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Song type matching as threat: a test using interactive playback

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Neighbouring song sparrows, *Melospiza melodia*, in our Seattle population share song types and sometimes respond to neighbour song by type matching (replying with the same song type being sung) or repertoire matching (replying with a shared song other than the type being sung). Based on our modification of the threat hypothesis of Krebs et al. (1981, *Animal Behaviour*, **29**, 918–923), according to which, type matching is a threat, we develop two predictions concerning type matching. (1) A bird will be more likely to escalate when type matched by his neighbour than when repertoire matched. (2) When type matched, birds who escalate will continue to sing the matched song type, while those who de-escalate will switch off the matched type or stop singing. To test these predictions we conducted an interactive playback experiment that simulated a bird in an adjoining territory issuing a song reply to a singing subject. We exposed subjects to three song playback conditions, each on a different day: a type match, a repertoire match and an unshared stranger song (to provide an estimate of each subjects maximum response for comparison with their responses to type matching). Subjects responded consistently and most aggressively to stranger song. Subjects responded more aggressively to type-matching playback than to repertoire-matching playback, supporting our first prediction. In type-matching trials, subjects did not always respond aggressively, and those who stayed on the same song type throughout the trial responded more aggressively than those who switched to a different song, supporting the second prediction.

In many songbird species with song repertoires, neighbours share song types (see Beecher et al. 1997). A bird who shares some song types with a neighbour can reply to the neighbour in several different ways: with a type match (the same song type his neighbour has just sung), a repertoire match (a song shared with but not recently sung by his neighbour), or a nonshared song type (Beecher et al. 1996). In this study, we focus on the communicative significance of type matching.

Song type matching has been observed in a number of species (e.g. Bremond 1968; Lemon 1968; Armstrong 1973; Krebs et al. 1981; Falls 1985; Stoddard et al. 1992; Nielsen & Vehrencamp 1995). In a study of type matching by great tits, *Parus major*, Krebs et al. (1981) hypothesized that type matching is a threat and made two predictions. The first prediction was that type matching would be correlated with other measures of strong response such as close approach and aggressive displays. The second prediction was that type matching would occur more often early in the breeding season when aggression is highest due to unstable territorial boundaries and insertions of newly established neighbours. Although Krebs et al. (1981) provided support for both predictions, subsequent studies on great tits and western meadowlarks, *Sturnella neglecta*, failed to support the first prediction (Falls et al. 1982; Falls 1985), and did not test the second prediction.

In a recent playback experiment designed to test both predictions of the threat hypothesis, we found that song sparrows, *Melospiza melodia*, who are new neighbours are indeed more likely to type match playback of a neighbour's song early in the breeding season (April), than later (June), supporting the second prediction of Krebs et al. (Beecher et al. 2000). However, we found no correlation between type matching and measures of aggression such as number of flights, closest approach to the speaker, and number of visual threat displays. Thus, Krebs et al.'s first prediction of a correlation between aggressive behaviour and type matching was not supported. Taken together, these results suggest that although type matching may be a threat, the temporal relationship between type matching and aggression may be more complicated than was assumed in the Krebs et al. hypothesis.

To address this issue, we propose a modification of the threat hypothesis. In our modified hypothesis, a bird

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signals his motivation to escalate or de-escalate an interaction by his reply to a neighbour's song. We develop four predictions from the modified threat hypothesis. The first two predictions concern when a bird should type match and how type matching relates to aggressive behaviour.

(1) A bird will be more likely to type match, the greater the perceived danger of a territorial conflict (e.g. the closer to encroaching on his territory his neighbour appears to be). Under high-danger conditions, the bird should type match, a high-threat signal that he will escalate if the neighbour escalates (e.g. crosses over the territory boundary). Under low-danger conditions, the bird should repertoire match, a low-threat signal specifically addressed to the neighbour. As mentioned earlier, this prediction was supported by our previous study: we predicted that for new neighbours, neighbour song from the territory boundary should be perceived as more threatening early in the breeding season than late in the season, and in fact early in the season neighbour song elicited more type matching than late in the season (Beecher et al. 2000).

(2) Type matching is a threat of future aggression, not a component of aggression. That is, type matching is given instead of and in advance of actual aggression, with escalation to aggression contingent on the recipient's response to the threat. The bird type matches first, and only escalates to aggression if the neighbour disregards the threat (e.g. moves onto the bird's territory). This line of reasoning would explain why we found no correlation between aggressive response and type matching in our earlier study, since the neighbour simulated by playback was singing from his own territory and never escalated the interaction by approaching closer (Beecher et al. 2000).

The next two predictions concern what the bird should do if he is type matched, and they are tested in the present study.

(3) On average, a bird should respond more strongly (e.g. approach closer, attack if the intruder is found) when type matched than when repertoire matched, because the former is a threat and the latter is not. That is, the next step in escalation when type matched is to attack, whereas the next step when repertoire matched is to type match (not yet to attack). In any particular instance, of course, a type-matched bird may choose not to respond to the threat.

(4) A bird choosing to de-escalate in response to a type match should switch off type, whereas one choosing to escalate should stay on type. That is, in response to a type match, switching to a repertoire match or nonmatch is a de-escalation signal, whereas staying on type is the bird's closest approximation to type matching (indeed, if we forget who started it, it is type matching). Our elaboration of the threat hypothesis is summarized in Fig. 1.

We report here an experimental test of the last two predictions using an interactive playback design that simulated a neighbour replying from an adjoining territory to a subject singing on his own territory. All subjects were tested in two playback conditions, each of which began when the subject sang: playback of the neighbour's type match (same song type), or of a repertoire match (another song type the two birds shared). By prediction 3, subjects inside their own territory should on average respond more aggressively to playback of a type match than to playback of a repertoire match. By prediction 4, those subjects who respond strongly to type-matching playback should stay on type, while those who respond weakly should switch off type or cease singing. Some subjects also received a third playback condition: a nonshared song of an unfamiliar bird (stranger song). Since stranger song has been found to be more threatening than neighbour song (Stoddard et al. 1992), we predicted that subjects would respond more strongly to stranger song than to either neighbour repertoire matching or type matching. Stranger song playback was used to establish an upper response limit with which to compare subjects' responses to type matching. We expected that the response to type matching would be intermediate on average to the response to repertoire matching (low-level threat) and stranger song (high-level threat).

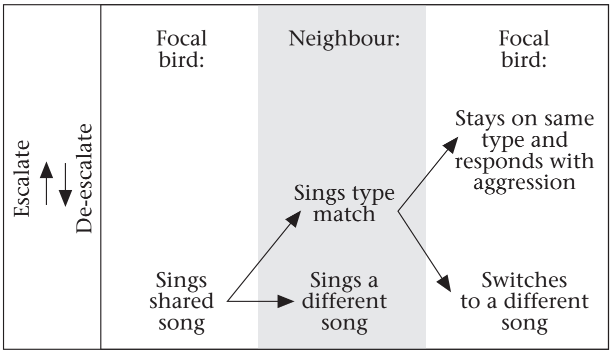

Figure 1. Diagram of singing interactions between a focal bird and a neighbour who shares his song types. Escalation is indicated by behaviours higher in the diagram, and de-escalation by behaviours lower in the diagram. In this figure, the interaction begins when the focal bird sings a shared song type. The neighbour can then either type match the focal bird (an escalation), or sing a different song. If the focal bird is type matched, he may respond to the escalation by staying on the same type and responding with aggression, a further escalation, or de-escalate by switching to another song type and not responding strongly.

METHODS

Study Area and Subjects

Our song sparrow study site is an undeveloped 3-km^2 park bordering Puget Sound in Seattle, Washington. The song sparrow population is sedentary (nonmigratory) and typically there are approximately 150 males on territories in a given year. Birds disperse into and out of the study population from surrounding areas. For the present experiment, we selected 10 pairs of colour-banded neighbouring males as subjects. Before the experiment we recorded the full song repertoires of each subject. Each male served both as a subject and as a source of stimulus songs for trials on his neighbour. We selected neighbour pairs at random from the population, the only requirement being that they shared at least two song types.

Subject repertoire sizes ranged from seven to 12 song types (mean 9.4) and the percentage of songs shared between pairs ranged from 17 to 100% (mean 60%).

Recording, Playback and Song Type Analysis

We recorded song repertoires of the subjects in the field with a Sennheiser ME88 directional microphone and a Sony TC-D5M tape recorder. We estimated a repertoire to have been completely measured (all song types) when we had recorded 20 or more consecutive song type switches (method and rationale described in Kroodsma 1982). We analysed songs on a Kay DSP-5500 sonagraph. We considered two songs to be matches if they shared at least half of their component phrases. In borderline cases, we put more weight on the more invariant early portions of the song and less on later parts of the song, which are more variable and less important in individual recognition (Nice 1943; Horning et al. 1993). The first five songs of birds A and B in Fig. 2 are examples of song pairs we classified as type matches.

We presented playback songs using a Panasonic CF-25 laptop computer with a 16-bit sound card, attached to an amplified speaker via a 10-m cable. Playback songs were digitized in 16 bits at a 22 050 Hz sample rate. A program written by J.M.B. ('Syrinx') allowed us to display playable spectrograms of all song types in the repertoires of the subject bird and his neighbour. The Syrinx program also displayed a real-time spectrogram of what the subject was singing, using a directional microphone as input to the computer. This set-up allowed us to identify the subject's song type quickly, then select and respond with the appropriate stimulus song playback. In addition, we recorded all trials onto tape for later analysis.

During a playback trial there was the possibility that the subject's neighbour would hear and respond to the playback by approaching or singing, in which case the trial would have to be aborted. To reduce this possibility, we built a highly directional speaker that consisted of an enclosed midrange tweeter (Radio Shack M40-1289A, frequency range 200–20 000 Hz) attached with the speaker output at the focal point of a Sony parabolic reflector. The apparatus was mounted on a tripod and could be aimed at a subject bird with little or no sound heard behind it (from the neighbour's direction). Peak playback sound levels were approximately 75 dB SPL at 10 m in front of the speaker with 35–40 dB attenuation from the peak level at 10 m directly behind the speaker.

Playback Conditions and Procedure

Three song playback trial conditions simulated a bird replying to the singing subject from within a neighbour's territory. The playback conditions were: (1) repertoire match (i.e. playback of one of the neighbour's shared song types, different from the one the subject was singing); (2) type match (i.e. playback of the neighbour's type match to the subject's song); (3) stranger song (i.e. playback of a nonshared song of a bird at least five territories distant).

We tested four subject pairs in 1997 and six pairs in 1998. We conducted playbacks during 25 April–14 July for 1997, and 16 April–29 May for 1998. The 1997 subjects received repertoire- and type-matching playback conditions only, while the 1998 subjects were given all three conditions (N=20 repertoire-matching and type-matching trials, and N=12 stranger song trials). For each subject, we presented all playback trials within the same year.

We conducted all trials in the morning between 0700 and 1000 hours. For each subject, we randomly determined trial type order, and administered only one trial per day. Neighbours were sometimes tested on the same day, but always after at least a 2-h delay between trials. Stranger song playback often affects the entire nearby neighbourhood, so we did not conduct further trials in an area on the same day a stranger trial had been administered there.

Before each trial, we set our playback speaker to broadcast towards the subject from 3 m within the neighbour's side of their contiguous territorial boundary. We did not begin a trial until the neighbour was quiet and well away from the playback area. The trial was aborted if the neighbour either sang a song or approached. When the subject sang, we first identified his song type on the computer display using Syrinx, then we selected a playback stimulus. If the predetermined trial type was to repertoire match, we selected one of the neighbour's songs that was shared with the subject but one the subject was not singing. For type match trials, we selected the neighbour's song that matched the subject's song. If the subject was singing a nonshared type, we always waited for him to switch to a shared type. For stranger trials we played the song of a distant Discovery Park song sparrow (at least five territories away), selected from the playback stimuli for a different subject; each subject received a different stranger song.

Playback trials lasted 3 min, starting from the first playback. We played the song at 10-s intervals (the modal singing rate of song sparrows) until the subject sang again, at which point we synchronized the playback with his singing to avoid song overlap. If he stopped singing (no song for >10 s), we continued our playback at 10-s intervals until the end of the trial. Synchronizing playback with the singer had no effect on other aspects of the playback trials; in particular, there were no significant differences between conditions with respect to the number of song playbacks per trial. During trials we noted whether the subject switched to a different song type, what song type he switched to, how many times he flew to a new perch, the closest approach distance to the speaker, the number of discrete threat displays (wing waves, or quiet song, Nice 1943) and the number of songs sung.

Data Analysis

We used number of flights, closest approach distance to speaker and number of threat displays as measures of aggressive response (we note that number of songs is not correlated with aggressive response in our song sparrows).

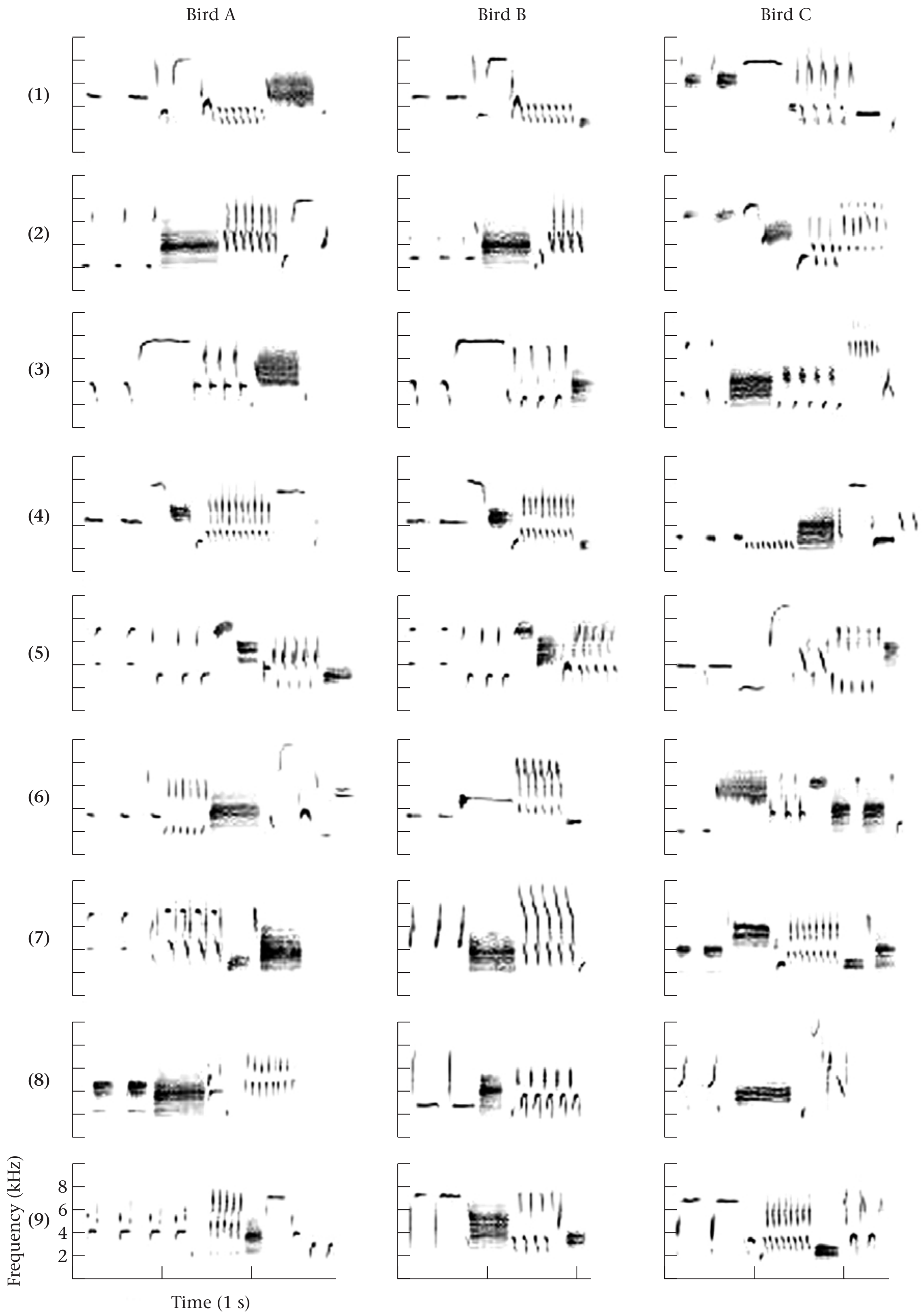

Figure 2. Song type repertoires of three song sparrow subjects. Birds A and B were neighbours and shared the first five songs in their 10-song repertoires (50% sharing). Bird C was located more than five territories away from birds A and B and did not share song types with either bird. The shared songs of birds A and B could be used as type- and repertoire-matching playback stimuli to each other, while songs from bird C's repertoire could be used as stranger songs for birds A and B. Songs A3 and B3 are examples of a borderline match.

These three measures were all significantly correlated with each other ($r=0.19$–0.59), so we used principal components analysis to generate a single composite aggressive response score for each trial using the method described in McGregor (1992). We first standardized the three response measures, then performed principal components analysis using the program Statistica. The first unrotated principal component factor accounted for 60% of the variance and was used to calculate the score. The formula for computing a score for each trial based on the first factor coefficients was: $(0.44 \times \text{number of flights}) + (0.34 \times \text{number of displays}) - (0.49 \times \text{approach distance})$. Larger values indicate a more aggressive response and so we refer to the measure as an 'aggression score'.

For the test of our primary prediction, that birds would respond more strongly to type-matching playback than to repertoire-matching playback, we used a Wilcoxon matched-pairs signed-ranks test, and conservatively, a two-tailed test. We performed a similar test to compare response to stranger song versus type-matching playback. In addition, to test for an overall response difference across experimental conditions, we applied a Kruskal–Wallis analysis of variance (ANOVA). Although our comparisons were within subjects, we used the unpaired Kruskal–Wallace test because many subjects were not tested in the stranger condition (it was present mainly to provide a baseline).

As a measure of song response, we scored each of the 52 trials for whether the subject continued singing the same song throughout the trial, switched to a new song type before the end of the trial, or stopped singing before the trial was half finished (1.5 min). Our prediction for song response during type-matching trials was that birds who stayed on the same type (and thus continued to match the playback song) would respond more aggressively than those who switched to a different type or stopped singing. To test this prediction, we compared aggression scores for birds who stayed on type to scores for birds who switched off type or stopped singing (Mann–Whitney *U* test). Since our hypothesis addressed only how birds would respond (stay on type or not) during type-matching trials, we had no specific predictions for repertoire-matching and stranger song playback and so there were no planned comparisons for song responses during these conditions. We could make no a priori predictions for response when birds stopped singing, because our experience has been that birds often stop singing when aggression is either very high, or very low. All *P* values reported are two-tailed.

We tested for differences in song rate between conditions (Kruskal–Wallis ANOVA using songs per trial as the dependent variable), and tested for a correlation between song rate and aggression score (Spearman rank correlations).

Variables we analysed for possible confounding effects were: trial date, trial year, order of playback condition and subject age. We used Spearman rank correlations to test for effects of trial date and subject age on aggression score. We used a Mann–Whitney *U* test to test for effects of trial year on aggression score. A Kruskal–Wallis ANOVA tested for effects of playback condition order on aggression score. We tested for effects of trial year and playback condition order on song response with chi-square analyses.

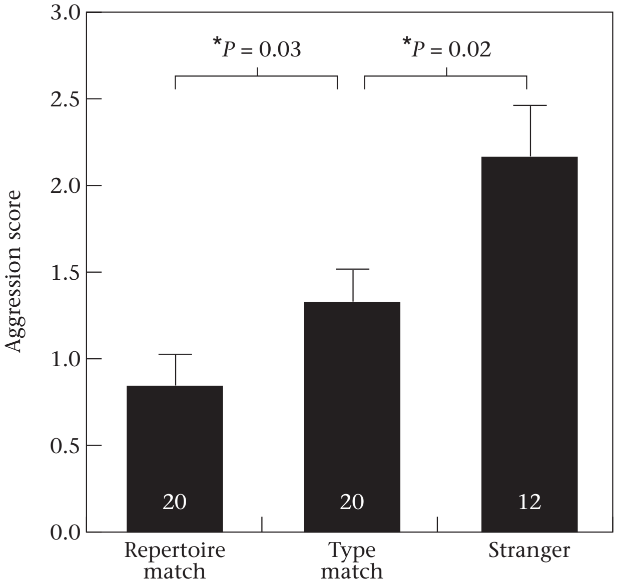

Figure 3. Aggression scores ($\bar{X}$+SE) for the three experimental conditions. Numbers of trials are shown at the base of each bar. *Wilcoxon matched-pairs signed-ranks test, two-tailed *P* values.

RESULTS

Aggressive Response

In the test of our first prediction, song sparrows responded with significantly higher aggression scores during type-matching playback than during repertoire-matching playback (median 1.2 versus 0.6; Wilcoxon matched-pairs signed-ranks test: $T=47$, $N=20$, $P=0.03$). Subjects also responded with higher aggression scores during stranger playback than during type-matching playback (median 2.1 versus 1.2; $T=9$, $N=12$, $P=0.02$; Fig. 3). In the overall test, aggression scores were significantly different between repertoire-matching, type-matching and stranger song playback conditions (Kruskal–Wallis ANOVA: $H_{2,52}=12.0$, $P<0.01$). Aggression score and trial condition were not correlated with subject age, trial date, trial order, playback year, or song rate.

Song Response

In a total of 52 trials (type match, repertoire match or stranger unshared song) subjects stayed on type in 15 trials, switched to a different type in 25, and stopped singing in 12 (frequencies of each response type for the different playback conditions are given in Table 1). In trials in which they were type matched, birds stayed on the same type in eight of the 20 trials. In the test of our second prediction, birds who stayed on the same type during type-matching trials had significantly higher aggression scores than those who switched off or stopped singing (stayed on type: median 2.0, range 1.3–3.0;

Table 1. Song response and aggression across playback conditions

	Playback condition								
	Repertoire match			Type match			Stranger song		
Song response	Number of trials	Aggression score	Songs per trial	Number of trials	Aggression score	Songs per trial	Number of trials	Aggression score	Songs per trial
Stayed on type	1	0.4	18.0	8	2.0±0.2	12.1±2.7	6	2.2±0.2	4.5±0.9
Switched off	11	1.0±0.3	9.4±1.6	10	0.9±0.2	8.5±2.2	4	2.4±0.8	10.5±4.8
Stopped singing	8	0.7±0.3	1.0±0.4	2	0.6±0.6	3.0±1.0	2	1.6±0.9	1.5±1.5

Listed for each playback condition are frequencies of occurrence, mean±SE aggression scores and mean±SE songs per trial for each type of song response.

switched off or stopped: median 0.8, range 0–2.1; Mann–Whitney *U* test: $U=7$, $N_1=8$, $N_2=10$ $P<0.01$; Table 1; Fig. 4). Song response (switching off, staying on type, or ceasing song) was not correlated with subject age, trial date, trial order, or playback year.

Song Rate

Song rate was not correlated with either aggression score or trial condition. Because birds who sing at a higher rate usually switch types sooner, we examined whether birds who switched during our trials had higher rates of singing than those who stayed on type (Mann–Whitney *U* test). Repertoire-matching trials were excluded because only one bird stayed on type. Although there were no significant differences, type-matching and stranger conditions showed opposite tendencies. In the type-matching condition, birds who stayed on type sang at higher rates than did birds who switched off type ($\bar{X}$+SE: stayed on type: 12.1 ± 2.7; switched off type: 8.5 ± 2.2). In contrast, in the stranger song trials, birds who stayed on type sang less than half the number of songs as birds who switched off type (4.5 ± 0.9 versus 10.5 ± 4.8). Songs per trial for all conditions and types of song response are given in Table 1.

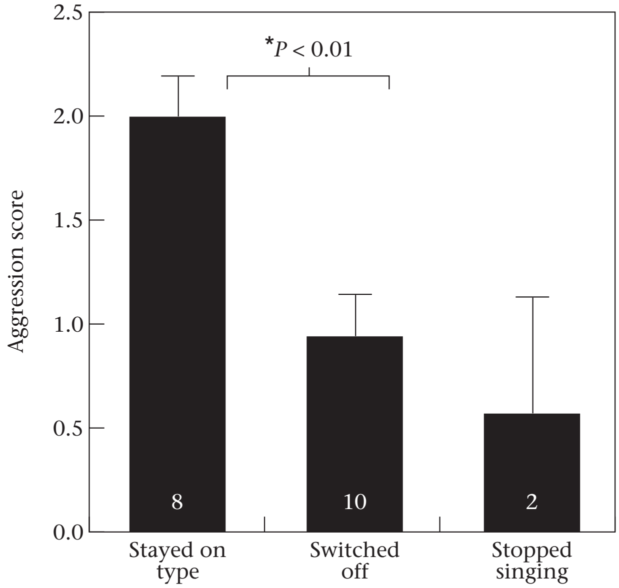

Figure 4. Relationship between song type switching during playback trials and aggression score ($\bar{X}$+SE) during type-matching trials. Numbers of trials are shown at the base of each bar. *Mann–Whitney *U* test, two-tailed *P* values.

DISCUSSION

Song sparrows responded to playback of neighbour song with significantly higher aggression scores when it was a type-matching playback than when it was a repertoire-matching playback, supporting the prediction that birds on their own territory will perceive a type match from a neighbour as a challenge and will be more likely to escalate. Birds did not always respond strongly when type matched, however, and whether or not they did was correlated with whether or not they stayed on the matched type: birds who stayed on the same type throughout the trial gave a stronger response than birds who switched types or stopped singing. This result supports our second prediction that staying on type is correlated with escalation, and switching off type with de-escalation.

Although we have no data on this point, it seems likely that uncontrolled contextual variables played a role in determining how aggressively a subject responded when type matched (similar arguments would apply to repertoire-matching trials). Relevant variables might include whether the subject had had recent conflicts with that neighbour, whether he had won or lost these battles, whether he was busy feeding nestlings or fledglings at the time of the test, whether the mate of one or the other bird had chosen to nest near the boundary, and so on. One implication of this view is that if we repeated these type-matching trials, some birds would flip-flop from weaker to stronger response, or vice versa, because of uncontrolled changes in one or more of these contextual variables. A different possibility is that the differences in aggressive response are determined by more permanent attributes of the neighbour relationship, such as dominance relationships. If stable dominance relationships between neighbours existed, we might expect on average half the birds to show dominant responses and half to show subordinate responses on type-matching trials.

During repertoire-matching trials birds gave relatively weak aggressive responses. They also usually either switched off the type they were singing, or stopped singing (only one stayed on type). These results support our hypothesis that repertoire matching is a low aggression signal, and suggest that the song responses of switching off type and ceasing singing may be either neutral or de-escalating signals.

Birds treated stranger song as more of a threat on average than a neighbour's type match. It is likely that birds react so strongly to stranger song because of the greater danger that a stranger might attempt to usurp his territory than an established neighbour. This 'dear enemy' phenomenon has been observed in many (but not all) territorial species (Fisher 1954; Jaeger 1981; Ydenberg et al. 1988; Getty 1987; Temeles 1994). In song sparrows, the effect disappears when the neighbour song is played from anywhere else than the neighbour's territory; for example, from the opposite (incorrect) boundary, or from within the subject's territory (Stoddard et al. 1991).

In the stranger playback trials, there was no correlation between staying on type and strong response. We suggest that a bird may stay on type as a threat only when the song type he is singing matches his adversary's song. A second possible reason for the difference between the subject's response to neighbour type match and stranger trials is that the most common reaction to stranger song is an immediate and aggressive approach, an escalation to direct aggression; the particular song sung in this context may be irrelevant (indeed, this same argument should apply to neighbour song when the neighbour is within the subject's territory).

When type matched by a neighbour, subjects generally gave a more restrained aggressive response than they did to stranger song, such that the mean aggressive score for those trials was approximately halfway in magnitude between scores to neighbour repertoire matching and stranger song (Fig. 3). Thus, although birds apparently did perceive the neighbour's type match as more of a threat than his repertoire match, the restrained aggression and use of further vocal signalling to indicate the probability of escalation or de-escalation suggest that, even at the later stages of an escalation, birds may continue to provide their neighbours with an avenue to de-escalate that they do not afford strangers. These results support our view that neighbours use type matching and switching as a signalling system for controlling conflict.

In song sparrows, there is normally a positive correlation between switching rate and singing rate (Nice 1943). This correlation raises the possibility that birds who stayed on type during playback trials may have done so because they were singing at a lower rate, rather than because they were avoiding switching. As it turns out, this may indeed have been the case during stranger playback trials: birds who switched off type sang more than twice as many songs as birds who stayed on type (see Table 1). However, during type-matching trials birds actually sang more songs when they stayed on type than when they switched off, the opposite of what would be predicted from the general correlation between singing rate and switching rate. Thus, only when they were type matched did birds who escalated both stay on type and maintain or even increase their rate of singing. We take this as evidence that staying on type is an escalation signal in response to being type matched. A similar finding was reported in Nielsen & Vehrencamp (1995). In that study birds dramatically lowered their song switching rate when synchronously type matched with playback while continuing to sing at about the same rate as they did for other trial types (cf. Table 1 and Figure 3b in Nielsen & Vehrencamp 1995).

Our previous study (Beecher et al. 2000) found support for Krebs' prediction that birds should type match more early in the season. In the present study, playback trial date was uncorrelated with either aggression or tendency to type match during repertoire match trials. The lack of correlation is probably due to most of the playbacks having been conducted later in the season than the previous experiment's early condition trials (present experiment trial date median 11 May, range 16 April–14 July, as compared with 14–28 April for the 'early period' of Beecher et al. 2000), thus at a time of year when neighbour boundaries were already well established and few, if any, new birds were trying to establish territories. In addition, most of the pairs in the present study were long-time neighbours, whereas all pairs in Beecher et al. (2000) were new that year.

Song sharing allows neighbours to type and repertoire match each other, and then use this ability to send graded, directed threats, as demonstrated by this study and others (Krebs et al. 1981; Stoddard et al. 1992; Beecher et al. 1996, 2000). Repertoire and type matching can occur only if neighbours share songs, however, and there are many neighbours in our population who share no song types. Furthermore, there are songbird populations in which neighbours typically share few song types; indeed, this seems to be the typical case in eastern song sparrows (Hughes et al. 1998). If song matching is an important element in a territorial communication system, as we suggest here, then how do nonsharing neighbours send threat signals? One possibility is that nonsharing neighbours use less stringent criteria to define song matches than we the experimenters do, allowing those birds to type match and repertoire match with those of their songs they consider similar enough. For example, in Fig. 2, birds A and C do not share any song types, but songs A8 and C7 both begin with a very similar phrase containing two brief buzzes followed by a longer buzz, note complex, and a trill. If birds A and C were neighbours, they might consider these songs to be matches, even though by our matching criteria they are not. We have provided evidence for this more general form of song matching in a recent study (J. M. Burt, S. C. Bard, S. E. Campbell & M. D. Beecher, unpublished data).

Acknowledgments

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