icterids on a walking gait on the ground. The icterids sometimes use the bilateral-scratch in short, erect, dense live grass while emberizines do not.

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THE EFFECT OF LARGE SONG REPERTOIRES ON NEIGHBOR "RECOGNITION" IN MALE SONG SPARROWS

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The occurrence of different life history strategies within a taxon often perplexes the evolutionary biologist, for adaptive significances of alternative habits are not always clear. Such is the case with the diversity of singing behaviors among the Oscines. Individuals of some species possess only one song (e.g., many fringillids listed in Borror 1961), while individuals of other species may have a thousand different songs (e.g., Brown Thrasher, *Toxostoma rufum*; Kroodsma, unpubl. data). Congeners may sing similarly—*Zonotrichia* species usually have one song per individual (Marler and Tamura 1962, Nottebohm 1969, Borror and Gunn 1965); or their singing may be quite different—the *Aimophila* species (Borror 1971) and the *Spizella* species (pers. obs.) are good examples.

Epigamic selection is one rather important selective force in the evolution of elaborate plumages, complex display patterns, and large song repertoires (see Nottebohm 1972, Otte 1972), but vocal diversity may also be important in male-male interactions, playing a role in the establishment and maintenance of territories in some songbirds. In several species with small song repertoires (table 1), territorial males respond more aggressively to songs of non-neighbors than they do to those of neighbors. Such reduced aggression to a specific and relatively unvarying stimulus at a specific location is presumed to be a considerable energetic savings (Falls 1969, Peeke and Veno 1973). Unclear, however, is the effect which a greater diversity of stimuli, such as a larger song repertoire, will have on this process of "neighbor recognition,"

or habituation (Petrinovich and Peeke 1973). With larger repertoires, the amount of exposure to and probably the familiarity with each song type of neighboring males will decrease proportionally; regardless of the neural mechanisms involved, distinguishing songs of neighbors from those of strangers may then become more difficult.

I examined this phenomenon of "neighbor recognition" in the Song Sparrow (*Melospiza melodia*), a species with a somewhat larger repertoire than has been used previously. The classic study by Nice (1937) as well as studies by Borror (1965), Mulligan (1966), and Harris and Lemon (1972) provide excellent background on the behavior of the species. Repertoire size varies geographically; minimum estimates for southern Quebec and Maine are nine and eight song patterns per individual respectively (Harris and Lemon 1972, Borror 1965), while on my study area they averge about ten.

I conducted 60 playbacks to 15 territorial paired males during late May and June 1973 at the Rockefeller University Field Reserch Center near Millbrook, New York. The birds were uniquely color-banded, and territories for each were mapped before starting playback experiments.

I recorded songs with a Uher 4400 tape recorder and 60 cm parabolic reflector. "Neighbors" in all cases had territories adjacent to the experimental male, while "strangers" were at least two territories removed. Most strangers held territories between 100–200 m but never more than 800 m from the experimental male. Over similar distances Harris and Lemon (1972) found much sharing of syllable types among males. Songs of Song Sparrows do, however, change over distance; if playback songs are selected from greater distances, any increased response to novel songs of the "local" population could be offset by a decreased response to songs of different dialects (Harris and Lemon 1974).

TABLE 1.   Species with small song repertoire sizes in which males respond more aggressively to songs of non-neighbors than to songs of neighbors.

Species	Song repertoire size	Source
Ovenbird (*Seiurus aurocapillus*)	1	Weeden and Falls (1959)
White-throated Sparrow (*Zonotrichia albicollis*)	1	Falls (1969)
Indigo Bunting (*Passerina cyanea*)	1	Emlen (1971)
Field Sparrow (*Spizella pusilla*)	1	Goldman (1973)
Yellowthroat (*Geothlypis trichas*)	1	J. M. Wunderle, Jr. (pers. comm.)
Great Tit (*Parus major*)	4–5	Gompertz (1961), Krebs (1971)

Songs were played back with a Nagra amplifier-speaker placed on the ground several meters inside (but see below) the territorial boundary of the subject male and connected by a 17 m line to a Nagra III tape recorder. The distances of potential song perches within 40 ft were measured to the nearest foot and distances of the bird from the speaker during playback were estimated using these reference points.

Each of the males was exposed to one randomly selected song type of both the neighboring and non-neighboring individuals between 0700 and 1000 hr on each of two successive days. The sequence of songs on the first day was chosen at random and then reversed on the second day. After the subject had been silent for several minutes, the playback tape was started; responses (table 2) were recorded with a cassette recorder during the 3-min playback session (1 song/12 sec, or a total of 15 songs) and the six following minutes. After the bird had been silent again for several minutes, the second playback, using the other song, was begun.

Playback experiments with five males were discarded before data analysis. With three males the speaker had been placed too close to the territorial boundary, evoking strong responses from and interactions between neighboring and experimental males. One male failed to respond and was not located until several days later. The fifth male was found to be feeding nestlings; the playback data were discarded rather than add further variability to response levels (see Verner and Milligan 1971). The remaining ten males were paired but did not have young at the time of playback.

The response categories are listed in table 2. In order to examine responses both during and after playback, I divided each nine-minute session into three 3-minute periods. Responses on a given day to the two playback songs were compared and analyzed with the one-tailed Wilcoxon's matched-pairs signed-ranks test.

The Wilcoxon test statistic in 13 of 14 response measures (table 2) indicated that male Song Sparrows *tend* to respond more strongly to the songs of non-neighboring individuals than they do to those of immediate neighbors. In three response measures this response was significantly stronger: during the actual playback of foreign songs the males approached the loudspeaker more quickly ($P = 0.052$), remained closer ($P = 0.005$), and flew more frequently ($P = 0.033$). The response intensity of different individuals varied considerably, and the standard error of median responses was large. Thus, although the median latency of song during playback indicated a more rapid response to song of neighboring individuals, the matched-pairs of the Wilcoxon's signed-ranks test indicated an overall tendency for more rapid response to songs of strangers.

In the Indigo Bunting (*Passerina cyanea*), Emlen

TABLE 2.   Song Sparrow responses to playback of recorded songs of neighbors and strangers.

	Median response to songs of[a]		Response stronger[b] to songs of
	Neighbor	Stranger	
Latency of song, in sec	16.5	20.5	S
Latency of approach to 10 ft, in sec	60.5	39.0	S* ($P = 0.052$)
Number of songs during			
1st 3 minutes (playback)	9.0	10.5	S
2nd 3 minutes	12.0	15.0	S
3rd 3 minutes	10.0	12.5	S
Number of flights during			
1st 3 minutes (playback)	11.0	13.0	S* ($P = 0.033$)
2nd 3 minutes	2.0	3.5	S
3rd 3 minutes	1.5	2.0	S
Flight lengths in sec during			
1st 3 minutes (playback)	18.1	16.2	S
2nd 3 minutes	3.8	4.4	S
3rd 3 minutes	1.9	1.7	S
Average distance from speaker in ft during			
1st 3 minutes (playback)	16.8	12.5	S** ($P = 0.005$)
2nd 3 minutes	19.5	20.0	N
3rd 3 minutes	51.8	21.8	S

[a] Sample size n = 20 for all medians.
[b] As indicated by Wilcoxon matched-pairs signed-ranks test statistic; e.g., when latency of singing in response to stranger's songs is subtracted from the latency of response to the neighbor's songs in each of the 20 playbacks and the absolute difference is ranked, the sum of the rank values for the positive differences is larger than the sum for the negative differences, indicating a more rapid response to strange songs. S = Stranger, N = Neighbor.

(1971:243) stated that "While stranger tapes evoked full attack, threat, and, in most instances, full submission responses, those of the neighbors evoked only curiosity, approach, and mild alarm." Krebs (1971) simply noted the presence or absence of any response by the experimental male during intensive playbacks to six male Great Tits and convincingly demonstrated more responses to novel songs. White-throated Sparrows (*Zonotrichia albicollis*) "By all criteria . . . responded more strongly to songs of strangers than to those of neighbors" (Falls 1969:219). The data of Weeden and Falls (1959) on Ovenbirds (*Seiurus aurocapillus*) and Goldman (1973) on Field Sparrows (*Spizella pusilla*) appear equally unequivocal. The Song Sparrow responses seem less polarized, for males responded strongly to songs of neighboring males. Unfortunately, quantitative interspecific comparisons of response intensities to playback of songs from neighboring and non-neighboring individuals are hindered by slightly different methods used by different investigators. Particularly critical variables include placement of the speaker relative to the territorial boundary, number of playbacks to each individual, the micro-geographical distribution of song variations in a particular species and the distance from which the stranger song is chosen, and the time of the breeding season.

It is not uncommon for a male Song Sparrow to have from four to seven neighboring males. Few song patterns are shared by neighboring males (Mulligan 1966), so birds are barraged with diverse song stimuli. A persistent human observer can learn to recognize many individuals by their songs, and the birds, with much more exposure to their neighbors' songs, also demonstrate this capability by their differential responses to the songs of neighboring and non-neighboring birds. It is entirely possible that powers of recognition (or rates of habituation) have increased proportionally with the evolution of larger repertoires. If this were the case, Song Sparrows might habituate to this great diversity of songs from neighboring males as rapidly as do those species with smaller repertoires. Interspecific differences in the polarization of response intensities might then be minimal.

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