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THE RESPONSE OF MALE AND FEMALE SONG SPARROWS TO GEOGRAPHIC VARIATION IN SONG[1]

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Abstract. We tested female and male Song Sparrows (*Melospiza melodia*) from a Pennsylvania site for discrimination between local songs and foreign songs recorded in New York. In Experiments 1 and 2 we measured the copulatory response of female Song Sparrows to playback of local and foreign songs. In Experiment 3 we measured the aggressive response of territorial males to playback. We used mean responses per subject as sample points in the statistical analysis in Experiment 1, but to avoid pseudoreplication we designed Experiments 2 and 3 with sufficient numbers of exemplars of local and foreign songs to use mean responses per exemplar as sample points. Responses in all three experiments were significantly stronger for local than for foreign songs. Song Sparrow songs show a great deal of variation within locales, and a pattern of gradual and subtle geographic change, so it is not obvious how or why our subjects performed the discrimination.

Key words: song, geographic variation, playback, Song Sparrows, Melospiza melodia.

INTRODUCTION

The species-typical songs of birds often vary from one geographic location to another, and individuals generally respond differently to local songs than to songs from more distant areas (Catchpole and Slater 1995). Several studies have reported, for example, that female birds court more in response to playback of songs recorded from their own population than to playback of foreign songs (King et al. 1980, Baker et al. 1982, Balaban 1988). An even larger number of studies have shown that male birds discriminate between local and foreign songs when these are played on their territories, usually responding more aggressively to local songs (Lemon 1967, Brenowitz 1983, Tomback et al. 1983), but sometimes responding more strongly to foreign songs (Petrinovich and Patterson 1981, Balaban 1988).

In some species, features that might be used to distinguish among songs from different locales are obvious to the human observer, and it therefore is not surprising that the birds themselves are able to perform the discrimination. This occurs, for example, when abrupt boundaries exist between geographic dialects made up of a limited number of discretely different song types (e.g., White-crowned Sparrow, *Zonotrichia leucophrys,* Marler and Tamura 1962; Corn Bunting, *Miliaria calandra,* McGregor 1980). In other cases, however, geographic changes are more gradual and songs are more variable within populations, so that population differences tend to be obscured against the background of individual differences. In such cases, it is less clear which features, if any, might allow a bird to discriminate local from foreign songs, and it seems less certain that the birds actually are able to make such discriminations.

The Song Sparrow (*Melospiza melodia*) provides a good example of this latter condition. Males of this species sing complex and highly variable song repertoires (Nice 1943, Podos et al. 1992). In some populations, males in local neighborhoods share few if any songs (Harris and Lemon 1972, but see Beecher et al. 1994, 1996). Levels of variation within and between populations are comparable, and there are no obvious structural differences that distinguish the songs of one population from those of another (Borror 1965, Nowicki et al., unpubl. data).

Song Sparrows and species with similar patterns of vocal variation raise questions both about the perception of geographic differences in song and about the functional consequences of such differences. The most basic question is whether individuals in these species are able to discriminate between foreign and local songs when both sets are recorded from nonfamiliar

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individuals. If birds are able to discriminate under such circumstances, then some set of features must be available to enable discrimination. The fact that these features are subtle or vary gradually, as compared to species with pronounced and discrete patterns of geographic variation, suggests different selective forces or historical factors may be acting on the evolution of song in the two cases. It is possible, for example, that gradual geographic differences generally result from cultural drift (Mundinger 1980) and lack significant functional consequences, whereas pronounced and discrete patterns of geographic variation might result from strong selective pressures on mate choice.

Complex repertoires and gradual patterns of geographic variation, as seen in the Song Sparrow, also make it more difficult to determine with confidence whether birds discriminate among dialects because of the potential for pseudoreplication in the design of playback studies (Kroodsma 1989b). Pseudoreplication can occur when one tests for discrimination between two classes of stimuli using small numbers of exemplars because "the stimuli almost certainly vary within each class as well as between classes, so that any difference in response cannot necessarily be ascribed to the between-class difference in stimuli" (McGregor et al. 1992). The seriousness of the pseudoreplication problem in playback studies has been debated (Catchpole 1989, Kroodsma 1989a, Searcy 1989), but a consensus has been reached that pseudoreplication does weaken confidence in results and ought to be avoided (McGregor et al. 1992). The problem is particularly acute in research on dialect discrimination if the structural differences between dialects are not identified, and thus it is not known whether the chosen exemplars well represent those differences.

Previous work with Song Sparrows has provided some evidence for discrimination of local and foreign songs in this species, although that evidence has sometimes been equivocal. Harris and Lemon (1974) tested male Song Sparrows at three sites for discrimination between local songs and songs recorded at distances of approximately 40–100 km. One to three songs were used to exemplify the song of each locale. Significantly greater response to local songs was found in most comparisons, but the analysis was done by subject rather than by exemplar. Searcy et al. (1985) tested female Song Sparrows from a Pennsylvania (PA) population for discrimination between four local songs and four New York (NY) songs recorded at a site approximately 400 km distant. Mean courtship response was higher for the local songs than for the foreign songs, but the difference was not significant. Similar results were obtained for the approach response of male Song Sparrows to the same PA and NY songs. The usual worry about pseudoreplication is that it will lead to spurious positive results, but failure to find significant differences also may be due to the use of too few exemplars; in this case, the PA songs used in the experiments may have poorly represented local song structure, or the NY songs may have been unusually similar to the local PA songs.

Our interest in geographic differences in Song Sparrow song was renewed by our discovery, incidental to an experiment on the functional significance of song variation, that PA females from the same population used by Searcy et al. (1985) discriminated against NY songs and in favor of local songs when a new set of exemplars was presented to them. This experiment (Experiment 1 below) was designed for analysis by subject, rather than by exemplar, and also could be faulted for pseudoreplication. Accordingly, we designed a new experiment without pseudoreplication to test for geographical discrimination in female Song Sparrows (Experiment 2). Patterns of song discrimination can differ between females and males within a species (Searcy and Brenowitz 1988, Ratcliffe and Otter 1996), so we designed Experiment 3 to test for geographical discrimination in male Song Sparrows, again avoiding pseudoreplication.

METHODS

Subjects for the first two experiments were female Song Sparrows captured in the vicinity of the Pymatuning Laboratory of Ecology in Linesville, Pennsylvania. Subjects for Experiment 3 were free-living males holding territories in the same area. We recorded the PA songs used in playbacks during 1992–1994 from males located 2–15 km from the sites where we obtained subjects. Dispersal distances of Song Sparrows average less than 300 m for both sexes (Nice 1937), so it is highly unlikely that any of our subjects had previous contact with the males we recorded. The foreign songs were recorded during 1987–1988 in the vicinity of the Rockefeller Field Research Station in Millbrook, New York, about 400 km from the PA sites. The NY recordings were made using either a Marantz PMD 221 or a Sony TC-D5M tape recorder with either a Sennheiser ME88 shotgun microphone or a Realistic 331070B microphone in a Sony PBR-330 parabola. The PA recordings were made using either a Marantz PMD 221 or a Sony TCM 5000EV tape recorder with either a Sennheiser ME88 shotgun microphone or a Sony ECM-170 microphone in a Sony PBR-330 parabola. Playback songs were chosen for high quality and low background noise from among hundreds of songs recorded from each source male.

We tested females for response to song using the solicitation display assay, as described in detail in Searcy et al. (1985) and Searcy (1992). Briefly, we gave each female a single, subcutaneous implant of 17-ß-estradiol in silastic tubing with an outside diameter of 1.96 mm and a length of 15 mm and containing 8–10 mm of hormone. Following treatment, we housed each subject singly in a small cage within a sound attenuation chamber. Testing began seven days after treatment. During testing, we played songs to one subject at a time through a speaker within the sound attenuation chamber. Songs were played from a Marantz PMD 221 cassette-tape recorder and over Realistic 40-1272 speakers (effective range 90–20,000 Hz). We observed responses by means of a video camera directed through a window on the chamber door. We used numbers of copulation displays performed as the sole response measure. We counted both full and partial displays.

For experiment 1, we captured 10 female Song Sparrows during the spring of 1993. We first tested these PA females on each of two days with two 3-min presentations of NY song, then on each of two days with two 3-min presentations of PA song, and finally on one additional day with two 3-min presentations of NY song. All playbacks were of 18 songs recorded at one song per 10 sec. On each day, one 3-min playback consisted of a single variant (Podos et al. 1992) of one foreign or local song type and the other 3-min playback consisted of four variants of the same song type, presented in the order abcdabcd, etc. A total of four local and four foreign song types were used in making the tapes. Response was summarized as mean number of displays per 6 min of playback. The statistical analysis for this experiment used number of subjects as the sample size, rather than number of exemplars.

For experiment 2, we captured 18 females during the spring of 1995. We tested these females on two days, each day with 3-min of foreign song and 3-min of local song. We randomized the order of presentation of foreign and local songs for each subject on the first day of testing, with the constraint that half heard foreign first and half local. We reversed the order for each bird on the second day. Each 3-min presentation contained 18 songs made up of nine repetitions of a single variant of each of two song types. Nine pairs of local and foreign tapes were used, each containing different song types. Each pair of tapes was presented to two subjects. Analysis was done using the mean response of subjects per tape as the sample points; thus the sample size is the number of tapes.

In experiment 3, we tested male Song Sparrows for discrimination between PA and NY songs. Subjects were 20 territorial males. We used 10 pairs of NY and PA tapes, with each pair played to two subjects. For each subject, we randomly chose one tape in the pair to present first, and returned two or more days later to present the contrasting tape. Each tape contained two song types from the appropriate area, recorded at the rate of 1 song per 10 sec, and in the order: 9 repetitions of the first song type, 9 of the second, 9 of the first, and 9 of the second. Playbacks thus lasted 6 min.

We played tapes using a Marantz PMD 221 cassette-tape recorder and a Nagra DSM speaker-amplifier. We placed the speaker face-up on the ground well within the territory boundaries, and marked its position with plastic flagging so that the same position could be used on the second test with the same male. We recorded distance of the subject from the speaker for the 6 min of playback and for a 3 min post-playback period, giving a total of three 3-min periods. Two observers were used; one kept track of the subject's position relative to the speaker while the other recorded the positions on a flow sheet broken into 5-sec intervals. We set out flags and/or poles at measured distances from the speaker prior to playback to aid in estimation of distances. Distance categories used were 0–2 m, 2–4 m, 4–8 m, 8–16 m, and > 16 m. We calculated mean distances for 3-min periods following the method in Peters et al. (1980). We used distance to the speaker as the sole response measure be-

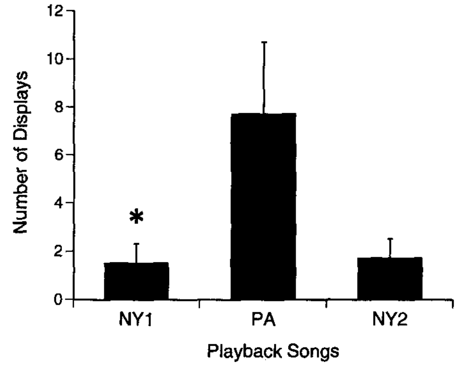

FIGURE 1. The number of copulation solicitation displays given by 10 female Song Sparrows to playback of local, PA songs and foreign, NY songs. Means + SE. Subjects were played first NY tape (NY1), then a PA tape, and then a second NY tape (NY2), all on different days. Four different PA and NY song types were used. Statistical analysis was done by subject rather than by tape. Friedman two-way ANOVA indicated significant variation in response across the three sets of stimuli. * indicates a significant difference at the 0.05 level between foreign and control.

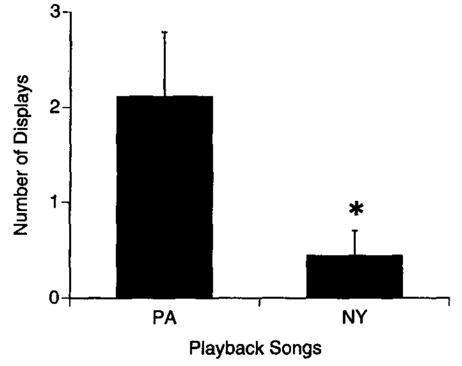

FIGURE 2. The number of copulation solicitation displays given by 18 female Song Sparrows to playback of local PA songs and of foreign NY songs. Means + SE. Nine PA tapes and nine NY tapes were used. Analysis was done by tape rather than by subject. * indicates a significant difference by a two-tailed Wilcoxon matched pairs signed ranks test.

cause past experience has shown this to be the most reliable measure of response (Peters et al. 1980, Searcy et al. 1981).

RESULTS

In the analysis of experiment 1, the sample points were mean responses per subject. The 10 PA females responded more strongly to the playback of PA Song Sparrow songs than to either the earlier or later playback of NY songs (Fig. 1). A Friedman two-way analysis of variance showed significant variation in response across the sets of playbacks ($\chi^2 = 9.07$, $P < 0.02$). Friedman dependent multiple comparison tests (Siegel and Castellan 1988) showed a significant difference in response between the PA songs and the first set of NY songs ($P < 0.05$), but not between the PA songs and the second set of NY songs ($P < 0.10$).

In the analysis of experiment 2, the sample points were the mean response of two PA females per tape. Response of the subjects was higher for 9 PA tapes than for 9 NY tapes (Fig. 2), and the difference was significant by a Wilcoxon matched pairs signed ranks test ($z = -2.20$, $P < 0.05$).

In the analysis of experiment 3, the sample points were again the mean response of two subjects per tape, in this case male subjects. Males approached more closely on average for the 10 PA tapes than for the 10 NY tapes during each of the three observation periods (Fig. 3), and each of the differences was statistically significant by Wilcoxon matched pairs tests ($z = -2.43$, $P < 0.02$ for period 1; $z = -2.07$, $P < 0.05$ for period 2; $z = -2.55$, $P < 0.02$ for period 3).

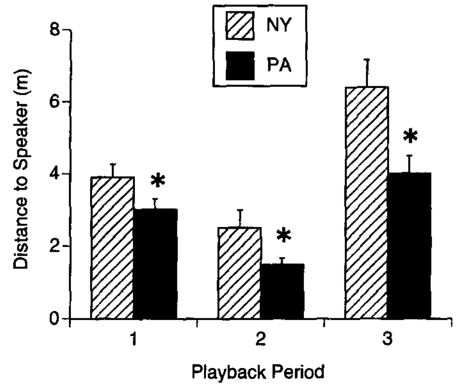

FIGURE. 3. Distance of 20 male Song Sparrows to speakers playing either local PA songs or foreign NY songs. Means + SE. Closer approach indicates a stronger response. Results are given separately for two 3-min playback periods (1 and 2) and one 3-min postplayback period (3). Ten PA and 10 NY tapes were used, and statistical analysis was performed by tape rather than by subject. * indicates a significant difference by a two-tailed Wilcoxon matched pairs test.

DISCUSSION

Our subjects, both male and female, responded more strongly to local songs than to conspecific songs recorded at a distant site. This result duplicates previous results on male Song Sparrows (Harris and Lemon 1974) and on males and females in several other passerine species (see references above). A difference between our results and those of most previous studies is that our experiments 2 and 3 were designed to use sufficient numbers of exemplars of the local and foreign songs that statistical analysis could be done with numbers of exemplars as the sample size. These two experiments then avoid pseudoreplication, at least in one sense.

In the context of playback experiments, pseudoreplication has been defined as "the use of an *n* (sample size) in a statistical test that is not appropriate to the hypothesis being tested" (McGregor et al. 1992); therefore, whether a playback study commits pseudoreplication depends upon how the hypothesis is stated. Given our design, our study avoids pseudoreplication if the hypothesis being tested is that Song Sparrows at our PA site respond preferentially to local songs over songs from one particular foreign site (our NY site). If we wished to test the hypothesis that our local Song Sparrows respond preferentially to local songs over foreign songs in general, then we would have to use as stimuli songs recorded from *n* foreign sites, making this *n* the sample size in our statistical analysis (McGregor et al. 1992). If we wished to test the hypothesis that Song Sparrows in general discriminate local and foreign songs, we would have to test subjects from multiple locales as well as using multiple foreign and local stimuli.

Our results differ from those of Searcy et al. (1985), who tested PA Song Sparrows from the same locality with songs from the same two locales used here. Searcy et al. (1985) found that both males and females responded more strongly to the local songs, but in both sexes discrimination was not significant. The difference in the results on males in the two studies may be due in part to differences in experimental design: Searcy et al. (1985) used a two-speaker, simultaneous choice design, whereas in the present study we used a single-speaker, sequential presentation design. Sequential presentations have sometimes proved more powerful in testing discrimination in male birds (Searcy et al. 1981), although they are often less powerful than simultaneous choice designs in other groups (Doherty 1985, Ryan and Rand 1993). The difference in the results on females in the two studies seems unlikely to have been caused by differences in experimental design, which were minor. Nor can the difference in results be ascribed to sample sizes, which were identical in our experiment 1 and the female experiment in Searcy et al. (1985). Female response actually differs quite markedly between the two studies: the ratio of response (PA:NY) found by Searcy et al. (1985) was 1.36:1, compared to ratios of 4.81:1 and 4.75:1 found in our two experiments. The difference may be due to chance differences in the songs chosen for playbacks in the different experiments, that is to pseudoreplication in the first experiment, but given that four songs of each category were used in that experiment, this explanation seems unlikely also. We are left with no satisfactory explanation at this time.

The ability of our subjects to discriminate between local and distant songs implies that acoustic differences exist between songs from the two populations that provide a basis for discrimination. What these differences are is not clear. In fact, given the variability of Song Sparrow song, i.e., the repertoires of two males from the same population may appear as different as those of two males from different populations, it is not even clear what *kinds* of cues might be involved. One possibility is that males in a locality share distinctive song types or parts of songs, in which case idiosyncratic song patterns could serve as labels for populations. Beecher et al. (1994) found that Song Sparrows in a western population do share entire song types, but sharing appears to be confined to neighborhoods of a few territories; song sharing over areas this small would not explain recognition of songs from sites 2–15 km distant, as we have found. Furthermore, sharing of entire song types appears to be quite rare over any distance in eastern populations, including our PA population (Harris and Lemon 1972, M. Hughes et al., unpubl. data). Sharing of parts of songs, such as particular trills, is more common in PA than is the sharing of entire songs, so conceivably our subjects might have recognized local songs by the presence of particular syllables that are widespread in the local population. We plan to explore this possibility. Familiarity with the particular individuals from which the songs were recorded is unlikely, because the distances between the sites of our recording and our subjects' territories so greatly exceed the usual dispersal distance of Song Sparrows (Nice 1937).

If particular song types or syllables do not serve to identify populations, then some more general acoustic features shared within locales might provide cues for discrimination. We have found, for example, that our PA songs exhibit characteristic modulation rates of "buzzy" notes which differ from those of our NY population. Although preliminary playback data do not support the hypothesis that this single feature adequately differentiates the songs of the two populations when played back to PA males (S. Nowicki et al., unpubl. data), we think it is probable that there are general acoustic features of songs (such as patterns of syllables in time and frequency) or syllables (such as frequency, duration or modulation rate) that differ between locales and which could provide cues for discrimination. We are currently searching for such features for our PA and NY locales.

Our results allow us to conclude that Song Sparrows in our study population discriminate between local songs and songs from at least one foreign locale. Why they should do so is still an open question. Given its gradual and subtle nature, the pattern of geographic variation observed in Song Sparrow song may simply be the result of cultural drift and may lack any significant functional consequences. If so, however, it seems unlikely that selection would act to promote dialect discrimination (as might be predicted for more pronounced patterns of geographic variation resulting from selection on male-male interactions or mate choice). If, on the other hand, selection has acted to promote discrimination of local from foreign songs in Song Sparrows, then one wonders why selection also has not favored more pronounced geographic differences in song structure. Demonstrating that Song Sparrows do attend to geographic differences in their songs is only the first step towards addressing these issues.

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