

## Recognition of individual neighbors by song in the song sparrow, a species with song repertoires

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**Summary.** Previous theory and research have suggested that bird species with song repertoires in general, and song sparrows (*Melospiza melodia*) in particular, cannot readily discriminate between the songs of neighbors and strangers. In a recent study (Stoddard et al. 1991) we showed that song sparrows can in fact discriminate neighbors from strangers on the basis of song. In this study we sought to demonstrate that song sparrows can make the finer discrimination between individual neighbors and that they can do so on the basis of a single song type. We compared the response of territorial males to song playback of neighbors and strangers at three locations: the neighbor's regular boundary, the opposite boundary, and the center of the territory. The birds showed strong neighbor-stranger discrimination at the regular boundary but not at the opposite boundary, nor in the center of the territory. The differences in song discrimination between different boundary locations indicate that song sparrows associate particular songs with particular territories, effectively discriminating between individual neighbors on the basis of song. Song repertoires themselves do not interfere with neighbor recognition to the extent originally postulated. As speakers are moved inside the territory from the border, however, the degree of discrimination diminishes. We believe that differences in speaker placement may have contributed to the variability in neighbor-stranger discrimination observed in previous studies of the song sparrow and perhaps other repertoire species as well. This interpretation is consistent with data from another song sparrow population showing that half the territory takeovers are by immediate neighbors.

### Introduction

Animals should benefit by recognizing all individuals with whom they have repeated contact. For instance, individual recognition is one of the prerequisite conditions for reciprocity among social animals. Among terri-

torial songbirds, we expect to find good recognition of songs that vary between individuals (Falls 1982; Getty 1987). A bird that can discriminate between its neighbors' vocalizations can save time and energy by gauging its territorial response according to the threat posed by that individual neighbor. There is considerable evidence, however, that individual recognition by song is poor in songbird species with medium song repertoires (6–20 song types) or large song repertoires (20–200) compared to that seen in single-song or small repertoire (2–5) species (Falls 1982). Several authors have suggested that an increase in song repertoire size inevitably causes a decrease in the ability of listeners to recognize the singer (Kroodsma 1976; Wiley and Wiley 1977; Krebs and Kroodsma 1980; Falls 1982). The general argument is that a male of a repertoire species must learn and remember more songs, in the face of greater similarity among songs and less exposure to each song, than his counterpart in a single-song species. When the number of songs to be recognized is large enough, the bird may reach the limits of his perceptual discrimination ability, learning speed, or memory capacity. These limitations may thus constrain the ability to recognize individuals by song; we will refer to this as the 'repertoire constraint' hypothesis. Under this hypothesis, the benefits of being recognizable to other individuals may act as stabilizing selective factors in a selection regime that otherwise favors larger repertoire size. The repertoire constraint hypothesis is of general interest because it proposes a constraint on sexual selection for vocal complexity. Further, repertoire constraint is perhaps the only hypothesis extant that poses a behavioral counteradvantage to evolution of progressively greater vocal complexity. Selection against large repertoires is also suggested by evidence that the emberizine sparrows have in fact undergone an evolutionary *reduction* in repertoire size (Irwin 1988).

The evidence for the repertoire constraint hypothesis comes from field playback studies of neighbor-stranger discrimination (hereafter NSD) and has been reviewed by Falls (1982). A major portion of this evidence comes

from three field experiments which found weak NSD in song sparrows, *Melospiza melodia* (Harris and Lemon 1976; Kroodsma 1976; Searcy et al. 1981). In a recent study, however, we found strong NSD in song sparrows (Stoddard et al. 1991). The discrepancy between the results of the earlier studies and ours has led us to a reconsideration of the repertoire constraint hypothesis and to the present study.

Male song sparrows have medium-sized song repertoires averaging eight discrete types per individual throughout most of their range in North America. A variety of evidence points to a role for these song repertoires in male-male competition in song sparrows (Stoddard et al. 1988; Hiebert et al. 1989) and in passerine birds in general (Searcy and Andersson 1986). Male-male competition in song sparrows centers on acquiring and holding a territory. In one population of song sparrows, Arcese (1989) found that males losing their territories were equally likely to lose them to neighboring males and to 'floater' males (typically young birds obtaining their first territory). Thus both floaters and neighboring males with inadequate or inferior territories pose a considerable threat to territorial males, compared with neighbors inhabiting high quality territories. Given this pattern of threat and territory loss, male song sparrows with territories have considerable incentive to discriminate between non-threatening neighbors, threatening neighbors and floaters. For this reason, the song sparrow is a good candidate to test for recognition of individual neighbors, which requires finer discrimination ability than discrimination between neighbors and strangers.

In the present study, we evaluated the idea that song sparrows are capable of recognizing their neighbors individually by song but respond differentially to neighbor (N) and stranger (S) song only in contexts where N song is less threatening than S song. Given the finding of Arcese (1989) that neighbors account for as many incidents of territory loss as strangers, and given that adult male song sparrows sing only on the territory they are defending, male song sparrows should respond as vigorously to N song as they do to S song, when the N song comes from anywhere other than the neighbor's established territory (where he normally sings). Such a song would signal territory expansion by that neighbor and would warrant territorial defense. Moreover, the bird should respond more strongly to song within his territory than to song from without or on the edge of the territory, regardless of whether this is N or S song.

Our design and terminology follow Falls and Brooks (1975). We systematically compared responses of territorial male song sparrows to a speaker placed in three locations: on the regular boundary of the neighbor that sang the song used as the N stimulus, on the edge of the subject's territory opposite the regular boundary of the N song neighbor, and in the territory center. We tested two specific predictions: (1) that the bird would respond less strongly to N song when N and S songs are played from the usual boundary, but not when they are played from the opposite boundary or the center of the subject's territory; (2) that the bird would respond more strongly in the center of the territory than at either

edge. As originally pointed out by Falls and Brooks (1975), this design represents a test of neighbor-neighbor discrimination (NND) as well as neighbor-stranger discrimination (NSD). If the subject responds to neighbor song weakly when the neighbor is singing on his own territory, but strongly when he sings from other adjoining territories, then effectively the subject recognizes this neighbor as a particular neighbor (vs. one of his several neighbors, merely a familiar singer).

## Methods

We selected as subjects 14 territorial males from the population of resident song sparrows inhabiting the deciduous woodlands and field margins of Discovery Park, a 200-ha tract on the edge of Puget Sound in Seattle, Washington, USA. Each male was color-banded on his territory at least 1 month before the study. We recorded the full repertoire of each subject and one of his neighbors. Two weeks before the playback experiment, we determined the territory of each subject by drawing the bird to his boundary with a playback of songs not used in the study (our netting tape). The day before the playback experiment, we rechecked the boundaries by observing interactions between the subject and his neighbors.

We conducted playback trials during the first 3 weeks of May 1989. Most of our subject males had incubating mates by this time. We ran trials between 08:00 and 12:00 PST in fair weather only.

As stimuli for each subject, we selected one song from a neighbor and one song from a bird at least 0.5 km distant, presumably a stranger. We selected our subjects, neighbors, and strangers in such a way that we could play each song to two subjects: to one subject as a neighbor song (N song), and to the other as a stranger song (S song). Thus we used 14 songs as stimuli for 14 subjects, avoiding pseudoreplication (Kroodsma 1989) while balancing for differences in song potency. Stimulus songs were recorded in the field onto metal tapes with a Sony WM-D6C cassette recorder and a Sennheiser RF condenser microphone MKH-816T-U. We chose a single rendition of one song type at random from the field recordings of each singer's repertoire, making sure only that the recording was of good quality. Note that in choosing a single song rendition, instead of a series of variations on a song type as would occur in a natural song bout, we biased the experiment against the predicted outcome. Each song was band-pass filtered to attenuate noise outside the frequency range of 1.7–10 kHz and digitized (30 ksamples/s, 12 bits). The computer standardized amplitudes and played the songs back onto a stimulus tape 18 times at 10 s intervals onset-to-onset. Labels on tapes and tape boxes were encrypted to reduce experimenter bias: field workers knew which tape to play on a given trial, but not whether it contained N or S song.

We played both N and S songs to each subject from 3 locations in and around his territory: the regular boundary shared with the neighbor who sang the N song, the opposite boundary, and the approximate geometric center of the territory. In the boundary conditions, we placed the speaker approximately 1 m outside the subject's territory. In each location, we placed the Sony APM-007 AV speaker 0.5 m off the ground in a spot devoid of obstructions in order to facilitate observation and sound transmission. We set playback volume by ear to match natural singing levels.

Each subject received two playback trials (N and S) on 3 consecutive days, one location per day, allowing at least 15 min between trials. Orders of presentation and location were varied with a randomized block design. This playback regimen represented a compromise between risks of habituation/sensitization from multiple presentation within days and birds' changing responsiveness between days due to extrinsic factors such as parental or territorial demands.

Before starting a trial we would lure a potentially reactive neighbor to the most distant part of his territory by quietly playing

**Table 1.** Summary of response of 14 male song sparrows to playback song in the 6 conditions of speaker placement and song origin

		Conditions					
		Reg N	Reg S	Ctr N	Ctr S	Opp N	Opp S
Mean	NFl	3.57	5.29	7.86	8.21	5.43	5.50
Response	ClAppr	14.93	5.93	4.64	4.29	9.57	9.79
Measures	PC1 <sup>a</sup>	-0.748	0.056	0.474	0.543	-0.160	-0.165
ANOVA	H1	-3	1	0	0	1	1
coefs	H2	-1	-1	2	2	-1	-1

Conditions: Reg=regular boundary shared with neighbor that sings N song, Ctr=center of territory, Opp=boundary opposite the regular boundary. N=neighbor song, S=stranger song.

NFl: Number of flights during 3-min trial. ClAppr: Closest approach during trial (m)

PC1: 1st principal component of NFl and ClAppr

H1: Hypothesis 1: Neighbor threat varies with location of playback (Neighbor-Neighbor Discrimination): (Reg N < Reg S = Opp N = Opp S)

H2: Hypothesis 2: Any song evokes a stronger territorial response played at the territory center than at the edge: (Ctr > Reg = Opp)

<sup>a</sup> All statistical analyses done on PC1

recorded songs (not experimental) from the netting tape before beginning the trial. This technique kept the neighbor quietly searching low in the underbrush away from the experiment during the trial. The few times the neighbor slipped back and sang at the boundary, we terminated the trial and rescheduled it at least 15 min later or for the following day. When the neighbor was safely occupied, we located the subject on his territory and waited until he had stopped singing before starting the playback. After a minimum wait of 15 min we conducted a second playback at the same location using the other stimulus. We delayed onset of the second trial until the subject was in approximately the same location he was before the first trial. We were able to run trials with 3 birds per day and we attempted to conduct playbacks to each bird at the same time each day. We avoided playback trials to neighboring birds on the same day. All 14 subjects received each playback condition, enabling each bird to serve as its own control for statistical analysis, eliminating differences in general responsiveness between individuals.

**Analysis.** As measures of response intensity we recorded the subject's number of flights and closest approach to the playback speaker during the 3-min playback. To avoid a 'fishing expedition' we confined ourselves to these two dependent variables and combined them into a single dependent variable, their first principal component (PC1). With only two original variables, PC1 is simply derived. One standardizes the two variables, takes their sum (if V1 and V2 are positively correlated) or difference (if negatively correlated), and standardizes the derived scores. We chose number of flights and closest approach on the basis of earlier studies; we feel that they are the best measures of response intensity. Latency measures are typically less reliable (they are influenced by other factors such as the bird's location when the trial begins, what the bird is doing, and how well it hears the playback) and they are redundant. We have found that song measures do not relate in a simple way to response intensity in this species. Playbacks inside the territory often elicit little song because the bird is actively trying to evict the singer.

We tested two specific predictions concerning response to playback song. The first prediction was that the subject would respond more strongly to stranger song at either boundary and neighbor song at the opposite boundary (taken together) than to neighbor song at the usual boundary. The second, independent prediction was that subject would respond more strongly to song from the center of his territory than to song at the boundaries. We tested these two hypotheses as planned comparisons in a repeated measures ANOVA (Sokal and Rohlf 1981). As is indicated by the contrast coefficients in Table 1, these two hypotheses are orthogo-

nal, hence we can partition the total treatment sum of squares into three components, the variation accounted for by each of the two hypotheses and the residual condition variation.

## Results

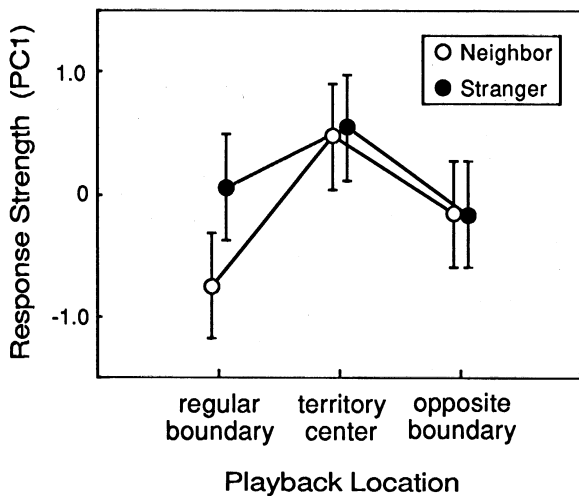
Mean number of flights, closest approach and the first principal component of these two variables (PC1) for the six conditions are presented in Table 1. There was a strong correlation between number of flights and closest approach (and PC1) across the six condition means ( $r = -0.89$ ), and analyses on any of the three variables gave essentially identical results.

The results are summarized in Table 1 (mean response), Table 2 (ANOVA summary) and Fig. 1 (means and 95% confidence intervals, SEs derived from the error mean square of Table 2). As can be seen, essentially all of the effect due to the treatments is accounted for by the two hypotheses: birds responded more to stranger song (both boundaries) and neighbor song at the opposite boundary than they did to neighbor song at the neighbor's regular boundary ( $P = 0.017$ ), and they responded more to song in the territory center than at the two boundary locations ( $P = 0.0001$ ). The first result indicates that the threat value of neighbor song increased when shifted to a different boundary location whereas the threat value of stranger song remained the same. The fact that a neighbor song elicits a weak response in its usual boundary location but a strong response

**Table 2.** Analysis of variance summary table

Source	Sum squares	df	Mean square	F	P
Hypothesis 1 <sup>a</sup>	4.55	1	4.55	6.05	0.017
Hypothesis 2 <sup>a</sup>	10.86	1	10.86	14.45	0.0001
Condition res.	0.47	3	0.16		
Error	48.82	65	0.75		

<sup>a</sup> Hypothesis coefficients: See Table 1



**Fig. 1.** Mean response (PC1) during playback given by 14 male song sparrows to songs of neighbors and strangers played in three locations: the regular boundary of the neighbor that sings the N song (where the neighbor song is ordinarily heard), at the center of the subject's territory and at the opposite boundary (opposite that where the neighbor song is ordinarily heard). Error bars are  $\pm 2$  SE (SE derived from the error mean square of Table 1) and represent 95% confidence intervals for the mean estimates

in a different boundary location, one often occupied by a different neighbor, indicates that neighboring males are treated as individuals rather than as a group of familiar singers. This finding meets the criteria of Falls and Brooks (1975) for a demonstration of recognition of individual neighbors by song. The second result, elevated response in the territory center, is consistent with results obtained for a closely related species, the white-throated sparrow, *Zonotrichia albicollis* (Falls and Brooks 1975). The clear absence of NSD at that location (Fig. 1) is consistent with the finding of reduced or absent NSD by earlier studies on the song sparrow.

## Discussion

The results of the present study indicate that song sparrows can discriminate among their different neighbors, and that a single song type, indeed, a single variant thereof, provides sufficient information for recognition. Moreover, results from the present study taken together with those of our earlier study (Stoddard et al. 1991), indicate that song sparrows are quite capable of discriminating between neighbors and strangers on the basis of song. It is also clear that in some contexts song sparrows *do not* discriminate between neighbors and strangers in their aggressive response to song, as our center and opposite boundary conditions reveal. Similar spatial effects in neighbor-stranger discrimination have been reported for the single-song white-throated sparrow, (Falls and Brooks 1975) and the small-repertoire great tit, *Parus major* (McGregor and Avery 1986).

Response to playback at or near the territory edge now has been compared with response in the center of the territory in five songbird species. Four of the five studies found significant NSD at the edge but not in

the center: common yellowthroat, *Geothlypis trichas* (Wunderle 1978), great tit (Falls et al. 1982), yellow-breasted chat, *Icteria virens* (Ritchison 1988), and the song sparrow (present study). In the fifth study white-throated sparrows showed a much weaker effect in the center than at the edge (Falls and Brooks 1975). In all cases, the aggressive response was stronger in the center of the territory, raising the possibility that the lack of discrimination in the center simply reflected a ceiling effect (i.e. no difference between N and S song can be detected because response strength is near its natural maximum). For two of these species, however, response at the opposite boundary was also compared (present study; Falls and Brooks 1975): In both cases, response levels at the opposite boundary were more similar to those seen at the usual boundary, but there was no discrimination between N and S song. This provides some support for a common interpretation of the lack of discrimination seen at the territory center and at the opposite boundary: N and S song in these locations are equally or nearly equally threatening and so elicit equal or nearly equal response.

The main implication of studies such as ours for the generalization that NSD is weaker in repertoire species concerns hypotheses about the mechanism of the effect, rather than the effect itself. In particular, we feel there is considerable evidence now against the repertoire constraint hypothesis, i.e. the idea that large repertoires per se reduce the ability of birds to discriminate between neighbors and strangers, or among different neighbors. In addition to the playback study described here, we have carried out a laboratory study showing that song sparrows can memorize a large number of songs with relative ease; birds learned exemplars of 64 songs, learned the last ones as quickly as they had learned the first ones, and gave no indication that they were near memory capacity (Stoddard et al. in prep.).

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