

STRONG NEIGHBOR-STRANGER DISCRIMINATION IN SONG SPARROWS¹

PHILIP K. STODDARD

Section of Neurobiology and Behavior, S. G. Mudd Hall, Cornell University,
Ithaca, NY 14853-2702

MICHAEL D. BEECHER, CYNTHIA L. HORNING, AND MARY S. WILLIS

Animal Behavior Program, Guthrie Hall, University of Washington,
Seattle, WA 98195

Abstract. Song Sparrows (*Melospiza melodia*) have medium-sized song repertoires and have been the main example for the generalization that neighbor recognition is weaker in species with larger song repertoires. Three previous studies of the Song Sparrow have indicated that neighbor-stranger discrimination by song is weak or absent in this species. In contrast to the previous studies, we found that territorial male Song Sparrows readily discriminated between neighbors and strangers based on a single song type from each. This result is strong and unequivocal evidence of neighbor-stranger discrimination in this species. We also present evidence that stability of neighbor boundaries may be required to demonstrate neighbor-stranger discrimination.

Key words: Song Sparrow; *Melospiza melodia*; song; recognition; neighbor; stranger; territoriality.

INTRODUCTION

Among the passerines, extreme complexity and variability of male song is thought to have evolved in the context of sexual selection (Darwin 1871, Searcy and Andersson 1986, Kroodsma 1988). One possible function of song complexity is to render the singer more readily identifiable to neighboring conspecifics (Beecher and Stoddard 1990). For example, a number of recent theoretical discussions of territorial dynamics in birds have implied that reliable identification would be beneficial to residents (Getty 1987) as well as to floaters avoiding dangerous residents (Ydenberg et al. 1988).

Despite considerable evidence that vocal complexity in birds has been shaped by selection for enhanced recognition (Beecher 1982, Jouventin 1982, Beecher et al. 1986), no theory of bird song function has attempted to relate interspecific variation in song complexity to individual recognition. Several authors have suggested, however, that one aspect of song complexity, song repertoires, may adversely affect neighbor recognition (Wiley and Wiley 1977, Krebs and Kroodsma 1980, Falls 1982). As repertoires increase in size across species, they should act to

reduce the ease of recognition for three reasons (Falls 1982). First, in order to identify the singer from a single song, listeners must learn to identify many songs instead of one or a few. Repertoire elaboration should thus tax memory and increase the listener's learning time. Second, because the singer divides singing time among several song types, each song type is heard fewer times and therefore should take longer to learn. Third, the average differences between songs of different individuals will diminish as more songs are added to each bird's repertoire, provided the total diversity remains constant (i.e., if the new songs remain within the bounds of the existing song characteristics of the population).

Falls (1982) and others have noted an apparent inverse relation across species between repertoire size and the magnitude of neighbor-stranger discrimination measured with response to playback experiments of one song type. Species in which each male sings a single song type almost invariably show strong differences in response to songs of neighbors and strangers (see Falls 1982). Species with small repertoires of two to five song types per male likewise show pronounced neighbor-stranger discrimination (NSD). Of the few species tested with medium-sized (6-20 types) or large (>20 types) repertoires, some have shown NSD, e.g., Western Meadowlark (*Sturnella neglecta*) (Falls and d'Agincourt 1981), Red-winged

¹ Received 25 April 1990. Final acceptance 28 June 1990.

Blackbird (*Agelaius phoeniceus*) (Yasukawa et al. 1982) and Yellow-breasted Chat (*Icteria virens*) (Ritchison 1988), and others have not, e.g., Song Sparrow (*Melospiza melodia*) (Harris and Lemon 1976, Kroodsma 1976, Searcy et al. 1981) and Eastern Meadowlarks (*Sturnella magna*) (Falls and d'Agincourt 1981). The experimental results from these latter few species have been heavily weighted in the generalization that individual recognition breaks down as repertoire size increases. The Song Sparrow has been a key species, as three experimental field studies have indicated that this medium-repertoire species (6–12 song types over most of North America) has weak NSD (Harris and Lemon 1976, Kroodsma 1976) or no NSD (Searcy et al. 1981).

We propose an alternative explanation for why species with large repertoires have shown equivocal NSD. Conventional tests of NSD depend on the assumption that strangers constitute a greater threat than neighbors. If neighbors constitute a significant threat in a particular species, however, an individual bird may respond equally aggressively to playbacks of neighbor and stranger song, and conventional NSD test designs will not reveal an effect. The idea that neighbors may pose a threat is compatible with all contemporary male-male competition theories of song repertoires (reviewed by Searcy and Andersson 1986, Beecher and Stoddard 1990). These theories assume that repertoire size is positively related to the intensity of male-male competition (Kroodsma 1983, 1987). By implication, the extent of competition should be least for species with a single song type. If male-male competition is intense, neighboring males may be as great a threat as strangers or greater. There is recent evidence for the Song Sparrow that neighbors do, in fact, constitute a significant threat: Arcese (1989) found that in years of high population density, neighbors accounted for nearly half the territory takeovers.

The weaker NSD observed in repertoire species in general and Song Sparrows in particular may indicate that neighbors are greater threats in those species than in species with single songs or small repertoires. This failure to discriminate may be only indirectly related to repertoire size per se. If this hypothesis is correct, how can we carry out a valid test of NSD in a medium- or large-repertoire species? Even for species in which expansionist neighbors pose a significant threat, neighbor song should be less threatening than

stranger song in certain contexts. In particular, a bird should consider neighbor song a challenge when he hears it coming from within his own territory but *not* when it comes from the neighbor's territory. Stranger song, in contrast, *always* signals a newcomer and a potential takeover attempt. This argument suggests that strong NSD should be seen on the territory boundary, but not within the subject's territory. In fact, all three tests of NSD in Song Sparrows to date have been conducted with the speaker placed *within* the subject's territory: "... within the territory of the bird being tested, towards the boundary of his neighbour" (Harris and Lemon 1976); "... several meters inside the territorial boundary..." (Kroodsma 1976); "... near the boundary..." (Searcy et al. 1981).

Such a design simulates sequential intrusion by a neighbor and a stranger. We often see aggressive encounters when a neighbor crosses the boundary by less than a meter. Because Song Sparrow neighbors and strangers potentially pose equally high threat levels, it might be expected that they should respond equally strongly to neighbors and strangers. On the other hand, males with mates and high-quality territories have little incentive to intrude on their neighbors. Therefore, resident male Song Sparrows should habituate to the songs of neighbors singing on their territories. The appropriate design for demonstrating Song Sparrow NSD places the playback speaker on the neighbor's side of the common boundary, where neighbor song would not be unusual, and thus not especially threatening. Because speaker placement inside the territory boundaries may have diminished effects obtained in earlier studies of Song Sparrow NSD, and because discussions and hypotheses relating recognition to repertoires have hinged on this species, we retested the Song Sparrow for NSD with two playback speakers situated just outside the territory of the subject bird. Choice of a two-speaker design over a one-speaker design did not seem critical, however we favored the two-speaker design because it forced a response choice between neighbor and stranger song and because it seemed to better simulate a natural encounter. In a two-speaker playback design where neighbor and stranger songs are played to "countersing" from different speakers, the playback neighbor song might be perceived as the neighbor also responding to the unfamiliar song of their common enemy, the stranger.

METHODS

This study was conducted on a color-banded population of resident Song Sparrows in Discovery Park, a 200-ha tract of deciduous woodland and fields on the edge of Puget Sound in Seattle, Washington. We recorded repertoires in March and April 1987 and conducted playback trials during the first 2 weeks of May 1987 between 08:00 and 12:00 PST.

We wished to make our study comparable to previous studies. One concern was that birds in our sedentary population would have greater familiarity with their neighbors than birds in the migratory or semi-migratory populations tested by Harris and Lemon (1976), Kroodsma (1976), and Searcy et al. (1981). We therefore selected neighbor pairs from our banded study population where one of the males had established his territory for the first time that year.

We placed our two playback speakers 30 m apart to achieve a distinct spatial separation without exceeding the length of a typical boundary or the audible range of a normal song. This experimental geometry restricted our choice of neighbor pairs to those that shared a boundary >30 m long, with vegetation sufficiently sparse to allow observation of male responses.

From 80 banded males, we selected four neighbor pairs that met our criteria. Each pair was no closer than six territories from the next pair (ca. 0.5 km). Separation of territory pairs enabled us to use each bird as a subject, and to use one song from each as a neighbor song in one test and as a stranger song in another, thereby eliminating potential confounds with random differences in stimulus potency. Test songs were selected at random from the repertoires of the eight subjects (Fig. 1).

We recorded song repertoires with a Sennheiser RF condenser microphone MKH-816T-U and a Sony WM-D6C cassette recorder (noise reduction disabled) on 60-min metal tapes. We made every attempt to stay close to the bird during recording to minimize attenuation and degradation of sound quality. Stimuli were bandpass filtered and digitized with 12 bits resolution at 30 k samples/sec into files on computer disk. Once digitized, the stimuli were rescaled to equate loudness and edited to eliminate extraneous sounds. Stimulus tapes were made by reversing this process with a program that resynthesized songs, switched audio channels and controlled

timing. The computer system and software developed for these tasks are described elsewhere (Stoddard et al. 1988, Stoddard 1990). Songs played from the speakers were indistinguishable by ear from those of live birds. Neighbor and stranger songs were placed on separate, randomly assigned, tape tracks so that each was repeated at 10-sec intervals onset-to-onset, with a 5-sec offset between tracks. Stimulus names were encrypted on the tape boxes to eliminate experimenter bias in the field tests.

Neighbor response interference was minimized during playback by placing each amplified playback speaker (Sony APM 007AM) at the back of an open-ended plywood box lined with dry-wall and 10-cm Sonex acoustic foam. With the boxes opening toward the center of the territory and amplification set to a predetermined, realistic level, each speaker sounded like a normal Song Sparrow from anywhere in the territory (including at the other speaker) but sounded very distant when heard from behind in the neighbor's territory. When neighbor interference was anticipated, we lured the neighbor to the distant edge of his territory by playing the recorded songs of sparrows not used in the experiments.

A 3-min playback trial was begun once the subject had moved into a location in the center of his territory, roughly equidistant from the two speakers. Because most male Song Sparrows respond to intruders by approaching closely and giving threat displays or attacking, we measured a single response variable, the number of seconds that the bird spent nearest each of the two speakers after his first flight. Fifteen minutes after the first trial, we reversed the speaker cables and repeated the trial. Responses were summed for the two trials. Reversal of the cables and summation of responses cancelled any response differences due to speaker placement or amplified sound levels (peak sound levels of the playback tapes were initially set equal by the computer).

RESULTS

All eight subject males spent most of their response time closer to the speaker playing the stranger song (Fig. 2, $P < 0.005$; one-tailed sign test). The resolution of our proximity data was restricted to the number of seconds the subject was present in one of three zones of equal size: nearest L speaker, center, nearest R speaker. In practice, there were no judgement calls as the birds spent most of their time singing and calling

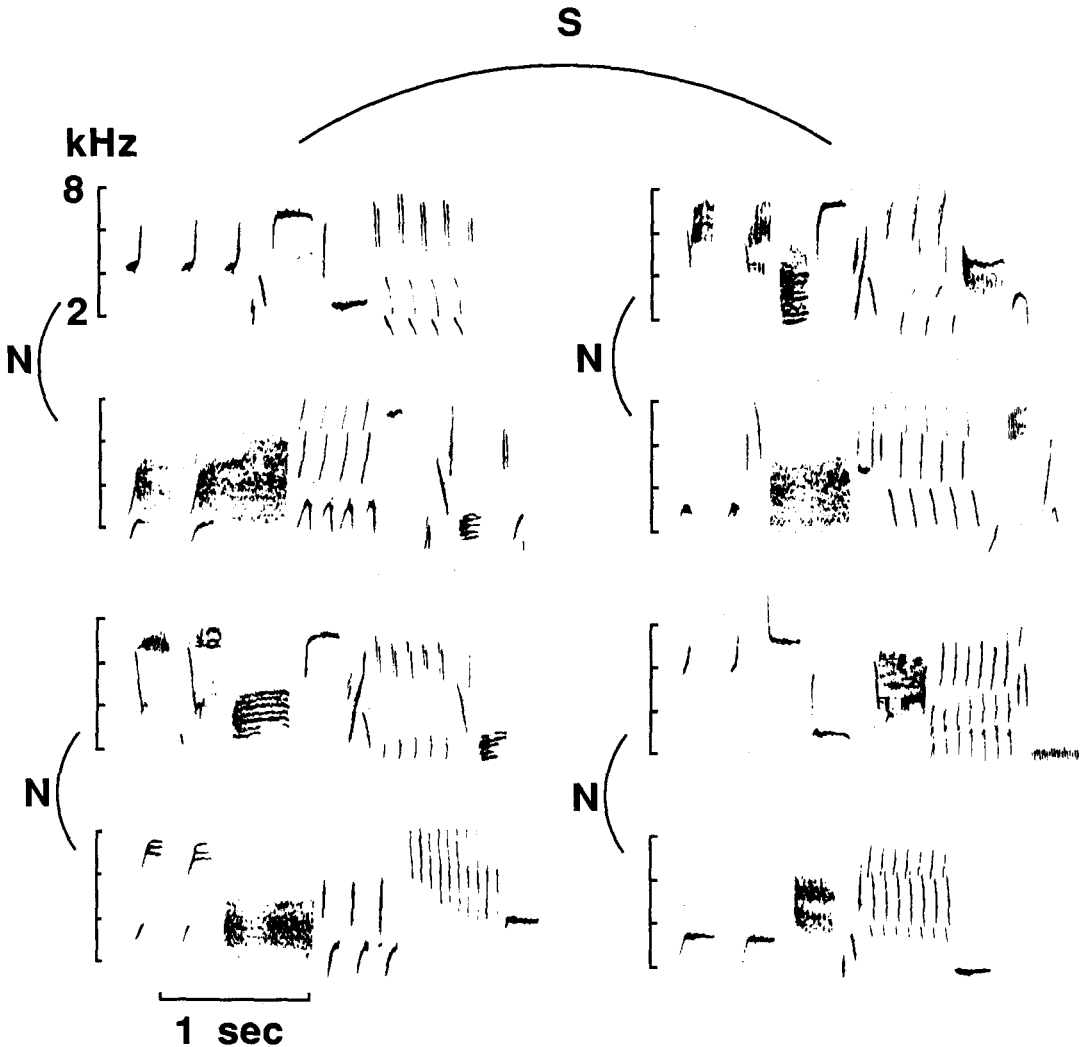


FIGURE 1. Stimuli used in experiments. S denotes a "stranger" relation, and N denotes a neighbor relation between experimental subjects. For any of the eight songs (of eight birds) shown, the bird whose song is shown received his stranger song (S) from the same row and his neighbor song (N) from the song above or below as indicated.

aggressively within 2 m of the speaker playing the stranger song, always remaining on their own side of the territory boundary. These data indicate a strong tendency of male Song Sparrows to discriminate neighbors from strangers on the boundary where the neighbor normally sings.

DISCUSSION

Although the repertoires of our subjects ranged from six to 11 discrete song types, we found strong positive discrimination based on one randomly

chosen song type from each male. This finding indicates that males attain familiarity with most or all of the song types in their neighbors' repertoires. Thus it is apparent that repertoires do not, of themselves, prevent NSD to the extent postulated by Falls (1982). Nor do these birds need to hear multiple song types in order to make this discrimination, as some have suggested (e.g., Falls 1982, Weary et al. 1987). It is still possible, of course, that although repertoires do not prevent discrimination they may require more time

to be learned and thus delay the onset of recognition.

In the year following our experiment, as part of another study, we ran an additional series of neighbor-stranger discrimination tests on birds whose territory boundaries we had monitored carefully for 3 months. This year, 1988, was marked by many territorial takeovers and insertions throughout the breeding season. Nearly all territory flux was attributable to neighbors with established territories. A post-hoc analysis showed a significant relation between territory stability and expression of NSD. Those males whose boundaries had been stable for the past 60 days showed strong NSD as expected. In contrast, males whose neighbor boundaries had changed within the past 15 days did not show NSD. Males in both groups had been neighbors for over 2 months. Thus the effect appears to be due to territory instability per se, rather than differential familiarity with neighbor song. These findings suggest that the *expression* of neighbor-stranger discrimination depends on a difference in the threat level posed by neighbors and strangers at the time of the test. We assume that discriminatory abilities are not affected by deteriorating neighbor relations. Rather, we believe that territorial instability (loss or gain) creates a condition of general defensiveness in which residents mistrust all singing males and thus do not express NSD.

Our two-speaker design may enhance the "paranoiac" response of the sparrows with unstable boundaries. Neighbor and floater Song Sparrows frequently engage in cooperative assault on a territorial male, gradually wearing him down with repeated intrusions and challenges (Arcese 1989, pers. observ.). If successful in expelling the resident from his territory, the neighbors may expand their holdings and a floater may acquire either the remainder or the territory abandoned by the neighbor. The two-speaker playback design on a territory boundary could be interpreted by a territory holder in two ways. If the territory had been stable, the neighbor song should seem like that neighbor responding to the stranger's threat to its own boundary. Alternately, if his territory had been recently challenged, the beleaguered resident might well interpret the dual playback as a dual assault on his boundary by both a neighbor and a stranger. Thus whether a resident responds exclusively to the stranger song or strongly to both neighbor and stranger

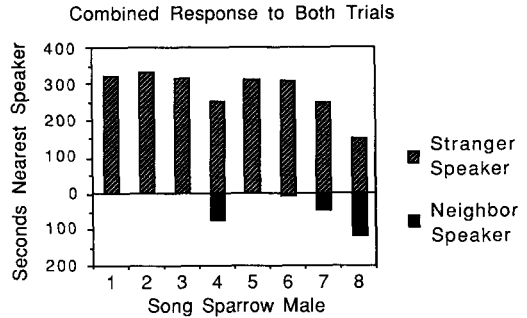


FIGURE 2. Response to the speakers playing stranger and neighbor song for the eight males tested. Note that all eight male subjects spent more time close to the speakers playing stranger song than the speakers playing neighbor song.

songs might reasonably depend on the recent history of interaction on that territory.

The Song Sparrow populations of the earlier studies in Quebec (Harris and Lemon 1976) and the Hudson Valley of New York (Kroodsmma 1976, Searcy et al. 1981) are both migratory. We attempted to simulate this feature in our 1987 experiment by choosing males who were spending their first breeding season as neighbors. Our laboratory studies suggest that Song Sparrows can learn their neighbors' repertoires in about 10 days (Stoddard, unpubl. data), and so both our birds and those of the earlier studies should have had ample time to learn neighbor songs.

There is recent evidence, however, that in at least some migratory populations, territory boundaries may be chronically unstable. In the Ontario Song Sparrow population studied by Weatherhead and Boak (1986) territory flux was the rule. For example, their males held a particular territory for only 2 months on average. In contrast, in the resident Song Sparrow populations in the Pacific Northwest most male Song Sparrows hold the same territory throughout their lives (P. A. Arcese, pers. comm.; Stoddard, unpubl. data). Where territories are in constant flux, neighbors represent a constant threat, and NSD should be difficult to demonstrate, depending as it does on neighbors being regarded as less threatening than strangers. This argument raises the possibility that territory instability may have been present in the populations of the earlier Song Sparrow studies and responsible for the reduced NSD observed in these studies. We cannot evaluate this possibility because background infor-

mation on the tested birds and their neighbors was not gathered in these earlier studies. In any case, we believe that if migratory Song Sparrow populations generally show weaker NSD than sedentary ones, the difference may be due not to weaker discriminatory abilities resulting from less listening experience, but rather to weaker expression of NSD resulting from the effects of territory instability.

Data from the Song Sparrow lead us to predict that the spatial dynamics of NSD in different species is related to the intensity of territorial interactions between neighbors. Future research should be directed to gathering comparative information on the details of male-male competition, such as the intensity of competition for territories, the frequency with which takeovers are initiated by residents vs. floaters, and the degree of territory trespassing and response to it by the resident. Such information will be needed for us to evaluate the role of male-male competition in neighbor-stranger discrimination and in the evolution of song repertoires.

ACKNOWLEDGMENTS

We thank the staff of Discovery Park for welcoming our field research. L. Beletsky, E. Brenowitz, S. Hiebert, D. Kroodsma, G. Orians, T. Quinn, W. Searcy, and K. Yasukawa commented on earlier drafts of the manuscript. This study was supported by the National Science Foundation (grants BNS-8408053 and BNS-8709854 to M. D. Beecher).

LITERATURE CITED

- ARCESE, P. A. 1989. Territory acquisition and loss in male Song Sparrows. *Anim. Behav.* 37:45-55.
- BEECHER, M. D. 1982. Signature systems and kin recognition. *Am. Zool.* 22:477-490.
- BEECHER, M. D., M. B. MEDVIN, P. K. STODDARD, AND P. LOESCHE. 1986. Acoustic adaptations for parent-offspring recognition in swallows. *Exp. Biol.* 45:179-193.
- BEECHER, M. D., AND P. K. STODDARD. 1990. The role of bird song and calls in individual recognition: contrasting field and laboratory perspectives, p. 375-408. *In* W. C. Stebbins and M. A. Berkeley [eds.], *Comparative perception*. Vol. 2. John Wiley and Sons, New York.
- DARWIN, C. 1871. The descent of man, and selection in relation to sex. Murray, London.
- FALLS, J. B. 1982. Individual recognition by sound in birds, p. 237-278. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.
- FALLS, J. B., AND L. G. D'AGINCOURT. 1981. A comparison of neighbor-stranger discrimination in eastern and western meadowlarks. *Can. J. Zool.* 59:2380-2385.
- GETTY, T. 1987. Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? *Am. Zool.* 27:327-336.
- HARRIS, M. A., AND R. E. LEMON. 1976. Response of male Song Sparrows *Melospiza melodia* to neighbouring and non-neighbouring individuals. *Ibis* 118:421-424.
- JOUVENTIN, P. 1982. Visual and vocal signals in penguins, their evolution and adaptive characters. Verlag Paul Parey, Berlin.
- KREBS, J. R., AND D. E. KROODSMA. 1980. Repertoires and territory defense. *Nature* 271:539-542.
- KROODSMA, D. E. 1976. The effect of large song repertoires on neighbor 'recognition' in male Song Sparrows. *Condor* 78:97-99.
- KROODSMA, D. E. 1983. The ecology of avian vocal learning. *BioScience* 33:165-171.
- KROODSMA, D. E. 1988. Contrasting types of song development and their consequences among passerine birds, p. 157-184. *In* R. C. Bolles and M. D. Beecher [eds.], *Evolution and learning*. Erlbaum, Hillsdale, NJ.
- RITCHISON, G. 1988. Responses of Yellow-breasted Chats to the songs of neighboring and non-neighboring conspecifics. *J. Field Ornithol.* 59:37-42.
- SEARCY, W. A., P. D. MCARTHUR, S. S. PETERS, AND P. MARLER. 1981. Response of male song and swamp sparrows to neighbour, stranger and self songs. *Behaviour* 77:152-166.
- SEARCY, W. A., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. *Annu. Rev. Ecol. Syst.* 17:507-533.
- STODDARD, P. K., M. D. BEECHER, AND M. S. WILLIS. 1988. Response of territorial male song sparrows to song types and variations. *Behav. Ecol. Sociobiol.* 22:125-130.
- STODDARD, P. K. 1990. Audio computers: theory of operation and guidelines for selection of systems and components. *Bioacoustics* 2:217-239.
- WEATHERHEAD, P. J., AND K. A. BOAK. 1986. Site infidelity in song sparrows. *Anim. Behav.* 34:1299-1310.
- WEARY, D. M., R. E. LEMON, AND E. M. DATE. 1987. Neighbour-stranger discrimination by song in the Veery, a species with song repertoires. *Can. J. Zool.* 65:1206-1209.
- WILEY, R. H., AND M. S. WILEY. 1977. Recognition of neighbors' duets by stripe-backed wrens (*Campylorhynchus nuchalis*). *Behaviour* 62:10-34.
- YASUKAWA, K., E. BICK, D. W. WAGMAN, AND P. MARLER. 1982. Playback and speaker-replacement experiments on song-based neighbor, stranger and self discrimination in male Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 10:211-215.
- YDENBERG, R. C., L.-A. GIRALDEAU, AND J. B. FALLS. 1988. Neighbors, strangers and the asymmetric war of attrition. *Anim. Behav.* 36:343-347.