

Testing the function of song-matching in birds: responses of eastern male song sparrows *Melospiza melodia* to partial song-matching

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Summary

Song-matching has been hypothesized to be a signal of aggressive intentions whereby matching an opponent signals that the singer is likely to attack. Theory predicts that an aggressive signal should impose a cost that enforces the signal's reliability. A receiver-dependent cost imposed by the matched bird's aggressive retaliation has been proposed for song-matching. We tested for such a cost for partial song-matching in an eastern population of song sparrows where males lack the shared song types necessary for song type matching, but can perform partial song-matching using shared song segments. We tested aggressive response, as measured by average distance to a playback speaker, to partial-matching songs and non-matching songs. We predicted a stronger aggressive response to partial-matching songs, as has been shown for whole song-matching in western song sparrow populations. The birds in our study responded no differently to partial-matching and non-matching songs. Neither the distance to the playback speaker nor singing responses differed between playback treatments. Our results do not support a receiver-dependent cost to partial song-matching, as would be expected if partial-matching is a direct threat. Instead, we suggest that partial song-matching functions as a signal of attention.

Introduction

A variety of singing behaviors used by song birds in aggressive contexts have been hypothesized to provide information about aggressive intentions.

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For example, singers may adjust the timing of their songs to overlap the songs of a rival (Dabelsteen et al., 1997; Naguib, 1999; Mennill & Ratcliffe, 2004) or they may match an opponent's song using a shared or similar song type (Krebs et al., 1981; McGregor et al., 1992; Burt et al., 2002). Evidence that such behaviors convey information during aggressive signaling contests comes from playback experiments in which the singing behaviors correlate with measures of aggressive behavior, such as approach to a playback speaker (Krebs et al., 1981; Kramer et al., 1985; Shackleton & Ratcliffe, 1994; Vehrencamp, 2001).

Honest signaling of aggression is vulnerable to cheating or bluffing by individuals that signal greater strength or aggressive motivation than they truly possess (Dawkins & Krebs, 1978; Maynard Smith, 1979). Theory suggests that reliable aggressive signaling can be maintained if the signal is sufficiently costly, and if signal costs are greater for weaker or less aggressive individuals (Zahavi, 1977; Enquist, 1985; Grafen, 1990). Yet, in song birds, many vocal behaviors hypothesized to signal aggression have no obvious production costs. Bird song in general appears to have surprisingly low metabolic costs (Oberweger & Goller, 2001; Ward et al., 2004). Even if time and vulnerability costs are considered, it is difficult to see how many of the singing behaviors proposed to be aggressive can be more costly than their non-aggressive alternatives.

Game theoretic models suggest that receiver-dependent costs can enforce the reliability of aggressive signals (Enquist, 1985; Adams & Mesterton-Gibbons, 1995; Hurd, 1997). Individuals who inaccurately signal their strength or willingness to fight will be attacked by truly stronger or more motivated individuals, making bluffing an unprofitable strategy. Vehrencamp (2000) applied the idea of receiver-dependent costs to explain the reliability of aggressive singing behaviors in song birds. Signal cost is imposed by a retaliation rule whereby strongly aggressive singing behaviors provoke a stronger aggressive response from receivers (Dabelsteen et al., 1997; Molles & Vehrencamp, 2001; Vehrencamp, 2001). Only signalers that are themselves truly strong or highly aggressive can pay the cost of this more intense aggressive response. In the present study, we test for evidence of a receiver-dependent cost to partial song-matching, a singing behavior that occurs in response to simulated territorial intrusion in eastern song sparrows *Melospiza melodia* (Anderson et al., 2005).

Song type matching occurs when an individual replies to a rival with an identical or highly similar song type (Krebs et al., 1981; McGregor et al., 1992; Stoddard et al., 1992). Krebs et al. (1981) proposed that matching functions as a graded signal of aggression, with matching signaling a higher likelihood of attack to a specific rival. In western song sparrow populations, neighbors frequently share whole song types, making song type matching possible for many or most territory owners (Hill et al., 1999; Wilson et al., 2000). Males match song types in response to playback at levels substantially above chance (Stoddard et al., 1992) and matchers approach the playback speaker more closely than do non-matchers (Vehrencamp, 2001). Further, song type matching playback elicits a stronger aggressive response than non-matching playback (Burt et al. 2001; Vehrencamp, 2001), consistent with the hypothesis that song type matching represents a greater threat, and also with the idea that the reliability of this signal is enforced by a receiver-retaliation rule.

Sharing of whole song types is uncommon in eastern song sparrow populations (Hughes et al., 1998, 2007) making signaling via song type matching difficult if not impossible. Eastern males do share parts of songs; however, song matching via partially shared songs could provide an equivalent strategy to matching of whole song types. We have shown that eastern song sparrow males perform partial song-matching in response to playback, and that birds that partially-matched playback approached the speaker more closely than those that did not match, consistent with the idea that partial-matching is an aggressive signal (Anderson et al., 2005).

In this study, we compare the response of male song sparrows in an eastern population to playback of partially-matching and non-matching songs. Previous studies have tested for receiver-retaliation as we do here, by measuring the mean aggressive response across all subjects (McGregor et al., 1992; Vehrencamp, 2001). A stronger aggressive response to partial-matching than to non-matching playbacks is predicted if the reliability of partial song-matching is enforced by a receiver-retaliation rule. However, models of receiver retaliation (e.g., Enquist, 1985) suggest that only strong, aggressive males will retaliate in response to a strongly aggressive signal, while weaker males may be intimidated. This idea predicts that variability in receiver response will be greater to a strongly aggressive signal compared to a weaker signal. We test this prediction here by comparing variability in response between partial-matching and non-matching playback treatments.

Methods

We tested the responses of 31 male song sparrows to partial-matching and non-matching playbacks between 23 May and 30 June, 2003. Trials were conducted between 0700 and 1030 hours. Our subjects held territories on Pennsylvania State Gamelands and in Pymatuning State Park, in Crawford County, PA, USA. The birds defended territories around the perimeter of fields and lawns, singing from trees and shrubs in hedgerows and interacting principally with neighbors on either side.

Playback stimuli

Each bird received a partial-matching playback and a non-matching (control) playback. Partial-matching playbacks were designed to simulate an intruder that performed a partial song-match to the singing territory owner. Partial-matching playbacks consisted of a self/stranger 'hybrid' song that we created by replacing the introductory trill of a stranger song with the introductory trill from one of the subject's own song types (Figure 1). The non-matching treatment was the unmodified version of the stranger song that was used to construct the subject's hybrid songs. We used introductory trills to construct partial-matching stimuli because males in our Pennsylvania population most commonly share song introductions (Hughes et al., 1998), and because we have recently shown that males in this population perform partial song matches when played a song with a shared introductory trill (Anderson et al., 2005).

To create playback stimuli we first 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 four or five song types in his repertoire. All songs were digitized at 22 050 pts/s and 16-bit resolution, and examined spectrographically at 172.3 Hz frequency resolution and 5.8 ms time resolution using the Syrinx-PC sound analysis program (John Burt, University of Washington, Pullman, WA, USA, available online at <http://www.syrinxpc.com>). From the four or five song types recorded from each male, we chose three 'target' song types to create partially-shared hybrid songs. To make the three hybrid songs for a given male, we used the introductions from the three target song types, substituting each introduction in turn into the same stranger song type (Figure 1). For each subject, only one of the three hybrid songs was used in

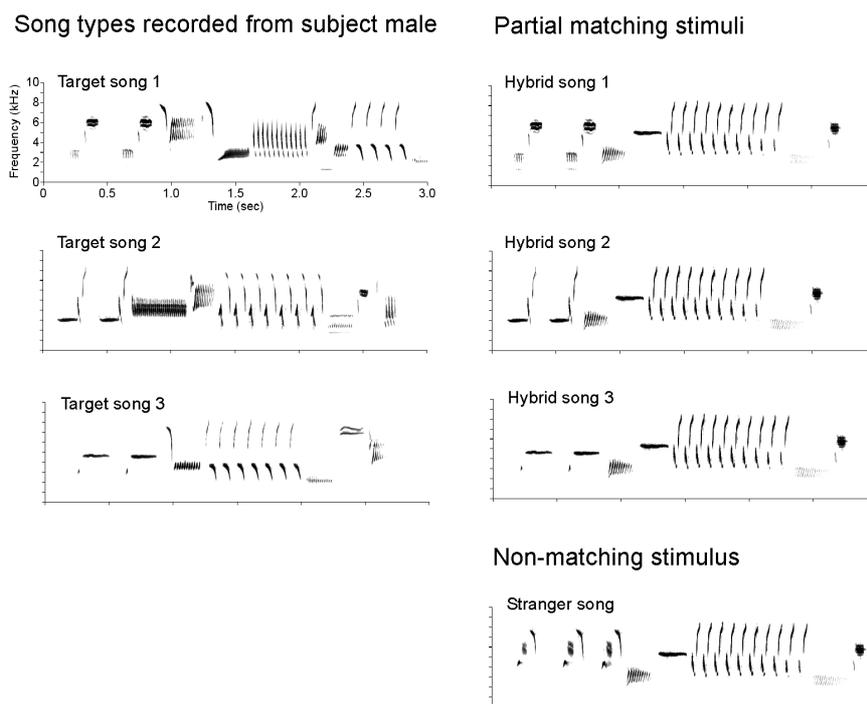


Figure 1. Three hybrid songs constructed for one subject male by removing the introduction of a stranger song and replacing it with the introductions from three of the subject's songs. In this example, Hybrid song 1 was played to partially-match the subject when he sang Target song 1. The Stranger song was the non-matching (control) treatment.

playback. We made three rather than one so that we could match a male without waiting for him to cycle through most of his repertoire before singing a song that we could match. Stranger songs were recorded from males holding territories at least 2 km distant from the subject, and we selected a different stranger song for each subject. Substitution of one song introduction for another was done by digitally cutting and pasting song segments using SIGNAL v.3.1 software (Engineering Design, Berkeley, CA, USA) as described in Anderson et al. (2005).

Playback protocol

One of us (R.A.) ran the trial and recorded data from a distance of approximately 20 m. Prior to each trial, we played a stranger song at 10-s intervals for 1 min to stimulate the subject male to sing. We recorded the subject's own

singing using a Realistic 33-1070B microphone in a Sony PBR-330 parabola connected to a Sony TCM-5000EV tape recorder. The tape recorder's output was connected to the audio input jack of a laptop computer running Syrinx-PC, allowing us to view spectrograms of the subject's songs on a real-time scrolling display. We compared the songs being sung by the subject male to spectrograms of the three hybrid songs we had created. For partial-matching trials, we waited until the subject sang one of the target songs used to construct a hybrid song, and then we partially-matched him by selecting that hybrid song for playback. During non-matching trials, we again waited until the subject sang one of the target songs, and we then began playback of the stranger song used to construct the subject's hybrid songs. In 84% of trials, subject males sang one of the three target songs within two or fewer song type switches. Five trials had to be cancelled and completed on another day because the subject males stopped singing and left the area, or because of interference by non-subject males.

Playbacks were performed using a laptop computer running Syrinx-PC software, connected to a Fender 'AmpCan' speaker/amplifier. The speaker was placed face up on the ground, at the base of a hedgerow, within the subject's territory. In similar studies on song-matching in western song sparrows, playbacks were conducted from outside the subject's territory, from a neighbor's territory or from an unoccupied area (Nielsen and Vehrencamp, 1995; Burt et al., 2001; Vehrencamp, 2001). We chose to place the speaker within the subject's territory because we were specifically interested in testing for a receiver-dependent cost to partial-matching in the form of aggressive retaliation by the subject. This kind of cost requires that the subject approach the singing intruder closely enough to attack him physically, and placing the speaker within the subject's territory allows for such close approach.

We marked the speaker's location during the first trial so that we could use the same placement in the second test. Each playback consisted of one song type (a hybrid or stranger song) presented at 10-s intervals for 3 min, broadcast at approximately 85 dB sound pressure level (SPL) measured at 1 m. We measured playback SPL using a GenRad 1565-D sound level meter (C-weighting, fast setting). Subject males received the experimental and control stimuli in a balanced design, with 16 males receiving the partial-matching (hybrid) playback first, and 15 receiving the control (stranger) playback first. Playbacks to each male were separated by at least 48 h.

Data collection and analysis

Our primary measure of aggressive response was the subject's averaged distance to the playback speaker. Recent data support this practice by showing that proximity to the speaker predicts whether an individual song sparrow male will attack a conspecific mount (Searcy et al., 2006). Each subject's distance to the speaker was recorded at 5-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 m, 2–4 m, 4–8 m, 8–16 m and > 16 m) and distance to the speaker was averaged across playback and post-playback periods following the methods of Peters et al. (1980). Our measures of aggressive response were (1) the mean distance to the speaker during the 3-min playback, (2) the mean distance to the speaker during the 3-min post-playback and (3) the amount of time spent in close proximity to the speaker (< 2 m) during the entire 6-min trial. To test the prediction that aggressive response would differ between partial-matching and non-matching playback conditions, we used paired *t*-tests (two-tailed) to make within-subject comparisons. In addition, we tested whether variation in response differed between the playback conditions using an *F*-test for equality of two variances.

We examined singing responses during partial-matching trials to ask whether birds that persisted in singing the same song type when matched by playback were more aggressive than birds that switched off the partially-matching song type. This relationship is expected if partial-matching is a threat, and was observed for whole song-matching in a western population of song sparrows (Burt et al., 2001). We scored each of the 31 partial-matching trials as to whether the subject continued to sing the song type that was matched by playback ('matchers'), or if the subject switched to a different song type during the 3-min playback ('switchers'). We used independent sample *t*-tests (two-tailed) to compare the average distance to the speaker between matchers and switchers for both the 3-min playback and 3-min post-playback periods.

We recorded each subject's song replies continuously through the 6-min trial using a Sony TCM-5000EV recorder and a Realistic 33-1070B microphone in a Sony PBR-330 parabola. All songs were digitized at 22 050 points/s and 16-bit resolution, and examined spectrographically at 172.3 Hz frequency resolution and 5.8 ms time resolution using Syrinx-PC. We measured song rate and the frequency of switching between song types because

increases in these singing behaviors can increase in aggressive contexts in some songbird species (Falls, 1969; Falls et al., 1982; D'Againcourt & Falls, 1983; Simpson, 1985), including song sparrows (Kramer & Lemon, 1983; Kramer et al., 1985; Searcy et al., 2000). We calculated song rate as the number of songs a subject male sang during the 3 min playback period, and during the 3 min post-playback period. We measured the frequency with which a male switched song types ('switching frequency') as the number of observed song type switches divided by the number of opportunities to switch song types (Searcy et al., 2000). We could not calculate switching frequency for two of the non-matching trials, once because a subject sang only one song during the playback period, and once because a subject sang no songs during the post-playback period. In each case we excluded the subject from analysis, resulting in a sample size of 30 for comparisons of switching frequencies during partial-matching versus non-matching trials. We used paired t-tests to make comparisons of song rate and switching frequency between the two playback types for 3 min playback and 3 min post-playback periods. All statistical tests were conducted using SYSTAT v.11.

Results

Mean distance to the playback speaker did not differ between partial-matching and control playbacks for either the playback or post-playback periods (Figure 2a). Time spent < 2 m from the playback speaker also did not differ between partial-matching and control trials (Figure 2b).

There was a larger variance in the approach response data during control playbacks (var = 6.3) than during partial-matching playbacks (var = 2.9; $F = 0.46$, $df = 30, 30$, $p = 0.04$). However, this difference appears to come largely from an outlier (a very weak response) in the control treatment (Figure 3). In any case, this result goes in the opposite direction of the prediction that response variability should be greater to the more aggressive signal. Response variability did not differ between the playback treatments during the post-playback period (partial-matching variance = 18.1, control variance = 25.9; $F = 0.70$, $df = 30, 30$, $p > 0.33$), nor was there a significant difference in variances for time (s) subjects spent < 2 m to the speaker (partial-matching variance = 10 217.5, control variance = 10 114.5; $F = 1.01$, $df = 30, 30$, $p > 0.97$).

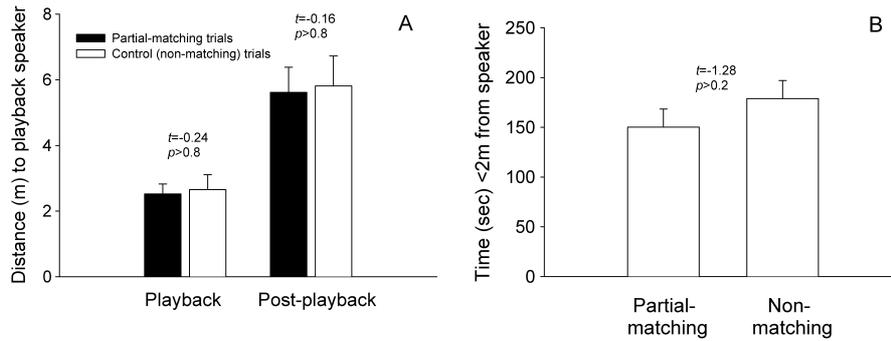


Figure 2. Measures of aggressive response (mean \pm SE) during partial-matching and non-matching (control) trials. Distance data refer to distance between subjects and the playback speaker during 3-min playback and post-playback periods. Values were calculated using means for individual trials averaged across the 31 subjects. Time spent (s) < 2 m from the playback speaker was averaged over the entire 6 min trial. Response measures were compared between partial-matching and control trials using the Wilcoxon matched-pairs signed-ranks test. $p > 0.30$ for all comparisons. $N = 31$ for all tests.

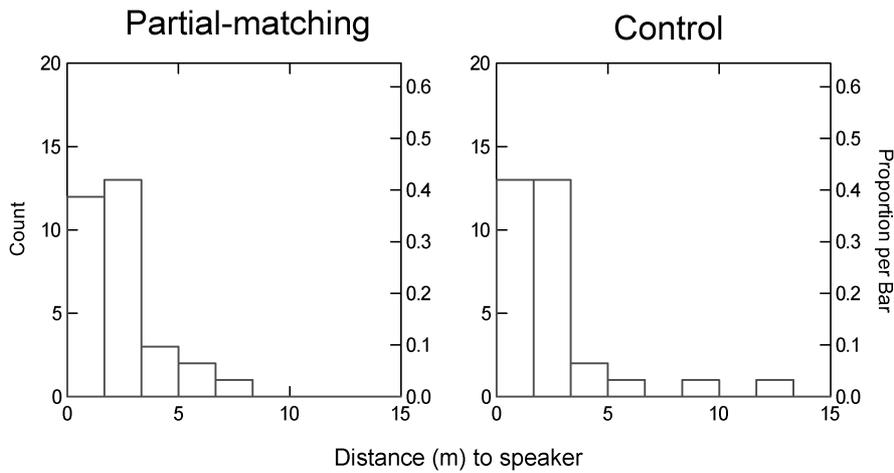


Figure 3. Histograms showing the range of aggressive responses during 3-min partial-matching and control (non-matching) playbacks. $N = 31$ subjects for all trials. Data values are distance to the playback speaker averaged across the playback period for each subject.

There was no difference in song rate during playbacks, nor in song switching frequencies during or following playbacks, between partial-matching and control trials (Table 1). Song rate during the post-playback period was higher

Table 1. Mean \pm SE for song rates and song type switching frequencies for the two playback types during 3-min playback and post-playback periods. Comparisons were made between partial-matching and control trials using paired *t*-tests (two-tailed). Sample sizes in parentheses.

	Partial-matching trials	Control trials	<i>t</i>	<i>p</i>
Song rate playback	5.6 \pm 0.3 (31)	5.5 \pm 0.4 (31)	0.25	>0.80
Song rate post-playback	5.7 \pm 0.3 (31)	4.7 \pm 0.5 (31)	-1.92	=0.06
Switching frequency playback	0.1 \pm 0.0 (30)	0.1 \pm 0.0 (30)	0.79	>0.40
Switching frequency post-playback	0.1 \pm 0.0 (30)	0.1 \pm 0.0 (30)	-1.07	>0.30

Table 2. Measures of aggressive response (mean \pm SE) compared between subjects that continued to sing the partially-matching song during playback vs. subjects that switched to a different song type. Distance data refer to the subjects' distance to the playback speaker. Time spent within 2 m of the speaker was averaged over the entire trial period (3 min playback + 3 min post-playback). Response means were compared using *t*-tests.

	Stayed on matching song (<i>N</i> = 10)	Switched songs (<i>N</i> = 21)	<i>t</i>	<i>p</i>
Distance (m) 3 min playback	2.8 \pm 0.6	2.4 \pm 0.3	0.49	>0.60
Distance (m) 3 min post-playback	8.7 \pm 1.8	4.1 \pm 0.5	2.45	=0.03
Time spent (s) < 2 m of speaker	95.5 \pm 23.3	176.2 \pm 22.5	-2.49	=0.02

following partial-matching playbacks than following control playbacks, although the difference is not significant at the $\alpha = 0.05$ level (Table 1).

Ten subjects (32%) continued to sing the partially-matching song throughout the 3-min playback ('matchers'), whereas 21 subjects (68%) switched to a non-matching song at some point during the playback ('switchers'). Of the 21 switchers, 10 (about 48%) switched off the matching song within the first 60 s of the playback. Matchers and switchers did not differ in their mean distance to the speaker during the 3-min playback period (Table 2). However, switchers were closer to the speaker on average than matchers during the 3-min post-playback period. Switchers also spent more time very close to the speaker (< 2 m) during the 6-min trials than did matchers. We suggest that adjusting α levels due to multiple comparisons is unnecessarily conservative for this analysis; nonetheless, these results should be interpreted with some caution.

Discussion

We found no difference in aggressive response, as measured by approach, to partial-matching versus non-matching songs. The mean approach distances during playback and post-playback periods were nearly identical between the two playback treatments. Our results do not provide support for the idea that there is a receiver-dependent cost to partial song-matching, as would be expected if partial-matching is a signal of aggressive intentions. The time spent close to the playback speaker (< 2 m) does not differ significantly between treatments, and in fact goes in the opposite direction to that predicted by the receiver-dependent cost hypothesis.

In addition, we found no support for the hypothesis that because individuals vary in their motivation and ability to retaliate against an aggressive intruder, one may expect greater variability in aggression in response to a more threatening signal. We did find a marginally greater variance in response during control playbacks than during partial-matching playbacks, but this result opposes the prediction that a more aggressive signal, here partial-matching, should evoke greater variability in response.

Our present results contrast with previous studies of whole song type-matching in song sparrows. Nielsen & Vehrencamp (1995; see also Vehrencamp, 2001) found in a western population that males spent significantly more time within 2 m of a playback speaker when song type matched by stranger song playback. Using the same measure of aggression, and a larger sample size (31 versus 10 subjects), we did not find a more aggressive response to partial song-matching in eastern song sparrows. Our results also contrast with those of Burt et al. (2001), who found a stronger aggressive response to a neighbor's whole song type match than to a neighbor's repertoire match (a shared but non-matching song) in western song sparrows. These authors used a composite aggression score including closest approach to the speaker, number of flights, and number of visual displays. Here again, we used a comparable measure of aggressive response but did not detect a differential response to partial song-matching versus non-matching. Thus, the more aggressive response to whole song type matching in western song sparrows does not appear to extend to partial song-matching in our eastern population.

One possible explanation for the difference between our results and those of other studies is that we used partial-matching song stimuli rather than

whole song-matching stimuli. Perhaps the birds in our study did not detect that they were being matched because the partial-matching stimulus heard by each male matched only the introductory trill of his song. We think this explanation is unlikely for two reasons. First, Horning et al. (1993) showed in a laboratory study that introductory elements are particularly salient to song type classification by male song sparrows. Second, previous field studies on partial song-matching in song sparrows (Horning et al., 1993; Anderson et al., 2005) and Burt et al.'s (2002) study of 'broad sense matching' in a western population, have shown that song sparrow males will perform partial song matches in response to playback songs that share only introductory song elements in common. In fact, in our previous study in the same Pennsylvania population (Anderson et al., 2005), matching replies were similar in response to partially-shared songs and wholly-shared songs. If song sparrow males are able to perceive shared introductory trills and perform partial or broad sense song matches at rates much greater than chance, we think it unlikely that they would fail to detect a partial-match when played a song with an identical introduction.

Another possibility is that a partial-match is detected but is interpreted as less threatening than a whole song-match. Burt et al. (2001) proposed that repertoire matching (replying to a rival with a shared but non-matching song type) is perceived as less threatening than whole song-matching in a Washington song sparrow population. Whole song-matching in our eastern population is precluded by low levels of song sharing among territory neighbors, but this does not exclude the possibility that partial-matching communicates a moderate threat analogous to repertoire-matching in western populations.

Another contrast between our study and studies of western song sparrows is a difference in the placement of the playback speaker during trials. We placed the speaker well within the subject's territory to simulate an unfamiliar intruder. Burt et al. (2001), Nielsen & Vehrencamp (1995) and Vehrencamp (2001) conducted playbacks from a neighbor's territory or from an unoccupied area outside the subject's territory. One possibility is that placing the speaker within the subject's territory evoked a ceiling effect; the birds gave their strongest aggressive response to both stimuli, overruling any differences in the effect of the treatment. The birds' approach data argue against this idea, however. The procedure used to obtain average distance values for each subject results in a lowest possible value of 1.0 m. A subject with an average distance near 1.0 m has spent nearly the entire trial period very close

to the speaker (< 2 m), and this level of response has been observed in other playback experiments with this population (Anderson, 2006). Most subjects did not respond at this level, however: only 17 of 31 subjects had a distance value less than 2 m during the playback period, and only 2 of 31 subjects had values less than 2 m during the post-playback period. A similar explanation is that the playbacks may not have evoked a ceiling effect *per se*, but that the subjects did not discriminate between the playback treatments because the simulated intruder was inside the subject's territory and was perceived as threatening regardless of his singing behavior. We cannot rule out this possibility. However, we think this an unlikely explanation because we have shown significantly different aggressive responses to playback treatments in numerous previous experiments with song sparrows using the same methods used here (Searcy et al., 1997, 2000, 2002; Nowicki et al., 2001; Anderson et al., 2005). Further, we argue that placing the playback speaker within the subject's territory, rather than placing it on a neighbor's territory, allows for a more direct test for a receiver-retaliation cost. Simulating a singing intruder within the territory allows for close approach by the defending subject, and a meaningful receiver-dependent cost requires that the defender approach closely enough to physically attack the intruder. We conclude that a ceiling effect in aggressive response is not a likely explanation for the lack of difference in response to partial-matching and non-matching stimuli in this study.

Burt et al. (2001) predicted that if song-matching is a threat, then "A bird choosing to de-escalate in response to a song type match should switch off the matching song type, whereas one choosing to escalate should stay on the matching song type". In Burt et al.'s playback study, 40% of males responded to a song type match by singing that song type for the duration of the 3-min playback period. Males that continued to match had significantly higher aggression scores than males that switched off the matching song. In our study, a similar proportion of birds (32%) continued to sing the partially-matching song. However, we found that aggressive response was, if anything, stronger in males that switched off the matching song than in males that continued to match. For the post-playback period, mean distance to the speaker for switchers was less than half of the mean distance for matchers (Table 2). Increased song type switching has been proposed as an aggressive signal in the song sparrow, and song type switching frequencies can increase in agonistic contexts (Kramer & Lemon, 1983; Kramer et al., 1985; Searcy et al.,

2000). Rapid song type switching provokes closer approach to the playback speaker by territorial males compared to a lower switching rate (Nielsen & Vehrencamp, 1995). For a male that is matched by another, continued matching and song type switching are mutually exclusive behaviors — a male that performs one cannot perform the other. Perhaps, then, the more aggressive males in our population on average choose to switch song types, leaving continued matching to the less aggressive males (see Mennill & Ratcliffe, 2004). This argument aside, our results do not support the prediction that continued song-matching should be associated with a stronger aggressive response than switching off the matching song.

Although we found no evidence of a stronger aggressive response to partial-matching songs, the results presented here do not allow for a complete rejection of the hypothesis that partial-matching may be a signal of aggressive intentions. Further studies of behaviors that are associated with partial-matching, and how receivers respond to partial-matching in different contexts, may help to clarify the function of this behavior. We suggest, however, that the available evidence best supports the idea that partial song-matching functions as a signal of attention. Brémond (1968) originally proposed that song-matching is a way of directing a reply to a particular individual. A signal of this type could function as a low-risk mechanism of avoiding a more escalated encounter with a rival by signaling awareness of, and attention to, that specific individual, without a close approach or other risky directed display. The attention hypothesis can explain the observed decline in the incidence of partial song-matching across the breeding season (Anderson et al., 2005) if males become occupied with parental behaviors and pay less attention to intruders or neighbors as the season progresses. This hypothesis also helps to explain why the average aggressive response is higher for birds that partial-match in response to a simulated intruder (Anderson et al., 2005). Males that are paying attention to an intruder are expected to be more aggressive on average than males that are not paying attention. Also, a male cannot partial-match in response to another singer at above chance levels unless he is paying attention to the singer, so if attention is all that is being communicated, the signal cannot be cheated upon. Thus, it is not necessary to invoke a cost to explain the honesty of the signal, which may help to explain why we found no evidence of a receiver-retaliation rule in response to partial song-matching in our study.

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References

- Adams, E.S. & Mesterton-Gibbons, M. (1995). The cost of threat displays and the stability of deceptive communication. — *J. Theor. Biol.* 175: 405-421.
- Anderson, R.C. (2006). Song as an aggressive signal in the song sparrow *Melospiza melodia*. — Doctoral dissertation, University of Miami, Coral Gables, FL.
- Anderson, R.C., Searcy, W.A. & Nowicki, S. (2005). Partial song-matching in an eastern population of song sparrows, *Melospiza melodia*. — *Anim. Behav.* 69: 189-196.
- Bremond, J.C. (1968). Recherches sur la semantique et les elements vecteurs d'information dans les signaux acoustiques du rouge-gorge (*Erithacus rubecula* L.). — *Terre Vie* 2: 109-220.
- Burt, J.M., Bard, S.C., Campbell, S.E. & Beecher, M.D. (2002). Alternative forms of song-matching in song sparrows. — *Anim. Behav.* 63: 1143-1151.
- Burt, J.M., Campbell, S.E. & Beecher, M.D. (2001). Song type matching as a threat: a test using interactive playback. — *Anim. Behav.* 62: 1163-1170.
- Dabelsteen, T., McGregor, P.K., Holland, J., Tobias, J.A. & Pedersen, S.B. (1997). The signal function of overlapping singing in male robins. — *Anim. Behav.* 53: 249-256.
- D'Againcourt, L.G. & Falls, J.B. (1983). Variation of repertoire use in the eastern meadowlark, *Sturnella magna*. — *Can. J. Zool.* 61: 1086-1093.
- Dawkins, R. & Krebs, J.R. (1978). Animal signals: information or manipulation? — In: *Behavioural ecology* (Davies, N.B. & Krebs, J.R., eds). Blackwell Scientific, Oxford, p. 282-309.
- Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behavior. — *Anim. Behav.* 33: 1152-1161.
- Falls, J.B. (1969). Functions of territorial song in the white-throated sparrow. — In: *Bird vocalizations* (Hinde, R.A., ed.). Cambridge University Press, Cambridge, p. 207-232.
- Falls, J.B., Krebs, J.R. & McGregor, P. (1982). Song-matching in the great tit (*Parus major*): the effect of similarity and familiarity. — *Anim. Behav.* 30: 997-1009.
- Grafen, A. (1990). Biological signals as handicaps. — *J. Theor. Biol.* 144: 517-546.
- 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*). — *Behav. Ecol. Sociobiol.* 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. — *Behav. Ecol. Sociobiol.* 42: 437-446.

- Hughes, M., Anderson, R.C., Searcy, W.A., Bottensek, L.A. & Nowicki, S. (2007). Song type sharing and territory tenure in eastern song sparrows: implications for the evolution of song repertoires. — *Anim. Behav.* 73: 701-710.
- Hurd, P.L. (1997). Is signaling of fighting ability costlier for weaker individuals? — *J. Theor. Biol.* 184: 83-88.
- Kramer, H.G. & Lemon, R.E. (1983). Dynamics of territorial singing between neighbouring song sparrows *Melospiza melodia*. — *Behaviour* 85: 198-223.
- Kramer, H.G., Lemon, R.E. & Morris, M.J. (1985). Song switching and agonistic stimulation in the song sparrow (*Melospiza melodia*) — 5 Tests. — *Anim. Behav.* 33: 135-149.
- Krebs, J.R., Ashcroft, R. & Van Orsdol, K. (1981). Song-matching in the great tit *Parus major* L. — *Anim. Behav.* 29: 918-923.
- Maynard Smith, J. (1979). Game theory and the evolution of behaviour. — *Proc. Roy. Soc. Lond. B Biol.* 205: 475-488.
- McGregor, P.K., Dabelsteen, T., Shepherd, M. & Pedersen, S.B. (1992). The signal value of matched singing in great tits: evidence from interactive playback experiments. — *Anim. Behav.* 43: 987-998.
- Mennill, D.J. & Ratcliffe, L.M. (2004). Overlapping and matching in the song contests of black-capped chickadees. — *Anim. Behav.* 67: 441-450.
- Molles, L.E. & Vehrencamp, S.L. (2001). Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. — *Proc. Roy. Soc. Lond. B Biol.* 268: 2013-2019.
- Naguib, M. (1999). Effects of song overlapping and alternating on nocturnally singing nightingales. — *Anim. Behav.* 58: 1061-1067.
- Nielsen, B.M.B. & Vehrencamp, S.L. (1995). Responses of song sparrows to song-type matching via interactive playback. — *Behav. Ecol. Sociobiol.* 37: 109-117.
- Nowicki, S., Searcy, W.A., Hughes, M. & Podos, J. (2001). The evolution of bird song: male and female response to song innovation in swamp sparrows. — *Anim. Behav.* 62: 1189-1195.
- Oberweger, K. & Goller, F. (2001). The metabolic cost of birdsong production. — *J. Exp. Biol.* 204: 3379-3388.
- Peters, S., Searcy, W.A. & Marler, P. (1980). Species song discrimination in choice experiments with territorial male swamp and song sparrows. — *Anim. Behav.* 28: 393-404.
- Searcy, W.A., Anderson, R.C. & Nowicki, S. (2006). Bird song as a signal of aggressive intent. — *Behav. Ecol. Sociobiol.* 60: 234-241.
- Searcy, W.A., Hughes, M. & Nowicki, S. (1997). The response of male and female song sparrows to geographic variation in song. — *Condor* 99: 651-657.
- Searcy, W.A., Nowicki, S. & Hogan, C. (2000). Song type variants and aggressive context. — *Behav. Ecol. Sociobiol.* 48: 358-363.
- Searcy, W.A., Nowicki, S., Hughes, M. & Peters, S. (2002). Geographic song discrimination in relation to dispersal distances in song sparrows. — *Am. Nat.* 3: 221-230.
- Shackleton, S.A. & Ratcliffe, L. (1994). Matched counter-singing signals escalation of aggression in black-capped chickadees (*Parus atricapillus*). — *Ethology* 97: 310-316.
- Simpson, B.S. (1985). Effects of location in territory and distance from neighbors on the use of song repertoires by Carolina wrens. — *Anim. Behav.* 33: 793-804.
- Stoddard, P.K., Beecher, M.D., Campbell, S.E. & Horning, C.L. (1992). Song-type matching in the song sparrow. — *Can. J. Zool.* — *Rev. Can. Zool.* 70: 1440-1444.
- Vehrencamp, S.L. (2000). Handicap, index, and conventional signal elements of bird song. — In: *Animal signals: signaling and signal design in animal communication* (Espmark, Y., Amundsen, T. & Rosenquist, G., eds). Tapir Academic Press, Trondheim, p. 277-300.

- Vehrencamp, S.L. (2001). Is song-type matching a conventional signal of aggressive intentions? — *Proc. Roy. Soc. Lond. Ser. B Biol.* 268: 1637-1642.
- Ward, S., Lampe, H.M. & Slater, P.J.B. (2004). Singing is not energetically demanding for pied flycatchers, *Ficedula hypoleuca*. — *Behav. Ecol.* 15: 477-484.
- 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.
- Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). — *J. Theor. Biol.* 67: 603-605.
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