

Repertoire matching between neighbouring song sparrows

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(Received 21 December 1994; initial acceptance 16 March 1995;
final acceptance 1 September 1995; MS. number: A7198)

Abstract. A male song sparrow, *Melospiza melodia*, has a song repertoire of about eight or nine distinct song types, and he typically shares several of these song types with each of his several neighbours. In the prevailing theoretical view, the song types in a bird's repertoire are interchangeable and multiple song types exist primarily to provide diversity. The present study was designed to test a contrary hypothesis concerning one particular context, counter-singing between neighbours. Specifically, the hypothesis was tested that song sparrows reply to the songs of particular neighbours with particular songs from their repertoire: they select a song type they share with that neighbour ('repertoire matching'). In a field experiment, neighbour song was played to the subject from just inside the neighbour's territory. Subjects responded with a song shared with that neighbour in 87.5% of trials (chance expectation for this sample is 42%). In control trials, where stranger song was presented from the same location, subjects responded with songs shared with the neighbour at that location in only 17% of the trials. It is suggested that 'repertoire matching' may be one advantage of a song learning strategy that produces song sharing between neighbours.

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Song is a signal by which a territorial male songbird advertises his breeding status and 'posts' his territory. Although a single species-specific song is sufficient for this purpose, in most songbird species the male possesses a repertoire of distinct song types. The function of song repertoires is a topic of considerable theoretical debate, but most theories of repertoires agree on one point: that the songs in the repertoire are interchangeable, functioning primarily to provide diversity (reviews in Krebs & Kroodsma 1980; Searcy & Andersson 1986; Catchpole 1987; Kroodsma 1988; Slater 1989; McGregor 1991). In the course of a long-term study of the song sparrow, *Melospiza melodia*, we have developed an alternative view of song repertoires that focuses on song sharing between neighbouring birds (Beecher et al. 1994). We have found that a young male song sparrow learns several songs from each of the older, established males in a

particular area. Eventually the young bird attempts to set up his own territory close to his song 'tutors', often by defending a small 'insertion' territory among the larger territories and later expanding its boundaries. Because the young bird's strategies of song learning and of territory establishment are correlated, he ends up sharing at least several song types with each of his future neighbours, both his 'tutor' neighbours, and other young birds who will have learned many of the same song types. We believe that sharing song types with his neighbours confers several advantages on the bird, and we focus here on one key advantage: it provides the bird with a mechanism for addressing or replying to a particular neighbour by singing a song type that he shares with that neighbour. We term this mechanism 'repertoire matching' because the reply song matches some song in the neighbour's repertoire. In this paper we provide evidence for such a mechanism in song sparrows.

One of the exceptions to the generalization that the bird uses the song types in his repertoire interchangeably is the case where the bird replies to a stimulus song by singing the same song type. This pattern of counter-singing has been referred

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to as 'song matching', but we will describe it as 'song type matching' (or 'type matching') to distinguish it from 'repertoire matching'. Bremond (1968) suggested that song type matching might function as a specific reply mechanism. If the singing bird is a neighbour, however, repertoire matching may be a better specific reply than type matching for three reasons. First, the bird can type-match a neighbour's song only if he has that song type in his repertoire, whereas to repertoire-match he need share only one song type with that neighbour. Second, the bird needs no knowledge of the singer to type-match, whereas he does to repertoire-match, and in this sense repertoire matching communicates 'I know who you are'. Third, if song type matching is a threat (Krebs et al. 1981), then repertoire matching may provide a mechanism for replying to a neighbour without escalating to a fight. A possibility for 'repertoire matching' is suggested by the finding that song sparrows do not type-match to neighbour song but do to self song or stranger song (Stoddard et al. 1992). This same pattern has been found in western meadowlarks, *Sturnella neglecta* (Falls 1985), and a similar pattern has been reported in great tits, *Parus major* (Falls et al. 1982).

In our study population, two neighbours share about 40% of their song types on average. Rarely does a bird share no song types with a neighbour. Figure 1 provides a representative example; it shows six song types each from the repertoires of two neighbouring song sparrows. The three song pairs in the top half of Fig. 1 are examples of the close resemblance we refer to as 'shared' types. We see this close similarity of song types only between neighbours (Beecher et al. 1994). 'Unshared' types are illustrated by any song comparison in the bottom half of Fig. 1.

In the present study we tested the hypothesis that a song sparrow will reply to the song of a neighbour from their joint territory boundary with a song type that he shares with that neighbour (repertoire matching). Thus, taking the two birds in Fig. 1 as an example, one bird could reply with a repertoire match to the other by singing any one of the top three (shared) types.

METHODS

Study Area and Subjects

Our study site is an undeveloped 3-km² park bordering Puget Sound in Seattle, Washington.

The population is resident (non-migratory), and typically about 100–150 males are on territories in a given year. Birds disperse into and out of the study population from surrounding areas. The present experiment is part of a long-term study (since 1986).

We selected as subjects 20 song sparrows who met the following conditions: (1) we had mapped the bird's territory (defined by the song posts he used); (2) we had recorded the bird's complete song repertoire; (3) we had recorded the complete song repertoire and mapped the territory of at least one of his adjacent neighbours; and (4) the subject and neighbour chosen for the test shared at least one song type. The repertoire sizes of the subjects in the experiment ranged from 7 to 11 song types (mean=9.1) and the number of songs shared with neighbours ranged from 1 to 6 (mean=3.8). We estimate that we have completely measured repertoires when we have 20 or more consecutive switches (method and rationale described in Kroodsmma 1982). In free singing, song sparrows sing their song types approximately equally often, and this is our basis for taking the reciprocal of the repertoire size as the chance expectation of singing a particular type.

The experiments were carried out over the years 1988, 1989 and 1991. Thirty-seven of the 40 tests were carried out between 23 May and 14 June (the other three were done on 10 May). These test dates are all well into the breeding season (defined here as the period from the first to last clutches), which is approximately March through June in our population. Of the 20 tests, 16 were on subject-neighbour pairs that were long-term neighbours; i.e. neighbours for at least two breeding seasons. In the four remaining tests, one or both members of the test pair were first-year birds.

Playback Procedure and Conditions

In an experimental trial, we played one song of the selected neighbour to the subject at the normal territory boundary, with the playback speaker placed 1–2 m inside the neighbour's territory. The playback speaker faced out of an acoustical baffle box which reduced sound spread to the back of the speaker, and thus made interference from neighbours less likely. If the neighbour was nearby, however, one experimenter lured him to

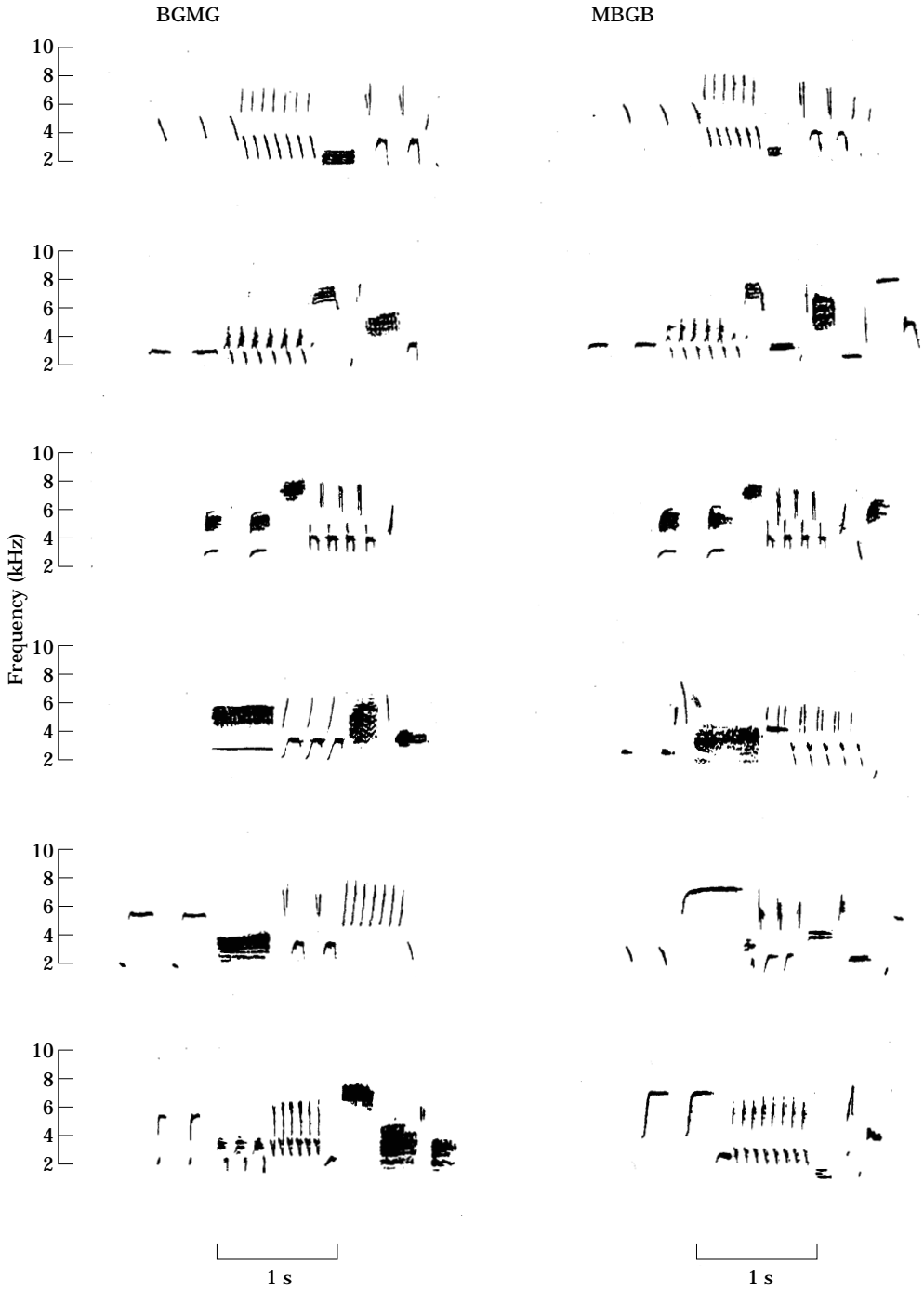


Figure 1. Left column shows 6 of the 11 song types of bird BGMG; right column shows 6 of the 9 song types of his neighbour MBGB. The top three rows show shared songs, the bottom three rows unshared songs. Spectrograms made on a Kay DSP-5500 Sonagraph. Bandwidth=117 Hz. Frequency scale 2–10 kHz, markers at 2-kHz intervals, time marker 1 s.

Table I. Does bird reply with 'repertoire match' to stimulus song?

Subject	N song types	N shared songs	Stimulus song		
			Neighbour shared song	Neighbour non-shared song	Stranger song
BGMG	11	5	No	—	—
BYMG	10	5	Yes	—	—
MBGB	9	5	Yes	—	—
GBMB	11	5	Yes	—	—
BBMB	11	3	Yes	—	—
RGMG	7	2	Yes	—	—
MGBB	10	5	Yes	—	—
MBGG	9	1	—	Yes	No
BMGB	7	2	—	Yes	No
RMR Y	8	2	Yes	—	No
RMYY	10	5	Yes	Yes	No
BBRM	7	5	Yes	Yes	No
BMRR	8	4	No	Yes	No
YBRM	10	5	Yes	Yes	No
MRGY	10	6	Yes	Yes	No
MYOO	10	6	Yes	No	Yes
RBMC	7	4	Yes	Yes	No
MRGK	10	4	Yes	No	No
PMRG	8	4	Yes	Yes	Yes
MPX	9	4	—	Yes	—
Proportion of neighbour matches			0.88	0.83	0.17

the back of his territory with playback song (a stranger song) for the duration of the trial (this song could not be heard at the location of the actual experiment).

The playback song was repeated every 10 s for 3 min. We recorded all songs that the subject sang during the trial and for 3 min afterwards. A subject usually sang the same song type throughout this period, but if he switched to a new song type, we counted the second one as his response. We ran three kinds of trials, counterbalanced across different days (not all birds were tested in all 3 conditions). The stimulus song was either (1) a shared neighbour song, $N=17$, (2) a non-shared neighbour song, $N=12$, or (3) a stranger song, $N=12$. Stranger song that did not closely resemble any song in the subject's repertoire served as a control condition. The stranger song was played to the subject from the standard location in the neighbour's territory. Each of the stranger songs was used also for a different subject as a neighbour song. We randomized the order of presentation of the three types of songs.

RESULTS

Birds replied to the neighbour stimulus song with a 'repertoire match' on 87.5% of the trials (Table I, each of the 20 subjects received equal weight in this calculation). We estimated the probability that the bird randomly chose a song type from his repertoire that matched a song type of his neighbour as the number of songs the bird shared with that neighbour divided by the total number of songs in the bird's repertoire. For the 20 birds in this sample, this chance expectation is 42% (3.8 shared song types per 9.1 song types in the repertoire). The observed 87.5% rate of repertoire matching is significantly higher than this chance expectation ($z=4.09$, $P<0.00003$).

It did not matter whether the neighbour stimulus song itself was shared. Of the 12 birds presented with an unshared neighbour stimulus song, 10 responded with a repertoire match (83%, $z=2.48$, $P<0.007$). Of the 17 birds presented with a shared stimulus song, 15 responded with a repertoire match (88%, $z=3.33$, $P<0.0004$). On

these trials with shared song, the subject had the opportunity to respond with the same song type (song type matching). In fact, however, only one bird of the 17 did so, which is less than the chance level (1/9.1), although not significantly so.

Of the 12 birds tested with stranger (control) song played from the neighbour's territory, only two (17%) responded with a song from the 'repertoire match' class, which is not only less than the rate in response to neighbour song (87.5% for these 12 birds, $z=3.46$, $P<0.0003$) but actually less than the expected chance level (46% for these 12 birds, $z=-2.05$, $P<0.04$). That is, the birds did not respond with repertoire matches to just any song heard from the neighbour's territory: the stimulus song had to be one of the songs of that neighbour.

DISCUSSION

Our playback experiment indicates that a song sparrow uses his song types selectively when replying to the song of a neighbour, choosing his reply from the subset of song types he shares with that neighbour. Moreover, the bird may actually avoid using songs he shares with the neighbour when replying to a stranger song, i.e. 'save' the neighbour-shared types for the neighbour. The present study thus extends our earlier demonstrations of neighbour recognition in song sparrows (Beecher & Stoddard 1990; Stoddard et al. 1990, 1991) to show that a bird's knowledge of his neighbours' repertoires forms the basis of a dynamic mechanism for long-distance communication between territorial neighbours.

Repertoire matching is a possible form of long-distance communication only if neighbours share song types. In our song sparrow study population, song sharing occurs because the young male learns his songs from three to four neighbouring territorial males, preferentially retains 'tutor'-shared types, and subsequently sets up his territory next to or among these 'tutor'-neighbours and other young birds who have done the same thing (Beecher et al. 1994). A high level of song sharing between neighbours has been observed in at least one other resident song sparrow population (Nielsen & Vehrencamp, in press). Comparable analyses have not been done for migratory populations, although Kramer & Lemon (1983) noted an apparently lower level of song sharing in

an Ontario population they studied (usually fewer than four shared types, average of one). We have two caveats about song sharing and the possibilities for repertoire matching in different populations. First, only one shared type is required for repertoire matching. Second, song sharing is not necessarily less in a migratory population than in a resident population (as is often assumed). If birds learn their songs following dispersal (as generally seems to be the case; review in Slater 1989), then sharing between neighbours will be high so long as birds return to the area where they learned their song types after migration, or retain the ability to learn or modify their songs into the spring following return from migration. With regard to the first pattern, in at least some migratory species, first-year breeding males return to the area to which they dispersed in their hatching summer, which is presumably where they learned their song types (review in Morton 1992). With regard to the second pattern, in some species, a bird's song repertoire may not crystallize until his first breeding season, following return from migration (e.g. indigo buntings, *Passerina cyanea*, and field sparrows, *Spizella pusilla*; Payne et al. 1987, 1993; Nelson 1992). Furthermore, in some species a male may add or drop song types in subsequent breeding seasons (e.g. great tits: McGregor & Krebs 1989; American redstarts, *Setophaga ruticilla*: Lemon et al. 1994; European starlings, *Sturnus vulgaris*: Mountjoy & Lemon 1995). The net effect in both cases is to increase song sharing with new neighbours.

A tendency to repertoire-match may provide a partial explanation for why song type matching rates are generally lowest when the stimulus song is a neighbour song compared to when it is either self song or stranger song. For example, earlier studies have shown that song sparrows type-match neighbour song at chance levels, while type matching self song or stranger song at much higher levels (McArthur 1986; Stoddard et al. 1992); the same pattern of results has been found for western meadowlarks (Falls 1985). The results of the present study suggest that a song sparrow does not reply to neighbour song with the same song type, even when he has it, because he instead replies with another song type he shares with that neighbour.

Why does a song sparrow type-match to playback of stranger song (if he has a similar enough type) or of his own song but repertoire-match to

a neighbour's shared song type? A hypothesis suggested earlier is that this difference in response may reflect a difference in perceived threat levels of these interchanges (Krebs et al. 1981): type matching may represent a stronger reply than repertoire matching (while repertoire matching is a more specific reply than non-repertoire matching, and of course a stronger reply than not singing at all). The failure to type-match neighbour song in this and earlier studies of song sparrows may be related to the fact that a neighbour's song was broadcast from the neighbour's territory. Perhaps counter-singing in this circumstance functions to confirm or preserve the territorial status quo. In the present study, most of the birds were long-term neighbours (2 or more years) and the tests were done well into the breeding season. In contrast, vocal interchanges with strangers may represent a more threatening situation (and self song is probably perceived as from a stranger, or perhaps worse yet, as a neighbour outside his normal territory). To examine the hypothesis that type matching is a stronger reply than repertoire matching, we have recently completed a playback experiment comparing a bird's response to neighbour song early in the spring, when territory boundaries are being established, versus later in the season. We have found that early in the season, birds respond to neighbour song with type matches, whereas later in the season they respond to these same songs with repertoire matches (S. E. Campbell, J. M. Burt, J. C. Nordby, C. E. Hill & M. D. Beecher, unpublished data).

ACKNOWLEDGMENTS

We thank Patti Mulligan for assistance in the field, and Les Beletsky, Eliot Brenowitz, Don Kroodsma, Patricia Loesche, Doug Mock, Patricia Schwagmeyer, Editor Meredith West and two anonymous referees for comments on the manuscript. This work was presented at the ABS Annual Meeting, June 1992. The research was supported by grants from NSF to M.D.B.

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