Song type matching as threat: a test using interactive playback

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Running head: Burt et al.: Type matching as threat

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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 a modification of the threat hypothesis of Krebs et al. (1981), 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. Subjects were exposed 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 maximum response to compare with response to type matching). Subjects responded more aggressively to type matching playback than to repertoire matching playback, supporting our first prediction. In type matching trials, subjects 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. Birds responded to neighbour type matching at a level intermediate to their response to neighbour repertoire matching (lowest) and stranger song (highest), suggesting that type matching represents an intermediate level of threat.
In many song bird 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 non-shared 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 in 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 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 behavior 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 signals his intention 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. The 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 it did 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, the 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 non-match 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 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 non-shared 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 to the response to repertoire matching (low level threat) and stranger song (high level threat).

METHODS

Study Area and Subjects

Our song sparrow study site is an undeveloped 3-km² park bordering Puget Sound in Seattle, Washington. The song sparrow population is sedentary (non-migratory) 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
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. Neighbour pairs were selected at random from the population, the only requirement being that they share at least two song types. Subject repertoire sizes ranged from 7 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

Song repertoires of the subjects were recorded 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). Songs were analyzed on a Kay DSP-5500 Sonagraph. Two songs were considered 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.

Playback songs were presented 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 22050 Hz sample rate. A program written by JMB ("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 setup allowed us to quickly identify the subject’s song type, select, and respond with playback of the appropriate stimulus song. Additionally, all trials were recorded 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 a Radio Shack enclosed midrange tweeter (Radio Shack M#40-1289A, 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 10m in front of the speaker with 35-40 dB attenuation from the peak level at 10m 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 non-shared song of a bird at least five territories distant.

Four subject pairs were tested in 1997 and six pairs were tested in 1998. Playback dates ranged between April 25 – July 14 for 1997, and April 16 – May 29 for 1998. The 1997 subjects
received repertoire match and type matching playback conditions only, while the 1998 subjects were given all three conditions (N=20 repertoire match and type match trials, and N=12 stranger song trials). For each subject, all playback trials were presented within the same year.

All trials were conducted in the morning between 0700 and 1000. For each subject, trial type order was randomly determined, and only one trial was administered per day. Neighbours were sometimes tested on the same day, but always after at least a two hour 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 three meters 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 which 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 non-shared 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 5 territories away), selected from the playback stimuli for a different subject; each subject received a different stranger song.

Playback trials lasted 3 minutes, starting from the first playback. We played the song at 10 s intervals until the subject sang again, at which point we synchronized the playback with his
singing to avoid song overlapping. If he stopped singing (no song for >10 s) we continued our playback with the 10-s intervals to the end of the 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**

Number of flights, closest approach distance to speaker, and number of threat displays were used as measures of aggressive response. These three measures were all significantly correlated with each other (r = 0.19 to 0.59), so principal components analysis was used to generate a single composite aggressive response score for each trial using the method described in McGregor (1992). The three response measures were first standardized, then run through 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 * number of flights) + (0.34 * number of displays) - (0.49 * approach distance). Larger values indicate a more aggressive response and so we refer to the measure as an “aggression score”.

To test whether there was an overall difference in aggression across experimental conditions, we applied a Kruskal-Wallis ANOVA using aggression score as the dependent variable. We predicted that birds would respond more strongly to type matching playback than to repertoire matching playback, and that they would respond more strongly to stranger song than to type matching playback. For our planned tests of the two predictions, we used paired comparisons of
aggression scores for type matching vs. repertoire matching playback, and type matching vs. stranger playback (Wilcoxon matched pairs tests).

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 analyzed for possible confounding effects were: trial date, trial year, order of playback condition, and subject age. Spearman rank correlations were used to test for effects of trial date and subject age on aggression score. A Mann-Whitney U test was used to test for
effects of trial year on aggression score. A Kruskal-Wallis ANOVA tested for effects of playback condition order on aggression score. Effects of trial year and playback condition order on song response were tested with Chi-Square analyses.

RESULTS

5

Aggressive response

Aggression scores were significantly different between repertoire matching, type matching, and stranger song playback conditions (Kruskal-Wallis ANOVA: $H_{2,52}=12.0$, $P<.01$). Song sparrows responded with significantly higher aggression scores during type matching playback than during repertoire matching playback (median 1.2 vs. 0.6, Wilcoxon matched pairs 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 vs. 1.2, Wilcoxon matched pairs test: $T=9$, $N=12$, $P=0.02$; Fig. 3). Aggression score and trial condition were not correlated with subject age, trial date, trial order, playback year, or song rate.

Song response

In the total 52 trials (type match, repertoire match or stranger unshared song) subjects stayed on type in 15 trials, switched off 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 8 of the 20 trials. 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 vs. switched off or stopped: median 0.8, range 0-2.1, Mann-Whitney U, P<.01; 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, there were opposite trends between the neighbour type match and stranger song conditions. In the type matching condition, birds who stayed on type sang at higher rates than did birds who switched off type (stayed on type mean±SE: 12.1±2.7, vs. 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 vs. 10.5±4.8). Songs per trial for all conditions and types of song response are given in Table 1.

DISCUSSION

Song sparrows responded to playback of neighbour song with significantly higher aggression scores when the playback was type matching playback than when it was repertoire matching playback, supporting the prediction that birds on their own territory would perceive a type match
as a challenge and thus 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, supporting our second
prediction that staying on type would be correlated with escalation, and switching off type with
de-escalation.

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.

As predicted, birds treated stranger song as more of a threat 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 might 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, this effect disappears
when the neighbour song is played from anywhere else than the neighbour’s territory, e.g., 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 signaling to indicate aggressive intent suggest that, even at the later stages of an escalation, birds may continue to provide their neighbours with a means to de-escalate that they do not afford strangers. These results support our view that neighbours use type matching and switching as a mutually beneficial signaling system for conflict resolution.

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 did 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 and 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 (c.f. Table 1, and Fig. 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 May 11, range April 16 – July 14, as compared with April 14 – 28 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, many of the pairs in this 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, which they use to send graded, directed threats, as demonstrated by this study and others (Krebs et al. 1981; Stoddard et al. 1992; Beecher et al. 1996; Beecher et al. 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. Moreover, 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 non-sharing neighbours send threat signals? One possibility is that non-sharing 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 don’t 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. In separate studies, we are investigating whether non-sharing neighbours might song match using songs that are similar but not ‘shared’ by our criteria.
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References


Table 1. Song response and aggression across playback conditions. 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

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<tr>
<th>Song response</th>
<th>Playback Condition</th>
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<tr>
<td></td>
<td>Repertoire Match</td>
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<td></td>
<td>number of trials</td>
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<tr>
<td>stayed on type</td>
<td>1 0.4 18.0</td>
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<tr>
<td>switched off</td>
<td>11 1.0±0.3 9.4±1.6</td>
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<tr>
<td>stopped singing</td>
<td>8 0.7±0.3 1.0±0.4</td>
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FIGURE LEGENDS

**Figure 1.** Diagram of singing interactions between a focal bird and his neighbour, who share song types. Escalation is indicated by behaviors higher in the diagram, and de-escalation by behaviors 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.

**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 5 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.

**Figure 3.** Aggression scores (mean±SE) for the three experimental conditions. Numbers of trials are shown at the base of each bar. *Wilcoxon matched pairs, two-tailed p-values.*
Figure 4. Relationship between song type switching during playback trials and aggression score (mean±SE) during type matching trials. Numbers of trials are shown at the base of each bar.

*Mann-Whitney U, two-tailed p-values.
sings shared song

Focal Bird:
sings type match

Neighbor:
sings a different song

Focal Bird:
stays on same type and responds with aggression

switches to a different song

escalate
des-escalate
Repertoire Match

Type Match

Stranger

aggression score

*P = 0.03

*P = 0.02

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<th></th>
<th>Repertoire Match</th>
<th>Type Match</th>
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<td>20</td>
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The aggression score is significantly higher when stayed on type (8) compared to switched off (10) and stopped singing (2). The difference is statistically significant at *P < 0.01.