SONG TYPES AND VARIATION IN INSULAR POPULATIONS OF LINCOLN'S SPARROW (*MELOSPIZA LINCOLNII*), AND COMPARISONS WITH OTHER *MELOSPIZA*

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ABSTRACT.—In contrast to the Swamp Sparrow (*Melospiza georgiana*) and Song Sparrow (*M. melodia*), vocal studies of the congeneric Lincoln's Sparrow (*M. lincolnii*) are essentially lacking. To provide comparative data on song variation in this species, we obtained and analyzed recordings from 58 males (4,537 songs) breeding in montane meadows of the Sierra Nevada and San Bernardino Mountains, California. Males sang from one to six song types, and repertoire size averaged 3.7 types. No two males shared an identical song type. Males varied their types by changing the number of repetitions of a syllable or by adding, deleting, or substituting one or more syllables (i.e. by changing syllable composition). The number of variants, identified on the basis of differences in syllable composition, averaged 2.6 per song type (range 1 to 12). Individual variability was highest in the terminal elements of the song. Production of variants appears to be a process of "open-ended improvisation" of song types. Similarity of songs on the basis of shared syllables, as calculated by simple matching coefficients, showed a strong pattern of concordance with geography. Pairwise similarity declined with increasing distance between meadows, and meadows from different geographic regions clustered separately in a UPGMA tree. Patterns of geographic variation in song of Lincoln's Sparrows are similar to those observed in Song Sparrows and Swamp Sparrows. Song complexity and repertoire size show different evolutionary trends within *Melospiza*. *Received 5 October 1998, accepted 28 April 1999.*

AMONG EMBERIZINE SPARROWS, model organisms for the study of song variation and development have included the Swamp Sparrow (*Melospiza georgiana*; Marler and Peters 1982, Marler and Pickert 1984), Song Sparrow (*M. melodia*; Mulligan 1966; Marler and Peters 1987, 1988; Podos et al. 1992), and White-crowned Sparrow (*Zonotrichia leucophrys*; Baptista 1977, Baptista and King 1980, Baptista and Morton 1988). Within *Melospiza*, a third species, the Lincoln's Sparrow (*M. lincolnii*), has been largely overlooked from the standpoint of song and many other aspects of its biology (Ammon 1995). Because Swamp Sparrows and Song Sparrows have different patterns of song variation (e.g. repertoire size) and complexity (e.g. single-syllabic vs. multisyllabic song, respectively), an analysis of song in Lincoln's Sparrows provides an additional comparative perspective on vocal differences in the genus. Furthermore, the fact that phylogenetic relationships among these three congeners have been well studied (Zink 1982, Zink and Blackwell 1996, Patten and Fugate 1998) enables assess-

ment of concordance between song evolution and phylogeny.

Of the three subspecies of Lincoln's Sparrow currently recognized (AOU 1957), the montane form (*M. l. alticola*) is especially well suited to a study of song variation because of its insular breeding distribution in mid- to high-elevation meadows in the western United States. Montane Lincoln's Sparrows have a narrow nesting preference for flooded or boggy meadows with low vegetative cover and minimal disturbance from livestock grazing (Cicero 1997). Although abundances may vary among sites, densities generally are low (Cicero 1997, unpubl. data). Meadows occupied by Lincoln's Sparrows are isolated from each other by coniferous forest that forms discrete boundaries around breeding populations. This distribution provides an ideal setting for the analysis of vocal variation at different geographic scales.

We studied songs of Lincoln's Sparrows in montane populations to document variation at four levels: (1) within individuals; (2) among individuals breeding in the same meadow; (3) among individuals occupying different clusters of meadows in the same geographic re-

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TABLE 1.   Geographic distribution and sample sizes of Lincoln's Sparrow song recordings, and number of song types and song-type variants found at each site. Sites are grouped into three geographic regions for analysis.

Region and study site[a]	No. males recorded	No. songs recorded	No. song types[b]	No. song-type variants[c]
Northern Sierra Nevada				
Church Meadow, Sierra Co.	6	646	22	55
Lincoln Valley, Sierra Co.	11	862	38	99
Haypress Creek, Sierra Co.	7	504	28	75
Webber Lake, Sierra Co.	2	132	5	13
Coppins Meadow, Sierra Co.	7	633	34	114
Central Sierra Nevada				
Hogdon Meadow, Tuolumne Co.	2	49	6	14
Beasore Meadow, Madera Co.	5	269	19	45
Dinkey Meadow, Fresno Co.	1	16	1	3
Long Meadow, Fresno Co.	2	75	7	10
San Bernardino Mountains				
Bluff Lake, San Bernardino Co.	7	648	25	56
Metcalf Creek, San Bernardino Co.	8	703	30	94
Total	58	4,537	215	578

[a] See Cicero (1997: figure 1) for specific locations of sites.

[b] Song type defined by unique syllable composition and order; songs easily classified into types.

[c] Song-type variant defined as a different rendition of the same basic song type created by the deletion, addition, or substitution of one or more syllables. Distinction between song types and variants on a single type was unambiguous.

gion; and (4) among individuals breeding in different geographic regions. We also compared the observed patterns of variation with those reported for Swamp Sparrows and Song Sparrows. A phylogenetic framework was used to interpret similarities or differences in song variation within this genus. Such a comparative approach (Irwin 1988, Brooks and McLennan 1991, Read and Weary 1992, Brenowitz 1997) is central to understanding the evolutionary and behavioral basis for vocal differences among taxa.

STUDY AREA AND METHODS

Recordings.—Songs were recorded during the breeding seasons (May through June) of 1988 and 1989 using a Sony TCM-5000EV cassette recorder, a Sennheiser ME88 directional microphone, and a SME-BA3 amplifier. We obtained 4,537 recordings from 58 males breeding in 11 meadows in the Sierra Nevada and San Bernardino Mountains, California (Table 1). The number of songs recorded per male ranged from 16 to 150 ($\bar{x} = 78$ songs). As many songs as possible were recorded for each male, with sample sizes dictated by the persistence of the singer. All males singing at each meadow were recorded. Because Lincoln's Sparrows are highly territorial during the breeding season, and males sing from conspicuous perches (Ammon 1995, Cicero 1997), individuals could be identified easily by their position in

the meadow. Exact locations of recordings are available from the senior author. Tapes are archived in the Museum of Vertebrate Zoology, University of California, Berkeley.

Sonographic analysis.—Digital sound acquisition, storage, and output were performed in the Laboratory of Natural Sounds, Museum of Vertebrate Zoology, on a Gateway 2000 microcomputer using Real-time Spectrogram (RTS) version 2.0 and SIGNAL version 3.0 programs and hardware (Engineering Design 1996). Real-time sonograms were examined for each song, and songs were easily classified into distinct types on the basis of unique syllable composition and order (Fig. 1). Because males often varied one or more syllables during a bout of singing a particular song type (Fig. 2), we also noted all song-type variants. Song types were initially classified for each male to determine individual repertoire size. Subsequently, individual song types were compared across all males in the sample to assess the degree of sharing of types.

Analysis of similarity at different geographic scales.—The complexity and variability in Lincoln's Sparrow songs made it impractical to compare entire songs with regard to geographic patterning. Thus, we used syllables as the main unit of geographic analysis, where a syllable is defined here as "the main recognizable, repeated component of songs, comprised of one or several notes" (Irwin 1988). This approach is similar to that employed by Harris and Lemon (1972) for Song Sparrows, which also have complex and variable songs. Using sonograms of all song
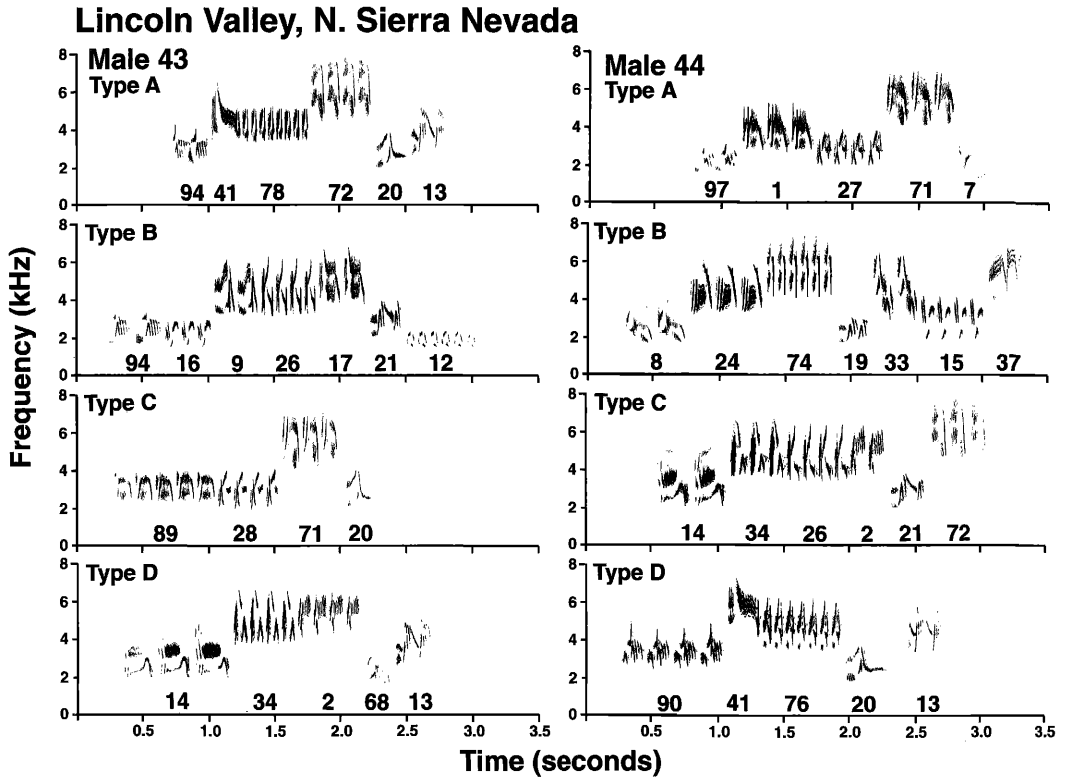
Lincoln Valley, N. Sierra Nevada

FIG. 1.   Four song types (A to D) recorded from two male Lincoln's Sparrows (43 and 44) in Lincoln Valley, California. Different types were comprised of some unique and some shared syllables, which are numbered as in our lexicon. Note the multisyllabic complexity of song types.

types and their variants, we developed a lexicon of unique syllables found in the entire sample of recordings by visually comparing each syllable with all syllables already in the lexicon. Differences between syllables generally were discrete and unambiguous. However, in cases where syllables had subtle variations, we took a conservative approach and did not distinguish these in the lexicon. Comparison of syllables in the lexicon was done "blindly" with regard to geographic origin. Once the lexicon was complete, the following data were recorded for each syllable: (1) the song type or variant in which the syllable occurred, (2) the meadow where that song type was recorded, and (3) the relative position of the syllable in the song (e.g. first syllable out of seven syllables total).

We used the simple matching coefficient (S_{SM}; Sneath and Sokal 1973) to quantify pairwise similarity among all males based on the presence or absence of syllables in their respective song repertoires:

$$S_{SM} = (a + d)/(a + b + c + d), \qquad (1)$$

where a is the number of syllables present in the repertoires of both individuals; b is the number of syl-

lables present in the repertoire of the first individual but absent in the repertoire of the second individual; c is the number of syllables present in the repertoire of the second individual but absent in the repertoire of the first individual; and d is the number of syllables absent in the repertoires of both individuals, using as a base list the number of syllables found in the repertoires of all individuals being compared. We chose the simple matching coefficient because it incorporates diverse kinds of information, including both positive and negative matches as well as mismatches. Although the number of negative matches (d) may be influenced by sampling effort, e.g. size of lexicon, exclusion of this variable, such as in Jaccard's (1908) coefficient, would result in loss of significant information for purposes of the present study.

Pairwise coefficients were averaged to obtain a mean similarity value for males breeding in the same meadow, in different meadows in the same region, or in different regions. Mean coefficients were analyzed with the sums-of-squares simultaneous test procedure (SS-STP; Gabriel 1964, Gabriel and Sokal 1969) to assess the effects of geographic scale. The SS-STP analysis was performed using a program modified
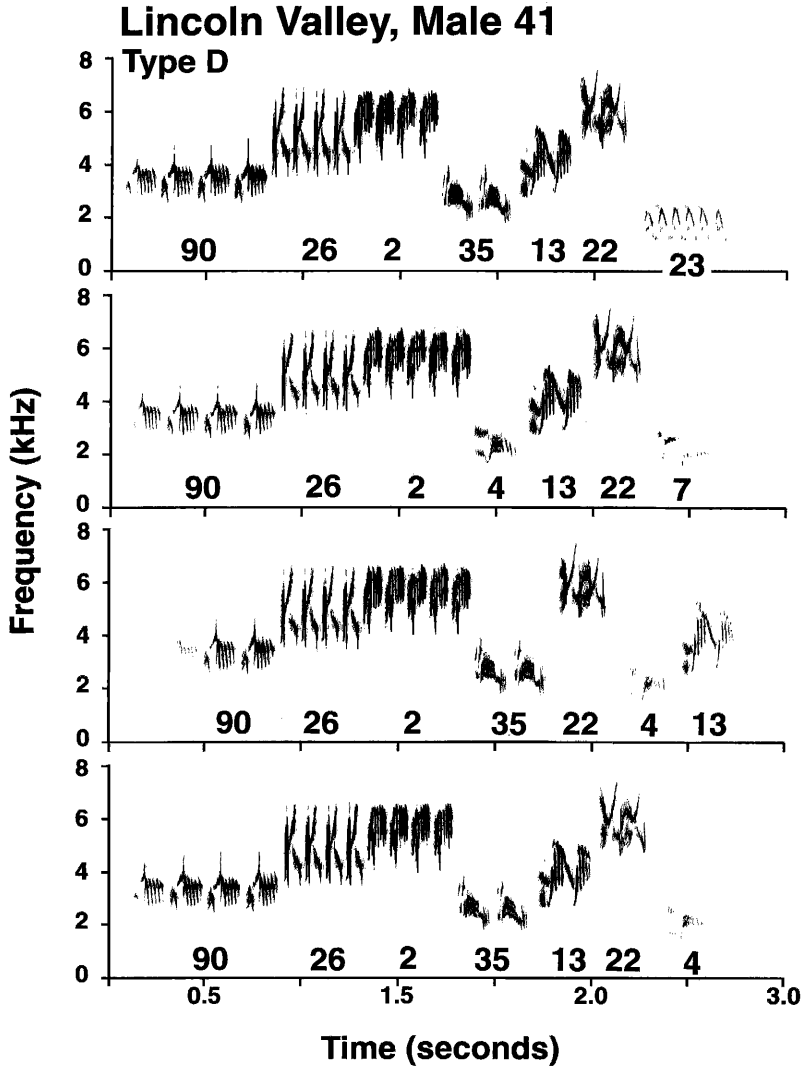
FIG. 2. Sonograms showing four variants of a single song type (type D) recorded from a Lincoln's Sparrow (male 41) in Lincoln Valley. Unique syllables are numbered as in our lexicon. Note the flexibility with which individuals can vary individual song types.

from that of Sokal and Rohlf (1969; see Johnson et al. 1997).

We also calculated simple matching coefficients for pairs of meadows using the entire repertoire of syllables found in each meadow. Mantel's (1967) test was used to regress this matrix of coefficients against a pairwise matrix of inter-meadow distances as determined from topographic maps. In addition, we used the UPGMA clustering algorithm (Sneath and Sokal 1973) to group meadows based on their similarity coefficients. NTSYS-pc (Rohlf 1988) was used to calculate simple matching coefficients and to perform the regression and cluster analyses.

RESULTS

Song types and repertoire size.—We classified the 4,537 songs into a total of 215 song types (Table 1). Each male sang from one to six types, and repertoire size averaged 3.7 ± SD of 1.1 song types. Males typically sang several renditions of one song type before switching to a new type or returning to an earlier type. The number of consecutive renditions of a song type was highly variable. For example, a sample of 31 recordings from one male yielded four

types (the same as the number of types in 136 recordings from another male), whereas a third male sang the same type repeatedly in 88 recordings. Although extremely large sample sizes are needed to ensure complete sampling of an individual's repertoire, repertoire size was not statistically correlated with the number of songs recorded per male ($r = 0.218$, $P > 0.05$).

Song types were composed of different combinations of syllables (Fig. 1), and no two males shared an identical type. Individual syllables, however, were incorporated into different types sung by a single male or by males from the same or another meadow. Of the 221 syllables that we identified in the lexicon, 126 (57%) were shared and 95 (43%) were unique to a single song type. Males in our sample had from 6 to 31 syllables in their repertoire ($\bar{x} = 20.4 \pm 5.9$); this value was correlated with number of songs recorded ($r = 0.44$, $P < 0.01$). The number of syllables per song varied from 1 to 12 ($\bar{x} = 5.4 \pm 1.5$; mode = 5).

Individual variability.—Although the number of song types per male was low, males varied their types in two ways: (1) by changing the number of times that a syllable was repeated in a given sequence; and (2) by adding, deleting, or substituting syllables within a type, i.e. by changing syllable composition (Fig. 2). Because essentially every song was distinct if the number of repetitive elements within songs was considered, our analysis of individual variability dealt solely with variation in syllable composition.

The first song type recorded from a male was used as the standard against which other songs were compared and variations in syllable composition identified. The total number of song-type variants (hereafter "variants") in the sample was 578 (Table 1). We recorded from 3 to 29
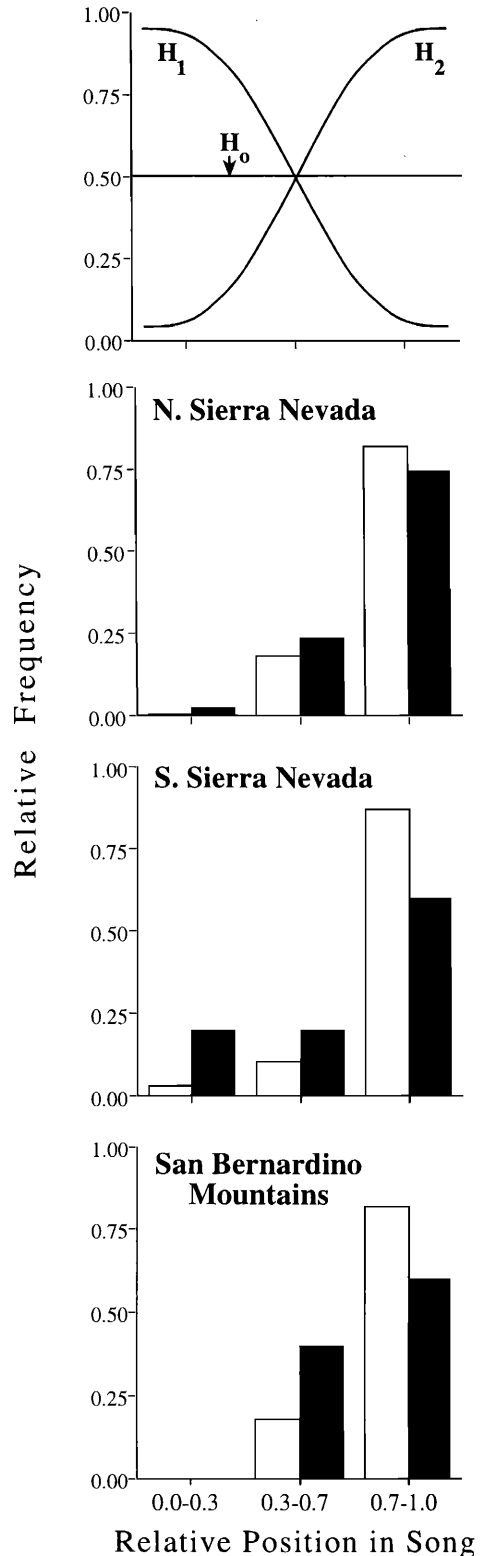
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FIG. 3. Proportion of song-type variants, by geographic region, with different kinds of changes in syllable composition as a function of position in the song (open bars, addition or deletion of syllable; solid bars, substitution of syllable). Data are for comparisons of song-type variants within individuals only. The top panel illustrates expectations based on the null hypothesis and two alternative hypotheses (indicated by idealized frequency distributions). Note the prevalence of changes of either kind toward the ending of the song.
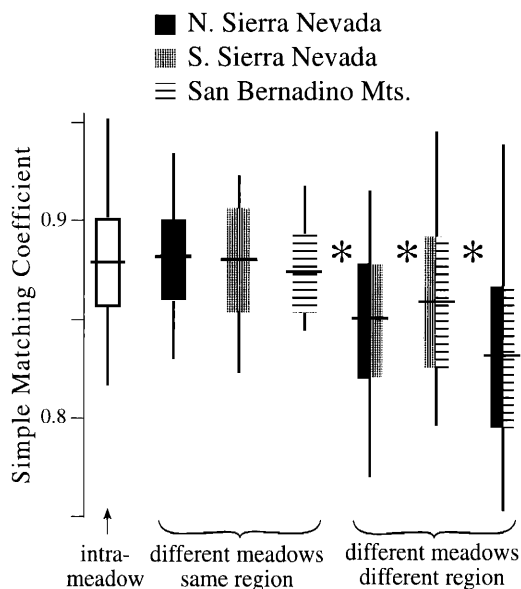
FIG. 4. Similarity (S_{SM}) in syllable composition of male song repertoires in Lincoln's Sparrows at different geographic scales. Coefficients were calculated for pairwise comparisons of all 58 males in the sample. Symbols show mean coefficients (horizontal lines) ±SD (bars) and range (vertical lines). Inter-regional comparisons are illustrated by contrasting patterns within a bar. Asterisks denote means that are significantly different from each other at $P = 0.05$, as determined by the SS-STP procedure.

variants per male ($\bar{x} = 10.0 \pm 4.9$), and the number of variants was positively correlated with the number of songs recorded from that male ($r = 0.49$, $P < 0.01$), as well as with the number of songs recorded per song type ($r = 0.43$, $P < 0.01$). Males sang an average of 2.6 ± 1.6 variants per song type, although one male had 12 variants on a single type. On a few occasions, males sang "hybrid" songs in which groups of syllables from two song types were combined. The mean number of variants per type did not differ geographically (northern Sierra Nevada, 2.7 ± 1.7; southern Sierra Nevada, 2.1 ± 0.9; San Bernardino Mountains, 2.8 ± 1.7).

To test whether some parts of the song were more stable than others (e.g. the introduction vs. the ending), we divided each variant song into three sections and calculated the frequency of changes in syllable composition that occurred at different relative positions in the song

(Fig. 3). The null hypothesis (H_0) predicts that males vary different parts of their songs with equal frequency, i.e. they show no preference for varying one part of their song over another. Two alternative hypotheses are possible: H_1, which predicts that the introduction is more variable than the ending; and H_2, which predicts that the ending is more variable than the beginning. Our data clearly support the second alternative hypothesis (H_2), with 60 to 87% of the changes in syllable composition (addition, deletion, or substitution) occurring in the terminal third of the song. The most common pattern was for males to add or delete one or more syllable types in the ending of the song. Whereas additions and deletions were more common than substitutions in the latter part of the song, the reverse pattern was observed in the introductory or middle segments. Males from different regions showed the same pattern of individual variation in song types.

Geographic variation.—Songs of males from the same meadow or region all had high coefficients of similarity (Fig. 4), indicating that many syllables were shared among song types at these geographic scales. In contrast, mean coefficients of similarity declined significantly in interregional comparisons, with males from the two most distant regions (northern Sierra Nevada vs. San Bernardino Mountains) having the lowest mean coefficients of similarity in all pairwise comparisons (Fig. 4). Regression of simple matching coefficients against geographic distance for pairs of meadows (Fig. 5) showed a strong negative correlation ($r = -0.856$) that was highly significant using Mantel's test ($t = -4.866$, $P < 0.001$).

UPGMA clearly separated meadows into different geographic clusters based on shared syllables in songs (Fig. 6). Meadows in the northern Sierra Nevada grouped separately from those farther south in the range, and all Sierran meadows clustered apart from sites in the San Bernardino Mountains of southern California. The high cophenetic correlation coefficient (0.841) indicates strong agreement between the cluster diagram and the original similarity matrix.

DISCUSSION

Song complexity, repertoire size, and phylogeny in Melospiza.—Lincoln's Sparrows have a com-
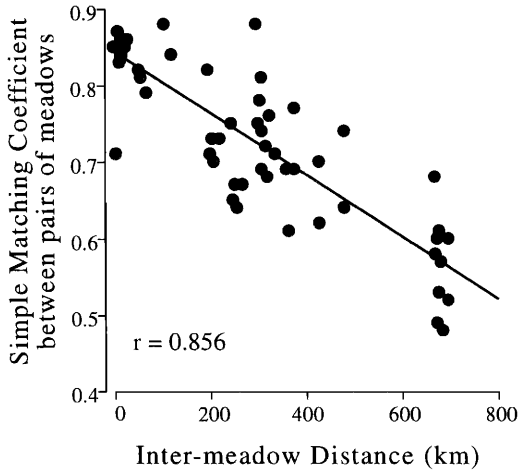
FIG. 5. Strong negative association between similarity (S_{SM}) of meadows, as determined by the presence or absence of syllables in Lincoln's Sparrow songs, and geographic distance between meadows. Each point represents comparison of a single pair of meadows.

plex song that consists of different syllables given in variable frequencies, often with a clear introduction, trill, and ending. Song Sparrows likewise sing a multisyllabic song that is characterized by an array of syllables (e.g. whistle, buzz, trill) at different frequencies. Both of these song patterns contrast sharply with the simple, single-syllabic trill sung by Swamp Sparrows.

Repertoire size also varies among species of *Melospiza* (Table 2). Lincoln's Sparrows recorded in this study sang an average of 3.7 song types per individual, which is consistent with the limited data previously available for this species. Brewster (1899) reported his observations on one Lincoln's Sparrow in Massachusetts and classified the songs of this individual into four types. Borror (1961) analyzed 12 recordings of Lincoln's Sparrows from Ontario and Wyoming and reported a song repertoire of "3 or more patterns." Baker (1982) compared several characteristics of "*Zonotrichia*" sparrows (inclusive of *Melospiza*) and reported "often two" songs per bird for Lincoln's Sparrows. The relatively small song repertoire of the Lincoln's Sparrow is comparable to that of the Swamp Sparrow, and both of these species have notably smaller average repertoire sizes than the Song Sparrow (Baker 1982). The behavioral implications of such differences in repertoire size have been well studied (e.g. Searcy et al. 1982; Searcy 1984, 1992; Hiebert et al. 1989; Williams and Slater 1990).

Whether bird song exhibits patterns that are concordant with phylogeny is of primary evolutionary interest (Irwin 1988, Read and Weary 1992). Based on morphometric, allozyme, and/or mitochondrial DNA data, several studies of emberizid sparrows (Zink 1982, Zink and Blackwell 1996, Patten and Fugate 1998) have shown that the Lincoln's Sparrow and Swamp
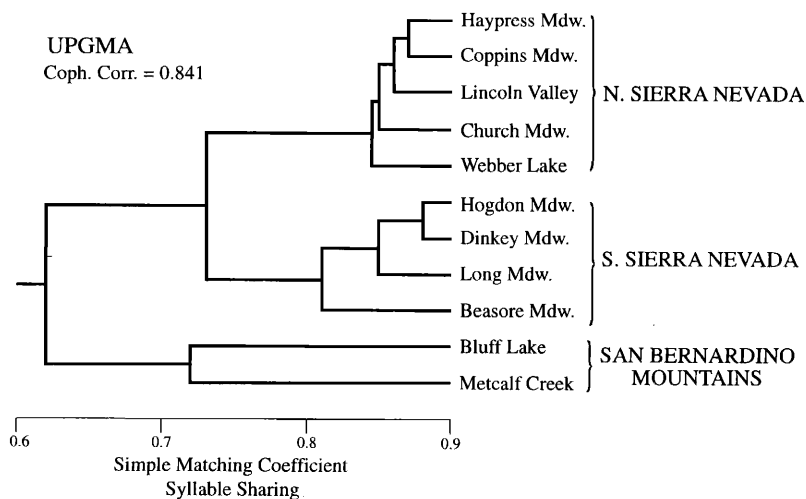

FIG. 6. UPGMA cluster diagram illustrating the similarity of meadows on the basis of syllable composition of Lincoln's Sparrow songs. Syllable sharing was highest among songs recorded from the same geographic region, as indicated by clustering of meadows.

TABLE 2. Summary of song characteristics of *Melospiza* sparrows.

Species	Song complexity	Individual variability	Repertoire size[a]	Source, location, and no. males[b]
M. melodia	High	High	8 (5–14)	Borror 1965; Maine (53)
			16 (10–23)	Mulligan 1966; California (13)
			9 (7–11)	Harris and Lemon 1972; Quebec (10)
			7 (5–12)	Eberhardt and Baptista 1977; California (7)
			9 (8–9)	Searcy et al. 1985b; New York (5)
			8 (4–12)	Hiebert et al. 1989; British Columbia (16)
			10 (8–20)[c]	Podos et al. 1992; New York (12)
			9 (7–11)	Beecher et al. 1996; Washington (20)
M. georgiana	Low	Low	3 (1–7)	Marler and Pickert 1984; New York (127)
M. lincolnii	High	High	4	Brewster 1899; Massachusetts (1)
			3+	Borror 1961; Ontario and Wyoming (unknown)
			4 (1–6)	This study; California (59)

[a] Average no. of song types per individual (rounded to whole number), with range of individual repertoire sizes in parentheses.

[b] Samples are based on the number of males for which repertoire size was determined, which may be less than the total number of males recorded in the study.

[c] Based on Monad method of classifying songs into types; see Podos et al. (1992) for explanation.

Sparrow are sister species, with Song Sparrow as the basal taxon. Although Irwin (1988) and Lanyon (1985) questioned this phylogenetic hypothesis, congruence among multiple data sets lends credence to the relationship (*M. melodia* (*M. lincolnii, M. georgiana*)). Using this tree, the evolution of song complexity among species of *Melospiza* does not appear to be concordant with their phylogenetic history (Fig. 7). Repertoire size (Fig. 7, Table 2), on the other hand, shows a congruent evolutionary pattern. Large repertoire size and high song complexity appear to be ancestral in *Melospiza* and may be the primitive state for emberizid sparrows. Irwin (1988) compared song characteristics among species of *Zonotrichia, Passerella, Junco,* and *Melospiza* and concluded that the most parsimonious hypothesis calls for a single transformation from large repertoires (>1 song type; e.g. *Melospiza*) to repertoires of a single song type (e.g. *Zonotrichia*). Likewise, fewer transformations are needed to explain the evolution of single-syllablic songs (e.g. *M. georgiana*) from more complex multisyllabic songs (Irwin 1988).

Patterns and significance of individual variability in song.—Lincoln's Sparrows exhibit a high degree of individual variability in song (changes in syllable composition within a song type), and even higher levels of individual variation characterize the songs of Song Sparrows (Mulligan 1966, Harris and Lemon 1972, Podos et al. 1992). In both species, the positive correlation between number of variants and number of songs recorded, and the lack of such a corre-

lation with number of song types, suggests that such variants are produced by "open-ended improvisations" of a crystallized number of song types in the repertoire (Podos et al. 1992). In contrast, Swamp Sparrows repeatedly sing the same single-syllabic trill (Marler and Pickert 1984). As with large repertoire size and high song complexity, the high individual variability in song types of Lincoln's Sparrows and Song Sparrows may be an ancestral behavior for *Melospiza.*

Individual variability in the songs of Lincoln's Sparrows as well as Song Sparrows (Horning et al. 1993) is concentrated in the later parts of the song. This nonrandom pattern of variation suggests a functional basis. For example, relative stability in the introduction may be important for species recognition, whereas terminal variability may promote individual recognition. The importance of different vocal cues in conveying alternate kinds of information has received recurrent attention (Emlen 1972, Nelson 1989, Beecher and Stoddard 1990, Kroodsma and Miller 1996). Laboratory and field studies of Song Sparrows (Horning et al. 1993) have shown that, although individuals use information from throughout the song to classify types, they weigh the beginning elements most heavily. Similar results have been obtained for other species with highly variable songs (e.g. *Sturnella neglecta*; Falls et al. 1988). Although male Song Sparrows perceive different song types as being more distinctive than variants on a single type (Searcy
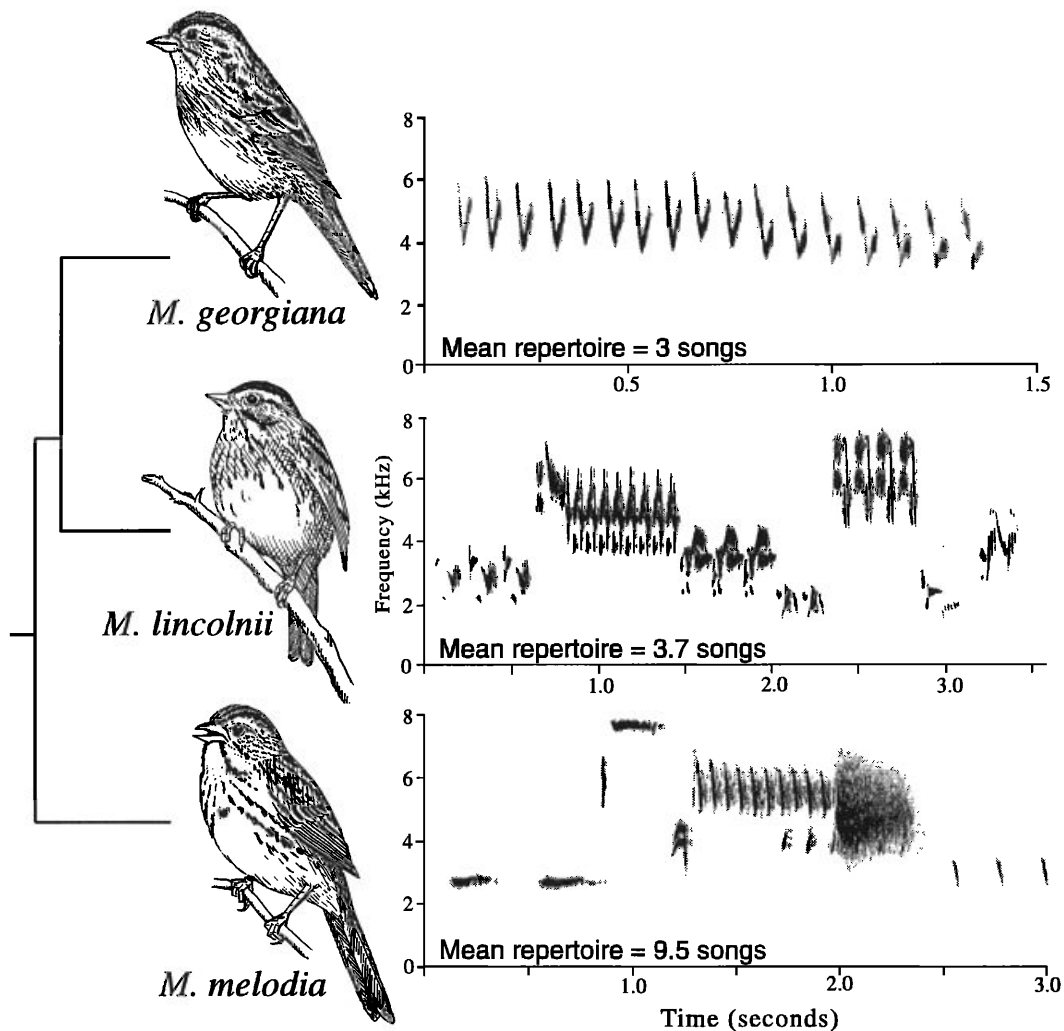
FIG. 7. Best-supported phylogenetic hypothesis of relationships among the three species of *Melospiza*, with sonograms of representative songs. Note that sister-taxon relationship is congruent with mean repertoire size but not with song complexity (i.e. single-syllabic versus multisyllabic song). The Swamp Sparrow song was recorded by S. L. L. Gaunt at Churchill, Manitoba, Canada (Borror Laboratory of Bioacoustics recording number 21225). The Lincoln's Sparrow song was recorded by C. Cicero at Church Meadows, Sierra County, California. The Song Sparrow song was recorded by V. Dziadosz at Tilden Regional Park, Contra Costa County, California (Museum of Vertebrate Zoology master tape number 135).

et al. 1995), a single song variant appears to provide sufficient information for recognition of different neighbors (Stoddard et al. 1991). Comparable studies are needed on Lincoln's Sparrows for comparison with the observed behavior in Song Sparrows.

Patterns and significance of geographic variation in song.—The songs of Lincoln's Sparrows showed clear geographic variation in syllable composition, with certain syllables becoming rare or absent in the songs of males from distant meadows (northern Sierra Nevada vs. San Bernardino Mountains). Similar variation has been observed between geographically separate populations of Song Sparrows (Borror 1965; Harris and Lemon 1972, 1974) and Swamp Sparrows (Marler and Pickert 1984). Playback experiments on Song Sparrows (Har-

ris and Lemon 1974) have shown that males respond more strongly to local versus foreign songs in some populations, although this is not universal. Balaban (1988a) found a correlation between variation in song syllables and allelic frequency in two populations of Swamp Sparrows and showed through playback experiments (Balaban 1988b, c) that geographic differences in syllable structure and song syntax are behaviorally meaningful in this species. Similar experiments have not been conducted on Lincoln's Sparrows to assess the response of individuals to songs from different regions.

Whether geographic variants in song of the Lincoln's Sparrow or other *Melospiza* species can be termed "dialects" depends on the definition that is applied (Mundinger 1982). We prefer the definition proposed by Mundinger (1982): "a *song dialect* is a *variant song tradition* shared by members of a local population of birds, with a dialect *boundary* delineating it from other variant song traditions" (italics his). Dialects in this sense are best exemplified by the White-crowned Sparrow, where all males within one dialect region sing the same song type, and clear boundaries exist between dialects (Orejuela and Morton 1975, Baptista 1977, Baptista and King 1980). Within *Melospiza*, the Swamp Sparrow comes closest to having local dialects (sensu Mundinger 1982) because of the relatively low amount of individual variation, the limited number of notes and syllable types, and the tendency for distinctive syntactical rules to apply within an area (Marler and Pickert 1984). The high degree of song-type variation observed in Lincoln's Sparrows as well as Song Sparrows, and the absence of any discrete vocal boundary between populations, makes it difficult to delineate dialects in these species as they apply to entire songs. Nonetheless, the geographic structuring of vocal variation seen in this study (Fig. 6) indicates that sharing of song traditions in the Lincoln's Sparrow occurs at the level of individual syllables. This has important implications for understanding vocal learning and cultural evolution in this species.

Song learning and development in Melospiza.— Studies of song ontogeny in Lincoln's Sparrows are lacking, although vocal mimicry by free-living birds provides indirect evidence of learning in this species (Baptista et al. 1981, Kroodsma and Baylis 1982). In contrast, pro-

cesses of vocal development in Song Sparrows and Swamp Sparrows, which show marked interspecific differences, are well understood (e.g. Marler and Peters 1982, 1987, 1988; Marler and Pickert 1984; Searcy et al. 1985a; Nelson 1987; Beecher et al. 1994). Because the variable multisyllabic song of the Lincoln's Sparrow is most similar to that of the Song Sparrow, one might expect that the Lincoln's Sparrow—like the Song Sparrow but not the Swamp Sparrow—uses cues from both syllable morphology and temporal arrangement of syllables (i.e. syntax) to learn and discriminate conspecific songs. On the other hand, the similarity in repertoire size between Lincoln's Sparrows and Swamp Sparrows, and the apparently innate basis for interspecific differences in repertoire size in this genus (Marler and Sherman 1983, 1985), suggests that Lincoln's Sparrows and Swamp Sparrows have similar developmental constraints on the size of their crystallized repertoire. Such predictions should be tested experimentally to shed further light on song learning and cultural evolution, and its relation to phylogeny, in *Melospiza*.

Needs for future research.—Our study provides a basis for future research on vocal communication, development, and behavior in Lincoln's Sparrow. Particularly needed are (1) broader geographic sampling of songs in both montane and non-montane populations to assess macrogeographic patterns of variation; (2) laboratory experiments on song ontogeny and development; (3) laboratory and field experiments to test the hypothesis that certain elements of song are more important in species versus individual recognition; (4) field experiments to assess the responses of males and females to songs from different geographic regions; (5) field studies that correlate repertoire size and individual variability as a function of population density; and (6) studies that use molecular markers to provide data on dispersal and breeding-site fidelity.

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