GEOGRAPHIC VARIATION IN THE ORGANIZATION
OF SONG SPARROW REPERTOIRES

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ABSTRACT.—We asked whether geographic variation exists in the complexity of song repertoires in Song Sparrows (*Melospiza melodia*) by quantitatively comparing four measures of repertoire organization across four geographically distant populations: (1) repertoire size (the number of distinct song types), (2) the number of ''minimal units of production'' per repertoire, (3) mean similarity among variants of the same song type (''within-type'' similarity), and (4) mean similarity among song types in a repertoire (''between-type'' similarity). We found significant geographic differences among populations in three of these four measures, with mean similarity among song types being the exception. In general, relatively sedentary populations in North Carolina and Washington were more similar to each other than to migratory populations in Pennsylvania and Maine. Contrary to our expectation based on prior interspecific analyses of variation in repertoire complexity, the relatively sedentary populations in our sample had more complex repertoires than did the more migratory populations. The origin and functional significance of population differences in repertoire complexity in this species remain uncertain. *Received 16 August 1999, accepted 27 April 2000.*

TREMENDOUS VARIATION exists among species of songbirds in the complexity of their songs. Complexity is most often measured as song repertoire size (i.e. the number of distinct song types sung by individual males), which can range from as few as one to as many as 2,000 across oscine species (Catchpole and Slater 1995). Comparative analyses by a number of authors have attempted to make sense of the diversity of song systems by correlating repertoire size with various behavioral and ecological factors, such as mating system and migratory pattern (Kroodsma 1977, Catchpole 1980, Shutler and Weatherhead 1990, Read and Weary 1992). Interspecific comparisons are hampered, however, by the fact that song types themselves may be more or less complex and may differ one from another to greater or lesser degrees in different species. This comparability problem means that repertoire size may be too simple a measure to describe adequately the relative complexity of song systems across species (Krebs and Kroodsma 1980, Kroodsma 1982). The problem can be circumvented to a large extent by making comparisons among different populations of the same species rather than among different species. Here, we undertake such an analysis for the Song Sparrow (*Melospiza melodia*).

Working within a species does not eliminate the comparability problem given that methods for defining and counting song types can differ across studies. Some level of subjectivity occurs in defining song types in Song Sparrows, for example, owing to the existence of extensive variation within song types. Renditions of the same song type by the same male may differ in minor ways, for example by the addition or deletion of syllables within trills, and in more substantial ways, such as by the addition, deletion, or substitution of entire trills or note complexes (Stoddard et al. 1988, Podos et al. 1992, Searcy and Nowicki 1999). Consequently, decisions about whether two songs differ enough to be considered separate song types, rather than two variants of the same type, can seem arbitrary. A method of classifying songs that minimizes this problem was suggested by Podos et al. (1992). In this method, songs are first broken into minimal units of production, or ''MUPs,'' defined as the smallest invariant units in a male's repertoire. Similarities for pairs of songs are calculated based on the pro-

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portion of MUPs shared. Cluster analysis is then performed on the set of songs produced by a given male, with songs assigned to categories at the level of clustering that produces maximal isolation between clusters.

We apply the Podos et al. (1992) method, which we call ''MUP analysis,'' to four distinct populations of Song Sparrows in Maine, Pennsylvania, North Carolina, and Washington. We also present data on a fifth smaller sample of males from a New York population. We first use our results to ask whether geographic variation exists in repertoire size. Differences in repertoire size have been reported between Song Sparrow populations (cf. Mulligan 1963, Borror 1965), but it is unclear whether these differences are biological rather than methodological. We further compare populations using three additional measures of repertoire complexity that are produced by MUP analysis: the number of MUPs per repertoire, the mean similarity among variants of the same song type (''within-type'' similarity), and the mean similarity among song types in a repertoire (''between-type'' similarity). Together, these four measures give a much fuller picture of repertoire complexity than does repertoire size alone.

Our results permit us to make preliminary within-species tests of trends in song complexity found in among-species comparisons. The most complete among-species comparisons made to date are those of Read and Weary (1992), using data on 165 passerine species. These data suggest that, among a large set of possible causal variables, song repertoire size appears to be most strongly associated with male parental care and migration: species with high male parental care tend to have larger song repertoires, as do species that are migratory rather than sedentary. Syllable repertoire size is associated with migration in the same way and also is correlated with mating system: polygynous species tend to have larger syllable repertoires than monogamous species. Of the three independent variables important in these interspecific comparisons, only migration is known to vary between populations of Song Sparrows. Two of our study populations (Washington and North Carolina) are nonmigratory, whereas the other three (Maine, Pennsylvania, and New York) are partial migrants. By analogy with the interspecific trends outlined by Read and Weary (1992), we predicted

that the Washington and North Carolina populations should have repertoires that are less complex than those of the Maine, Pennsylvania, and New York populations.

METHODS

Subjects and recording.—We recorded eight males in each of four geographically separate populations: Appledore Island, Maine (43°00′N, 70°40′W); Linesville, Crawford County, Pennsylvania (41°40′N, 80°30′W); Durham, Durham County, North Carolina (36°00′N, 78°50′W); and Seattle, King County, Washington (47°40′N, 122°20′W). All males were recorded as they sang on their territories during the breeding season. Numbers of songs recorded per male ($\bar{x} \pm$ SD) were 292 ± 68 in Maine, 371 ± 32 in Pennsylvania, 386 ± 118 in North Carolina, and 234 ± 68 in Washington.

The birds in these samples were recorded continuously for one to four hours on one or two consecutive mornings. We used the following sets of recording equipment: Sony TC D5M cassette recorder and Audio Technica Pro 2AX microphone with parabolic reflector (Maine); Sony TCM 5000EV cassette recorder and Realistic Omnidirectional microphone with parabolic reflector (Maine, Pennsylvania); Marantz PMD 221 cassette recorder and Realistic Omnidirectional microphone with parabolic reflector (Pennsylvania); Sony TC D5M cassette recorder and Sennheiser MKH 816 shotgun mircophone (North Carolina); Sony TCD-5 Pro II cassette recorder and Sennheiser ME 88 shotgun microphone (North Carolina); Sony WM-DC recorder with a Sennheiser RF condenser microphone MKH-816T-U (North Carolina); or Sony TC D5M cassette recorder and Sennheiser ME 88 shotgun microphone (Washington).

We also included recordings made at Millbrook, Dutchess County, New York (41°50′N, 73°40′W). These recordings represent a subset of those examined by Podos et al. (1992), who included laboratory as well as field recordings in their analysis. To ensure that the New York sample was comparable to the other samples, we used only the field recordings from that sample, which were from four males singing on their territories ($\bar{x} = 282 \pm 107$ songs per male). Recording methods for the New York birds were described in Podos et al. (1992). Because of the small sample size from New York, we did not include these results in our statistical analysis.

Song analysis.—We used MUP analysis to define song types and measure within-type and between-type variation. Briefly, we first visually reviewed the complete song sample of an individual using spectrograms produced on a Princeton Applied Research Real Time Spectrum Analyzer (model 4512) or a Kay Elemetric Sona-Graph (model 5500). Based on this review, we made an initial subjective classification of

TABLE 1. Summary of four measures of song repertoire complexity from five Song Sparrow populations. Values are $\bar{x} \pm$ SD. Within columns, values with the same superscript do not differ significantly (post-hoc analysis; $P > 0.05$). Values from New York are not included in statistical analyses.

Population	No. of song types	No. of MUPs	Within-type similarity	Between-type similarity
Maine	8.1 ± 1.0[A]	53.3 ± 6.1[A]	0.96 ± 0.03[A]	0.16 ± 0.03
Pennsylvania	8.4 ± 1.3[A]	56.3 ± 10.0[A]	0.96 ± 0.02[A]	0.18 ± 0.06
North Carolina	10.4 ± 1.4[B]	69.1 ± 14.5[B]	0.93 ± 0.02[B]	0.13 ± 0.06
Washington	12.4 ± 1.3[C]	70.1 ± 10.9[B]	0.92 ± 0.02[B]	0.13 ± 0.03
New York	8.8 ± 1.5	61.3 ± 7.9	0.95 ± 0.02	0.11 ± 0.06

song types in a bird's repertoire and produced sonograms of multiple copies of each type using a Kay Elemetric Digital Sona-Graph Model 7800 or a DSP Sona-Graph Model 5500 (0 to 8 kHz range and 300 Hz filter bandwidth). We divided sonograms into their component notes, pooled all note sonograms from all sonograms, and grouped identical notes according to fine acoustic features such as frequency, duration, amplitude, and frequency modulation. This categorization was done without reference to the song types in which the notes originally occurred. By identifying all of the notes we defined an individual's "note repertoire." Each unique note received an identification number. We then reviewed the complete song sample again, using "RTS" real-time spectrographic software (Engineering Design 1996), this time annotating the sequence of notes for each song recorded from the male.

Although a note is the smallest distinct acoustic unit in a song, it is often the case that two or more notes invariably occur together and in the same order. From the annotated song data, we identified the smallest such units, the MUPs (Podos et al. 1992), by searching the entire recorded sample from a given male to make sure that each was never subdivided. Most MUPs were individual notes, although some included as many as four or five notes that always occurred in sequence together. All songs were converted from a note sequence annotation to a MUP sequence annotation. All unique MUP sequences for an individual's recorded sample were identified, and each unique sequence was considered a song variant.

We calculated pairwise similarities between all song variants using a modified Jaccard's coefficient of correlation (Podos et al. 1992). This similarity score is a function of the number of MUPs held in common by two songs relative to the total number of MUPs in both songs. We then performed cluster analysis on these pairwise similarity measures using the UPGMA method (Sneath and Sokal 1973) to objectively group song variants into song types. We calculated moat indices (Wirth et al. 1966) to describe the degree to which cluster groups are isolated from each other. Our assignment of song variants to song types corresponded to the level at which the moat index reached a maximum. Further details on MUP analysis are given in Podos et al. (1992).

We present four measures of song variation. Song repertoire size is the number of song types as determined by cluster analysis, and MUP repertoire size is the number of MUPs identified in a male's sample. Within-type similarity is the average linkage similarity of adjacent variants clustered within each song type. Between-type similarity is the average linkage similarity of adjacent clusters of song types. These last two measures vary from 0 to 1, with lower values indicating more variation (i.e. a lower average similarity score among variants of a song type means that the song type is more variable; a lower average similarity score among song types in a repertoire means that the song types are more different from each other).

RESULTS

Among the four populations for which we had samples from eight males, we found significant heterogeneity in song repertoire size ($H = 21.1$, $P = 0.001$), MUP repertoire size ($H = 11.1$, $P = 0.011$), and within-type similarity ($H = 12.5$, $P = 0.006$) and found no significant differences in between-type similarity ($H = 6.7$, $P = 0.084$). We used post-hoc analyses to test for differences between pairs of populations for the three measures that differed significantly among populations. Song repertoire size was smallest in Maine and Pennsylvania, with 8.1 and 8.4 song types per male, respectively, and these values did not differ statistically from each other (Table 1). The Maine and Pennsylvania populations had significantly smaller song repertoires than did North Carolina, with 10.4 types per male. Song repertoires in Washington (12.4 types per male) were significantly larger than in each of the other three populations (Table 1).

MUP repertoire sizes were smallest in Maine

and Pennsylvania, with means of 53 and 56 MUPs per male. These populations also did not differ statistically from each other, but both had significantly smaller MUP repertoires than either North Carolina or Washington (Table 1). MUP repertoire size was nearly identical in North Carolina and Washington, with about 70 MUPs per male (Table 1).

Within-type similarity in songs showed the same pattern as did MUP repertoire sizes. Maine and Pennsylvania clustered together with the highest similarities, and thus the lowest degree of within-type variation. Each of these populations was significantly different from North Carolina and Washington for this measure (Table 1). North Carolina and Washington had similar low values of within-type similarity (i.e. a higher degree of within-song type variation).

The New York population tended to be intermediate in song repertoire size, MUP repertoire size, and within-type variation (Table 1), falling closer to Maine and Pennsylvania (at the low end) than to North Carolina and Washington (at the high end). As noted earlier, these results are not included in the overall statistical analysis because of the small sample size. The New York value of between-type similarity in song was closer to that of North Carolina and Washington; however, this measure did not differ significantly among the four main populations in our study.

DISCUSSION

We found significant differences among populations in three of the four measures of repertoire complexity that we examined. Geographic variation in song has been demonstrated previously in a great many passerine species, often on much smaller spatial scales than we report here (see Catchpole and Slater 1995). Most such demonstrations, however, concern geographic differences in the structure of individual songs, for example in features such as song duration, minimum or maximum frequency, or the occurrence of particular note or syllable types. The measures we examined are higher-order measures in the sense that they assess the structure and complexity of a male's entire song repertoire rather than the structure of individual songs. Evidence for this kind of geographic variation is much rarer. In a comparison of two Song Sparrow populations in Ontario, Harris and Lemon (1972) found a small difference in average repertoire size (8.4 vs. 9.4). This difference was not statistically significant, but the fact that the two populations were separated by only 37 km, and that repertoires of only five males were analyzed for each site, suggested to the authors that this trend was biologically meaningful. Kroodsma (1985) found more convincing evidence of geographic differences in repertoire sizes of song type and phrase types in Bewick's Wrens (*Thryomanes bewickii*), the differences being correlated with the complexity of the avifaunal assemblage. The strongest evidence for geographic differences in repertoire complexity comes from a study of Eastern Towhees (*Pipilo erythrophthalmus*) in which the mean number of song types per male was 8 for a sedentary population in Florida and only 3.5 for a migratory population in New York (Ewert and Kroodsma 1994). Similarly, relatively sedentary populations of Marsh Wrens (*Cistothorus palustris*) appear to have larger repertoires than do migratory populations (Kroodsma and Verner 1997).

The estimate of repertoire size we obtained for the Washington population (12.4) is higher than earlier reports (i.e. 9.1 to 9.2; Beecher et al. 1996, 2000). The difference arises because the earlier studies used a bout-based definition of song types, whereas our study used a MUP-based definition. Because male Song Sparrows sing with eventual variety, i.e. they sing a bout of similar songs before switching to a bout of distinctly different songs, one has the option of lumping songs that are sung in the same bout into the same song type, or classifying them purely acoustically on the basis of MUP analysis. For most song types, these two schemes coincide (Nowicki et al. 1994). But at least in the Washington population, some song bouts include extreme variation and can be broken down into two song types by MUP analysis. These sibling song types, which are distinct MUP types, are not sung with eventual variety, but rather are sung interchangeably with one another. Thus, the bout classification lumps these sibling types as one song type, whereas the MUP classification splits them into two song types. This difference points to the importance of using the same quantitative method to describe song organization when com-

paring different populations, as we have done in the present study.

The existence of geographic variation in song structure often is taken as prima facie evidence that the examined differences are learned. Whether the geographic differences we found in repertoire structure of Song Sparrows are learned versus innate is not clear, however. Male Song Sparrows reared in isolation had smaller song repertoires than did males with more normal experience, indicating that learning plays a role in determining song repertoire size in this species (Marler and Sherman 1985). Marler and Sherman (1985) also showed that Song Sparrows reared in isolation had larger song repertoires than did Swamp Sparrows (*Melospiza georgiana*) reared in isolation, which parallels the difference between the two species in nature and indicates that differences in song repertoire size also can be innate.

The development of other aspects of song complexity in oscine passerines has received little attention, although Nowicki et al. (1999) recently found that tutoring young Song Sparrows with variable versus invariant song types had no measurable effect on the within-type song variation subsequently produced by adults. Consequently, this aspect of song variation does not seem to be affected by learning, although it does differ significantly among populations of Song Sparrows (Table 1).

Whether the geographic differences in repertoire complexity we identified are adaptive also is unknown. Comparative analyses suggest that male parental care, mating system, and migratory behavior are correlated with repertoire complexity across species (Read and Weary 1992), and one might predict similar correlations to be observed across populations of the same species. Song Sparrow populations are not known to vary in the degree of parental care or in social mating system, although it is possible that the genetic mating system (i.e. the frequency of extrapair fertilizations) may turn out to differ among populations in a way that would select more intensely for repertoire complexity in some populations than in others. In the laboratory, female Song Sparrows perform more copulation-solicitation displays in response to larger song repertoires (Searcy and Marler 1981, Searcy 1984); in other species, males with larger repertoires are more successful in obtaining extrapair fertilizations in

the field (e.g. Hasselquist et al. 1996). It is possible that adaptive differences in repertoire complexity occur among Song Sparrow populations because extrapair fertilizations are more common in some populations than in others, but this hypothesis is purely speculative at the moment.

Some populations of Song Sparrows differ in migratory behavior, allowing us to ask whether interspecific trends in repertoire variation also occur within species. The interspecific trends are for song repertories and syllable repertoires to be larger in species that migrate than in year-round residents (Read and Weary 1992). The adaptive significance of these trends is unknown, but one argument is that because migratory males are under more pressure to obtain a territory and a mate quickly, both intersexual and intrasexual selection favor complex repertoires more strongly in migratory species than in sedentary ones (Catchpole 1980). The within-species trend we found runs directly opposite to the between-species pattern. Males in our Washington study population are definitely known to be year-round residents (Beecher et al. 1996). The North Carolina population, which is near the southeastern border of the species' range, is relatively sedentary (unpubl. data). All three of the populations in the northeastern United States (Maine, Pennsylvania, and New York) are north of Nice's (1937) Ohio study population, in which just over 50% of the male population migrated each fall; we believe we can safely assume that these three populations also are at least partially migratory. The two nonmigratory populations had higher song repertoire sizes, MUP repertoire sizes, and within-type variability than did the partially migratory populations. Thus, our results for Song Sparrows do not support the hypothesis that some aspect of migratory behavior selects for greater song complexity.

Our Pennsylvania and Washington populations of Song Sparrows also differ in the degree to which neighboring males share song types (Beecher et al. 1994, 1996; Hughes et al. 1998). It is possible that differences in repertoire complexity between these two populations are related to this difference in song-type sharing; for example, the larger average song type and MUP repertoire sizes of Washington birds may reflect the outcome of selection for the increased song sharing observed in this popula-

tion, or vice-versa. Consistent with this idea, birds in our North Carolina population also appear to exhibit a greater degree of song-type sharing than the Pennsylvania population, although less than is exhibited by Washington birds (unpubl. data). It is less obvious how increased song-type variability, which also is characteristic of the Washington birds, might be explained in this way. A fuller explanation for the differences in repertoire variation we have described here awaits a better understanding of the selective forces that influence the expression of song-type complexity and how songs are used in different populations.

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Associate Editor: D. E. Kroodsma