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The Organization of Song Repertoires in Song Sparrows: Themes and Variations

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Abstract

Although songtypes are generally considered to be important functional units in birdsong, they have not been well-characterized in terms of within- and between-songtype variation. We analyzed the song repertoires of 12 adult male song sparrows (*Melospiza melodia*) from a population in New York. We identified minimal units of production (MUPs), and calculated the degree to which song variants within a bird's repertoire were similar to each other based on an analysis of MUP sharing. Using statistical techniques from numerical taxonomy, we assessed how song variants clustered into songtypes, and we derived quantitative measures of within-songtype and between-songtype similarity. We found that birds produced a limited number of songtypes, but constantly produced new song variants within the framework of these types. Most song variants were produced very rarely; over 43 % of song variants were produced only once. Repertoires differed in the degree of between-songtype similarity and in the number of songtypes defined, but there was comparatively less variation in within-songtype similarity. Between-songtype similarity and repertoire size were positively correlated. We argue that song sparrow songtypes are probabilistic units of song production, and discuss the functional and evolutionary implications of having vocal motor patterns organized in this way.

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Introduction

The behavior patterns of animals, especially those associated with communication, are often treated as if they belong to discrete natural categories or "packets" of structure and function (BARLOW 1977). Close examination, however, always reveals some degree of structural variation among and within these categories. Similarities among categories may be meaningful as, for example, in a

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graded communication system (MARLER 1982), or they may instead reflect the use of common motor patterns in the production of functionally distinct behaviors. Even the most stereotypic behaviors are likely to differ from one performance to the next, if for no other reason than limitations on the precision of motor control (SCHLEIDT 1974). Understanding these patterns of variation is a requisite for both functional and evolutionary analyses of behavior.

Birdsong provides a case in point. In many passerine species, individual males sing a "repertoire" that includes more than one distinctive pattern or "songtype" (KROODSMA 1982). Differences in both repertoire size and repertoire delivery are thought to play important roles in the perception and function of birdsong as a communication signal (HARTSHORNE 1956; KREBS 1977; SEARCY & ANDERSSON 1986). But in some species, different performances of the same songtype vary. If intra-songtype variation is substantial, some songs may be difficult to classify to a given type either because they are intermediate between types or because they are not easily associated with any type. In such cases, analyses of song complexity must not only consider typical songtypes, but must also account for the distribution of variation among and within songtypes (KROODSMA 1982).

Studies of song sparrow (*Melospiza melodia*) song illustrate the problem of quantifying variation. WHEELER & NICHOLS (1924) first noted that males of this species produce a repertoire of different song "patterns" (i.e., songtypes), but reported that these patterns are themselves variable, and also that patterns vary in the degree to which they are different from each other. NICE (1943) and SAUNDERS (1951) confirmed these observations and reported that birds tend to repeat songs of the same type during bouts. Using sonagraphic techniques for sound analysis, both MULLIGAN (1963, 1966) and BORROR (1965) were able to document several levels of variation in the structure of song sparrow songtypes including variation in note sequences and in "the character of particular phrases" (BORROR 1965). They also noted that different songtypes often share common elements. Thus, song sparrow songs can be classified into songtypes but there is considerable structural variation within songtypes, and different songtypes might be more or less distinct based on the number of elements they share.

The function of song variation in the song sparrow has been the subject of several studies (SEARCY & MARLER 1981; SEARCY 1983, 1984; SEARCY et al. 1985; HIEBERT et al. 1989), as have the processes by which this species learns (MARLER & PETERS 1987, 1988, 1989) and perceives its songs (KROODSMA 1976; PETERS et al. 1980; MCARTHUR 1986; NELSON 1987; STODDARD et al. 1988; BEECHER & STODDARD 1990). In general, these studies measure vocal complexity simply in terms of the number of songtypes an individual produces. At best, this approach provides an approximation of the relationships between vocal complexity and its functional consequences, because it does not reflect variation within songtypes or similarities among different types. An exception is the work of STODDARD et al. (1988), who found within-songtype variation to be as salient as the differences between songtypes in a field playback experiment. Although this study did not quantify within- and between-songtype differences, it illustrates that such differences may be functionally important.

In this paper we quantify structural variation in the song repertoires of 12 adult male song sparrows from a New York State population. We use numerical taxonomic techniques to partition songs objectively into statistical "songtypes" and to calculate within-songtype and between-songtype variation. We describe how variation is patterned in the repertoires of individuals in this population, and discuss the problem of quantifying variation in song repertoires in general. We also discuss the implications of our findings for song sparrow song learning, production and perception.

Methods

A. Subjects and Song Recording

12 adult male song sparrows were recorded as they sang under one or more of the following conditions: in the field during territory advertisement (F), in the laboratory (L), and in the laboratory following testosterone therapy (T) (Table 1). All birds were from study sites near the Rockefeller University Field Research Center, Dutchess County, New York, and all were at least two years old.

We recorded birds in the field continuously for about 3 h on one or two consecutive mornings using a Nagra 4.2L recorder and Sennheiser MKH 816 shotgun microphone. Birds in captivity (L and T) were recorded for 3 h each morning with a Marantz PMD 221 cassette tape recorder and a Tandy #1070A microphone. Birds recorded in the L condition were maintained on a normal photoperiod and sang, as they do in the field, with seasonally increasing daylength. Birds recorded in the T condition were induced to sing above normal seasonal rates by administering subcutaneous implants of crystalline testosterone and exposing them to long day lengths (18 : 6 h L : D).

B. Song Analysis

We generated sound spectrograms of the 6028 songs in our sample (Table 1) using a real time analyzer (Princeton Applied Research 4512). Song sparrow songs typically last for 2—3 s and appear on spectrograms as sequences of discrete tracings (Fig. 1). We defined spectrogram tracings separated by at least 8 msec of silence as "notes." Thus "buzzes" modulated at 125 Hz or greater were classified as single notes rather than as a rapid series of repeated notes. We also made sonagrams of songs using a Kay Elemetric Digital Sona-Graph (Model 7800, 0—8 kHz range, 300 Hz filter bandwidth) to reveal more accurately the fine structure of notes.

To quantify song variation, we first identified the smallest units of song that were produced intact throughout each bird's recorded sample (see BARLOW 1977). Songs are strings of discrete notes and different songs sung by an individual can share some or many notes. Notes are the smallest units in a song, but it is often the case that particular sequences of notes invariably occur together. We defined "minimal units of production" (MUPs) as groups of notes that always occur together and in sequence whenever they occur in a bird's song repertoire. Because song sparrow notes are stereotypic and distinctive, it is operationally simple to recognize MUPs in different songs sung by the same individual (e.g., Fig. 2). Comparing and equating MUPs across the repertoires of different individuals is more difficult and was not attempted here. Most MUPs were individual notes, although some include up to four notes (Fig. 3 A). MUPs were determined separately for each bird.

We annotated all songs in each bird's sample as MUP sequences. Individuals produced an average of 71.5 ± 12.6 ($\bar{x}$ ± SD) MUPs. Typically, songs comprised 10—13 MUPs (Fig. 3 B). Songs composed of identical strings of MUPs were thus exemplars of the same "song variant." A total of 1100 unique song variants were identified from 6028 songs recorded from 12 birds (Table 2). Song sparrow song has been described previously as a series of alternating trill and note cluster phrases (e.g., BORROR 1965; MULLIGAN 1966; HARRIS & LEMON 1972). By our definition, trills are sequential repetitions of the same MUP or MUPs (Fig. 2). We did not distinguish song variants from one another on the basis of the number of repeated MUPs in trills.

Table 1: Recording dates and number of songs recorded from 12 male song sparrows

Bird	Field (F) recordings Date recorded	Field (F) recordings Songs (n)	Laboratory (L) recordings Date recorded	Laboratory (L) recordings Songs (n)	T-implant (T) recordings Date recorded	T-implant (T) recordings Songs (n)	Total songs
1	3/82	324	—	—	—	—	324
2	3/82	122	—	—	—	—	122
3	—	—	5/87	452	—	—	452
4	—	—	5/87	514	11/87	308	822
5	—	—	—	—	11/87	578	578[1])
6	—	—	7/87	329	—	—	329
7	—	—	—	—	3/88	408	408[1])
8	—	—	8/87	164	3/88	221	385
9	—	—	8/87	714	—	—	714
10	4/88	337	—	—	4/88	253	590
11	4/88	344	4/88	207	4/88	351	902
12	—	—	5/87	402	—	—	402
Totals		1127		2782		2119	6028

[1]) One song comprised of a single MUP was omitted from the analysis

C. Classification of Song Variants into Songtypes

Our general approach was to first calculate pairwise similarities between all song variants (i.e., unique MUP strings) and then to group similar song variants into "songtypes" using a clustering procedure. We calculated pairwise similarities between song variants for each bird separately using Jaccard's coefficient of correlation (SNEATH & SOKAL 1973; BAULIEU 1989):

$$(CC_j)_{a,\,b} = c \;/\; (c + u_a + u_b)$$

where a and b are the song variants being compared, c = number of MUPs common to both a and b, u_a = number of MUPs unique to song variant a, and u_b = number of MUPs unique to song variant b. The coefficient is a function of the number of MUPs held in common by both songs and the number of MUPs unique to each song. We modified CC_j such that when two strings of unequal length were compared, the longer string was truncated to match the length of the shorter string. This modification was necessary because of the wide disparity of MUP string lengths (i.e., song lengths; Fig. 3B).

We performed cluster analyses on these pairwise similarity comparisons for each bird separately using the unweighted pair-group method of arithmetic averages (UPGMA) for dendrogram construction (Fig. 4; ROHLF 1988). The UPGMA method yielded the highest cophenetic values with our data as compared to other methods of dendrogram construction (SNEATH & SOKAL 1973). Cluster analysis does not by itself provide an objective means for determining the level of similarity at which individual cases (i.e., song variants) are most efficiently assigned to groups (i.e., songtypes). To this end, we calculated moat indices (WIRTH et al. 1966) for all possible levels of clustering (numbers of groups) of song variants from each bird's dendrogram. The moat index describes the degree to which cluster groups are isolated or externally discontinuous to each other (WIRTH et al. 1966; SNEATH & SOKAL 1973), and is calculated as

$$M_n = [\Sigma(\min B - \max W)] \;/\; n$$

where M_n = moat index for a particular bird with song variants partitioned into n clusters, min B = minimum between-group linkage dissimilarities of each cluster to other clusters, and max W = maximum within-group linkage dissimilarities found within each cluster. Our assignments of song

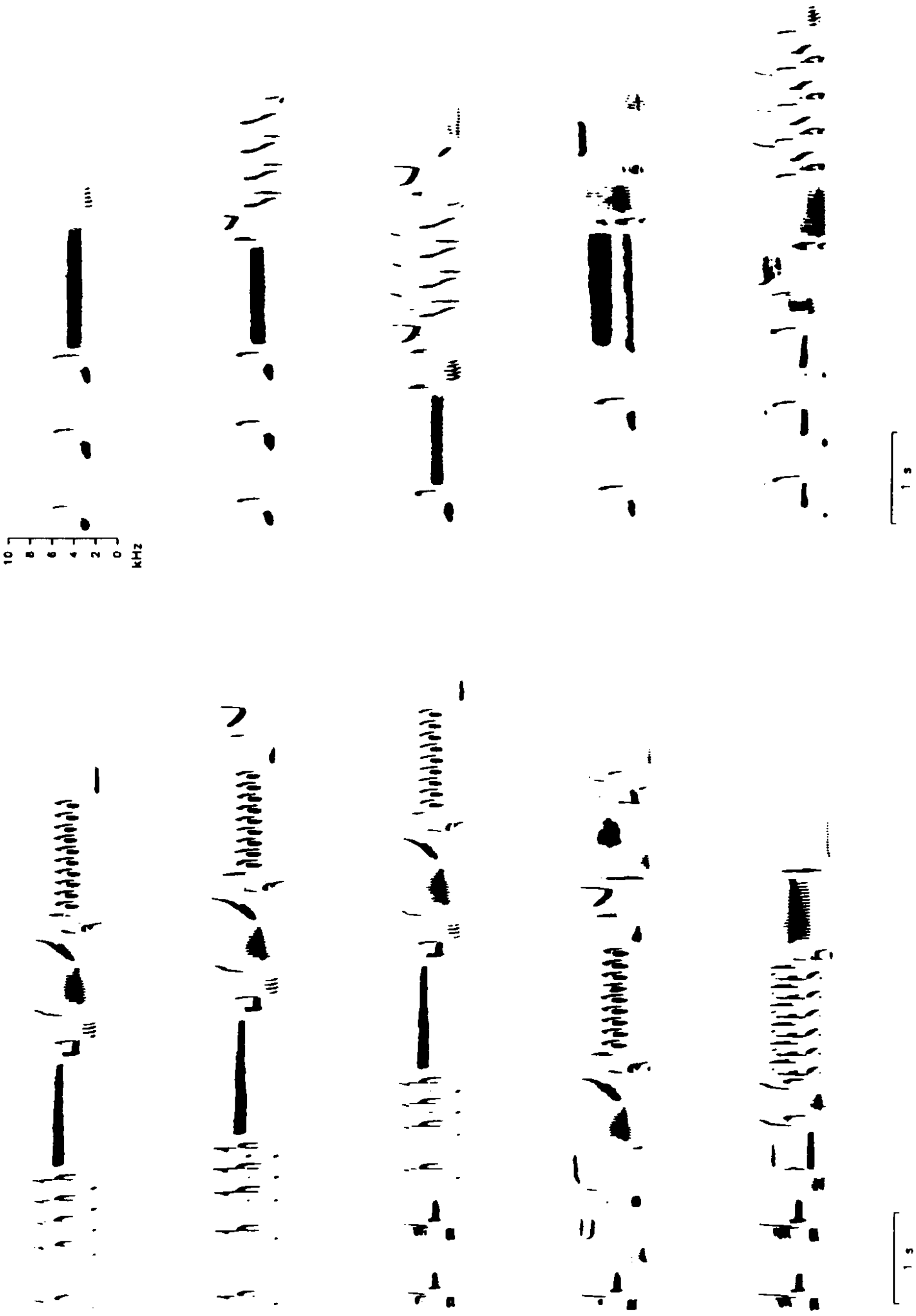


Fig. 1: Sonagrams of song sparrow songs illustrating typical variation within the same songtype and between different songtypes. The five songs on the left were sung by Bird 3 and the five on the right by Bird 8. In both cases, the uppermost four songs were assigned by the monadic clustering procedure to the same songtype, while the bottom song was assigned to a different songtype

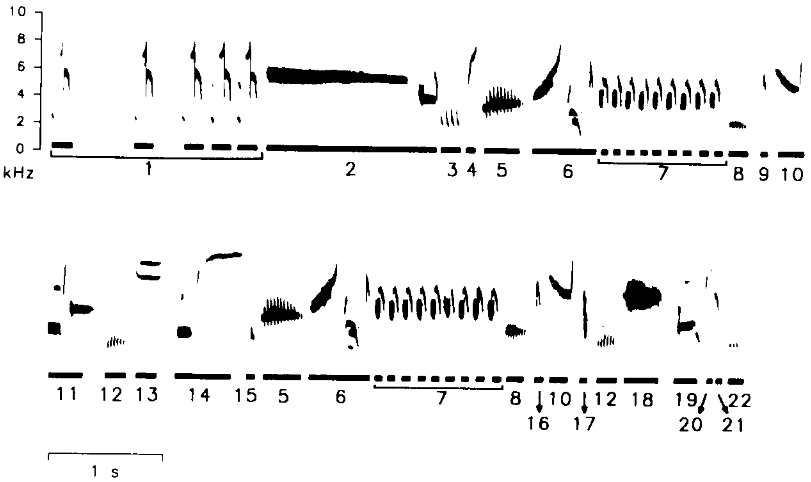


Fig. 2: Two songs of Bird 3 (second and fourth songs on left in Fig. 1) annotated as MUP strings. Numbered horizontal lines designate each MUP. Note that some MUPs consist of more than one note (see also Fig. 3 A). MUPs were determined separately for each bird and were easily identified by eye. When a MUP was immediately repeated as in a trill (e.g., MUP 7 here), we annotated the trill as a single MUP. The same MUPs often appear in different song variants, as is the case for MUPs 5, 6, 7, 8 and 10 in this example. The value of CC_j between these two songs is 0.25

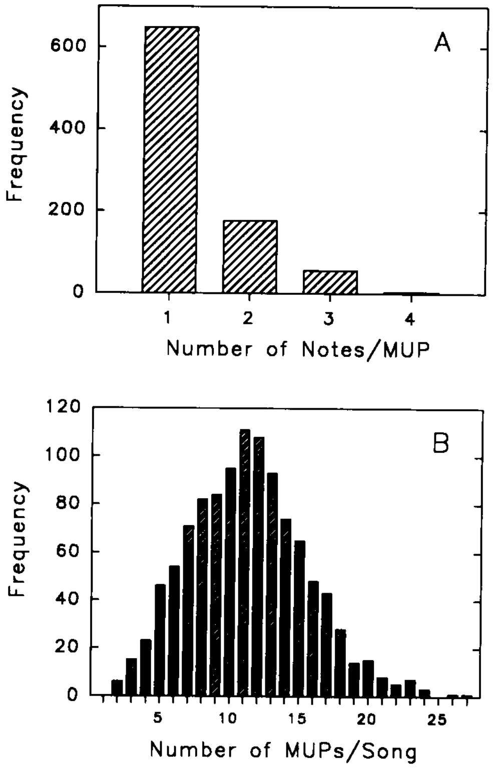


Fig. 3: A. Frequency distribution of the number of notes per MUP. B. Frequency distribution of the number of MUPs per song

Table 2: Number of song variants and songtypes in the repertoires of 12 male song sparrows. The results of three songtype classification methods are shown

Bird	No. of song variants	No. of songtypes Visual classification	Monad classification	Dyad classification
1	32	7	7	8
2	52	9	11	15
3	82	10	11	15
4	135	11	8	10
5	145	9	9	33
6	72	16	20	25
7	35	8	8	10
8	108	10	13	16
9	60	8	8	10
10	131	8	9	10
11	175	8	9	10
12	73	6	10	19
	Total: 1100	$\bar{x}$: 9.2	10.3	15.1
		SD: 2.6	3.5	7.5

variants to songtypes corresponded to the level of clustering at which the moat index reached a maximum (Fig. 4).

The calculation of CC_j described above is based solely on the presence or absence of shared MUPs between song variants with no regard to the ordering of those units within strings. Such an approach may seem incomplete given the highly ordered nature of note sequences in songs. To evaluate the influence of sequential information on song classification, we transformed the original song variant strings (referred to below as "monadic") into "dyadic" strings, in which every ordered pair of MUPs was recoded with a single designator signifying that ordered-pair relationship. For instance, the monadic strings "1 2 3 4" and "1 2 4 5" for a given bird would be transformed into dyadic strings "a b c" and "a d e," respectively, "a" signifying the dyad "1—>2," "b" signifying "2—>3," and so forth. Similarity matrices of these dyadic strings were generated and songtype assignments were made based on cluster analyses as outlined above. We calculated correlations between monadic and dyadic similarity matrices using the Mantel test (SCHNELL et al. 1985).

Finally, two of us (SP and TR), without prior knowledge of the outcome of the cluster analysis of types, classified all variants into songtypes using a subjective assessment of similarity based on visual inspection of sonagrams, comparable to the approach taken in previous visual classifications (e.g., KROODSMA 1976; SEARCY & MARLER 1981; SEARCY 1984; MARLER & SHERMAN 1985; SEARCY et al. 1985; HIEBERT et al. 1989; MARLER & PETERS 1989; BEECHER & STODDARD 1990).

Results

A. Assignment of Song Variants to Songtypes

The numbers of songtypes that each bird produced, as determined by cluster analyses of monad and dyad CC_j similarity matrices and as determined by visual classification, are presented in Table 2. The visual classification and the classification based on monad similarities identified comparable numbers of songtypes ($\bar{x}$

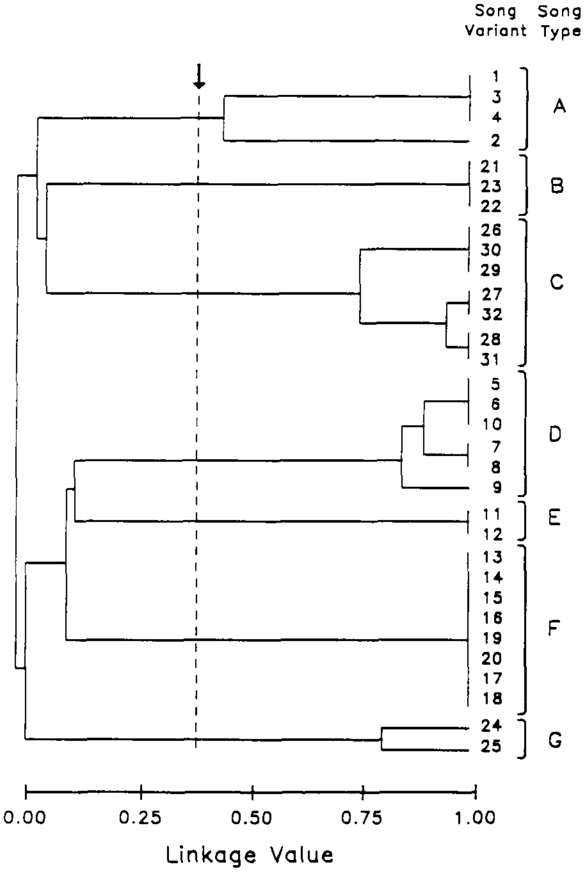


Fig. 4: Cluster analysis dendrogram of Bird 1's song repertoire. Numbers to the right indicate the 32 song variants that were identified in this bird's song repertoire. Song variants were classified into songtypes (indicated by brackets and letters to the right) by determining the clustering level, or equivalently the number of cluster groups, at which the moat index reached its maximum value (indicated by arrow and vertical dashed line). Bird 1 is shown because the number of variants in its repertoire could be illustrated easily, but this pattern of clustering is typical of all birds

± SD = 9.2 ± 2.6 and 10.3 ± 3.5, respectively; sign test, ns). The classification based on dyad similarities, by contrast, recognized significantly more songtypes (15.1 ± 7.5; sign test, $p < 0.01$). There was an average of 3.5 % disagreement between visual and monad similarity classifications in the assignment of particular song variants to types. There was considerably greater disagreement between the dyad and monad clustering classifications and between the dyad clustering and visual classifications (10.0 % and 11.2 %, respectively).

Although more songtypes were recognized by the cluster analysis based on dyad similarities as compared to monad similarities, these two classification schemes were in fact largely redundant. The 10.0 % disagreement between these classifications was, with only a single exception, accounted for by cases in which the dyad classification cleanly split songtypes defined by the monad classification into two or more sub-groups. Further, monad and dyad similarity matrices were highly correlated (Mantel test, $p < 0.001$ in all cases evaluated). Thus, the classifications based on clustering of monad and dyad similarity scores differed not in their general patterns of clustering, but in the resolution with which they split song variants into songtypes. Given that the two schemes were redundant, we based our subsequent analyses of variation on songtype categories as delimited by the monad procedure because it is operationally simpler than the dyad procedure.

Song sparrows are commonly observed to repeat songs in bouts of the same songtype before switching to a new type (e.g., NICE 1943; BORROR 1965). We examined how two birds in our sample (10 & 11) delivered songtypes in their field recordings. Songs of the same songtype, as defined by the monad procedure, were delivered in bouts that were 8.2 ± 3.1 and 14.9 ± 7.8 songs long ($\bar{x} \pm$ SD). The boundaries between delivery of successive songtypes were defined unambiguously by our methods. The pattern of variation in songs within songtype bouts will be addressed more completely in a subsequent paper (NOWICKI et al., unpubl. data).

B. Correlates of Song Variation

There was no relationship between the total number of songs recorded and the number of songtypes observed in an individual's repertoire (Fig. 5A, $r_s = -0.38$, ns). This was expected, given that previous estimates of the number of songs needed to sample exhaustively the repertoire of songtypes from male song sparrows range from 200—300 (BORROR 1965; SEARCY et al. 1985) and that we recorded over 300 songs from all but one bird (Table 1). By contrast, the number of song variants in a bird's repertoire was significantly, positively correlated with

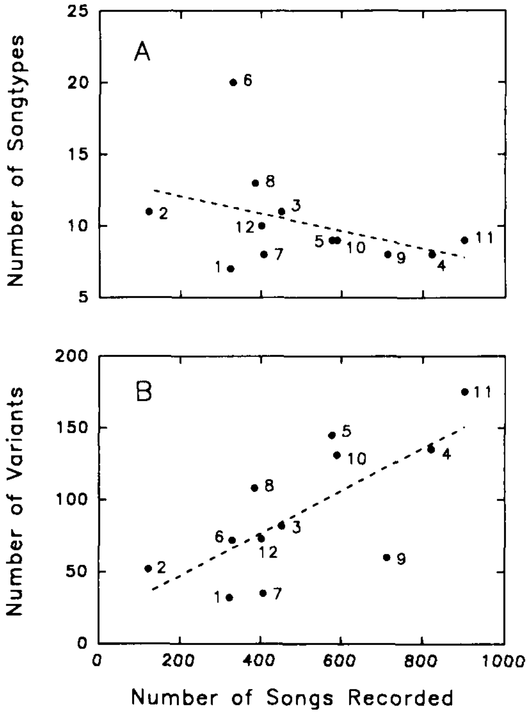


Fig. 5: Number of songtypes (A) and number of song variants (B) as a function of the total number of songs recorded from individuals. Data point labels refer to individual birds (see Table 1). Dashed lines are the regression of the two variables in each case ($r_s = 0.38$, ns, and $r_s = 0.69$, $p < 0.01$)

the total number of songs recorded from that bird (Fig. 5B, $r_s = 0.69$, $p < 0.01$). Thus, as the number of songs recorded from a bird increases, the number of song variants observed also increases, at least up to the size of our largest sample (Bird 11, 902 songs).

To evaluate whether the different recording conditions from which we obtained our total sample had any effect on song variation, we divided subjects into three groups of four birds each, as follows: F — Birds 1, 2, 10, and 11; L — Birds 3, 6, 9, and 12; T — Birds 4, 5, 7, and 8. Using only the subsample of recordings made under the condition to which a bird was assigned (Table 1) and pooling data by recording condition, there was a trend toward fewer song variants produced by birds in the field ($\bar{x} \pm$ SD: F = 44 ± 14; L = 72 ± 9; T = 81 ± 46). These differences were not statistically significant (Kruskal-Wallis H = 4.93, p = 0.09). Additionally, the apparent lower number of variants observed in our field sample was confounded by the fact that the three recording conditions differed in the average number of songs recorded (F = 282 ± 106; L = 474 ± 168; T = 378 ± 152). While these differences also were not statistically significant (Kruskal-Wallis H = 2.81, p = 0.25 and H = 1.89, p = 0.39; respectively), the F sample stands our for having a low average number of songs recorded as compared to the L and T samples, a factor that correlated with the number of variants produced (Fig. 5B). Thus, we found no evidence for quantitative differences in the production of song variants under different recording conditions (see also BALL & NOWICKI 1990).

C. Frequency of Production of Song Variants and Songtypes

Are the different song variants in a bird's repertoire sung with equal frequency, or are some variants produced more commonly than others? We calculated how often a bird sang each song variant in its recorded sample as a percentage of the total number of songs recorded from that individual. We found that a surprisingly large majority of song variants were produced rarely, with almost 70 % of all variants being sung less often than 1 % of a bird's total recorded song sample. In fact, an astonishing 43.6 ± 10.7 % ($\bar{x} \pm$ SD) of all song variants were sung only once. The proportion of rare variants in a bird's repertoire did not correlate with the number of songtypes recorded from that bird or with the total number of songs in its sample.

We performed a comparable analysis based on the frequency of production of songtypes by calculating how often a bird sang each songtype as a percentage of the total number of songs in its sample. Most songtypes were sung relatively frequently as compared to song variants, with over 72 % of all songtypes being sung frequently enough to include at least 10 % each of the total number of songs recorded from a bird. A notable proportion of songtypes (over 13 %), however, were sung only rarely (less than 1 % of sample). In all cases but two, these rare songtypes represented single song variants that were not readily lumped with others into songtypes by our analysis of similarity scores. Such rare songtypes were, in fact, rare variants that were highly dissimilar from the "major" songtypes in a bird's repertoire.

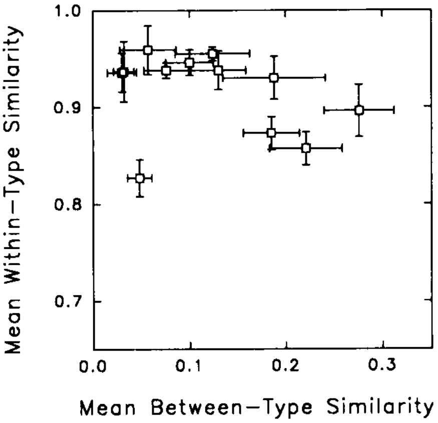


Fig. 6: Mean within-type similarity as a function of mean between-type similarity for all 12 birds. Error bars are SE of the mean for both variables

D. Within- and Between-Songtype Variation

Having assigned song variants to songtypes based on cluster analysis of similarity scores, we quantitatively assessed the average similarity among variants grouped together as a type, and the average similarity among songtypes in a bird's repertoire. To determine within-type similarities, we calculated the average linkage similarity of adjacent variants within each songtype as determined by the cluster analysis. To determine between-type similarities, we calculated the average linkage similarities of adjacent songtypes. The coefficient of variation across individuals of between-type similarities was far greater than that of within-type similarities (Fig. 6; $c.v._{between} = 65.61$, $c.v._{within} = 4.65$). Within- and between-type similarity scores were not significantly correlated ($r_s = -0.29$, ns).

There also was no relationship between the number of song variants grouped together in a particular songtype and that songtype's average within-type similarity score (Fig. 7, $r_s = -0.16$, ns). This was surprising given that one might expect songtypes that include many variants to have an inherently greater range of variation than songtypes that only include a small number of song variants.

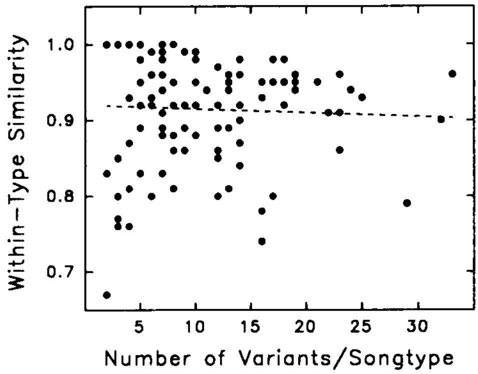


Fig. 7: Within-type similarity as a function of the number of variants per songtype, for all songtypes in our sample that included two or more song variants (n = 106). The dashed line is the regression of the two variables ($r_s = -0.16$, ns)

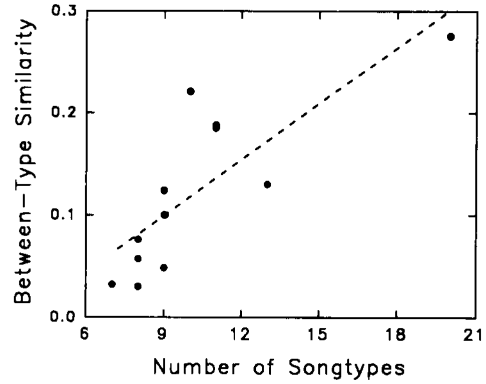


Fig. 8: Between-songtype similarity as a function of the number of songtypes in birds' repertoires (n = 12). The dashed line is the regression of the two variables ($r_s = 0.79$, $p < 0.005$)

Neither within- nor between-type similarities were correlated with the total number of songs recorded from a bird ($r_s = 0.29$, $r_s = -0.41$, respectively; both ns) nor with the rate of song production ($r_s = 0.06$, $r_s = -0.34$, respectively; both ns). By contrast, the number of songtypes in the repertoire of an individual was highly significantly correlated with that bird's average between-type similarity score (Fig. 8, $r_s = 0.79$, $p < 0.005$).

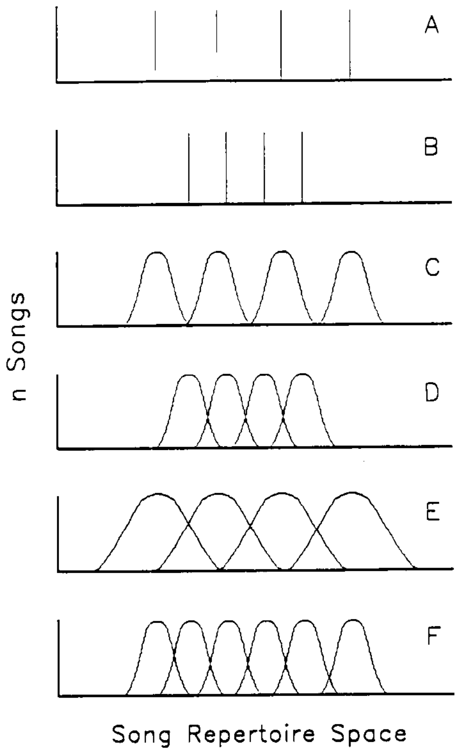
Discussion

A. Organization of Song Repertoires

Because song sparrow songtypes exhibit considerable variation and often overlap in structure (i.e., by sharing notes), describing songtypes in a song repertoire can be subjective and arbitrary (BORROR 1961, 1965; MULLIGAN 1963, 1966; STODDARD et al. 1988). This difficulty represents a fundamental problem in ethology, that of quantitatively delineating behavioral categories in functional and evolutionary studies of behavior. BARLOW (1977) outlined the general strategy we have employed here, which entails (1) identifying the smallest distinguishable units of behavior (MUPs in our case), and (2) statistically grouping behaviors that share those units using numerical taxonomic procedures. A distinguishing feature of this approach is that it does not take into consideration behavioral context. Instead, it is based exclusively on the structure of behavior itself. As such, this approach avoids the potential circularity of assessing the functional significance of behaviors that have in turn been defined on the basis of inferred function or by associations with other behaviors. The utility of this method may extend to other signalling systems and to the analysis of behaviors not associated with communication.

Beyond simply delineating songtypes, our quantitative analysis of song similarities demonstrates how a vocal repertoire can exhibit variation in dimensions other than in the number of songtypes produced. Take, for example, the simple case in which songtypes are invariant from one performance to the next. A repertoire of highly dissimilar songtypes might be functionally different from a

Fig. 9: Schematic representation of possible within-songtype and between-songtype similarity relationships in a song repertoire. See text for description and explanation



repertoire of the same size but with more similar songtypes (Fig. 9A vs. B). In this case, a measure of "between-songtype similarity" needs to be included as part of the description of vocal complexity.

In song sparrows, however, songtypes are not invariant. Thus, the evaluation of vocal complexity in this species must also consider the degree to which songs lumped in a given type vary, or "within-songtype similarity" (e.g., Fig. 9C). By definition, all renditions of an invariant songtype have a within-songtype similarity of 1.0. This value decreases as the song variants in a given songtype become increasingly divergent.

Between-songtype similarity in song sparrows depends not only on the similarity of "modal" songtypes (if such could be defined, sensu Barlow 1977), but also on the degree of within-songtype similarity observed. To illustrate, consider two repertoires with equal numbers of songtypes. Between-songtype similarity will increase with increasing similarity of the central tendencies (or modes) of these songtypes (Fig. 9C vs. D). But even if the songtype modes in these two repertoires are equally dissimilar, between-songtype similarity will also increase as a function of increasing within-songtype variation (Fig. 9C vs. E). In this sense, between-songtype similarity may be thought of as a measure of songtype "overlap". Our use of Jaccard's coefficient based on shared MUPs encompasses both aspects of between-songtype similarity without relying on the definition of a modal songtype.

The song sparrow repertoires in our sample exhibit variation in all three measures of vocal complexity (number of songtypes, between-songtype similarity, and within-songtype similarity), but to differing degrees. Between-songtype similarity is considerably more variable across individuals than is within-songtype similarity (c.v. = 65.61 vs. 4.65, respectively; Fig. 6). The number of songtypes in a repertoire, as determined by our cluster analyses, also varies considerably (c.v. = 34.08), albeit to a lesser extent than between-type similarity. Thus, repertoires include different numbers of songtypes, and those songtypes differ in how similar they are to each other, but the amount of diversity in song variants that comprise songtypes is comparatively low. The relative constancy of within-type variation is also reflected in the lack of correlation between within-type similarity and the number of song variants classified together in a songtype (Fig. 7).

Despite the low variance in within-songtype similarity, one still might predict that song sparrow repertoires with more variable songtypes should tend to have higher between-songtype similarities because of increased overlap (e.g., Fig. 9C vs. E). A trend in this direction is seen in our data, but it is not significant ($r_s = -0.29$, ns). Thus, observed differences in between-songtype similarity are relatively independent of differences in overlap due to within-songtype variation in our sample.

By contrast, between-songtype similarity is strongly positively correlated with the number of songtypes in a bird's repertoire (Fig. 8; $r_s = 0.79$, $p < 0.005$). That is, the more songtypes in a bird's repertoire, the more similar they are to each other. This result, along with the low variation observed in within-songtype similarity, suggests that song sparrows in our population produce variation in their repertoires along a continuum. One extreme of this continuum includes relatively few, but highly dissimilar songtypes, and the other extreme includes relatively many, but highly similar songtypes (e.g., Fig. 9C vs. F). There is one caveat — in 7 of 12 birds, some songtypes represent rare song variants (< 1 % of total songs produced) that were sufficiently dissimilar from other songs so as to be classified as their own songtypes. The number of rare songtypes was positively correlated with the total number of songtypes in a bird's repertoire ($r_s = 0.81$, $p < 0.005$), and with between-songtype similarity ($r_s = 0.66$, $p < 0.025$). Both relationships suggest that rare songtypes essentially "fill in the gaps" between more common songtypes in a bird's repertoire, and in this way contribute to higher between-songtype similarities.

This pattern of song repertoire organization implies that vocal complexity is best summarized as a "space" characterized by several parameters rather than in terms of any single measure. It may be useful to think of a "repertoire space," analogous to the concept of an "acoustic space" that has been used to characterize the features of song involved in species-recognition (BRÉMOND 1978; DABELSTEEN & PEDERSEN 1985; NELSON 1988, 1989; NELSON & MARLER 1990). The difference is that dimensions of repertoire space are based not on primary measures of acoustic structure (such as frequency or duration), but are instead measures derived from variation in structure or structural similarity.

This way of organizing song repertoires also has implications for understanding the functional and evolutionary consequences of vocal complexity. For example, female song sparrows respond preferentially in the laboratory to large song repertoires measured as numbers of songtypes (SEARCY & MARLER 1981; SEARCY 1984), but field studies have failed to find consistent correlations between repertoire size and indicators of female mating preference (GILBERT 1983; SEARCY et al. 1985; HIEBERT et al. 1989). Our results might account for this inconsistency if, for example, males in the field with few but highly dissimilar songtypes were as successful in mating as males with many but highly similar songtypes.

B. Songtypes as Units of Learning, Production and Perception

Like many songbirds, the song sparrow is a "close-ended" or "age-limited" learner (MARLER & PETERS 1987, 1988). This label implies that the endpoint of song development is marked by a profound loss of vocal plasticity ("crystallization") and that songs, once learned, are encoded by the brain in some sort of packet ("template") that remains immutable after development is complete (THORPE 1961; KONISHI & NOTTEBOHM 1969; MARLER 1970, 1981; MARLER & MUNDINGER 1971; NOTTEBOHM 1984). The analogy of a "motor tape" has been used to connote the invariance that characterizes the production of song as dictated by this template (KONISHI 1965; NOTTEBOHM 1970; but see CYNX 1990). Because song sparrow songtypes are variable, they cannot correspond to the concept of a crystallized song template or motor tape in the strictest sense. Does this then imply that song variants are the unit of memory and production?

Two lines of evidence contradict this view. First, whereas the number of songtypes we observed did not increase with the number of songs recorded (Fig. 5A), we found no upper limit to the number of song variants produced (Fig. 5B). One might argue that we simply did not sample enough songs to reach an asymptote in the number of variants observed, but theoretically one could never record enough songs to prove that an asymptote does not exist (KROODSMA 1982). Second, most song variants are rare. Although the entire sample of a song sparrow's singing behavior is divided approximately equally among its songtypes, most song variants (almost 70 %) are produced exceptionally infrequently. Indeed, over 43 % of all song variants in our sample were produced only once even when hundreds of songs were recorded from an individual. The two birds in our sample with the most songs recorded, Bird 4 (822 songs) and Bird 11 (902 songs), sang 42 % and 49 %, respectively, of their song variants only once.

In contrast to the open-ended nature of song variant production, our data suggest that the variation within songtypes is restricted. Most of the song variants we recorded (about 90 %) were easily assigned to a songtype with no disagreement between our objective methods and the subjective visual classification. Extensive recording failed to reveal more songtypes after some minimum number of songs was recorded (Fig. 5). The low variation we observed in within-songtype similarity scores (c.v. = 4.65) is also consistent with the idea that songtypes are limited in the degree to which they express variation. The most direct support for this point comes from the surprising lack of correlation between within-type similarity and the number of variants clustered in a particular songtype (Fig. 7). Additional song variants in a songtype do not translate into greater variation in that type.

We conclude that song variants produced by song sparrows are open-ended improvisations, in many cases unique utterances, that fit into the circumscribed framework of songtype themes. In this sense, the motor representation of song appears to be probabilistic, with each songtype stored as an abstract average that carries with it probabilities describing an allowable range of within-type variation.

The concept of probabilistic representation also has been applied to the problem of perceptual categorization of variable stimuli. A probabilistic model contrasts with an exemplar-based model of category representation in which multiple and related variants are stored individually and used as perceptual referents (SMITH & MEDIN 1981; see also NELSON & MARLER 1990). An exemplar-based motor representation of songtypes, with each song variant stored as its own crystallized template, seems unlikely given the open-ended nature of variant production.

What of the perception of songtypes? Other than the demonstration by STODDARD et al. (1988) that song sparrows are sensitive to within-songtype variation, there are few data to instruct us on this point. Recent studies of birdsong perception in general tend to favor an exemplar-based model of song categorization (see NELSON & MARLER 1990 for review), although some studies are also consistent with a probabilistic model of perceptual representation (e.g., NELSON 1988). The demonstrated link between production and perception of birdsong (e.g., MARGOLIASH & KONISHI 1985; WILLIAMS & NOTTEBOHM 1985) might suggest that both production and perception share a common kind of representation in the brain. Even if this proves not to be the case, the patterns of variation we observe in song sparrow repertoires help to define the necessary properties of brain mechanisms that mediate vocal behavior.

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