

Song features and singing heights of American warblers: Maximization or optimization of distance?

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By discriminant analysis we examined the multivariate relationships between quantifiable features of song and the usual rank of singing height in 19 species of warblers (Family *Parulidae*) resident in New Brunswick, Canada. We found a correlation of higher frequencies with higher singing heights, although the lowest singing group was not different from the second lowest in this respect. Associated with higher frequencies are repeated groupings of two phone types, low numbers of total phone types and fast frequency sweeps in the last phone of the song. Warblers with lower frequencies tend to have more phone types per song. Warblers singing at lowest levels, however, have large numbers of unrepeated phones or alternatively three to five separate phone types repeated in the series in their songs. Overall, the results indicate that in addition to frequency, structural characteristics of the songs are related to singing height. The results are not consistent with the view that warblers are maximizing the distance over which their songs are transmitted since low-frequency sounds should be preferred on an acoustical basis at most singing heights, if not the very lowest. Warblers may be producing songs which by their frequency and structure carry mainly to individuals of biological significance to the singers, probably individuals on adjacent territories. Other possible explanations are also considered.

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INTRODUCTION

A number of studies have indicated that physical attributes of natural environments may determine some of the features of animal sounds.¹⁻¹⁰ Often these studies have been concerned with problems of attenuation and other distortions of sounds produced by birds. For example, in reporting that the mean frequency of songs of American warblers (Family *Parulidae*) correlates positively and significantly with foraging height, Ficken and Ficken¹ suggested that the low-level singers used sounds of low frequency to carry further in an environment with obstacles. All these studies have emphasized one or a few, frequency-related features of the vocalization.

We have examined a broader spectrum of song features in relation to singing heights for 19 species of American warblers resident in New Brunswick. We consider the results relative to several current ideas presented in the biological literature.

I. MATERIALS AND METHODS

A total of 337 songs from 19 species of warblers (Table I) were recorded in June 1978 and June and July 1979 in an area within roughly 10 miles north or south of St. George, New Brunswick, Canada. Recordings were made by a Uher 4200 tape recorder, using a Dan Gibson microphone and parabolic reflector. The number of songs analyzed per species ranged from 7 to 39, with a mean of 17.8. Analysis of features of individual continuous sounds (here called phones) and of the whole song were made from sonograms (Kay Elemetrics, Pine Brook, NJ). In addition we measured the frequency of modal intensity in the power spectrum of entire songs as obtained from a ubiquitous spectrum analyzer (Federal Scientific).

Each song was characterized by 15 objective variables. These variables fell into two categories, those related to frequency and those related to temporal se-

quence or song structure. Frequency related variables included the maximum frequency and bandwidth for the entire song and for the song's last phone, and the frequency of modal intensity for the entire song. Structural variables for the entire song included duration, number of phone types, maximum number of a single phone type, and a measure of grouping pattern of phones. The last phone was characterized by its duration, the duration of the silent interval preceding it, and the rate at which frequency changed within the phone. These measures are reduced from 35 original variables which thoroughly described the frequency-related and structural characteristics of bird song (manuscript). In this paper we use the SPSS discriminant analysis programs¹¹ to compare the song characteristics of birds in four groups defined by the typical heights in the vegetation at which they sing.

We subjectively ranked species of warblers by singing height into four categories from high (A) to low (D) (Table I). The area in which we worked is an ecotone of coniferous spruce-balsam fir (*Picea-Abies*) and deciduous maple-birch (*Acer-Betula*) forests with the warbler species widespread across this vegetation continuum. Our estimates of singing height are relative to the available mature stands of the dominant forest types. Some species such as blackburnian and Cape May warblers sing mainly from the tops of tall conifers, whereas others, such as yellow-throats and ovenbirds sing close to the ground, either in low shrubs or open country in the first species or under mature deciduous forest in the second. We recognize that members of all of these species may at times sing at levels other than those stated but our estimates are based on where as naturalists we most often noted these birds at the time of recording.

II. RESULTS

Ficken and Ficken¹ used average frequency of songs from 16 species of warblers obtained from measures

TABLE I. Body length versus singing height of 19 species of wood warblers (*Family Parulidae*). Singing heights were first grouped by proximity from tree top to ground and then were placed from highest (A) to lowest (D).

Species	Singing height group	Average body length (cm) ¹⁴
(1) Blackburnian (<i>Dendroica fusca</i>)	A	12.7
(2) Cape May (<i>Dendroica tigrina</i>)	A	13.2
(3) Bay-breasted (<i>Dendroica castanea</i>)	A	14.0
(4) Tennessee (<i>Vermivora ruficapilla</i>)	A	12.2
(5) Black-and-White (<i>Mniotilta varia</i>)	B	12.7
(6) Nashville (<i>Vermivora peregrina</i>)	B	12.2
(7) Parula (<i>Parula americana</i>)	B	11.7
(8) Yellow-rumped (<i>Dendroica coronata</i>)	B	14.0
(9) Black-throated Green (<i>Dendroica virens</i>)	B	12.5
(10) Redstart (<i>Setophaga ruticilla</i>)	B	13.2
(11) Yellow (<i>Dendroica petechia</i>)	C	12.7
(12) Magnolia (<i>Dendroica magnolia</i>)	C	12.2
(13) Chestnut-sided (<i>Dendroica pennsylvanica</i>)	C	12.5
(14) Mourning (<i>Oporornis philadelphia</i>)	C	13.7
(15) Ovenbird (<i>Seiurus aurocapillus</i>)	D	15.2
(16) Northern Waterthrush (<i>Seiurus noveboracensis</i>)	D	14.0
(17) Yellowthroat (<i>Geothlypis trichas</i>)	D	13.0
(18) Wilson's (<i>Wilsonia pusilla</i>)	D	10.7
(19) Canada (<i>Wilsonia canadensis</i>)	D	13.7

of the maxima and minima provided by Brand,¹² and related these to the subjective rankings of foraging heights of the species into high, medium, and low as provided by Griscom and Sprunt.¹³ They found a positive correlation of such heights with mean frequency. We related the Ficken's data to average body length as provided by Godfrey¹⁴ and found a significant correlation of frequency with this measure (Spearman's $r = +0.76$, $P < 0.01$). Hence in the Ficken's data, the largest warblers which sing near the ground sing the lowest frequencies and, to some extent, the converse is true. Therefore the correlation of song frequency with singing height could be secondary.

Based on averages of maximum and minimum frequencies of each song, we subjected our own data to a correlation of mean frequency of song with average body length. This yields a correlation coefficient of only +0.12, a value not close to significance. Hence in our data the importance of frequency is to a great extent

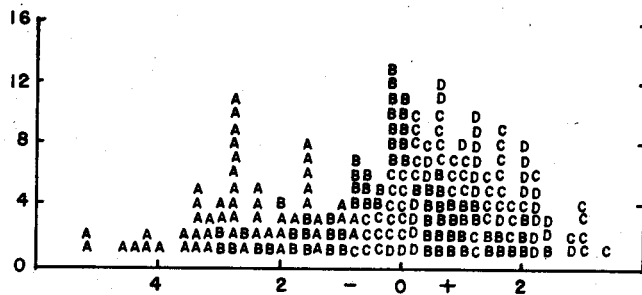


FIG. 1. Single function discriminant analysis of singing height groups (A highest to D lowest) using only frequency-related variables. Histogram shows frequency of songs by coefficient interval. The function accounts for 91.5% of the information in the raw data and is highly significant by the Wilks' λ criterion ($p < 0.0001$).

independent of body size, so that its correlation with singing height would therefore seem of biological significance as originally interpreted.

To examine further the relationships of frequency variables to singing height, we performed a discriminant analysis using seven measures of frequency: the maximum and minimum frequency in the first measurable phone, the last phone, and the whole song, and the modal frequency of the entire song. These multivariate descriptors show a trend in songs from the highest-level singers (Fig. 1). Group A singers stand out clearer than the rest as members of groups B, C, and D intermingle.

Four frequency variables of song are examined independently and by species in Fig. 2 to illustrate the primary univariate relationships underlying the multi-

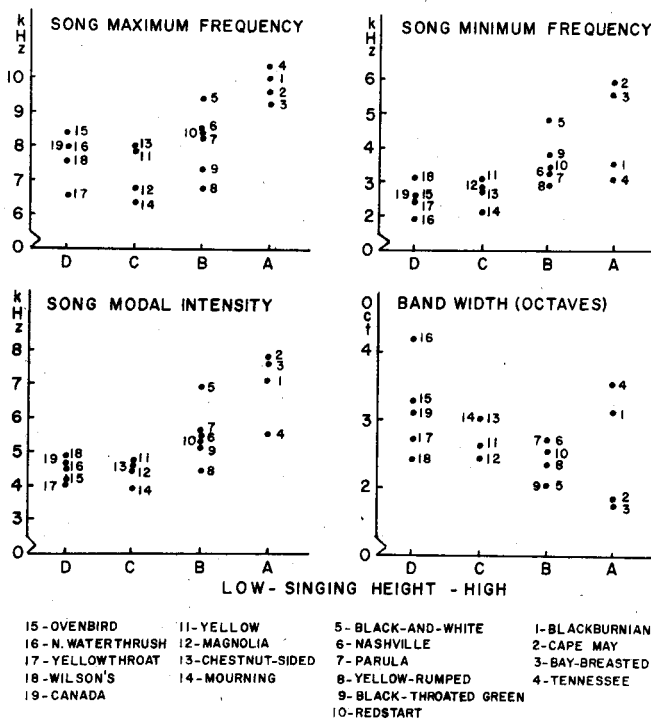


FIG. 2. Mean values by species of some frequency variables used in discriminant analysis of Fig. 1, except bandwidth, which was not so used.

variate trend. The highest values for all four variables are found in group A warblers, three of whose members, bay-breast, Cape May, and blackburnian, sing high in conifers. The Tennessee warbler differs most from the others in group A with the lowest frequency of modal intensity (Fig. 3). Its songs and those of the blackburnian warbler have the broadest frequency sweeps in the group. However, species in group A do not have the highest values in all cases: Black-and-white warbler, placed in group B, has high values also. There is a downward trend in bandwidth from low-level (D) to high-level singers (A), although group A tends to be split. (Bandwidth was not used in the discriminant analysis.) It is worth noting that the lowest singers (group D) differ little from group C across these variables, except possibly in wider bandwidths. Sonograms in Figs. 3, 4, and 5 illustrate typical songs by species and emphasize the necessity for multivariate characterization of these songs. Despite the strong effect of a few univariate trends (Fig. 2), the multivariate relationships in Fig. 1 reflect dependence on interrelated frequency variables that more fully characterize a given song.

There are features of song other than those of frequency which might also relate to singing height. Consequently, we performed a multiple discriminant analysis using only three frequency variables of songs and 12 of other details of the phones and sequential aspects of the whole song. These variables listed in Table II are essentially self-explanatory. However, the following require some comment.

A phone type is a subjectively judged pattern type of individual sound, the number of such types being judged for each song. Maximum phone types is the largest number of any type per song. Last phone interval is the time interval immediately preceding this phone. In some songs, phones of different types occur in repeated series as illustrated in the songs of Fig. 5. In these particular examples, four phones are repeated

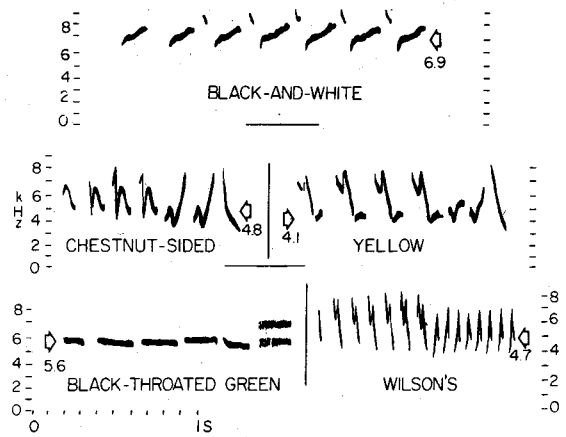


FIG. 4. Representative songs of warblers in groups B, C, and D. Note accented endings of chestnut-sided and yellow warblers wherein last phone is not a member of a preceding group and hence stands out. Song of Wilson's warbler included here because its songs differ somewhat from those of most in group D (see Fig. 5). Song of Wilson's warbler has a different frequency scale from others.

in groups in the yellow-throat, whereas three phones are repeated by the ovenbird. Combinations of such repetitions can occur as in the waterthrush song with sequences of 2, 2, 1, 1. In the song of the Canada warbler illustrated, only one repeated pair occurs.

The last phone of many warblers stands out as different from the preceding repeated phones or groups of phones. This "accenting" feature is characteristic of many songs used by chestnut-sided and yellow warblers as shown in Fig. 4. It should be noted that the literature on warbler songs often used the term "accented" in reference to particular songs in the repertoire of an individual whereas by the definition used here, the repertoire considered might have more than one accented song. Finally, the sweep rate of the phone is the rate of frequency change of the longest continuous sweep in the same "direction."

The discriminant analysis using the 15 variables of

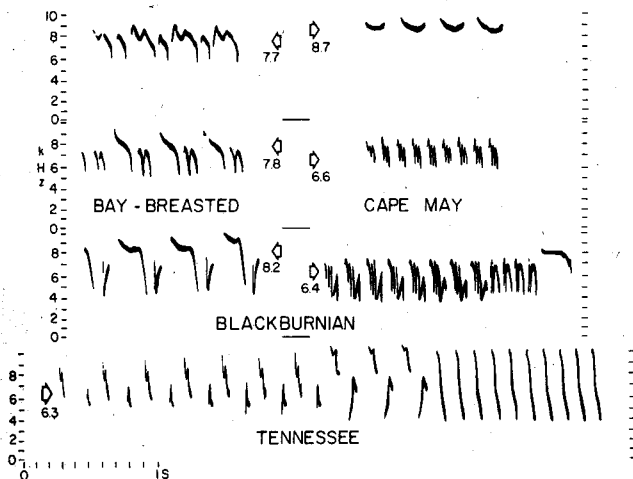


FIG. 3. Representative songs of warblers in group A (highest singing height). Different songs of three species intended to illustrate occurrence of repertoires of songs in individuals. Arrows show frequency of modal intensity.

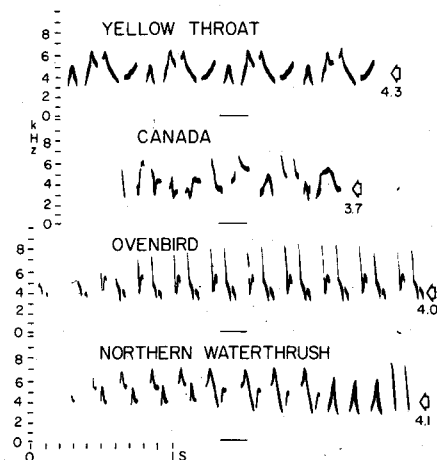


FIG. 5. Songs of certain warblers in group D, notably those with several phones per group, or in the Canada, different phones usually of entirely different types.

TABLE II. Standardized canonical discriminant function coefficients for 15 variables in a discriminant analysis of singing height groups (S—song, LP—last phone). The larger the absolute value of the coefficients for a character, the greater the influence of that character in the analysis.

Function 1		Function 2	
Bandwidth (octaves)	+0.3199	Phone types	+0.4339
LP accented	+0.2208	Bandwidth	+0.3056
Phone types	+0.1871	S Frequency modal intensity	+0.2563
Phone group 1	+0.0866	Phone group 4	+0.2276
S duration	+0.0018	Phone group 5	+0.2095
S Maximum frequency	-0.6836	S duration	+0.1579
S Frequency modal intensity	-0.4729	Phone group 3	+0.1465
Phone group 2	-0.3955	LP sweep rate	+0.1336
Maximum phone repetitions	-0.3263	Interval preceding LP	+0.0804
LP sweep rate	-0.2507	LP duration	-0.6236
LP duration	-0.1514	Phone group 1	-0.4832
Phone group 3	-0.0812	LP accented	-0.4607
Interval preceding LP	-0.0444	Phone group 2	-0.4373
Phone group 5	-0.0422	S Maximum frequency	-0.0929
Phone group 4	-0.0044	Maximum phone repetitions	-0.0358

Table II effectively separated the four singing height groups and did so much better than the discriminant analysis using seven frequency variables alone (Fig. 6). Function 1 clearly separates group A through C, while function 2 separates group D from the rest.

Separation on function 1 is mainly by high negative scores of group A in frequency variables, song maximum frequency and frequency of modal intensity. Phones in repeated groups of two and many repetitions of the same phone as well as other variables also contribute (Table II). On the positive side are high scores for bandwidth, last phone accented, and others.

Differences across the four groups seem to be linear in phone types, group D having the most (Fig. 7).

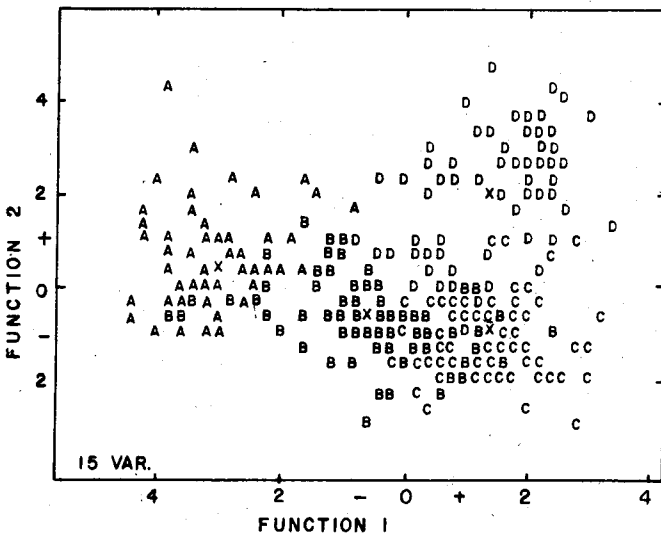


FIG. 6. Discriminant analysis of singing height groups (A highest to D lowest) as determined using 15 variables related to both frequency and structural characteristics of the song. Together the two axes account for 91.9% of the information in the raw data; both axes are highly significant by the Wilk's λ criterion ($p < 0.0001$).

Other univariate relationships (Fig. 7) tend to be less clear and sometimes groups A and D seem to be more similar overall than do the other two groups despite their clear multivariate separation. Last phone especially contributes to the more similar location of groups A and D on axis 2 (Fig. 6, Table II). However, group D stands out from the rest in having, on the one hand, either more ungrouped phones (Canada warbler, Fig. 5), phones in groups of two as in the waterthrush (Fig. 5), or alternatively more phones repeated in groups of three to five, as in the yellow-throat and ovenbird. This suggests then that the lowest singers differ from the others in temporal sequencing of phones.

III. DISCUSSION

There has been considerable recent interest by physicists as well as by biologists in the effects of environmental factors on the transmission of sound, with detailed reviews now published.^{15,16} A number of important physical factors have now been identified and quantified. These include attenuation with distance, temperature, and humidity; wave interactions resulting in either reinforcement and interference or reverberations; amplitude variations; background noise; and others. Actual situations can be enormously complicated with several of these factors being involved.

It is assumed that animals facing problems of sound transmission can accommodate by structuring signals in ways to insure their sufficient integrity at biologically important receivers. In apparent consequences of the foregoing, correlations have been noted between certain features of bird sounds and the environments in which they are used. Chappuis² noted that in African birds, sounds of comparable or identical taxonomic groups were lower in frequency in areas of high vegetation density than in more open or semi-open areas. He offered limited experimental evidence to support the argument that sound signals traveled further at lower frequencies in the closed environment.

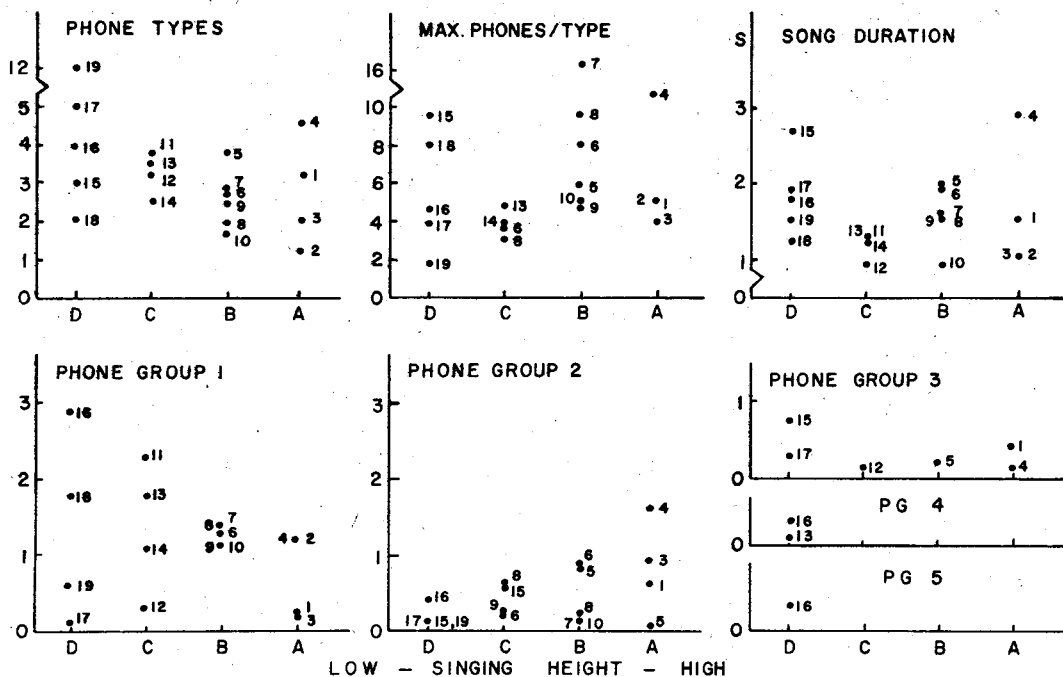


FIG. 7. Mean values by species of several variables used in discriminant analyses. Phone groups refer to number of types occurring singly (1) or in repeated groupings of two to five. For example, yellow-throats (Fig. 5) have phones repeated in groups of four. Species numbered as in Fig. 2.

Morton³ broadcast sounds of different frequencies and at different height from the ground in certain habitats in Panama: under forested canopy, forest edge, and grassland. In the forest he found a sound "window" with relatively little or no excess attenuation between frequencies of roughly 1.5 to 2.5 kHz. In forest edge and in grasslands, no such windows occurred; instead attenuation was directly related to frequency. He presented evidence that forest birds on average emphasized frequencies in the "window" range and also used sounds with slow modulations of frequency. In the other habitats, birds used higher frequencies and sounds of faster modulation. In the latter habitats he argued that information transmitted through frequency modulation should be more distorted and that instead the birds should use sounds with more timing information as apparently given by more rapid frequency modulations. Flight songs were particularly common among grassland birds, apparently avoiding some of the attenuation problems associated with low levels. He assumed that song is "used for communicating over relatively long distances" and that "selection should favor the use of sounds that give the greatest broadcast area for the given sound pressure level."

Marten *et al.*⁵ followed Morton's studies by broadcasting sounds in three habitats in Panama. The three areas constituted gradations in maturity of tropical lowland secondary forest. At the heights of transmission studied, up to 12 m, the vegetation was thicker in the younger forests. Above 1 m, lower frequencies carried better than higher. At 1 m and on the ground, sounds below 2 kHz attenuated more. They found "sound windows" in all habitats and restricted close to the ground in most. They suggest that such may occur in open country with short grass as well.

Bowman⁹ claims that songs of Galapagos Island finches are locally adapted to sound transmission

properties of different islands. In particular, the frequency of modal amplitude of songs is adapted to "least disturb the integrity of the sound signal over the greatest distance." Evidence in support of this claim was gathered from songs of three species of finches and from transmission of sounds from a standard source 1 m in height from the ground. In his study, however, song frequency of modal intensity apparently correlates highly with body size and mean width of internal tympaniform membrane.

Richards and Wiley¹⁰ examined two sources of signal degradation other than attenuation. These were amplitude, fluctuations, and reverberations. Amplitude modulations should have little effect on the frequencies perceived in the range used by most song birds. Reverberations, on the other hand, can have a serious effect on the signal. They found that reverberations were especially important for signals of low frequency (below 2 kHz) or high (above 8 kHz). At lower frequencies, the reverberations occur as clear echoes, whereas at higher frequencies they are present as long, indistinct echoes lasting up to 250 ms.

A. Frequencies and singing height

We can consider the correlations of song features of warblers with singing height in relation to possible explanations or hypotheses. We shall deal first with the dominant features of frequency. A number of possibilities may be suggested to explain the observed relationships.

(1) We have rejected the relationship of frequency with body size, assuming the laws of proportionality to apply to the syrinx as well as to the body length. Note, too, that the largest warblers, ovenbirds and waterthrushes, in our study do not sing frequencies as low as might be expected if this trend were to apply, in

fact, the songs of group D are no lower than group C. Although it does not apply to our data, we have noted that a frequency-size relationship apparently applies to Galapagos finches, and certainly applies across species groups, although it is rarely considered in biological studies to date. Our own analysis assumes not only reliability of the data, but that one measure of size, body length, is a true index of body size.

(2) The choice of frequencies by warblers might relate to the need to maximize the distance over which their signals may travel. If this were the case, however, we should expect them to avoid high frequencies because of the stronger effects of attenuation with frequency in relation to distance.¹⁷ For birds singing in foliage, reverberations should also be stronger with high frequencies.¹⁰

A reader of the manuscript for this study suggested that high-frequency singers could compensate for attenuation by singing louder. This may indeed be so, but it would not explain the claimed frequency-height relationship.

(3) Considering frequencies simply in relation to supposed transmission "windows," the correlation of singing height with frequency would require such windows at all levels used. Experimental studies in a number of field sites indicate that such windows are restricted to levels close to the ground.⁵ There is a suggestion that a window occurs between 1 and 3 kHz in northern deciduous forests occupied by some of our species.⁴ However, none of our warblers sing mainly in this low-frequency range.

(4) It may be that partitioning of frequencies is a way of avoiding jamming by other species or simply the effects of background noise. If larger birds of other taxa which use even lower frequencies were to sing closer to the ground, then the relationship we found might arise. But there is no reason to believe that they do.

(5) There is evidence that warblers interact inter-specifically. Species at roughly the same foraging or singing heights might be expected to interact most. In some species, such as yellows and chestnut-sideds, the songs and phrases are often strikingly similar (Fig. 4). The same applies to the songs of the species singing from tops of conifers (Fig. 3). However, one would hardly expect the simple relationship of frequency and singing height observed.

(6) One last suggestion remains which may be more satisfactory. It is that warblers are not trying to maximize the distance their songs carry but rather are optimizing the distance, sometimes greater, sometimes lesser, so as to communicate mainly with those individuals who are most significant to them biologically.

To expand this point, there are five classes of individuals of the same species toward whom another warbler might direct its songs: immediately neighboring males holding territories, males of a floating population who do not have territories, and either un-

mated or mated females, and their offspring. The territories of neighboring males are apparently stabilized by a number of factors, including song. The floating population of males is probably looking for empty territorial spaces, especially in species with high densities or limited habitat. The females early in the season are seeking mates. In these last two cases one might expect the males to sing as loudly as possible in order to repel intruders and to attract the mates. As far as the intruders are concerned, however, it is possible that males might be equally attracted from afar as much as repelled. The "Beau Geste" hypothesis of Krebs assumes repulsion.¹⁸

There is evidence that warblers take steps to increase or decrease the distance over which their songs travel. Some species in our group D have long complicated flight songs. Ovenbirds, for example, occasionally use such songs above the forest canopy much higher than their usual singing level. No such songs were analyzed here. Waterthrushes apparently do the same.¹ Yellow-throats leave their usual singing sites in shrubs close to the ground to sing above shrubs in the open, perhaps 10 m above the ground. One such song was included in our analysis. Also, although we have not emphasized the point, many species of warblers have repertoires of songs (see Fig. 3) and they switch from one song or set of songs to another depending somewhat on the circumstances. Redstarts, for example have 4 to 7 songs per male. Most of these are used when singing directly against neighboring males. The impression to the listener is that redstarts sometimes sing more quietly with a number of these songs than when using a particular "accented" song often used more centrally in the territory away from the neighbors. The accent is of low frequency, a fact that may help the song to carry further. Lein¹⁹ makes a similar argument for songs of chestnut-sided warblers. However, our overall impression is that warblers tend to sing at the same amplitude output for all but short distance interactions.

Obviously, the distance over which sounds might be important could relate to density of the species. In practice densities can vary enormously, by situation, species, and year. Consequently, in spite of published accounts, one would have to gather much information on a number of related aspects, including song, to make any critical assessments. We note that often one finds males apparently countersinging against each other at close distance as if by choice and without regard to density.

If this last hypothesis (6) is valid, then the following interpretation of the song-frequency singing height relationship should prevail. Those warblers singing at the tops of conifers limit the carrying power of their songs by singing at high frequencies. Directionality should not be greatly increased at the frequencies used since the heads are small. Warblers at lower levels in the forest, deciduous or coniferous, face increasing problems from obstacles like foliage, branches, and tree trunks, and perhaps noise from other species of warblers or other birds; overall then, it becomes more important to use lower frequencies in songs.

Moreover, in lower vegetation structural song features may become more important as high-frequency transmission becomes more quickly attenuated.

B. Low-level singers

Of additional interest is the separation of the lowest singers, group D, from group C. One could not argue that they were simply misclassified as a separate group for the songs of four group D species would still separate from the others of group C, the exception being those of the Wilson's warbler. However, it may be that the four species for the most part do not sing closer to the ground than do the warblers in group C; instead they might be separated by other reasons. Ovenbirds often sing close to the forest floor where they feed and nest, their congeners the waterthrush sing in similar areas but along streams, and yellow-throats sing in open areas covered with shrubs. The Canada warbler sings often from thickets, but only a few feet above the ground. Birds in group C sing close to the ground but often higher as well.

Group D species differ from the others in having large numbers of phone types (Canada) or phones in groups of up to five in the waterthrush, ovenbird, and yellow-throat. These facts suggest that these warblers are employing possibly the overall temporal rhythm of the song rather than the details of the frequencies. The reasons for this may be different in the different locations.

Most warblers in groups C and D sing loudly to our ears, with the ovenbird and waterthrush appearing possibly the loudest in three groups. The reason for the high intensity may be associated with the low singing height, or it may be that these species send their songs over longer distances in relation to lower population densities. The yellow-throat lives in open areas where distortions of wind and of density of air by temperature are likely to be strong.

C. Reverberations

Those warblers living under or in forest canopy would seem especially influenced by reverberations, the species most likely affected including ovenbird, waterthrush, Canada (group D), Tennessee (group A), and Nashville (group B).

From their experimental studies, Richards and Wiley¹⁰ argue that birds might avoid or reduce effects of reverberations in the following ways:

(1) They should avoid singing at either low frequencies (below 2 kHz) because they produce strong echoes, or above 7 kHz because of the strong but indistinct reverberations.

We note that our low-level frequency singers avoid such problems by not singing in these frequencies. Note, again, that the largest of these, the ovenbird and waterthrush, do not sing any lower than their somewhat smaller warblers of groups C and D.

By way of comparison at the upper end of the scale, the highest frequency singers do so in the open where reverberations do not occur. The one possible excep-

tion to this is the Tennessee warbler which often sings in foliage. However, its modal frequency lies well below the main problem frequency (also see below).

(2) Songs might incorporate slowly modulated sounds. Such were noticed in the under the forests canopies by Morton³ in Panama. None of our warblers use such, with the exception of the black-throated green which sings some phones with hardly any modulation at all (Fig. 4).

(3) It is the nature of reverberation or echo that the frequencies and their structure replicate the signal to varying extents. Consequently, if successive phones in the songs have different FM patterns, then they should retain some recognizable integrity; and

(4) Alternatively the phones may be separated by longer intervals such that the decay of the reverberations will have reduced their importance. This would be the case with time intervals of longer than 50 to 100 ms.

The songs of the ovenbird include clusters of phones which replicate in part the frequency sweeps of those immediately preceding (Fig. 5). Also some are considerably closer than the minimum duration proposed. Reverberations are especially noticeable in recordings of this species.

In songs of the Tennessee warbler (Fig. 3), the successive phones are simple frequency sweeps which are often identical. Should reverberations occur, they might have strong masking effect. In this case, though, the intervals between such phones are somewhat longer, say 60 ms. In the waterthrush and Canada, the FM patterns of phones may avoid echoes.

D. Attenuation and bandwidth

Perhaps overall, the most predictable effect on sound is attenuation of amplitude with distance, which is directly related to frequency as well as to other factors like temperature and humidity.¹⁷ Therefore, with increasing distance, a song with broad frequencies will progressively lose more and more information from the high frequencies down. Looking over different species, then, one can predict rather dramatic effects by such filtering if one assumes the same distances and amplitudes involved. For example, let us imagine that the distance and attenuation are such as to effectively remove all frequencies above 8 kHz. Then one song of the Cape May would be completely lost (upper right, Fig. 3); much of the Tennessee song would be lost but the loudest part would be retained (Fig. 3); and none of the yellow-throat song would be affected (Fig. 5).

A number of important corollaries of this effect may now be recognized. One is that narrowband signals can give sharp focus for distance and the higher the frequency the sharper it is. Very few species of any taxonomic group use this principle. In the warblers the high-frequency singers have songs which have much emphasis in a narrow range which would seem to make these particular songs especially sharp. Note that each species of these high-frequency singers has also another song which is much broader in bandwidth.

Actually, the black-throated green warbler has the narrowest band of all (Figs. 2 and 4). In the white throated sparrow (*Zonotrichia leucophrys*) which sings narrowband whistles, higher frequencies occur in more open country.²⁰ Since most species cannot afford the luxury of limiting distance so finely, the FM signals are likely to be more useful in general, as seems to be the case with warblers.

We note that Roberts *et al.*,²¹ have produced a model to explain the results of Marten *et al.*,⁵ based on certain assumptions. One prediction of this model is that bandwidth should increase with frequencies, a feature which does not apply clearly to warblers.

One might argue that with a large number of species involved, the simplest way to achieve a song characteristic of the species might be to restrict it to a particular bandwidth. One can see, however, that the tuning would have to be as fine as AM radio, and such might be impossible to achieve across so many species over large geographic areas. The use of frequency modulation through a broader bandwidth allows the carrying of large amounts of information in the channel.

In addition to advantages of frequency modulation, one should recognize advantages of either separate phones or continuous sweeps with changes in direction of sweep. Although we have not analyzed this in detail, it does appear that in a number of species, change in direction of sweep occurs more at higher frequencies than at low and hence should be more sensitive to attenuation.

This filtering with distance could have important effects on species recognition especially for non-neighbors, floaters, females searching for mates, or for occasional contacts. Although experimental studies suggest that songs have more information in them than is essential for species identification, identification as such may not be an all or nothing process, but may be quantitative on the basis of available information. Thus warblers may respond to some extent to songs of other species.

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