phone features were involved both negatively and positively, they were not outstanding as such. Function 2 (37% of the variance) polarized mainly the Magnolia Warbler against the remainder by its long last phones, plus a number of positive features. Function 3 also exploited phone features in improving the classification.

This group is particularly interesting be-

TABLE 7. Standardized canonical coefficients and mean values of discriminating variables (song + phones) for songs of warblers in Group 5.

Variable	Discriminant coefficients			Species means of variables*			
	Function 1 (45.9%)**	Function 2 (36.7%)	Function 3 (14.5%)	Yellow Warbler	Magnolia Warbler	Chestnut- sided Warbler	American Redstart
SMAEFR	+0.24	+0.43	-0.24	7.83	6.73	7.96	8.41
SMINFREQ	+0.37	+0.18	+0.54	3.06	2.79	2.71	3.37
SMODFR	-0.02	+0.02	0.00	4.71	4.49	4.65	5.36
SDUR	-0.41	+0.55	-0.25	1.26	0.94	1.28	0.92
PHONTYP	-0.22	-0.35	-0.11	3.75	3.17	3.50	1.64
MAXTYP	+0.45	-0.03	-0.36	3.64	3.03	4.43	4.87
DIVERS	-0.11	+0.31	+0.17	0.89	0.64	0.86	0.38
FPDUR	+0.01	+0.21	+0.41	0.12	0.08	0.10	0.12
LPDUR	+0.26	-0.63	-0.19	0.09	0.16	0.13	0.15
FPINFPTS	+0.25	+0.39	-0.44	2.69	1.41	2.82	3.38
LPINFPTS	+0.25	-0.05	+0.02	1.14	2.97	1.54	4.90
FPUP	-0.11	-0.18	+0.04	43.6	48.2	39.5	39.1
LPUP	-0.30	+0.26	+0.53	59.2	38.6	25.7	37.4

* Units in Table 2.

** Percent of total variance.

cause of the large repertoires of three species and the occurrence of both accented and unaccented ending songs in all four species. Consequently there is much variety in the songs of all, thereby contributing to the overlap.

Certain phones of any of these four species might be considered similar to those of any of the others. In fact, a discriminant analysis on separate first and last phones for these four species correctly classified to species only 45% (114 of 264). Despite this statistical confounding, Magnolia Warbler phones were consistently slightly lower than the others in frequency (SMODFR = 4.5 kHz) and American Redstart phones somewhat higher (SMODFR = 5.4 kHz). The phones of Yellow and Chestnut-sided warblers were particularly similar. A discriminant analysis based on only six features of each first and last phone of these two species alone correctly classified 66% of the 128 phones considered. Figure 6 shows examples of these phones and their classifications. In addition to duration, inflection points and percentage UP, we used percentage of sustained frequency and maximum and minimum frequencies. Since the discriminations were based on phone variables, not their overall shapes, phones with different shapes could conceivably have different scores. We believe, however, that many phones of Yellow and Chestnut-sided warblers could be interchanged with little or no effect on species identification. This re-emphasizes the dominance of song features as discriminators, as noted in the analyses of earlier groups.

DISCUSSION

In this study we have used the statistical technique of canonical discriminant analysis to determine whether certain features of song alone

could act as functional discriminators among coexisting species of warblers. This was shown to be the case in four of five groups selected, while in the last group, additional information of phones was essential for discrimination equivalent to that in the other groups. In all groups, however, and especially in Group 2, phones were often similar between species. Groups 2 and 4 were sufficiently alike that addition of phone features to the discriminations did not enhance separation; in Group 4 the inclusion of phone features actually decreased the degree of discrimination. In Group 2, the lack of difference in phones was related to the near absence of frequency modulation throughout the duration of the phones, which were brief but broad frequency sweeps with no more than one inflection point. In group 4, the similarity of phones was related to the repeated vibrato modulation on a sustained carrier frequency.

These discriminations suggest that most warbler songs can be recognized on the basis of rhythm (i.e., timing of amplitude modulations), and modal frequency. These are the characteristics that enable us to discriminate songs and do so by simple word descriptors (e.g., Peterson 1980). We believe that at low-signal-to-noise ratios, warblers would probably do much the same. High frequencies attenuate rapidly with distance, and details of frequency modulation are likely to be obscured further through interference, echoes, and other disturbances. At higher signal-noise levels, however, the birds' perception is certain to be much better than ours, especially in time.

Let us consider further the detailed structuring of warbler songs, which contribute to the rhythm. The sequential organization of each warbler song may be considered relative to

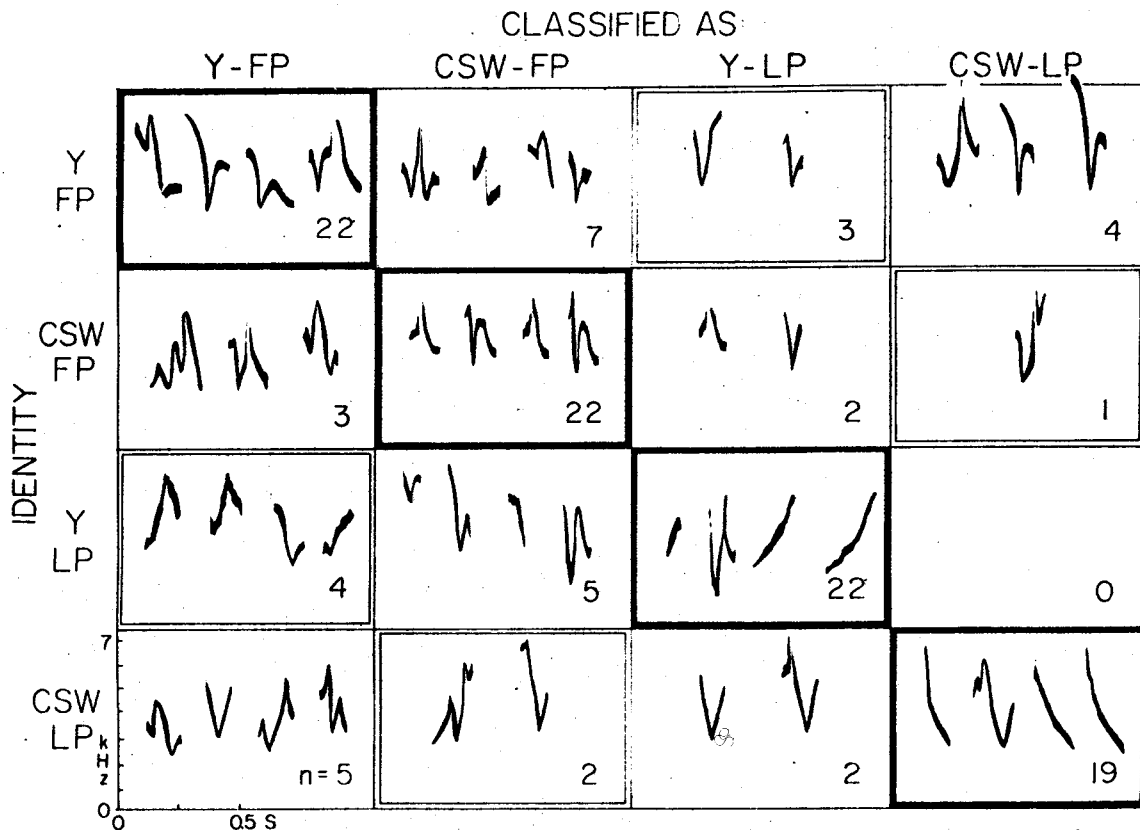


FIGURE 6. A classification of phones of Yellow (Y) and Chestnut-sided (CSW) warblers. The chart shows first and last phones (FP, LP), both as they are correctly identified to species and as classified by the discriminant analysis. Those in the black boxes were correctly classified by the analysis both to species and to position in the song, while those in the white boxes were correctly identified only to species. The remaining phones were incorrectly classified.

three points: 1) whether phones are repeated or not; 2) if repeated, whether they are sung alone or in groupings of two or more phones; 3) whether the last one or two phones stand out sequentially from the others in being un-repeated. Considering each species according to this simple scheme (Table 8) shows that songs of most species use repetitions of either a single phone or of groups of phones. Both features are exhibited by several species and also most genera. The Canada Warbler is the only species that, to a great degree, does not repeat phones, except for the first.

This sequential organization of song was represented in our discriminant analysis by phone types, maximum number per type and sequential diversity. All three of these variables were useful and sometimes important discriminators, especially diversity in Group 1 and phone type in Group 3.

Song duration is also an important discriminator; a longer song can include more repetitions of more diverse phones. Songs of the Tennessee Warbler are three times longer than those of the Magnolia Warbler and American Redstart. Conversely, within some of our

groupings song lengths are similar (e.g., the last two species). Also, the duration in certain species (e.g., Blackburnian Warbler) is highly variable.

Accenting of the terminal phone might be partly due to the lack of repetition of that phone, which may explain its absence in songs of Canada Warblers. Terminal phones, however, often differ in form from those preceding. In American Redstarts and Northern Parulas, they are of lower frequency and often have a second vibrato imposed on the up-down carrier form. In Yellow and Chestnut-sided warblers they are frequency sweeps either upward or downward. Even in the Northern Waterthrush, which repeats its terminal phones, these also lack inflection points. Similarly, terminal phones of the Common Yellowthroat, Ovenbird, and Tennessee and Wilson's warblers have few, if any, inflection points. By our definition, accenting is primarily a feature of *Dendroica* warblers although it is also used by the Northern Parula and American Redstart. The redstart is considered a close relative of the Chestnut-sided and Yellow warblers (Parkes 1961, Ficken and Ficken 1962). In general,

TABLE 8. A summary by warbler species of within-song repetition of phones and terminal accent. Genera in parentheses e.g. (D) = *Dendroica* (Table 1).

		Phone sequences			
No repetition: A only		Repetitions successive AA ... or AA ... BB			
No species	Cape May	(D)	N. Waterthrush	(S)	
	Bay-breasted	(D)	Yellow-rumped	(D)	
	Black-and-white	(M)	Black-throated Green	(D)	
	Redstart	(S)	Magnolia	(D)	
	Nashville	(V)	Yellow	(D)	
	Tennessee	(V)	Chestnut-sided	(D)	
	Wilson's	(W)	Canada	(W)	
(0)					(14)
ABCDEFG ...		Repetitions of multi-phone groups ABAB ... ABCDABCD ...			
Canada (W)	Blackburnian	(D)	Mourning	(O)	
	Bay-breasted	(D)	Common Yellowthroat	(G)	
	Nashville	(U)	Yellow-rumped	(D)	
	Tennessee	(U)	N. Parula	(P)	
	N. Waterthrush	(S)	Magnolia	(D)	
	Ovenbird	(S)			
(1)					(11)
		Terminal phone accented (i.e., not repeated)			
	Magnolia	(D)	Black-throated Green	(D)	
	Yellow	(D)	N. Parula	(P)	
	Chestnut-sided	(D)	Blackburnian	(D)	
	Am. Redstart	(S)			
					(7)

then, we have not found any generically distinctive sequential features of song except for the accentuation of terminal phones in some. Where this treatment occurs, however, not all songs of the same individual are so accented, as exemplified by redstarts and Yellow Warblers.

Accented songs stand out in a warbler's repertoire and they are given early, more than they are later, in the season. Hence, they may be especially suited to male-female interactions, possibly as attractants for females (Ficken and Ficken 1962; Morse 1966, 1967; Lein 1978; Kroodsma 1981; Monette and Lemon, unpubl. data). The remaining song(s) appear to serve different functions, which may not require species identification under conditions as extreme as low-signal-to-noise ratios. Close encounters between males would exemplify such conditions, as have been observed in redstarts.

The amount of information in the phones encoded in terms of modulation pattern differs considerably among warbler species. We would predict, therefore, that under standardized conditions of playback, species should differ considerably in response. Of course birds in Group 2 with phones of simple modulations, such as yellowthroats and waterthrushes, tend to sing the phones in repeated clusters that probably replace the continuous pattern of modulation.

Weeden and Falls (1959) and Falls (1963) manipulated the three phones, ABC, of Ovenbird song in playback experiments. Considering three possible combinations, they got decreasing responses from the maximum of ABC, to BC, random ABC, and ACB. Consequently, the rhythm and, to some extent, the frequencies seem important, C being the lowest after A and B. Wunderle (1979) found that Common Yellowthroats give a good response to repetitions of phone pairs in which one of the pair sweeps upward in frequency and the other downward in alternating fashion. In both species, simple frequency relationships and rhythm seem especially important, as we have found in this study.

Repertoires occur in Group 5, where the patterns of frequency modulation are greatest. There would seem to be strong pressures on the birds to discriminate the songs individually by the phone modulations, yet at least in redstarts, repertoires often differ among individuals.

Recognition can proceed in stages, as one appreciates when trying to identify persons at a distance or in unfamiliar circumstances. Likewise, birds hearing songs at a distance may make judgments that are not substantiated when the songs are heard more clearly (i.e., at high signal-to-noise ratios). It is possible that different sources of information have different values, depending on the circumstances. Ex-

perimental evidence, in fact, supports the view that certain parts of a song may be more important than others at certain times, especially over varying distances (Brenowitz 1981, Richards 1981). On the contrary, the different parts of a song may have complementary values, with the result that there is an overall additive effect (Shiovitz and Lemon 1980). The differences between these two approaches are somewhat semantic. Future experimental studies should consider the psychological literature on perceptual confusion beginning with Miller and Nicely (1955).

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