ANIMAL BEHAVIOUR, 2005, **69**, 189–196
doi:10.1016/j.anbehav.2004.02.019

Partial song matching in an eastern population of song sparrows, *Melospiza melodia*

RINDY C. ANDERSON*, WILLIAM A. SEARCY* & STEPHEN NOWICKI†
*Department of Biology, University of Miami, Coral Gables, Florida
†Department of Biology, Duke University, Durham, North Carolina

*(Received 5 May 2003; initial acceptance 7 August 2003;
final acceptance 9 February 2004; published online 23 November 2004; MS. number: A9604R)*

One hypothesis for the function of vocal repertoires in songbirds is that singing multiple song types facilitates song matching, a behaviour in which one male replies to a rival's song with a song of the same type. In eastern populations of song sparrows, low levels of whole song sharing restrict opportunities for matching of entire song types. A male in this population might still match a neighbour by replying with a partially shared song (i.e. a song that contains one or more phrases in common with the neighbour's song). We tested for partial matching in a Pennsylvania population using playback of three categories of song: self song (allowing a full match), stranger song (a control allowing no match) and hybrid self/stranger song (allowing a partial match). We also tested the hypothesis that matching is a directed signal of aggressive intentions by comparing subjects' approach distances between trials in which they did and did not match. Males in our study matched in response to both self song (21 of 39 trials) and hybrid song (23 of 40 trials) at levels significantly greater than expected based on control trials (5 of 40 trials). Males that performed a partial match to a hybrid song approached the speaker more closely than males that did not match, consistent with the hypothesis that partial matching is a directed signal of aggression. Self song matching did not predict approach as successfully.

A common feature of aggressive signalling systems is the ability to direct a signal to a particular rival (see Andersson 1994; Bradbury & Vehrencamp 1998). In contrast to conspicuous display signals, which may advertise signaller status, resource ownership and defence ability to all potential competitors (e.g. Davies & Halliday 1978; Fugle et al. 1984), directed signals can convey information about aggressive motivation and likely intentions to specific receivers (e.g. Nelson 1984; Capp & Searcy 1991). During close-range contests, postural and other visual displays can be directed at specific individuals. Examples include the head forward display in birds (reviewed in Hurd & Enquist 2001), and teeth baring in some canids (Fox 1971) and primates (Estes 1991). Agonistic olfactory signals also can be directed at particular rivals by spraying or by waving scent-marked body parts, as has been described in ringtailed lemurs, *Lemur catta* (Jolly 1966). In acoustic signalling systems, a common means for directing signals to a particular rival is the immediate reply to the rival's signal with the same signal type, a behaviour termed 'matching' (Brémond 1968; reviewed in Catchpole & Slater 1995; Bradbury & Vehrencamp 1998). Matching is best known in birds but also occurs in frogs (e.g. Narins et al. 2000).

Song matching, in which a male bird replies to a rival's song with an acoustically similar song, occurs during bouts of countersinging between males in many songbird species. The most obvious cases of song matching occur when males of species having song repertoires countersing with an exactly matching song type they share in common ('type matching'), as has been shown to occur in northern cardinals, *Cardinalis cardinalis* (Lemon 1968), great tits, *Parus major* (Krebs et al. 1981; Falls et al. 1982), western meadowlarks, *Sturna neglecta* (Falls 1985), tufted titmice, *Baeolophus bicolor* (Schroeder & Wiley 1983) and song sparrows (Stoddard et al. 1992; Beecher et al. 2000a), among others.

In western populations of song sparrows, males not only perform song type matching when they interact (Stoddard et al. 1992; Beecher et al. 2000a; Burt et al. 2001), but also show a more complex matching behaviour referred to as 'repertoire matching' (Beecher et al. 1996).

Correspondence: R. C. Anderson, Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, FL 33124-0421, U.S.A. (email: rindy@bio.miami.edu). S. Nowicki is at the Department of Biology, Duke University, Box 90325, Durham, North Carolina 27708-0325, U.S.A.

0003–3472/04/$30.00/0

In repertoire matching, a male replies to an opponent using a song type that differs from the one just sung by the opponent, but which the two birds nevertheless share in common in their repertoires (Beecher et al. 1996). Clearly, both type matching and repertoire matching require that interacting males share at least some complete song types, and the ability of males to engage in these behaviours increases as the number of song types they have in common increases. In western populations that have been studied, estimates of song type sharing among neighbouring song sparrow males range from 21% to 40% (Beecher et al. 1996; Hill et al. 1999; Wilson et al. 2000).

The occurrence of song type sharing and song matching can be quite different in other song sparrow populations. In a Pennsylvania population, for example, Hughes et al. (1998) found that neighbouring males shared on average only 3% of their repertoires with a given neighbour, and most neighbours (81%) shared no song types at all. Sharing of whole songs was also low between nonadjacent neighbours. Hughes et al. (1998) suggested that low song sharing in the Pennsylvania population probably precludes song matching in most cases. Such need not be the case, however, if matching in vocal interactions can occur with songs that are similar in some dimensions, even if they are less than completely identical (Krebs et al. 1981; Hill et al. 1999; Beecher et al. 2000a; Burt et al. 2001, 2002). Work with one western population of song sparrows has demonstrated this possibility, showing that males perform 'partial matching' by replying with songs that share a subset of identical phrases (Horning et al. 1993) and 'broad-sense' song matching by replying to nonshared songs with songs containing acoustically similar cadences or phrases (Burt et al. 2002). Song sparrows in Pennsylvania share parts of songs, such as trills and note complexes, more commonly than they share whole songs (Hughes et al. 1998). Sharing of introductory trills, in particular, occurs at substantial frequencies, both between immediate neighbours and more distant birds, which suggests that partial matching via shared introductions is a possible signalling strategy.

Song type matching is assumed to function in male–male competition. Brémond (1968) originally proposed the hypothesis that type matching serves as a mechanism for addressing a signal to a specific rival (the 'addressing hypothesis'), thereby facilitating interactions among competing males. Krebs et al. (1981) expanded on this idea by proposing that type matching functions as a graded signal of aggression, with the occurrence of matching signalling a higher likelihood of attack to a specific rival (the 'threat hypothesis'). Krebs et al. (1981) predicted that if matching is a signal of aggression, then (1) type matching should be associated with other strongly aggressive behaviours, such as close approach and threat displays, and (2) type matching should be more prevalent early in the breeding season, when neighbouring males engage more frequently in territory boundary disputes. Results of a playback experiment on western song sparrows by Vehrencamp (2001) supported the first prediction, in that males that type-matched spent more time in close proximity to the playback speaker than did males that did not match. Beecher et al. (2000a), however, found no difference in aggressive response between males that did and did not match in another western population. The second prediction has been addressed by Beecher et al. (2000a) with western song sparrows. Type-matching responses by new neighbours are significantly higher early in the breeding season (April) than late (June).

Our principal goal in this study was to determine whether song sparrow males in an eastern population, where whole song sharing is rare, are capable of using partial song matching using songs with shared introductions. Our second goal was to ask whether partial matching, if it does occur, serves as a signal of aggression as proposed for whole song type matching. To these ends, we performed playbacks of three song categories to territorial male song sparrows from the same Pennsylvania population as studied by Hughes et al. (1998). The playbacks were designed to simulate an intrusion by a distant neighbour or stranger male. The three song categories were: (1) 'self song,' which was a song selected from the repertoire of a given subject male, and thus a song to which the subject could respond with a complete type match; (2) 'stranger song', which was a song recorded from a distant male and allowed no match; and (3) self/stranger 'hybrid song', created by substituting the introductory phrase of a self song for the introduction of a stranger song, thus allowing the subject to partial match by replying with the source self song. Song sparrow songs typically consist of three or more phrases, in an alternating series of trills and note complexes. We used introductory phrases as shared song elements between self and hybrid songs in part because sharing of introductions is common in this population (Hughes et al. 1998), and in part because there is evidence to suggest that introductory phrases are particularly salient to song type classification by male song sparrows (Horning et al. 1993).

METHODS

We conducted playback trials from 16 May to 3 July 2002, between 0700 and 1030 hours. Our subjects were 46 adult male song sparrows holding territories on State Gamelands 213 and 214 and Pymatuning State Park, all in Crawford County, Pennsylvania, U.S.A. The subjects defended territories around the perimeter of fields and lawns, singing from trees and shrubs in hedgerows and interacting principally with neighbours on either side.

We tested males for song type matching and partial matching using three categories of experimental stimuli (Fig. 1): (1) 'self song' was a song type recorded from the subject male himself; (2) 'stranger song' was a song type recorded from a male at least 2 km away; and (3) 'hybrid song' was a song type created by replacing the introductory trill of a stranger song with the introductory trill from a self song. Males could perform a partial match to hybrid song because it contained the introductory phrase from one of their own song types.

Use of self song for matching experiments would be suspect if male song sparrows were able to identify self songs as their own and consequently responded to self songs as unnatural stimuli. For some other songbird

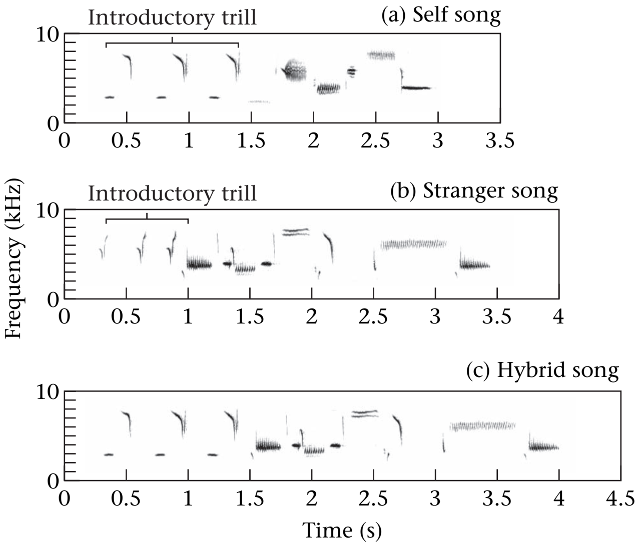

Figure 1. Examples of the three playback categories presented to each subject. Hybrid songs (c) were constructed by removing the introduction of a stranger song (b) and replacing it with the introduction of a self song (a).

species there is evidence that males discriminate self and stranger songs, showing lower aggressive response to self song than to stranger song (Brooks & Falls 1975; Searcy et al. 1981; Yasukawa et al. 1982). Response to self song in these species, however, tends to be higher than response to neighbour song, which suggests that self songs are treated as being of intermediate familiarity rather than as being unnatural. In song sparrows, the response of males to self song is no different than response to stranger song, both in terms of matching (Stoddard et al. 1992) and aggression (Searcy et al. 1981). Moreover, song sparrows seem to recognize songs of particular individuals by learning the details of each song type, rather than by learning a 'voice quality' common to all (Beecher et al. 1994; Searcy et al. 2003). Without the ability to recognize voice quality, a self song ought to be perceived as a fully shared stranger song. Burt et al. (2002) have also suggested that male song sparrows probably perceive self song as stranger song. Use of self song in matching experiments with song sparrows has an advantage over the alternative of using a similar song type recorded from a different bird in that the experimenters need not make subjective judgements about what stimuli do and do not match a subject's songs. Self song has a further advantage over the use of neighbour song as a playback stimulus in that responses are not confounded by a subject's past interactions with the source male.

We recorded males singing on their territories using a Sony TCM-5000EV tape recorder and a Realistic 33-1070B microphone in a Sony PBR-330 parabola. Each male was recorded until we had clear recordings of five to six song types in his repertoire. It was not necessary to record each male's full repertoire because we chose as our measure of the expected chance probability of matching the proportion of trials where the focal self song was sung in response to stranger song playback (e.g. Stoddard et al. 1991), rather than measures based on the reciprocal of the repertoire size (e.g. Krebs et al. 1981; Beecher et al. 1994, 2000a; Burt et al. 2001).

All songs were digitized at 22 050 points/s and 16-bit resolution, and examined spectrographically at a 172.3-Hz frequency resolution and a 5.8-ms time resolution using the Syrinx-PC sound analysis program (John Burt, http://www.syrinxpc.com). From the five to six song types recorded from each male, a good exemplar of one song type was chosen as a focal song to be used as the self song playback stimulus for that individual. Criteria for selecting self songs were (1) that we had a clear recording of the song type, with low background noise and no extraneous sounds, and (2) that the focal self song did not have a first phrase that was similar to any other recorded song type in the bird's repertoire. Thus, if two recorded songs in the bird's repertoire began with a similar trill or note complex at roughly the same acoustic frequencies, neither song was chosen as the focal self song.

Males separated by at least 2 km were defined as strangers and paired such that one song from a given bird's repertoire was used as the self song for that bird and as the stranger song for the other bird in the pair. Because we did not record full repertoires from each male, we could not be sure that a subject's repertoire did not include the stranger song type. Males in our song sparrow population rarely share whole songs, but they do commonly share parts of songs, making it possible for a pair of males to each have song types with the same introductory phrases. To reduce the likelihood that a male could match a stranger song with a song having a shared introduction, we checked the five to six song types recorded from both males in a pair and excluded any types that had shared introductions from consideration as stranger playback songs. Because the five to six song types compared for paired males represent 63–75% of the population mean repertoire size (8 song types), we were fairly confident that subject males would not be able to match in response to stranger songs. As an additional precaution, however, we compared each subject's song responses to the stranger playback song to check for partial matching using an unrecorded song type (see Results).

Hybrid songs were constructed by digitally cutting and pasting song segments using Signal software (Engineering Design, Belmont, Massachusetts, U.S.A.). Each hybrid song was examined carefully for artefacts that may have resulted from digital splicing (e.g. clicks resulting from waveform discontinuities, excess spacing between elements, etc.). Our prior work has shown that such manipulations do not affect the response of male song sparrows to song (Searcy et al. 2003). To ensure that amplitude did not vary greatly between playback stimuli or between the components of hybrid songs, song files were normalized to a common amplitude (by scalar multiplication of the digital source files) before other manipulations were done. An example of a hybrid song is shown in Fig. 1, together with the self and stranger songs from which it was derived. Playback stimuli were recorded directly to tape from digitized files.

Playbacks were performed using a Sony TCM-5000EV recorder and an Acoustics Research Powered Partner speaker/amplifier. The playback speaker was placed on the ground, face up, near the centre of the subject's territory and in close proximity to one or more bushes in a hedgerow. One of us (R.C.A.) ran the trial and recorded data from a distance of approximately 15 m. Each playback consisted of one song type (self song, stranger song, or hybrid song) presented at 10-s intervals (3-min total duration), broadcast at approximately 85 dB sound pressure level, SPL (measured at 1 m). We recorded the subject's song replies continuously through a 5-min preplayback period, a 3-min playback period and a 2-min postplayback period, using a Sony TCM-5000EV recorder and a Realistic 33-1070B microphone in a Sony PBR-330 parabola. The subject's distance to the speaker was recorded at 10-s intervals throughout the entire trial, with markers placed at 2, 4, 8 and 16 m on either side of the speaker to aid in distance estimation. Distances were binned into five categories (0–2 = 1 m, 2–4 = 3 m, 4–8 = 6 m, 8–16 = 12 m, > 16 = 24 m) following the method of Peters et al. (1980), and averaged across the 3-min playback periods and across the 2-min postplayback periods. Subject males received the three playback types in random order, with each playback separated by at least 48 h.

We conducted 39 self playbacks, 40 hybrid playbacks and 40 stranger playbacks for a total of 119 playbacks to 46 males. Different self, hybrid and stranger songs were used in each trial. Thirty-four of the 46 males were tested with all three playback types. Twelve additional males were tested with only one or two of the playback types to bring the number of trials for each stimulus type as close to 40 as possible. Not all males were tested with all three playback types because several trials had to be cancelled or excluded from the analysis. Trials were cancelled or excluded for one of the following reasons: (1) the subject sang the focal self song during the pretrial period, (2) the subject male was not detectable on his territory at any point during the trial, (3) neighbour interference occurred, or (4) human disturbances such as mowing disrupted the trial.

Song matching was determined by visual assessment of spectrograms using Syrinx-PC (1–10-kHz analysis bandwidth, 172.3-Hz frequency resolution, 5.8-ms time resolution). If the subject male did not sing during the 5-min preplayback period, then the first song he sang following the start of playback was considered his response to the playback stimulus. If the subject sang during the preplayback period, the first song type he switched to during playback was considered his response. We defined the level of self song matching as the proportion of focal males that replied to self song playback by matching with the focal self song. We defined the partial matching level as the proportion of males that replied to hybrid song playback by matching with the focal self song. We used the proportion of males that replied to stranger song playback with the focal self song as the control matching level. Using the replies to the stranger song to define the random expectation of replying with the focal self song is superior to using the reciprocal of the population mean repertoire size in that the former procedure controls for the possibility that not all song types are sung with equal frequency.

We used a 2 × 3 contingency test to compare matching responses across the three playback types, and then used chi-square tests with a Bonferroni adjustment of alpha to make the following three comparisons: (1) control matching level versus focal self song matching level; (2) control matching level versus partial matching level; (3) focal self song matching level versus partial matching level. Thirty-six birds were tested with both self song and hybrid song, and thus were given two opportunities to match. If some individuals are consistent matchers and others are consistent nonmatchers, then we would expect many individuals to match on both opportunities or on neither, and few individuals to match on one opportunity and not the other. We used a 2 × 3 contingency test to examine matching consistency by comparing the frequency of matching responses during both opportunities, neither opportunity, or during one opportunity but not the other, to frequencies expected by chance.

Our measures of aggressive response were the subject's mean distances to the speaker during the 3-min playback period and during the 2-min postplayback period. We used the Friedman ANOVA for overall comparisons of approach distances during self, hybrid and stranger 3-min playback and 2-min postplayback periods, confining this analysis to the 34 subjects that were tested with all three stimuli. We used Mann–Whitney *U* tests (two-tailed) to compare the distance values for the playback and postplayback periods between males that matched playback and those that did not match.

To examine the frequency of matching responses over the course of the season (16 May–3 July), we calculated the number of trials where the response was a match divided by the total number of self and hybrid trials performed for each 5-day period (Krebs et al. 1981). For example, between 16 and 20 May we performed three focal self and two hybrid trials (five total), and four of these resulted in a matching response, so the 'matching proportion' for 16–20 May was 4/5 or 0.8. We then performed a correlation between the matching proportion and the first day of each 5-day period. We performed a similar procedure for the speaker approach data to test whether aggressive response declined over the season.

RESULTS

Matching Responses

Birds replied to playback with the focal self song in 21 of the 39 self song playback trials (53.4%), in 23 of the 40 hybrid song playback trials (57.5%), and in five of the 40 stranger song playback trials (12.5%). The probability of singing the focal self song differed significantly across the three playback types (contingency test: $\chi^2_5 = 20.57$, $P < 0.001$). Pairwise comparisons revealed that the frequencies of replying with the focal self song were significantly greater in response to playback of self song and hybrid song than to playback of stranger song (chi-square test: self versus stranger: $\chi^2_1 = 15.29$, $P < 0.0001$; hybrid versus stranger: $\chi^2_1 = 17.80$, $P < 0.0001$; $\alpha = 0.017$ with Bonferroni adjustment). The frequency of replying with the focal self song did not differ between self song and hybrid song playbacks (chi-square test: $\chi^2_1 = 0.11$, $P = 0.744$). In no case did a subject perform a partial match to a stranger song using a song type that we had not recorded.

Thirty-six birds were tested with both self song and hybrid song, and thus were given two opportunities to match. Matching response patterns did not deviate from chance expectations (contingency test: $\chi^2_2 = 0.11$, $P = 0.944$; Table 1). Thus, whether a subject matched on one opportunity did not predict whether it would match on its other opportunity. This result cannot be explained by a seasonal decline in matching response (see below), because birds that matched in one playback and not the other (17 of 36 subjects) were no more likely to match on the first opportunity (eight individuals) than on the second (nine individuals).

Approach Response

There were no differences overall in mean distance (m) to the speaker during 3-min playbacks of self, stranger and hybrid songs ($\bar{X} \pm$SE distance: during self playbacks = 3.69 ± 0.64 m; during stranger playbacks = 4.22 ± 0.53 m; during hybrid playbacks = 4.31 ± 0.63 m; Friedman ANOVA: $\chi^2_2 = 4.28$, $N = 34$, $P = 0.118$), nor during 2-min postplayback periods (self playbacks = 4.16 ± 0.64 m; stranger playbacks = 4.94 ± 0.84 m; hybrid playbacks = 4.29 ± 0.64 m; Friedman ANOVA: $\chi^2_2 = 0.11$, $N = 34$, $P = 0.947$).

There were no differences when distances for birds that matched or did not match to the focal self playback were averaged over the 3-min playback period only (Mann–Whitney U test: $U = 168.5$, $N_1 = 18$, $N_2 = 21$, $P = 0.564$; Fig. 2). However, subjects that matched the hybrid playback were on average closer to the speaker during the 3-min playback period than subjects that did not match ($U = 109.0$, $N_1 = 17$, $N_2 = 23$, $P = 0.018$; Fig. 2). There were no differences when distances were averaged over the 2-min postplayback periods and compared for birds that matched or did not match to self playbacks (match self = 4.93 ± 0.89 m; no match self = 3.78 ± 0.72 m; $U = 155.0$, $N_1 = 21$, $N_2 = 18$, $P = 0.338$), nor for birds that matched or did not match to hybrid playbacks (match hybrid = 4.27 ± 0.75 m; no match hybrid = 3.88 ± 0.83 m; $U = 183.5$, $N_1 = 23$, $N_2 = 17$, $P = 0.743$.

Table 1. Consistency in matching response to hybrid and focal self song

	Matched to hybrid and self song	Matched to neither hybrid nor self song	Matched to either hybrid or self song
Observed	11 (0.31)	8 (0.22)	17 (0.47)
Expected	11 (0.31)	7 (0.20)	18 (0.50)

Thirty-six birds received both hybrid and self playbacks. Values are the observed numbers (and proportions) of subjects that gave a matching response to one, both, or neither of the playback categories and the numbers expected if individuals show no consistency.

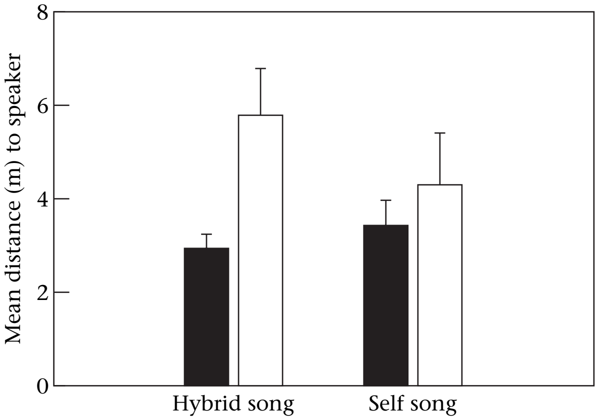

Figure 2. Distance (m) between subjects and the playback speaker during 3-min playback periods. ■: mean distances during trials when subjects sang the focal self song in response to self and hybrid playbacks (matching trials); □: mean distances during trials when subjects did not sing the focal self song (nonmatching trials). Responses to focal self playback: 21 match responses, 18 no match responses; hybrid playback: 23 match responses, 17 no match responses. Values are mean ± SE.

Seasonal Change

A correlation between the proportion of matching responses and the first day of each 5-day period between 16 May and 3 July revealed that matching responses became less frequent over the course of the season (Pearson correlation: $r_8 = -0.797$, $P = 0.006$; Fig. 3). We also found a significant positive relationship between the mean distance to the speaker during trials and trial date, demonstrating a decline in aggressive response over the season (Pearson correlation: $r_8 = 0.758$, $P = 0.011$; Fig. 4).

DISCUSSION

When presented with a song type from their own repertoire (‘self song’) during playback, male song spar-

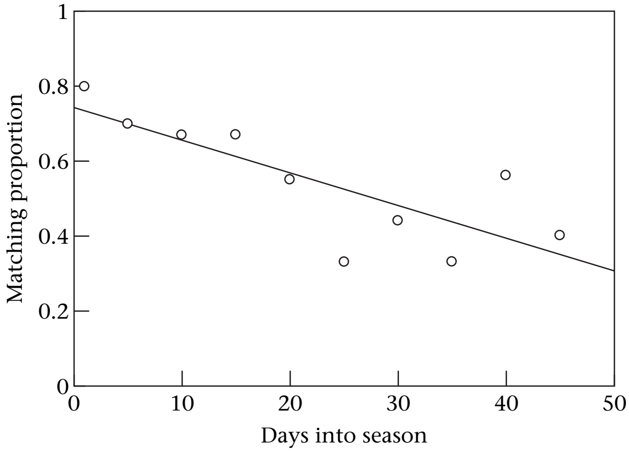

Figure 3. Seasonal decline in matching response. Trials were arbitrarily divided into 5-day blocks. Data points are proportions of trials in which the birds matched during each 5-day block.

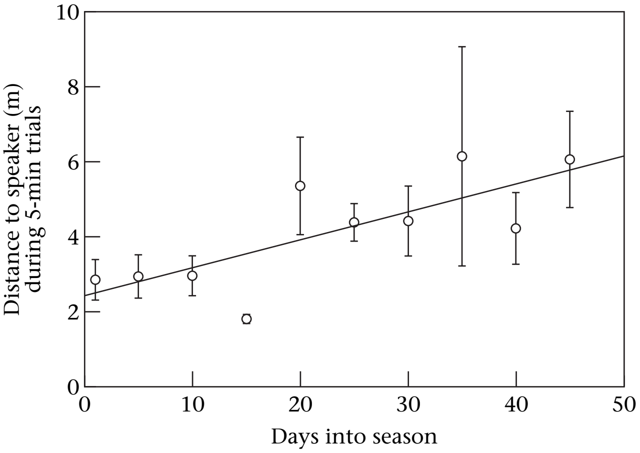

Figure 4. Increase in mean approach distance to the playback speaker over the study period 16 May–3 July. Trials were arbitrarily divided into 5-day blocks. Mean distances were calculated for each trial (combined 3-min playback and 2-min postplayback), then averaged over each 5-day block. Data points are 5-day mean values ± SE.

rows in our Pennsylvania population responded by matching that song type significantly more often than expected by chance. Males also responded with a matching song type significantly more often than chance when played a hybrid song to which they could make a partial match. There was no significant difference in the level of matching in response to a wholly shared song type or a partially shared song type. Subjects rarely overlapped playback, and never overlapped the first playback song of a self or hybrid trial, so the similar matching levels to self and hybrid playbacks cannot be attributed to subjects beginning their matching response before hearing the entire playback song. These results support the idea that the sharing of parts of songs rather than of whole song types is sufficient to allow song matching to play a role in interactions between males (Burt et al. 2002).

In several west coast populations of song sparrows, neighbouring males tend to share a large number of entire song types in common (Beecher et al. 1994; Hill et al. 1999; Wilson et al. 2000), probably as the result of a song learning strategy whereby males copy whole song types from tutor males (Beecher et al. 1994, 1996). This high level of whole song sharing among neighbouring males allows for the occurrence of both type matching (Stoddard et al. 1992) and repertoire matching (Beecher et al. 1996) in male–male interactions. By contrast, males in our Pennsylvania population appear to copy and recombine parts of songs to create their own adult songs (Hughes et al. 1998), paralleling the learning pattern found in laboratory studies of eastern song sparrows (Marler & Peters 1977, 1988). As a result, neighbouring males share parts of their repertoires as discrete song phrases rather than as whole songs. This song learning pattern reduces opportunities for the matching of entire song types (Hughes et al. 1998), but our present results demonstrate that males in this population none the less could interact using complex matching patterns via partial matching.

Krebs et al. (1981) originally suggested that birds that do not share exactly matching song types might still match using songs that are similar in some way. For example, species that produce single song types can respond to particular rivals by adjusting the pitch of their songs to match the rival's song ('frequency matching'), as has been shown in Kentucky warblers, *Oporornis formosus* (Morton & Young 1986), black-capped chickadees, *Poecile atricapillus* (Otter et al. 2002), and nightingales, *Luscinia megarhynchos* (Naguib et al. 2002). Partial matching is another alternative to song type matching. Naguib et al. (2002) recently showed partial matching of whistle songs in the nightingale. Subjects responded to playback of conspecific whistle songs with their own whistle songs at greater than chance levels, and often matched either the whistle component only, or the entire whistle song type. Horning et al. (1993) first showed partial matching in Washington song sparrows using playback of hybrid songs, and Burt et al. (2002) recently demonstrated 'broad-sense' matching in the same Washington population. We now have shown that eastern song sparrows are able to use partial matching in vocal interactions. These results suggest that matching interactions among songbirds may be more widespread than previously realized.

Individual subjects were not consistent in their matching responses. Of the 36 subjects tested with both self song and hybrid song, 17 (53%) matched on one but not the other opportunity, almost exactly as expected if the probability of an individual matching when given the opportunity was random. This pattern differs from that reported for a California population where subjects were generally consistent matchers or nonmatchers (Nielsen & Vehrencamp 1995).

Vehrencamp (2001) found that male song sparrows that matched either shared neighbour songs or shared stranger songs were more aggressive in other respects than were males that did not match. Beecher et al. (2000a), however, found that males that type-matched neighbour songs were no more aggressive on other measures than males that did not type-match. In our experiments, males that type-matched partially shared songs were more aggressive in terms of approach than were males that failed to match this stimulus, but no such difference in aggressiveness was found for matching to self song. It seems, then, that matching in song sparrows sometimes is and sometimes is not a predictor or correlate of aggressiveness, and no simple explanation for the differences in results is apparent. In particular, we have no explanation for why matching to partially shared songs was a better predictor of aggressiveness than matching to self songs in our experiments. One possible explanation is that self song types are perceived as unnatural in some way. If true, then we might expect subjects to have been less responsive overall to self songs than to hybrid songs, but this is not what we observed. Instead, subjects matched to self and hybrid songs at nearly equal frequencies, and did not show a reduced approach response overall during self song trials compared to hybrid and stranger song trials. Given that we found only a single significant relationship between partial matching and one measure of aggressiveness (mean distance to speaker across the 3-min playback period), we interpret this result with caution at present and are conducting further experiments to test how well matching predicts aggression in our study population.

Both the probability of matching and the mean aggressive response (as measured by approach to the speaker) decreased over the breeding season. Matching responses decreased from about 80% of trials in mid-May to about 40% of trials in early July. A similar decline was observed for matching by Washington song sparrows that were new neighbours (Beecher et al. 2000a). We observed an increase in mean distance to the speaker from less than 3 m to near 6 m, suggesting a decline in aggressive response similar to the observed decline in matching response. These results are consistent with the idea that matching is an aggressive signal, but do not help to explain why partial matching is, and self song matching is not, a predictor of aggressive response.

Song sharing has been proposed as a mechanism for the evolution of vocal repertoires in song sparrows (Beecher et al. 1996, 2000b; Wilson et al. 2000). The rationale is that singing multiple song types facilitates song sharing with multiple neighbours, and that song sharing in turn improves territory retention by allowing males to interact in ways (such as matching) that birds that do not share cannot achieve (Krebs 1977; Krebs & Kroodsma 1980; Slater 1981; Craig & Jenkins 1982). Support for this hypothesis comes from the observation that males with higher song type sharing have longer territory tenures (Beecher et al. 2000b) and that males sharing more song types with neighbours are more likely to survive and return to the same territory in subsequent years (Wilson et al. 2000). The relative rarity of whole song sharing in eastern song sparrow populations (Hughes et al. 1998) has proven a puzzle in light of this hypothesis. Our present results show that whole song sharing is not necessary for complex matching interactions. This observation explains at least part of this puzzle, but at the same time raises additional questions about how selection on male–male interactions might influence the evolution of song repertoires.

Acknowledgments

We thank Michael Beecher, John Burt and two anonymous referees for helpful comments on the manuscript, the Pennsylvania Game Commission for access to field sites, and the Pymatuning Laboratory of Ecology, University of Pittsburgh, for logistical support. Financial support was provided by National Science Foundation grants IBN-9974740 and IBN-0315566 to W.A.S. and IBN-9974743 and IBN-0315377 to S.N.

References

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Beecher, M. D., Campbell, S. E. & Burt, J. M. 1994. Song perception in the song sparrow: birds classify by song type but not by singer. *Animal Behaviour*, **47**, 1343–1351.

Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. L. 1996. Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, **51**, 917–923.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000a. Song-type matching between neighbouring song sparrows. *Animal Behaviour*, **59**, 21–27.

Beecher, M. D., Campbell, S. E. & Nordby, J. C. 2000b. Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour*, **59**, 29–37.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.

Brémond, J. C. 1968. Researchers sur la semantique et les elements vecteurs d'information dans les signaux acoustiques du rougegorge (*Erithacus rubecula* L.). *Terre Vie*, **2**, 109–220.

Brooks, R. J. & Falls, J. B. 1975. Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers. *Canadian Journal of Zoology*, **53**, 879–888.

Burt, J. M., Campbell, S. E. & Beecher, M. D. 2001. Song type matching as threat: a test using interactive playback. *Animal Behaviour*, **62**, 1163–1170. doi:10.1006/anbe.2001.1847.

Burt, J. M., Bard, S. C., Campbell, S. E. & Beecher, M. D. 2002. Alternative forms of song matching in song sparrows. *Animal Behaviour*, **63**, 1143–1151. doi:10.1006/anbe.2002.3011.

Capp, M. S. & Searcy, W. A. 1991. Acoustical communication of aggressive intentions by territorial-male bobolinks. *Behavioral Ecology*, **2**, 319–326.

Catchpole, C. K. & Slater, P. B. J. 1995. *Bird Song: Biological Themes and Variations*. New York: Cambridge University Press.

Craig, L. C. & Jenkins, P. F. 1982. The evolution of complexity in broadcast song of passerines. *Journal of Theoretical Biology*, **95**, 415–422.

Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.

Estes, R. D. 1991. *The Behavior Guide to African Mammals*. Los Angeles: University of California Press.

Falls, J. B. 1985. Song matching in western meadowlarks. *Canadian Journal of Zoology*, **63**, 2520–2524.

Falls, J. B., Krebs, J. R. & McGregor, P. 1982. Song matching in the great tit (*Parus major*): the effect of similarity and familiarity. *Animal Behaviour*, **30**, 997–1009.

Fox, M. W. 1971. *Behaviour of Wolves, Dogs, and Related Canids*. London: Jonathon Cape.

Fugle, G. N., Rothstein, S. I., Osenberg, C. W. & McGinley, M. A. 1984. Signals of status in wintering white-crowned sparrows, *Zonotrichia leucophrys gambelii*. *Animal Behaviour*, **32**, 86–93.

Hill, C. E., Campbell, S. E., Nordby, J. C., Burt, J. M. & Beecher, M. D. 1999. Song sharing in two populations of song sparrows (*Melospiza melodia*). *Behavioral Ecology and Sociobiology*, **46**, 341–349.

Horning, C. L., Beecher, M. D., Stoddard, P. K. & Campbell, S. E. 1993. Song perception in the song sparrow—importance of different parts of the song in song type classification. *Ethology*, **94**, 46–58.

Hughes, M., Nowicki, S., Searcy, W. A. & Peters, S. 1998. Song-type sharing in song sparrows: implications for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, **42**, 437–446.

Hurd, P. L. & Enquist, M. 2001. Threat display in birds. *Canadian Journal of Zoology*, **79**, 931–942.

Jolly, A. 1966. *Lemur Behavior*. Chicago: Chicago University Press.

Krebs, J. R. 1977. The significance of song repertoires: the beau geste hypothesis. *Animal Behaviour*, **25**, 475–478.

Krebs, J. R. & Kroodsma, D. E. 1980. Repertoires and geographical variation in bird song. *Advances in the Study of Behavior*, **11**, 143–177.

Krebs, J. R., Ashcroft, R. & Van Orsdol, K. 1981. Song matching in the great tit *Parus major* L.. *Animal Behaviour*, **29**, 918–923.

Lemon, R. E. 1968. The displays and call notes of cardinals. *Canadian Journal of Zoology*, **46**, 141–151.

Marler, P. & Peters, S. 1977. Selective vocal learning in a sparrow. *Science*, **198**, 519–521.

Marler, P. & Peters, S. 1988. The role of song phonology and syntax in vocal learning preferences in the song sparrow. *Ethology*, **77**, 125–149.

Morton, E. S. & Young, K. 1986. A previously undescribed method of song matching in a species with a single song type, the Kentucky warbler (*Oporornis formosus*). *Ethology*, **73**, 334–342.

Naguib, M., Mundry, R., Hultsch, H. & Todt, D. 2002. Responses to playback of whistle songs and normal songs in male nightingales: effects of song category, whistle pitch, and distance. *Behavioral Ecology and Sociobiology*, **52**, 216–223.

Narins, P. M., Lewis, E. R. & McClelland, B. E. 2000. Hyperextended call note repertoire of the endemic Madagascar treefrog *Boophis madagascariensis* (Rhacophoridae). *Journal of Zoology*, **250**, 283–298.

Nelson, D. A. 1984. Communication of intentions in agonistic contexts by the pigeon guillemot, *Cepphus columba. Behaviour*, **88**, 145–189.

Nielsen, B. M. B. & Vehrencamp, S. L. 1995. Responses of song sparrows to song-type matching via interactive playback. *Behavioral Ecology and Sociobiology*, **37**, 109–117.

Otter, K. A., Ratcliffe, L., Njegovan, M. & Fotheringham, J. 2002. Importance of frequency and temporal song matching in black-capped chickadees: evidence from interactive playback. *Ethology*, **108**, 181–191.

Peters, S., Searcy, W. A. & Marler, P. 1980. Species song discrimination in choice experiments with territorial male swamp and song sparrows. *Animal Behaviour*, **28**, 393–404.

Schroeder, D. J. & Wiley, R. H. 1983. Communication with repertoires of shared song themes in tufted titmice. *Auk*, **100**, 414–424.

Searcy, W. A., McArthur, P. D., Peters, S. & Marler, P. 1981. Response of male song and swamp sparrows to neighbor, stranger, and self songs. *Behaviour*, **77**, 152–163.

Searcy, W. A., Nowicki, S. & Peters, S. 2003. Phonology and geographic song discrimination in song sparrows. *Ethology*, **109**, 23–35.

Slater, P. J. B. 1981. Chaffinch song repertoires: observations, experiments and a discussion of their significance. *Zeitschrift für Tierpsychologie*, **56**, 1–24.

Stoddard, P. K., Beecher, M. D., Horning, C. L. & Campbell, S. E. 1991. Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behavioral Ecology and Sociobiology*, **29**, 211–215.

Stoddard, P. K., Beecher, M. D., Campbell, S. E. & Horning, C. L. 1992. Song-type matching in the song sparrow. *Canadian Journal of Zoology*, **70**, 1440–1444.

Vehrencamp, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions?. *Proceedings of the Royal Society of London, Series B*, **268**, 1637–1642.

Wilson, P. L., Towner, M. C. & Vehrencamp, S. L. 2000. Survival and song-type sharing in a sedentary subspecies of the song sparrow. *Condor*, **102**, 355–363.

Yasukawa, K., Bick, E. I., Wagman, D. W. & Marler, P. 1982. Playback and speaker-replacement experiments on song-based neighbor, stranger and self discrimination in male red-winged blackbirds. *Behavioral Ecology and Sociobiology*, **10**, 211–215.