

# Geographic Song Discrimination in Relation to Dispersal Distances in Song Sparrows

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**ABSTRACT:** Whether geographic variation in signals actually affects communication between individuals depends on whether discriminable differences in signals occur over distances that individuals move in their lifetimes. We measure the ability of song sparrows (*Melospiza melodia*) to discriminate foreign from local songs using foreign songs recorded at a series of increasing distances and compare the results with previous measurements of dispersal distances. We test discrimination in males using playback of songs on territories and measuring approach and in females using playback to estradiol-treated captives and measuring courtship display. Females fail to discriminate against foreign songs recorded at 18 km but do discriminate against foreign songs recorded at 34, 68, 135, and 540 km. Males fail to discriminate against foreign songs recorded at 18, 34, 68, 135, and 270 km but do discriminate against foreign songs from 540 km. Females are more discriminating, but even they do not discriminate at a distance three times the root-mean-square dispersal distance, as estimated from mtDNA variation. We suggest that female preference for local songs benefits females not because it allows them to reject foreign males but because accurate production of local song serves as a test of song-learning ability.

**Keywords:** geographic variation, song, dialects, female choice, *Melospiza melodia*, dispersal.

Vocal signals vary geographically in many animal groups, including insects (e.g., Ritchie 1991; Claridge and Morgan

1993), frogs (Ryan and Wilczynski 1991; Ryan et al. 1996), birds (Slater et al. 1984; Baker and Cunningham 1985; Wright 1996), and mammals (Cavalli-Sforza and Wang 1986; Esser and Schubert 1998; Mitani et al. 1999). Animals, in many cases, have been found to discriminate between geographic variants of their signals, usually responding less to foreign than to local variants, and this discrimination ability is often assumed to be selectively advantageous (Nottebohm 1969, 1972). Whether the ability to discriminate local from foreign signals actually confers any advantage must depend to a large extent on the geographic scale over which changes in the signals occur. In species in which signals change abruptly across discrete boundaries, we would expect frequent interaction between individuals that produce different variants, and therefore, that geographic variation might play some important role in communication. In most cases, however, signals change gradually with distance, and it is not clear that individuals will ever interact with others whose signals vary perceptibly from their own. Whether such interactions occur depends on how rapidly signals change relative to dispersal distances. Here, we address this question in song sparrows (*Melospiza melodia*) by measuring how discrimination of local from foreign songs changes as the foreign songs are recorded at greater and greater distances and comparing the resulting pattern to what is known about dispersal distances in this species.

Certain songbirds, such as white-crowned sparrows (*Zonotrichia leucophrys*), corn buntings (*Emberiza calandria*), and redwings (*Turdus iliacus*), exhibit well-defined, microgeographic dialects; here, each male sings only one or a very few song types—all males in a local population sing the same song type or types—and boundaries between adjacent dialects are abrupt, sometimes passing between pairs of adjacent territories (Marler and Tamura 1962; McGregor 1980; Bjerke and Bjerke 1981). Males in these species learn the details of the local dialect, although there is still argument about whether such learning occurs before or after natal dispersal (Kroodsma et al. 1985; Baptista and Petrinovich 1986; Nelson 1998a). Females also appear to learn the dialect they will prefer (Baker et al. 1981a). Re-

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ardless of when learning occurs in either sex, the potential seems high for encounters between individuals who have learned different dialects, given that populations of such individuals may be separated by no more than an apparently arbitrary line. In species with this kind of discrete dialect structure, geographic variants of song have been suggested to affect important aspects of life history, notably territory defense and mate choice. When tested for aggressive response to songs played on their territories, males of dialect species generally respond more strongly to their own dialect than to others (McGregor 1983), although they may give an even greater response to an adjacent dialect than to the home dialect (Baker et al. 1981*b*). Estradiol-treated females tested for response to song in captivity give more solicitation displays in response to home than to foreign dialects (Baker 1983; Baker et al. 1987*a*). The extent to which preferences for home dialect carry over to the formation of long-term pair bonds is controversial (Kroodsma et al. 1985), but in any event, these preferences can be expected to affect extra-pair copulation. Thus, the dialect that a particular male sings may well affect his fitness because he encounters males and females that have learned other dialects and dialect affects communication with these individuals.

The pattern of geographic variation in song is more complex in those species in which each male sings a repertoire of many song types and not all song types are shared among the males in a population. Here, local songs typically are not all marked by possession of a particular phrase or syllable, which makes it much more difficult to define how local songs differ from foreign ones. That such differences exist has nevertheless been shown in many cases, either by acoustic analysis (e.g., in chaffinches *Fringilla coelebs* [Marler 1952; Slater et al. 1984]) or by demonstrating that the birds themselves have the ability to discriminate foreign from local songs (e.g., in great tits *Parus major* [Baker et al. 1987*b*] and red-winged blackbirds *Agelaius phoeniceus* [Searcy 1990]). Differences between songs can be expected to increase progressively with distance, although this hypothesis has rarely been tested. If song differences do increase with distance, then at some distance, a threshold must be crossed where the differences in songs are great enough to affect communication. The question we address here is whether this threshold is crossed in song sparrows within the range of normal lifetime movement. If not, then individuals will not encounter others with discriminable geographic differences, and geographic variation in song is unlikely to have direct adaptive consequences.

Song sparrow males sing complex songs, usually of 2–3 s duration (Borror 1965). A song typically contains four or five major parts, or phrases, and these in turn each contain several to many notes (Mulligan 1966; Podos et

al. 1992). Each male sings five to 16 different basic patterns of phrases, or song types, plus an open-ended number of variations on these types (Borror 1965; Podos et al. 1992). In some populations, notably in western North America, sharing of song types is frequent between territorial neighbors (Hill et al. 1999; Wilson et al. 2000), although even here unique song types are fairly common (Wilson et al. 2000). In eastern North America, song-type sharing is less common (Borror 1965; Hughes et al. 1998), and most song types appear to be unique. In these eastern populations, geographic variation is especially hard to discern against the background of high within-site variation. Nevertheless, evidence exists that the song of eastern song sparrows does vary geographically. Borror (1965) reported that the frequency of shared syllable types found in the songs of Maine song sparrows declines with distance from his study site, although the data are reported in a way that makes it difficult to evaluate this claim. Harris and Lemon (1974) used playback experiments to show that territorial males in Ontario respond more strongly to songs recorded locally than to songs recorded 37 or 95 km distant, but these experiments can be criticized for pseudoreplication because of the small number of examples of each dialect used (Kroodsma 1989). Searcy et al. (1997) found that both males and females in Pennsylvania respond more strongly to local songs than to songs recorded in New York, approximately 540 km distant. This last study was conducted with an appropriate level of replication, but 540 km is certain to be greater than the dispersal distance of song sparrows; therefore, the study does not show that song varies over a scale that would affect communication between individuals likely to encounter each other.

Male song sparrows isolated at an early age produce highly simplified songs, which implies that the details that contribute to geographic variation are largely learned from others (Kroodsma 1977; Marler and Sherman 1985). Studies of song learning in the field indicate that males learn songs after they disperse to the area where they will establish territories (Beecher et al. 1994; Nordby et al. 1999). Presumably, female song preferences are also influenced by learning, but whether such learning takes place before or after natal dispersal is unknown.

To estimate the furthest distance over which song sparrows are likely to encounter one another, we can use the two traditional sources of data for estimating dispersal: observations of the movements of marked individuals and geographic patterns of genetic variation. In Nice's (1937) classic study of marked song sparrows in Ohio, males were highly site faithful as adults, and females were only slightly less so. For 54 females, mean movement between breeding seasons was about 90 m, with a maximum of 700 m. Natal dispersal (from hatching to first breeding) ranged from 100 to 1,400 m for 22 males, with a median of 280 m,

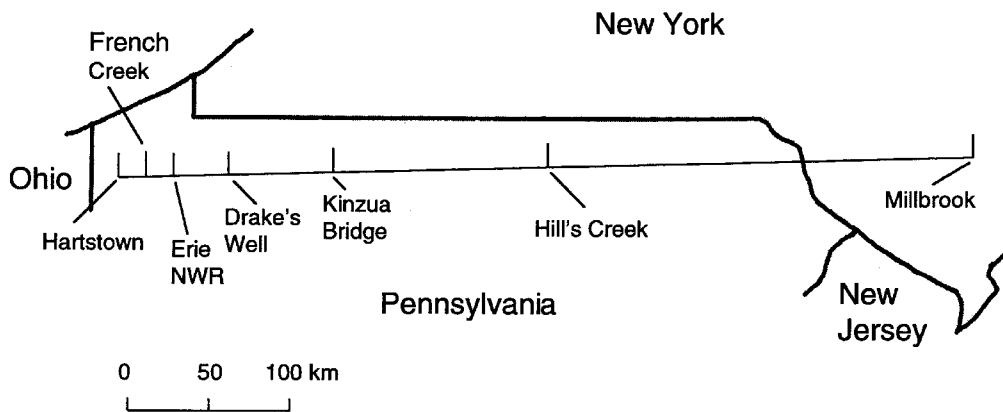


Figure 1: Map of recording sites

and from 45 to 1,300 m for 12 females, with a median of 270 m. Combining Nice's data on natal and breeding dispersal and using a correction for the bias against observing high dispersal distance (Barrowclough 1978), Barrowclough (1980) estimates the root-mean-square dispersal distance for song sparrows as 350 m. A second dispersal estimate comes from Zink and Dittman's (1993) study of mitochondrial DNA variation in song sparrow populations throughout North America. Root-mean-square dispersal distance is estimated from the mtDNA data using the method of Neigel et al. (1991), which models the dispersal distance required to produce the existing distribution of mtDNA lineages, assuming each had a single origin. Zink and Dittman (1993) arrive at an estimate of root-mean-square dispersal distance of 6.1 km per generation. Note that the two estimates are off by a factor of about 17. The genetic method may give the truer estimate because the method of direct observation is known to underestimate dispersal as a result of the impossibility of registering dispersal distances longer than the diameter of the study site (Koenig et al. 1996, 2000).

The root-mean-square dispersal distance is the standard deviation of the distance of an individual from its birth site after dispersal. If dispersal distances were normally distributed, then 99.74% of individuals would disperse less than three times the root-mean-square dispersal distance. Dispersal has not been measured accurately enough to define the distribution, but regardless of the true distribution, the proportion dispersing more than three times the standard deviation must be very small. We therefore will assume that virtually no song sparrows disperse beyond three times the greater estimate of root-mean-square dispersal distance, or approximately 18 km.

Here, we attempt to estimate the distance at which song sparrow songs become discriminably different from local

songs. We do this by testing both female and male song sparrows for discrimination between local and foreign songs, using as subjects birds from the same Pennsylvania site used in our earlier study of geographic variation in song (Searcy et al. 1997). Foreign songs are taken from various points along a 540-km transect running from the Pennsylvania local site to a site in New York.

## Methods

### *Study Sites and Recording*

We recorded male song sparrows at sites along a transect (fig. 1) running from Hartstown, Pennsylvania, to Millbrook, New York, the two sites used in our earlier study of geographic variation in song sparrow song (Searcy et al. 1997). Starting from the Hartstown end of the transect, the sites were Meadville Access to French Creek (the one-thirty-second point at 18 km from Hartstown), Erie National Wildlife Refuge (the one-sixteenth point at 34 km), Drake's Well State Park (the one-eighth point at 68 km), Kinzua Bridge State Park (the one-fourth point at 135 km), and Hill's Creek State Park (the one-half point at 270 km). We recorded male song sparrows at Drake's Well and Erie National Wildlife Refuge in June 1997, at Kinzua Bridge and Hill's Creek in July 1997, and at French Creek in June and July 1998. At all sites, we recorded at least five song types from at least eight males. Local songs were recorded in May and June 1996 at a site 2 km south of Hartstown. Recordings were made with Sony TC-D5M and Sony TCM 5000EV cassette recorders and either Shure SM 57, Realistic 33-1070, or Sony ECM-170 microphones in Sony PBR-330 parabolas.

*Experiments with Females*

We performed four discrimination experiments with females: local versus Erie songs (1998), local versus French Creek (2000), local versus Drake's Well (2000), and local versus Kinzua Bridge (2000). We did not test females with songs from Hill's Creek. Subjects were adult female song sparrows captured at sites 2–3.5 km south of Hartstown. For the Erie and Drake's Well experiments, the female subjects were captured 1.5 km from the site where the local playback songs were recorded. For the Kinzua Bridge experiment, four of 10 subjects were captured in the field where the local playback songs were recorded, five were captured in adjacent fields, and one was captured in a field 200 m distant. For the French Creek experiment, the same 10 subjects were used as in the Erie experiment plus 10 more captured 2 km from the recording site. The possibility that some of the subjects in the Kinzua Bridge and French Creek experiments had direct prior experience with the original singers of the playback songs is important because female song sparrows are known to respond preferentially to songs of mates and neighbors over those of strangers (O'Loughlin and Beecher 1997, 1999). We deem it unlikely that the subjects actually had prior familiarity with the original singers, however, because the playback songs were recorded 4 yr before these two experiments. Nice (1937) found that only 20%–65% of adult males and 13%–44% of adult females returned to the same area to breed from one year to the next.

Females were tested using the solicitation display assay as described in Searcy (1992). After capture, each female was given a single, subcutaneous implant of 17- $\beta$ -estradiol in silastic tubing of 1.96 mm outer diameter, sealed at both ends with adhesive. Implants were 15 mm long and contained 8–10 mm of hormone. We injected the implant under the skin of the ventral body surface after application of a topical anesthetic. After treatment, we housed females in individual cages within sound attenuation chambers.

We began testing females 7 d after treatment. We played songs to one female at a time from a Nagra DSM speaker, with the subject's chamber door open and the other chamber doors closed. We observed the subject's response from another room using a video camera directed through the open chamber door. We used the number of copulation solicitation displays performed as the sole response measure, counting both full and partial displays. The display is described by Nice (1943).

In each experiment, individual females were tested with both local and foreign songs in separate trials. Each female was tested on 2 d, with the order of trials (local/foreign) randomized on the first day and reversed on the second. The two tests of one subject within a day were spaced by at least 3 h. In each trial, females heard nine repetitions

of one song type followed by nine repetitions of a second song type, both recorded from the same male. Songs were presented at a rate of one song per 10 s (3 min total). Each recording site was represented by 10 stimulus sets (and thus 20 song types). The local (Hartstown) stimulus sets included songs from six males, whereas the French Creek, Erie, Drake's Well, and Kinzua stimulus sets each included songs from five males. For the Erie, Drake's Well, and Kinzua experiments, each pair of local and foreign stimulus sets was presented to just one subject. For the French Creek experiment, each pair of stimulus sets was presented to two subjects, whose responses were averaged for statistical analysis.

*Experiments with Males*

We performed five discrimination experiments with males: local versus Erie (1998), local versus Drake's Well (1998), local versus Kinzua (1999), local versus French Creek (2000), and local versus Hill's Creek (2000). Subjects for the male playbacks were free-living adult males occupying territories located between 2 km north and 3.5 km south of Hartstown. A small proportion of the male subjects held territories either in the field where the playback songs were recorded (1%) or in an adjacent field (10%). It is thus possible that these few males had some prior familiarity with the playback songs, although this chance is diminished by the fact that the playback songs were recorded 2–4 yr before the playback trials. In any event, male song sparrows of eastern populations show little or no discrimination of neighbor, stranger, and self songs from within a local population in the type of playback design we employ (Kroodsma 1976; Searcy et al. 1981).

We tested males using territorial playback as described in Searcy et al. (1997). Males in each experiment were tested twice: once with local and once with foreign song, with order randomized. The two trials with one male were separated by at least 2 d. All trials were run between 0600 and 1000 hours. We placed a single speaker (Nagra DSM) faceup on the ground well within a territory's boundary and marked the speaker's position with flagging so we could use the same position in the second test. We also set out flagging at measured distances of 4 and 8 m on either side of the speaker to aid in estimating the subject's distance to the speaker during the trial. Two observers stood with the tape recorder (Sony TCM 5000EV) 15–20 m from the speaker. The observers noted the subject's distance to the speaker in the categories 0–2, 2–4, 4–8, 8–16, and >16 m.

Each trial was 9 min long and consisted of 6 min of playback and 3 min of postplayback observation. We calculated mean distance of the subject to the speaker over the entire trial using the method of Peters et al. (1980).

Distance was our sole response measure. As in the female experiments, we used 10 local and 10 foreign stimulus sets in each experiment, and again, as in the female experiments, each set contained two song types recorded from one male in the appropriate population. The same song types were used as in the female experiments, with the addition of 20 song types recorded from eight males at Hill's Creek. The songs were recorded at the rate of one song per 10 s and in the order of nine repetitions of song A, nine of song B, nine of song A, and nine of song B. Each pair of local and foreign stimulus sets was presented to two males, and their responses were averaged for analysis.

*Statistical Analysis*

We compared responses of both females and males to local and foreign songs using Wilcoxon matched-pairs signed-ranks tests. In all cases, the sample size for the statistical test is the number of stimulus sets rather than number of subjects. In cases where the same stimulus set was presented to two subjects, the responses of the two were averaged, and the statistical test was performed on the means. The experimental design thus avoids pseudoreplication (Kroodsma 1989; McGregor et al. 1992). All tests are two tailed.

**Results**

Female song sparrows failed to discriminate between local songs and foreign songs recorded at the closest foreign site, at 18 km (table 1). Females did discriminate against songs recorded at the 34-, 68-, and 135-km sites, in each case giving significantly stronger responses to local than to foreign songs (table 1). We include (in table 1) the results of tests with foreign songs from Millbrook, New York, from Searcy et al. (1997) for comparison. We can describe the strength of discrimination in terms of the proportion of total displays given by females to local songs. This proportion increases with distance of the foreign site from the local site (fig. 2), with much of the increase occurring between 18 and 34 km.

Male song sparrows failed to show significant discrim-

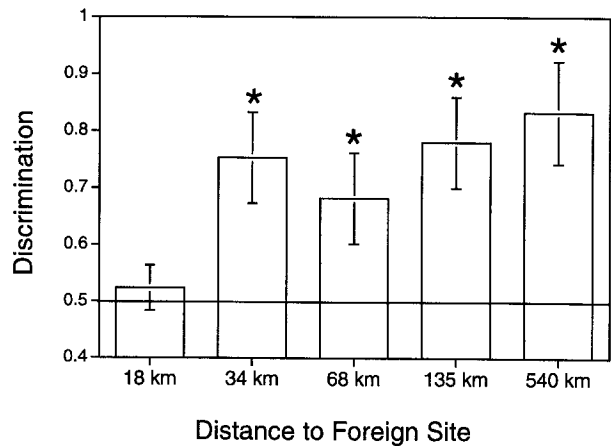


Figure 2: Female discrimination at each study site expressed as the mean proportion (± SE) of displays given to local song out of the total given to both local and foreign song. The line at 0.5 gives the expected proportion if females respond equally to local and foreign songs.

ination in any of our tests of local versus foreign songs using foreign sites extending out to the 270-km point (table 2). Only with foreign songs recorded at Millbrook, at 540 km, do males show significantly greater response to local songs (data reanalyzed from Searcy et al. 1997 to be comparable to the male playback data presented here). We can describe the strength of discrimination by males in terms of the ratio of distance to foreign songs/distance to local songs; this ratio shows little increase above 1 : 1 until the end point of the transect is reached (fig. 3).

**Discussion**

Our results suggest that discrimination by song sparrows of foreign from local songs grows stronger as the foreign songs are recorded at greater and greater distances from the local site. In females, the strength of discrimination increases mainly between 18 and 34 km (fig. 2), whereas in males, discrimination increases between 270 and 540 km (fig. 3). The overall pattern of discrimination by both sexes is consistent with the hypothesis that songs grow more different with increasing distance from a given point.

Table 1: Responses of female song sparrows in tests of local versus foreign songs

Source of foreign songs	Distance from Hartstown (km)	Mean no. of displays for local songs	Mean no. of displays for foreign songs	z	P
French Creek	18	4.1 ± 1.0	3.9 ± .8	.26	>.10
Erie National Wildlife Refuge	34	5.4 ± 2.2	2.7 ± 1.3	2.09	.036
Drake's Well	68	5.0 ± 1.5	2.9 ± 1.4	2.06	.040
Kinzua Bridge	135	6.9 ± 1.3	2.7 ± 1.1	2.24	.025
Millbrook	540	2.1 ± .7	.4 ± .2	2.20	.028

A pattern of increasing differences with distance is not surprising because such a pattern would be expected whether the details of songs are learned or genetic and whether the differences arise by selection or by drift. Nevertheless, only a few studies of bird vocalizations have shown this pattern in a systematic fashion, either by acoustic analysis or by analyzing patterns of discrimination (Baker 1983; McGregor 1983; Baker et al. 1984; Miyasato and Baker 1999). Better evidence for increasing differences in vocal signals with distance can be found in analyses of human dialects and languages (Cavalli-Sforza and Wang 1986; Barrantes et al. 1990).

Female song sparrows showed preferential response to local songs over foreign songs recorded just 34 km distant. Female birds in species with small-scale dialects may show discrimination over even smaller distances (Baker 1983; Baker et al. 1987a), but in those cases, song variation is limited within populations, and between-population differences are readily apparent. In song sparrows, the opposite is true; song variation is extreme within populations, and between-population differences are very difficult to discern against this background variation. Indeed, we have not yet been able to identify any consistent acoustic or organizational differences between our local (Hartstown) songs and those recorded at the 34-km point (S. Peters, S. Nowicki, and W. A. Searcy, unpublished data).

Male song sparrows overall showed weaker discrimination of local from foreign songs than did females. Males did not show a significant difference in response to local and foreign songs except in tests using foreign songs from the end of the transect, at 540 km. Females, by contrast, showed significant discrimination against foreign songs from the one-sixteenth, one-eighth, and one-fourth points as well as from the end point. Our results, then, support the general rule that female birds show stronger discrimination when tested for mating preferences based on songs than do male birds when tested for aggressive response to territorial intruders (Searcy and Brenowitz 1988; Searcy 1990; Ratcliffe and Otter 1996; but see Dabelsteen and Pedersen 1988, 1993).

O'Loghlen and Beecher (1997, 1999) have shown that female song sparrows prefer the songs of their mates and

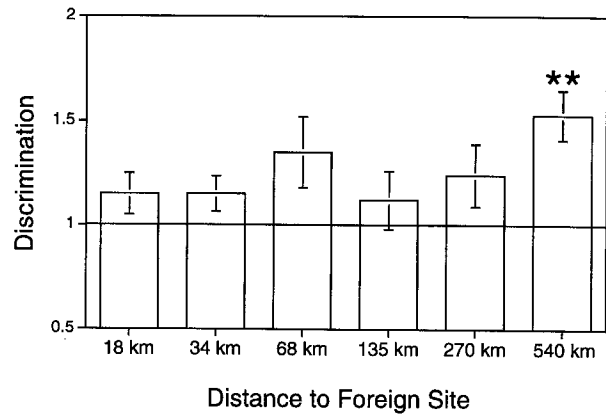


Figure 3: Male discrimination at each study site expressed as the mean ratio ( $\pm$  SE) of distance to foreign song/distance to local song. The line at 1 gives the expected ratio if males respond equally to foreign and local songs.

neighbors to the songs of strangers from their own population, and they prefer stranger songs that resemble mate songs to those that do not. These within-population preferences may provide a mechanism that would account for the between-population preferences we have observed. The familiar songs of mates or neighbors may be used by song sparrows of both sexes as ideal standards, to which they give their highest response, with response to other songs being lower in proportion to how much those songs depart from the ideal. What dimension or dimensions might be used to measure similarity to the ideal is not clear, however. One obvious possibility is note composition or phonology, with birds responding to foreign songs in proportion to how many notes those songs share with the familiar set of songs. This possibility has not been supported, however, by experiments with male song sparrows in which we have substituted local notes for notes in foreign songs; such substitutions have not increased response to foreign songs (S. Nowicki, W. A. Searcy, M. Hughes, and S. Peters, unpublished data). Other possible dimensions of similarity include order of elements (syntax) and sharing of larger song elements such as trills and note complexes.

Table 2: Responses of male song sparrows in tests of local versus foreign songs

Source of foreign songs	Distance from Hartstown (km)	Mean distance to local songs	Mean distance to foreign songs	<i>z</i>	<i>P</i>
French Creek	18	4.4 $\pm$ .6	4.9 $\pm$ .7	1.84	>.05
Erie National Wildlife Refuge	34	2.9 $\pm$ .2	3.3 $\pm$ .5	1.53	>.10
Drake's Well	68	3.8 $\pm$ .9	4.3 $\pm$ .5	.97	>.10
Kinzua Bridge	135	3.8 $\pm$ .5	4.6 $\pm$ 1.2	.31	>.10
Hill's Creek	270	3.9 $\pm$ .5	4.6 $\pm$ .7	1.12	>.10
Millbrook	540	2.8 $\pm$ .2	4.3 $\pm$ .4	2.70	.0066

Although female song sparrows perform remarkably well in discriminating foreign from local songs on small spatial scales, they do not perform well enough that they are ever likely to encounter foreign songs against which they can discriminate. Female song sparrows in our experiments discriminated local songs from foreign songs recorded at 34 km but showed no sign of discriminating local songs from foreign songs recorded at 18 km. We therefore assume that songs become discriminably different at some distance between 18 and 34 km. Root-mean-square dispersal distances for song sparrows are estimated at 350 m from observations of marked birds (Nice 1937; Barrowclough 1980) and at 6.1 km from mtDNA variation (Zink and Dittmann 1993). As we argued earlier, if the 6.1-km estimate is assumed to be correct, then 18 km represents roughly three times the root-mean-square dispersal distance, and we would expect a very small proportion of individuals to disperse more than this distance. If we assume that 350 m is closer to the actual root-mean dispersal, then 18 km is 50 times the dispersal distance, and the proportion of individuals moving this far would be effectively zero.

If females never, or almost never, encounter foreign males whose songs they would discriminate against, why do they show this discrimination ability? One answer is that discrimination of geographic variants arises as a by-product of selection against mating with heterospecific males (Nelson 1998*b*). Reinforcement of premating isolation because of selection against hybrid mating has in the past been controversial, but strong evidence in favor of such reinforcement now exists for several taxa (Coyne and Orr 1989, 1997; Rundle and Schluter 1998), including birds (Sætre et al. 1997). In song sparrows, selection against hybridization might have brought about a system in which females learn the cues to be used in identifying males of their own species by listening early in life to songs of older, conspecific males; because these song tutors would almost always be local males singing local songs, this learning mechanism might automatically create a bias for local over foreign songs. While this explanation seems satisfactory for species with well-defined dialects and little within-dialect variation, it does not lend itself as well to species such as song sparrows in which there is enormous within-population variation as compared to between-population variation. Given that the differences in song between song sparrow populations are so much smaller than the differences in song between song sparrows and closely related species, the degree of discrimination displayed by female song sparrows seems to be far more specific than warranted simply to avoid interspecific pairing.

An alternative hypothesis, which we think better explains the extreme specificity of female preferences in song

sparrows, is that female preferences have been shaped by the selective consequences of mating with conspecific males of varying quality. In other species of songbirds, females have been shown to benefit selectively from song-based preferences for certain conspecific males over others (Catchpole and Slater 1995; Searcy and Yasukawa 1996). Female sedge warblers (*Acrocephalus schoenobaenus*), for example, prefer males with larger repertoires of syllable types (Catchpole 1980; Buchanan and Catchpole 1997), and such males have lower parasite loads and provide greater parental care than males with smaller repertoires (Buchanan et al. 1999; Buchanan and Catchpole 2000). Female sedge warblers thus obtain direct benefits from their preference, but in other cases, the benefits of song-based preferences may be indirect, that is, experienced through more fit offspring (Hasselquist et al. 1996; Hasselquist 1998).

Whether preferences for local over foreign songs are similarly adaptive is unknown, but one popular hypothesis has been that females benefit from mating with local males because such males have genes adapted to local conditions (Nottebohm 1972; Baker and Cunningham 1985). Song sparrows show substantial geographic variation in size and color (Aldrich 1984), consistent with the strong local adaptation assumed by this hypothesis. Because of the observed geographic variation in morphology, song sparrows have been divided into numerous subspecies (American Ornithologists' Union 1957). It is not yet known, however, whether the observed geographic variation has a genetic basis. Song sparrows exhibit a low level of geographic structure in neutral genetic markers (Zink and Dittmann 1993; Zink and Blackwell 1996), which weighs against the hypothesis of strong local genetic adaptation. In any event, our comparison of dispersal distances to distances over which female song sparrows discriminate foreign from local song implies that females cannot be benefiting from discrimination against conspecific males with foreign genes.

The hypothesis that female preferences for local song represent a test for the quality of male song learning provides an alternative idea on how such preferences might be adaptive (Nowicki et al. 1998, 2000). Song may be a reliable indicator of male quality because young males learn their songs and the brain structures that underlie song learning and production develop early in life during a period of rapid growth. Any stress, such as undernutrition or parasitism, which occurs during this period and which affects general phenotypic development, will also affect song development (Nowicki et al. 1998). Females might, therefore, use any aspect of male song that reflects the quality or quantity of song learning as an index of male phenotypic quality (Nowicki et al. 1998). Male phenotypic quality might be important to females because

males that are phenotypically superior provide better parental care, better territorial resources, and/or better genes. The accuracy with which males copy local songs would be one obvious measure of the quality of male song learning. This hypothesis suggests that selection does not act on females specifically to discriminate against foreign songs. Instead, discrimination against foreign songs is an indirect consequence of selection on females to choose those males that have learned best. Foreign songs are discriminated against because they seem, to a female, to have been poorly learned. Further testable predictions of the hypothesis include that females should prefer accurately learned songs to poorly learned songs, learning accuracy should be positively correlated with male phenotypic quality, and females should benefit directly or indirectly from choosing males possessing accurately learned songs.

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