

THE IMPORTANCE OF INVARIANT AND DISTINCTIVE FEATURES IN SPECIES RECOGNITION OF BIRD SONG¹

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Abstract. Two hypotheses concerning the relative importance of different acoustic features in species-song recognition were examined. The invariant-features hypothesis predicted that a feature's accuracy in song recognition is inversely proportional to its intraspecific variability, as expressed by the coefficient of variation. The sound-environment hypothesis assumes that both variability and a feature's central tendency relative to other species in the local acoustic environment determine a feature's importance in species-song recognition. These hypotheses were compared in an acoustic analysis of 14 features of songs of two focal species, the Field Sparrow (*Spizella pusilla*) and Chipping Sparrow (*S. passerina*), and 11 other species found in open habitats in the eastern United States. In both focal species, maximal note frequency was one of the two least-variable features within conspecific song, and the most accurate single feature in classifying songs in a canonical discriminant analysis. In neither species was a feature's accuracy in classifying songs correlated with its relative variability within conspecific song. These results, in conjunction with recent experimental studies, contradict the common assumption in the literature that invariant features provide the most important song recognition cues.

Key words: *Bird song; species recognition; Chipping Sparrow; Field Sparrow; discriminant analysis; song variation.*

INTRODUCTION

Breeding birds must recognize their own species' song against a background of songs from many other species. For north-temperate songbirds this is particularly true during the "dawn chorus" when song activity is at its daily peak. The attributes of song used in species recognition have been extensively studied (reviewed in Becker 1982). Two hypotheses have been advanced to predict which attributes songbirds use to discriminate conspecific songs from the songs of other species occurring in the same habitat.

One hypothesis predicts that song features that vary little intraspecifically (hereafter referred to as "invariant features") will be preferentially used in song recognition (Marler 1960, Falls 1963, Emlen 1972) because such features would be less likely to overlap with other species' songs. Emlen (1972) concluded from his study of Indigo Buntings (*Passerina cyanea*) and a review of four other studies that only invariant song features provided important recognition cues. This conclusion was repeated by Becker (1982) in his literature review. However, Emlen (1972) noted that not all invariant song features were appar-

ently used by the birds, and a recent study has shown that variable features are used in species recognition by Eurasian Blackbirds, *Turdus merula* (Dabelsteen and Pedersen 1985). These results raise questions about the predictive ability of the "invariant-features hypothesis."

A second hypothesis, hereafter referred to as the "sound environment" hypothesis, emphasizes the relationship between a species' song and the songs of sympatric species in "acoustic space" (Marler 1960; Emlen 1972; Brémond 1976, 1978; Dabelsteen and Pedersen 1985) in predicting which features provide accurate song-discrimination cues. Acoustic space is a multidimensional representation of song structure, formed by measurements describing song (e.g., frequency, song duration). The sound-environment hypothesis assumes that variation is only one component of species distinctiveness; the other component is the separation between mean values (or other measure of central tendency) of different species along whatever acoustic dimensions are believed to play a role in song recognition (Miller 1982). If an invariant feature's mean was similar to that of other species the feature would not provide reliable information about species identity. This latter possibility could explain Emlen's finding that not all invariant features within a species' song seem to be used in song recognition.

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There has been no quantitative attempt to compare these two hypotheses, although Lemon et al. (1983) analyzed song features as discrimination cues in warbler communities. In this paper I describe patterns of variation in songs of the Field Sparrow (*Spizella pusilla*), Chipping Sparrow (*S. passerina*), and 11 other species that inhabit old fields in the eastern United States. My goal was to identify acoustic features of songs that, according to either the invariant-features hypothesis or the sound environment hypothesis, might encode information about species identity in Field Sparrows and Chipping Sparrows. Experimental attempts to identify species-distinctive features of songs have been limited to comparing the songs of two or three closely-related species (e.g., Becker 1976, Boughey and Thompson 1976, Romanowski 1979, Peters et al. 1980). However, the most difficult song-discrimination problems do not necessarily arise among congeneric species. My goal in comparing sympatric close relatives was to examine, in light of the two hypotheses just described, whether species differences in the use of song-recognition features were predictable, and whether invariant features were also necessarily the best cues for discrimination.

Here I employ a canonical discriminant analysis to identify song features that discriminate Field Sparrow or Chipping Sparrow songs from those of 12 other species. Discriminant analysis is a multivariate technique that reduces a set of variables to a smaller set of variables that maximally separate groups, in this case, species. I use it here to model the process of acoustic pattern recognition in a local community of birds. One component of pattern recognition is feature extraction, the process of identifying a smaller set of variables that efficiently describe the stimuli, yet are capable of distinguishing stimuli belonging to different classes (e.g., conspecific vs. heterospecific song). Thus, feature extraction involves a reduction of dimensionality in which some potentially misleading or distracting information is discarded, while perceptually important distinctions are preserved (Howard and Balas 1981, Schleidt 1982).

METHODS

SONG RECORDINGS

In addition to Field and Chipping sparrows, 11 other species were chosen to be studied because

they were commonly found in old fields in Dutchess County, New York, and most had a simple song structure that could be described by a few measurements. Representative sonograms of songs from each species are shown in Figure 1. The Rufous-sided Towhee (*Pipilo erythrophthalmus*) and Song Sparrow (*Melospiza melodia*) were exceptional in that many syllables comprising their songs had a complicated structure composed of many elements (see below). Towhees were added to the analysis after four towhees approached some of the initial song playback tests I made to male Field Sparrows (Nelson 1988). Prairie Warblers (*Dendroica discolor*) sing two or more song types (Nolan 1978). Only songs composed of tonal notes ("Group B" songs, Nolan 1978) were included in this analysis. White-throated Sparrows (*Zonotrichia albicollis*) and Dark-eyed Juncos (*Junco hyemalis*) migrated through the study area and sang simple songs. Swamp Sparrows (*M. georgiana*) also sang simple songs and occupied territories near Field Sparrows or Chipping Sparrows.

Song recordings came from four sources: the Library of Natural Sounds at the Cornell Laboratory of Ornithology, the Borror Laboratory of Bioacoustics, record albums (Federation of Ontario Naturalists, Vol. 4, Warblers and Vol. 6, Finches), and recordings I made in Dutchess County from 1984–1987. One song per individual bird was sampled, with the exception of five songs (of different types) sung by one Yellow Warbler (*D. petechia*).

SONG MEASUREMENTS

Songs of six species (Group I species: Chipping Sparrow, Field Sparrow, Prairie Warbler, Rufous-sided Towhee, Northern Cardinal, *Cardinalis cardinalis*, and Tufted Titmouse, *Parus bicolor*) were analyzed on a Kay Elemetrics Model 7800 Digital Sona-Graph. Measurements were made using a plastic overlay. Note-level (see below) temporal variables were measured on amplitude-time plots or sonograms made with the 300 Hz analyzing filter to the nearest 3 msec. Frequency measures were made on narrow-band (40 Hz filter) sonograms to the nearest 80 Hz. Songs of the remaining seven species were analyzed on a computer-based analysis system (Engineering Design 1987). Songs were displayed as spectrographic plots on a computer terminal. Sixty-four point (temporal resolution = 3 msec) and 256 point (frequency resolution = 81 Hz)

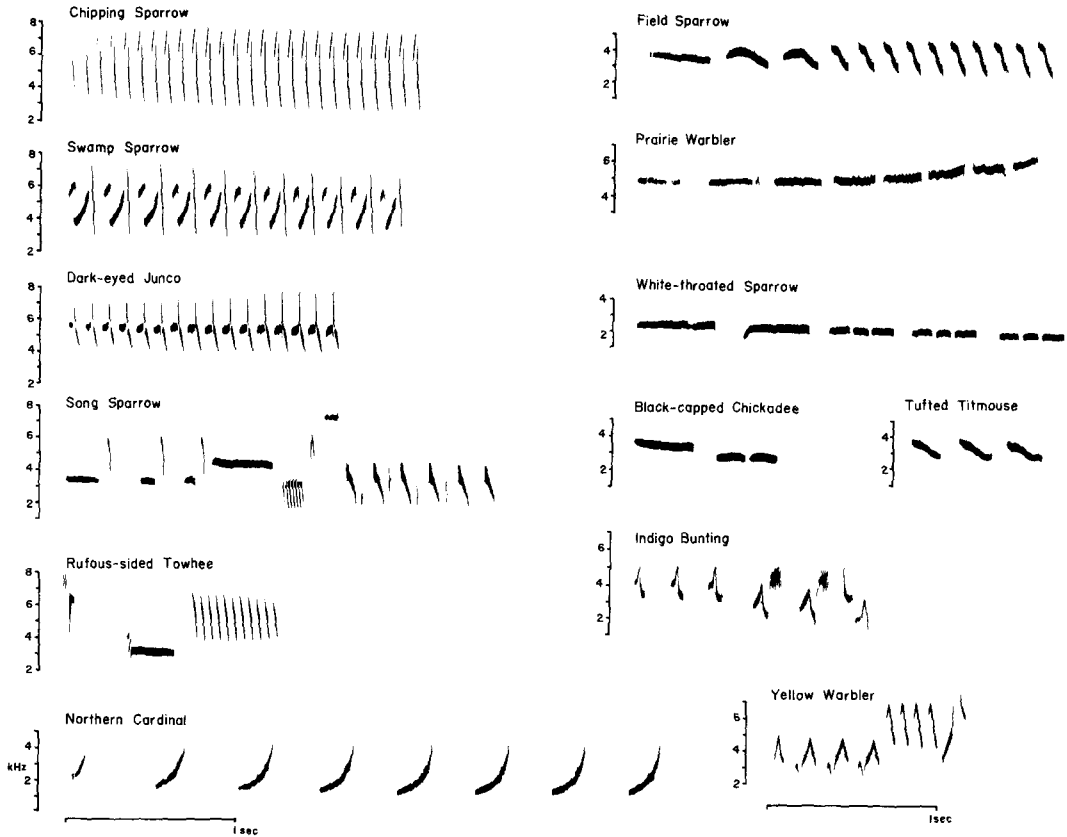


FIGURE 1. Wide-band (300 Hz filter) audiospectrograms of the songs of each of the 13 species studied.

digital Fourier transforms were used to produce the plots for temporal and frequency measures, respectively. Measurements were made with a graphics cursor.

Fourteen variables were measured on each song (Fig. 2). Three variables (song duration, number of phrases, and number of notes) described the entire song. A note was defined as a sonogram tracing not interrupted by more than 3 msec of silence. A syllable was defined as a repeated unit composed of one or more notes. A phrase was defined as a sequence of repeated identical syllables (trill) or a sequence of unrepeated notes. Thus, for a song to contain two or more phrases, it had to contain at least one trill.

A limitation of multivariate statistical methods is that they require complete data for each observation. Because some species sang songs composed of only one syllable type, I could only include one note or syllable from each song. To

include replicate measurements of identical syllables would create problems due to singular group covariance matrices in the discriminant analysis. I randomly chose one phrase from each song, and selected one syllable or note from it for measurement. Notes were chosen from the middle of trill phrases and were randomly-chosen from nontrill phrases.

I tried to devise a framework that represented acoustic variation across a diverse sample of notes. After preliminary visual examination of sonograms, I measured note duration, internote interval, and number of elements within a note (Fig. 2). An element was defined as a note subunit with nearly constant rate of frequency modulation, separated from other such units by a "marked" change in FM. Marked changes in FM were judged visually, and were usually obvious, although some Northern Cardinal and Tufted Titmouse elements consisted of frequency sweeps

in which the FM rate changed constantly at a uniform rate, thereby describing a semicircle on a sonogram. These were coded as one element. Most of the species considered here sang syllables composed of one note. For those species in which syllables were made of two or more notes separated by silence, I ignored the intrasyllable internote intervals, and measured the variables described below on the first two elements within each syllable.

Four variables were measured on each of the first two elements within a note: maximal and minimal frequency, element duration, and rate of frequency modulation (FM). The four frequency variables measured on each note proved to be highly correlated. In all subsequent analyses I used two frequency variables: note maximal and minimal frequency. To preserve information about the direction of FM, frequency upsweeps were coded as positive rates, and downsweeps as negative rates. A constant was added to FM rates prior to their being log-transformed. All variables except number of elements and number of phrases were log-transformed to better approximate normality and equal variances.

A limitation of this system is that it did not fully describe the element structure of notes with more than two elements. Ninety-five percent of Chipping Sparrow, Field Sparrow, and Prairie Warbler notes had one or two elements, but only 51% of the remaining species had two elements or less. Single-element notes (28% of 347 notes) were bisected, and element durations and frequencies were measured as if the notes were composed of two elements each with half the total note bandwidth and duration.

STATISTICAL ANALYSES

Relative variation. I used Levene's median-ratio test (Sokal and Braumann 1980, Schultz 1985) to compare relative variation within species of three song variables and seven of nine note variables. Duration and FM rate of the second element within a note were excluded from the analysis because their coefficients of variation were nearly identical to the corresponding measurements made on the first element. Fifty-one Chipping Sparrow songs and 60 Field Sparrow songs were used. Schultz (1985) recommended Levene's test using the median as a measure of central tendency as a robust test of relative variation. Each variable is transformed as:

$$|x - \text{Median } x| / \text{Median } x$$

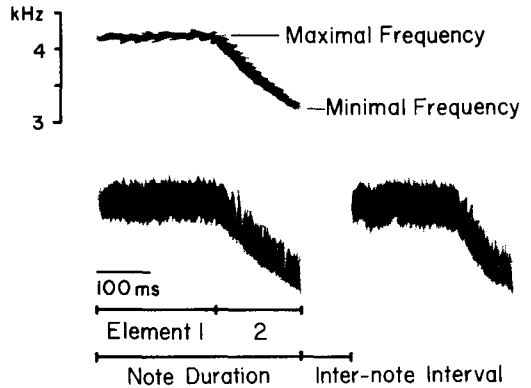


FIGURE 2. An illustration of a Field Sparrow note, and six variables measured on every note. The two note frequency variables were measured on narrow-band spectrograms (40 Hz analysis, top) and four temporal variables were measured on wide-band spectrograms (300 Hz analysis, bottom). The frequency modulation rate of each element was calculated as: (Element maximal - minimal frequency)/element duration.

The null hypothesis that the relative variation across all 10 transformed variables was the same was tested with a Kruskal-Wallis nonparametric ANOVA with each variable treated as a group. Pair-wise comparisons between variables, with $P < 0.05$ were made using the procedure described in Conover (1980). The mean rank of each group in the ANOVA was used to order variables by their relative variability.

Distinctive features. To test whether songs recorded in Dutchess County differed from songs obtained from other sources, two-group discriminant analyses using all 14 variables were performed for each Group I species. I had too few recordings for the remaining species to perform this check.

To equalize sample sizes across species, half the songs from each primary species were randomly allocated to one of two sets: a modeling set, and a validation set. The modeling set was combined with all songs from the seven remaining species for use in the discriminant functions analysis to find variables that effectively discriminated either Chipping Sparrow or Field Sparrow song from songs of the other species. The validation set was reserved for testing the predictive ability of the model derived from the modeling set.

Canonical discriminant analysis was used to identify song features that distinguished the songs of either target species (Chipping Sparrows or

TABLE 1. Rankings of 10 acoustic features according to relative variability and classification accuracy in Field Sparrow and Chipping Sparrow song.

Field Sparrow (<i>n</i> = 60)				Chipping Sparrow (<i>n</i> = 51)			
Variable ^{1,2}	Coefficient of variation	Group	Percent correct	Variable	Coefficient of variation	Group	Percent correct
Maximal frequency	10.4	1	92	Number of phrases	0.0	1	87
Minimal frequency	10.6	1	83	Number of elements	24.0	2	71
Number of phrases	28.9	1	87	Maximal frequency	9.7	2	93
Song duration	17.0	1, 2	87	Minimal frequency	20.6	3	87
Number of elements	36.0	2, 3	87	Internote interval	25.7	3	84
Number of notes	30.9	3	87	Song duration	27.3	3	87
Internote interval	39.5	4	87	Note duration	46.1	4	90
Note duration	55.0	4	87	Number of notes	42.0	4	93
Element duration	61.6	5	87	Element duration	64.1	4	83
Element FM rate	87.5	5	80	Element FM rate	58.5	4	90

¹ Variables are ranked within each species according to their mean rank in the Kruskal-Wallis ANOVA used in Levene's test.

² Variables sharing a number are equally variable, and differ significantly from variables with different group numbers.

Field Sparrows) from the other 12 species. Discriminant analysis is a two-step technique, consisting of identifying and interpreting intergroup differences, and then classifying cases into groups predicted by the analysis (Klecka 1980). I used separate group-covariance matrices and assumed equal prior probabilities of group membership in classifying cases (SPSS 1986).

It seemed most reasonable to model this as a two-group, conspecific song vs. alien song discrimination problem. However, discriminant analysis does not perform optimally when a group, in this case the alien-song group, has a multimodal distribution. Therefore, the discriminant functions were calculated for all 13 groups (species) but decisions on whether to add or delete a variable from the model were based solely on the variable's contribution to accurately classify songs as conspecific or alien. This was achieved by collapsing the 13 × 13 classification matrix that resulted from an analysis into a 2 × 2 matrix (conspecific × alien). Off-diagonal entries in the 2 × 2 matrix were considered to be classification errors. The analysis was done separately for Field Sparrows and Chipping Sparrows as the target conspecific species. The goal for both species was to derive the simplest statistical model that maximized the percentage of songs correctly classified.

The procedure of deriving a discriminant model and classifying cases was repeated, adding and deleting variables one by one to assess how important each was in accurately classifying songs. Finally, each of the 10 variables was used singly in a discriminant analysis to measure how effective each was in classifying songs.

RESULTS

RELATIVE VARIATION

Table 1 lists the 10 variables in order of increasing variability for both Field Sparrows and Chipping Sparrows. Within each species, the variables differed in relative variability (Field Sparrow: Kruskal-Wallis $\chi^2 = 210$, $n = 600$, $P < 0.01$; Chipping Sparrow: Kruskal-Wallis $\chi^2 = 229$, $n = 510$, $P < 0.01$). In Field Sparrow song, frequency variables were the least variable and differed significantly from the other eight variables. In Chipping Sparrow song, the pattern of variation was similar to Field Sparrow song, as reflected in the significant correlation between the variability rankings of the two species (Spearman's $\rho = +0.79$, $n = 10$, $P < 0.01$). The rankings based on Levene's test do not agree perfectly with the ranks by coefficients of variation listed in Table 1 because Levene's test uses the median as the estimate of central tendency while coefficients of variation are based upon the sample mean. In neither species was the relative variability correlated with the measurement error for each feature (Field Sparrow: Spearman's $\rho = -0.16$, $P > 0.3$; Chipping Sparrow: Spearman's $\rho = 0.47$, $P > 0.05$).

DISTINCTIVE FEATURES

Chipping Sparrow, Field Sparrow, Rufous-sided Towhee, Northern Cardinal, and Tufted Titmouse songs recorded locally did not differ significantly from songs obtained from other sources (Discriminant function analyses, $P > 0.10$ for each species). Prairie Warbler songs did differ, primarily because local songs were longer than

TABLE 2. Descriptive statistics for nine variables used to describe songs. Values are mean \pm standard deviation. Temporal variables are in msec, frequency measures in Hz.

Species	<i>n</i>	Maximal frequency	Minimal frequency	Note duration	Internote interval	FM rate	Number of elements	Number of phrases	Song duration	Number of notes
Chipping Sparrow	51	8,016 \pm 774.3	3,585 \pm 739.7	45.1 \pm 20.78	26.1 \pm 6.71	184.7 \pm 108.19	2.0 \pm 0.49	1.0 \pm 0.00	2,435 \pm 663.6	39.6 \pm 16.62
Field Sparrow	60	4,263 \pm 445.1	3,122 \pm 330.9	187.6 \pm 103.11	55.4 \pm 21.89	8.4 \pm 7.34	1.6 \pm 0.56	2.8 \pm 0.80	2,428 \pm 411.9	15.4 \pm 4.76
Prairie Warbler	24	5,127 \pm 436.7	4,628 \pm 317.9	178.5 \pm 85.08	55.6 \pm 26.87	8.6 \pm 19.92	1.2 \pm 0.41	1.4 \pm 0.58	2,569 \pm 545.9	12.1 \pm 3.59
Northern Cardinal	46	4,545 \pm 1,485.9	1,626 \pm 405.3	292.6 \pm 185.18	148.9 \pm 82.56	79.8 \pm 133.27	2.3 \pm 1.09	2.1 \pm 0.83	3,381 \pm 1,190.9	12.5 \pm 8.21
Rufous-sided Towhee	41	4,574 \pm 1,362.6	2,852 \pm 760.5	155.7 \pm 110.74	76.2 \pm 74.75	68.6 \pm 98.96	2.9 \pm 1.37	2.0 \pm 0.22	1,168 \pm 204.5	9.7 \pm 3.18
Tufted Titmouse	24	3,149 \pm 478.8	2,169 \pm 278.1	227.9 \pm 51.91	117.2 \pm 47.49	17.6 \pm 51.74	2.4 \pm 1.09	1.0 \pm 0.00	994 \pm 243.5	3.3 \pm 0.85
White-throated Sparrow	12	3,666 \pm 489.5	3,441 \pm 472.3	408.6 \pm 170.46	126.2 \pm 36.49	2.2 \pm 4.79	1.8 \pm 0.94	2.0 \pm 0.00	2,752 \pm 405.8	8.0 \pm 3.52
Indigo Bunting	13	6,702 \pm 963.9	4,257 \pm 800.9	161.0 \pm 57.62	80.9 \pm 24.78	61.2 \pm 89.44	3.8 \pm 1.36	5.9 \pm 2.22	2,857 \pm 1,172.2	11.8 \pm 4.68
Yellow Warbler	16	6,032 \pm 1,026.6	3,948 \pm 664.9	124.2 \pm 44.91	56.2 \pm 23.82	39.3 \pm 21.71	3.2 \pm 1.42	3.1 \pm 0.81	1,364 \pm 259.8	8.3 \pm 1.82
Dark-eyed Junco	15	5,330 \pm 648.4	3,830 \pm 696.3	70.1 \pm 24.48	21.4 \pm 4.01	43.1 \pm 44.68	2.7 \pm 0.80	1.1 \pm 0.26	1,711 \pm 231.5	21.1 \pm 9.7
Swamp Sparrow	15	5,905 \pm 696.6	3,415 \pm 309.9	106.1 \pm 30.24	33.1 \pm 7.58	45.1 \pm 47.00	3.1 \pm 0.74	1.0 \pm 0.00	2,213 \pm 340.3	16.9 \pm 5.01
Song Sparrow	15	5,973 \pm 1,863.2	3,107 \pm 803.8	127.7 \pm 71.59	51.5 \pm 38.78	33.2 \pm 23.67	2.5 \pm 0.92	3.8 \pm 0.94	2,354 \pm 351.4	15.7 \pm 8.43
Black-capped Chickadee	15	3,980 \pm 389.8	3,672 \pm 335.1	392.7 \pm 36.06	120.4 \pm 24.72	0.6 \pm 0.19	1.3 \pm 0.49	2.0 \pm 0.00	910 \pm 51.1	3.0 \pm 0.00

TABLE 3. Simplest discrimination model resulting in 100% classification accuracy of Chipping Sparrow songs.

	Discriminant function ^a		
	1	2	3
Chi-square	796	371	74
Variance explained	64%	32%	4%
Function by variable correlations			
Number of phrases	-0.39	0.81	0.44
Maximal frequency	0.41	0.55	-0.73
Number of notes	0.63	0.38	0.67

^a All three functions were significant at $P < 0.001$.

other songs. I conclude that the different recording methods and locations did not introduce significant heterogeneity in the data. Table 2 presents descriptive statistics for each of nine variables for all 13 species.

Chipping Sparrows. Three variables (note maximal frequency, number of notes in a song, and number of phrases in a song), were sufficient to correctly classify all 230 songs in the model set, and 97% of 116 songs in the validation set (Table 3). Two other variables were strongly correlated with number of notes in a song. Note duration could replace number of notes with no loss of classification accuracy. Number of elements in a note could replace number of notes with only one classification error resulting. No other variables could replace maximal frequency or number of phrases without causing six or more classification errors. The most accurate variables in classifying songs were note maximal frequency and number of notes in a song (Table 1).

Field Sparrows. Maximal classification accuracy (98% correct) of Field Sparrow song required seven variables that were correlated with six discriminant functions (Table 4). The vari-

ables were: note maximal and minimal frequencies, note duration, internote interval, song duration, and number of notes and number of phrases in a song. This model also correctly classified 97% of the songs in the validation set. Classification accuracy remained the same when the number of elements in a note, and FM rates of each element were included.

IS RELATIVE VARIABILITY RELATED TO CLASSIFICATION ACCURACY?

If classification accuracy derives in whole or part from a feature's relative variability, then the two rankings of features based on increasing variability and increasing univariate classification accuracy (Table 1) should be negatively correlated. The two rankings were not correlated in Chipping Sparrow song (Spearman's rho = +0.26, $P > 0.20$, $n = 10$) nor in Field Sparrow song (Spearman's rho = -0.15, $P > 0.60$, $n = 10$).

It is also apparent from Table 1 that there was a high degree of redundancy among variables. The best variable at discriminating Field Sparrow song was maximal frequency, which, used alone, correctly classified 92% of 230 songs (Ta-

TABLE 4. Simplest discriminant model resulting in 98% classification accuracy of Field Sparrow songs.

	Discriminant function ^a					
	1	2	3	4	5	6
Chi-square	947	599	303	107	33	14
Variance explained	45%	24%	18%	9%	2%	1%
Function by variable correlations						
Number of notes	0.54	0.28	0.35	0.12	-0.51	0.08
Number of phrases	-0.30	-0.14	0.83	-0.07	-0.40	-0.01
Minimal frequency	-0.10	0.58	0.22	0.72	0.28	0.07
Song length	0.42	-0.45	0.49	0.51	-0.32	0.04
Maximal frequency	0.29	0.38	0.49	-0.06	0.64	0.17
Internote interval	-0.19	-0.47	-0.06	0.01	0.49	0.40
Note duration	-0.28	-0.45	-0.16	0.18	0.10	0.77

^a Functions 1-5 significant at $P < 0.001$, Function 6 at $P < 0.05$.

ble 1). The poorest variable, minimal frequency, classified 83% correctly. The seven-variable model was 98% accurate; however, deleting any single variable from the model only decreased performance by 1–2%. Error rates increased two- to five-fold when only five variables were used. This indicates that no single variable was of major importance in discriminating Field Sparrow songs, and additional variables made only small improvements in performance. In Chipping Sparrow song, there was greater variation among variables in their classification accuracy (71–93%), and the three-variable model was 7% more accurate than the best single variables, maximal frequency or number of notes.

DISCUSSION

The results of this study indicate that the invariant-features hypothesis does not predict the accuracy of song features in distinguishing conspecific from heterospecific songs. The canonical discriminant analysis used to classify songs uses information about both a feature's mean relative to other species and its variability. The invariant-features hypothesis ignores a feature's central tendency and only uses estimates of feature variability to predict which features provide accurate recognition information. Because the predictions generated by the two hypotheses did not agree in either Field Sparrows or Chipping Sparrows, I conclude that the invariant-features hypothesis does not satisfactorily identify features that distinguish conspecific from heterospecific songs.

These results may provide an explanation for the paradox noted by Emlen (1972), namely, that not all invariant features are necessarily used by birds in species-song recognition. With the exception of maximal frequency, feature invariance did not contribute significantly to accurate classification of either Field Sparrow or Chipping Sparrow song. Some invariant features may be ignored by birds because the features' means do not differ from those of other species, while other invariant features are used because they do contrast with other species.

Recent experiments on Field Sparrows indicate that the process of species song recognition is more subtle than simply involving the qualitative effects of use or nonuse of features. Rather, all features are attended to, but some features are perceptually more important than others (Nelson 1988). Field Sparrows were more attentive to alterations to an invariant, distinctive feature, song

frequency, than to features that this analysis identified as being less accurate species-recognition cues (number of phrases, note duration, internote interval). The experimental results on Field Sparrows and Eurasian Blackbirds (Dabelsteen and Pedersen 1985), both of which show that birds use information from variable features, along with the results of this study, lead to the conclusion that the invariant-features hypothesis is an over-simplified view of species-song recognition.

Accurate classification of Field Sparrow songs required twice as many variables as for Chipping Sparrow song. Since the variables had the same relative variability in both species, the species contrast must be the result of the different relationship each species' song has to other species in the acoustic environment. The reason for the species difference is apparent from an examination of a plot of the species in "acoustic space" formed by the first two discriminant functions derived from the seven-variable model in Table 4 (Fig. 3). Field Sparrow songs are centrally located in this space with close acoustic neighbors in all directions. To overcome the greater opportunities for acoustic confusion, more variables are required to discriminate Field Sparrow song from songs of other species.

In contrast, Chipping Sparrow songs inhabited the margins of this acoustic space with fewer close neighbors. Chipping Sparrow songs differed sufficiently from the songs of other species that a highly variable feature, number of notes, was the second best classification cue. Conversely, the second-least-variable feature—number of elements—was the single poorest distinctive feature (Table 1). Number of elements might therefore be expected to be an invariant feature that Chipping Sparrows would not rely on in song recognition. No experiments have been conducted on Chipping Sparrow species-song recognition.

In both species there is a high degree of statistical redundancy among features. This is consistent with the results of many experimental studies indicating that birds use multiple cues in song recognition (Brémond 1968, 1976; Emlen 1972; Becker 1976, 1982; Peters et al. 1980; Shiovitz and Lemon 1980; MacNally et al. 1986; Nelson 1988). Redundancy was particularly apparent in Field Sparrow song, in which maximal frequency was the only feature much more important than the others in classifying songs. The

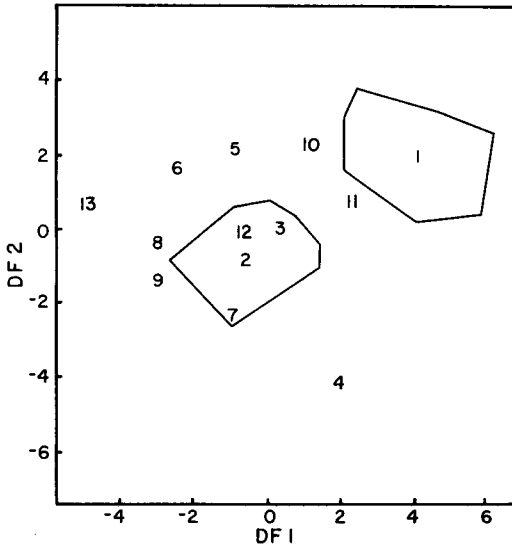


FIGURE 3. Polygons enclosing the songs of Field Sparrows and Chipping Sparrows plotted against the first two discriminant functions derived from seven acoustic variables (Table 4). DF 1 is positively correlated with song duration and number of notes in a song, while DF 2 is correlated with minimal note frequency, and negatively correlated with internote interval and note duration. Numbers indicate the centroids for each species. 1 = Chipping Sparrow, 2 = Field Sparrow, 3 = Prairie Warbler, 4 = Northern Cardinal, 5 = Rufous-sided Towhee, 6 = Tufted Titmouse, 7 = White-throated Sparrow, 8 = Indigo Bunting, 9 = Yellow Warbler, 10 = Dark-eyed Junco, 11 = Swamp Sparrow, 12 = Song Sparrow, 13 = Black-capped Chickadee (*Parus atricapillus*).

small incremental improvements in discrimination performance resulting from the addition of variables to the model is consistent with the additive-redundant model of song recognition of Shiovitz and Lemon (1980).

While the methods employed in this study yielded very good recognition performance, one assumption of the method deserves comment. This concerns how closely the discriminant model resembles the psychological processes involved in song recognition. In particular, the model assumes that a Field Sparrow, for example, stores representations of conspecific song as well as prototypes of alien songs, and that a stimulus is compared to each prototype, before a "decision" is made about the species identity of the stimulus. While there is behavioral and neurophysiological evidence indicating that a stimulus' similarity to a bird's own song is an impor-

tant determinant of response strength (Margoliash 1983, 1986; McGregor et al. 1983; MacArthur 1986), the assumption that other species' songs are also memorized is an open question.

Discriminant analysis is a multiple-distance model, whereby a song to be classified is compared to each prototype, and classified as the species to which it is closest. An alternative, single-distance model, involves comparing a stimulus only to a prototype of conspecific song. Recognition as conspecific song occurs if the stimulus is within a certain tolerance of the prototype, as in the signal variation tolerance model of Shiovitz and Lemon (1980). However, there is no way to know a priori what the appropriate tolerance should be. Instead, these tolerances must be measured empirically (Nelson 1988). Experiments on Field Sparrows revealed that males' territorial responses decreased significantly when each of four song features was altered by two to three standard deviations relative to a control song synthesized to resemble the species' mean on each feature. That is, males appear to tolerate song variants that fall within the normal limits of variation encountered in conspecific song. Dabelsteen and Pedersen (1985) have also demonstrated a correlation between song variation and responsiveness in the Eurasian Blackbird.

I simulated a single-distance recognition model using this data set. A song was classified as a Field Sparrow if its measurements on the seven features used in the Field Sparrow model (Table 4) were all within two standard deviations of the species mean. Ninety-three percent of the 347 songs were correctly classified. Only 86% and 85% were correctly classified when the tolerances were one and three standard deviations respectively. One-standard-deviation tolerances were too narrow, and missed Field Sparrow songs, while three-standard-deviation tolerances were too wide. Thus there appears to be a good match between the bird's behaviorally-measured tolerance of song variation, and the statistical limits of variation that yield maximal classification accuracy in a simulation. What is needed, obviously, are experiments that distinguish the comparative- and single-distance models. Field experiments using heterospecific songs as stimuli are consistent with either model. These experiments have shown that response strength is a function of how closely the alien songs resemble conspecific songs (Helb 1973, Becker 1976, Nelson 1987). Laboratory approaches (e.g., Dooling

et al. 1987) may be useful in distinguishing these two ideas.

Finally, modelling species song recognition in terms of an acoustic space formed by the songs of sympatric species generates testable predictions about variation in species-song recognition behavior. Interspecific comparisons with the Chipping Sparrow have been discussed above. Intraspecific tests are also possible. For example, in a different bird fauna containing Chipping Sparrows, an analysis similar to that conducted here might reveal that different song features would be favored as recognition cues. There are indications that song-discrimination behavior differs between populations that are allopatric or sympatric with close relatives (Gill and Murray 1972, Becker 1977). It is not known whether these differences, which may be learned, result from the use of different song features in different populations.

The prediction of geographic variation in the use of species-song recognition features differs from Marler's (1960) original suggestion that song structure may be determined by the complexity of the sound environment. Independently of whether the complexity or variability of the target species' song changes in a depauperate fauna (see Miller 1982 and Kroodsma 1985 for discussion), the *relationships* among species may change, thereby altering the discrimination effectiveness of song features.

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