



A test of a hierarchical signalling model in song sparrows



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Hierarchical signalling may be a common adaptation for aggressive signalling. In this strategy an animal progresses through a series of discretely different signals of escalating level of threat before eventually proceeding to physical aggression. A model of such hierarchical aggressive signalling has been proposed for song sparrows, *Melospiza melodia*, in which a core part of the sequence is: song type match → soft song → attack. The model predicts that song type matching is a strong predictor of soft song, but only a weak predictor of attack. We used a two-part playback design to test these predictions, with an initial edge playback from just off the subject's territory using a song type that the subject could match, followed by a centre playback from a speaker placed well within the territory. Each male was tested twice with this design. We found that matching the edge playback did not predict soft song production at the centre. A second strong threat, wing waving, was actually negatively associated with matching. Matching the edge playback also was not associated with physical measures of aggression such as approach and latency to approach. Thus, this particular model of hierarchical aggressive signalling was not supported for our study population. Song type matching in our study population may have some function not associated with aggressive signalling to the matched individual, or no function at all.

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Many animals possess multiple aggressive displays (Hazlett & Bossert 1965; Andersson 1980; Waas 1990; Bradbury & Vehrencamp 2011). A logical explanation for the evolution of multiple, seemingly redundant threat displays is that each communicates a different level of aggressive intention, so that the repertoire as a whole allows for a graded series of threats. A simple extension of this hypothesis is that animals tend to progress upwards through such a graded series as an aggressive encounter continues, successively switching to displays that are more and more reliable as predictors of attack. A functionally similar outcome can be accomplished by varying properties of a single display, as cricket frogs, *Acris crepitans*, do by lengthening their calls (Wagner 1989). We reserve the term 'hierarchical signalling' for cases in which animals escalate aggressive signalling using a progression of discretely different signals. Here we test a specific model of hierarchical signalling proposed for song sparrows, *Melospiza melodia*, by Beecher and colleagues (Beecher & Campbell 2005; Searcy & Beecher 2009; Akçay et al. 2013).

Various animals have been suggested to employ a hierarchy of aggressive signals, including mammals (Clutton-Brock & Albon 1979; Bartos et al. 2007), birds (Popp 1987; Waas 1991a, b), insects (Chen et al. 2002; Egge et al. 2011) and spiders (Fowler-Finn & Hebets 2006). Red deer, *Cervus elaphus*, provide a classic example. Two displays are especially prominent during aggressive contests between red deer stags: roars and parallel walks. Typically, roars lead into parallel walks, and parallel walks lead into fights (Clutton-Brock & Albon 1979). A similar system has been described for fallow deer, *Dama dama*, with groans substituted for roars, and here it has been explicitly shown that both displays predict aggression, with one (parallel walks) being a stronger predictor than the other (Bartos et al. 2007). Another classic example involves little blue penguins, *Eudyptula minor*. Among a large variety of agonistic displays given by these birds (Waas 1990, 1991b), two vocalizations, growls and hisses, appear to form a hierarchy of threat. When confronted with a model penguin at their burrows, lone males that give growls are more likely to attack than males that remain silent, and males that give hisses are more likely to attack than those that growl (Waas 1991a). Thus hisses are a more reliable threat than growls.

The model of hierarchical aggressive signalling in song sparrows emerged from work by Beecher and colleagues on matching behaviours. In song type matching, one individual replies to another

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with the song type that the latter has just sung. Matching at above chance levels has been demonstrated for a number of species of songbirds (Hinde 1958; Falls 1985; Rogers 2004; Burt & Vehrencamp 2005; Gammon et al. 2008; Price & Yuan 2011) and has been suggested to be an aggressive signal (Krebs et al. 1981). Stoddard et al. (1992) found that western song sparrows matched playback of self song types and shared stranger song types at frequencies far above chance levels. Sharing of whole song types is more frequent in western populations of song sparrows (Hill et al. 1999; Wilson et al. 2000) than in eastern ones (Hughes et al. 1998; Stewart & MacDougall-Shackleton 2008), but eastern individuals are nevertheless able to interact through matching by using partially shared song types (Hughes et al. 1998; Burt et al. 2002; Anderson et al. 2005). Some evidence suggests that type matching is an aggressive signal in song sparrows: males are more likely to match stranger than neighbour songs (Stoddard et al. 1992) and are in general more aggressive towards strangers than neighbours (Stoddard et al. 1990); males are more likely to match neighbours early in the breeding season when relationships are more aggressive than later when relationships are more relaxed (Beecher et al. 2000); and males that stay on a type match in response to playback show stronger aggressive reactions than males who switch to a different song type or stop singing (Burt et al. 2001; Akçay et al. 2013).

In a second matching behaviour, termed 'repertoire matching' by Beecher et al. (1996), one male replies to another not with the song type that the other has just sung, but with another shared song type. Beecher et al. (1996) found that male song sparrows reply to playback of neighbour song with a shared song type at much higher than expected frequencies, regardless of whether the playback song is itself shared. Male song sparrows respond less aggressively to playback of a repertoire match than to playback of a song type match (Burt et al. 2001), suggesting that a repertoire match is a lower level of threat than is a type match. Beecher & Campbell (2005) showed that song sparrows de-escalate more quickly in response to playback of unshared songs than to a repertoire match, implying that singing an unshared song is an even lower level of threat than is repertoire matching. Together these results suggest a hierarchical system with three levels of threat (Beecher & Campbell 2005): unshared song → repertoire match → song type match.

One problem with this model is that evidence is equivocal on whether even the highest level of threat in the hierarchy actually predicts physical aggression. Although type matching has been positively correlated with aggressive measures such as approach to a playback speaker in some studies (Burt et al. 2001; Vehrencamp 2001), in others no such correlations were found (Beecher et al. 2000; Anderson et al. 2005). In a study of eastern song sparrows, Searcy et al. (2006) found that type matching did not predict attack on a taxidermic mount: 19.5% of 41 males that matched attacked the mount, compared with 22.2% of 54 males that did not match. In contrast, production of low-amplitude soft songs proved to be a strong predictor of attack, as has since been found in other songbirds as well (Ballentine et al. 2008; Hof & Hazlett 2010).

The confluence of the soft song and matching results led to an expanded model of hierarchical signalling in song sparrows (Searcy & Beecher 2009). Here the basic progression of escalation is hypothesized to be: unshared song → repertoire match → type match → soft song → attack. The full progression could only be used in signalling to others whose repertoires are known by the subject; strangers would have to be dealt with using the latter part of the progression: type match → soft song → attack. Under this hypothesis, type matching is an aggressive signal, in that it predicts aggressive escalation, but it is only a weak predictor of attack,

weaker in particular than soft song. Matching should instead be a strong predictor of an escalation in aggressive signalling, and specifically of soft song production.

Here we test the hierarchical signalling hypothesis using a two-part playback design. The first part consists of playback of a shared song type from just outside a subject's territory. This 'edge playback' gives the subject an opportunity to type match, but does not allow close approach to the speaker. Once the subject has replied to the edge playback, playback switches to a second speaker placed well within the subject's territory. This 'centre playback' gives the subject the opportunity to approach the speaker and produce soft songs. The hierarchical signalling model predicts that type matching of the edge playback should be associated with higher soft song production for the centre playback.

METHODS

The experiment was carried out in Crawford County, Pennsylvania, U.S.A., during May and June of 2011 and 2012. The study was approved by the Institutional Animal Care and Use Committee of the University of Miami (Protocol 11-073). Subjects were 40 male song sparrows holding territories on the edges of old fields in state gamelands and mown lawns in parks. Prior to playback trials we mapped territories and recorded partial repertoires from each subject (with a Marantz 660 digital recorder and a Realistic omnidirectional microphone in a Sony Parabolic Reflector-330). Males were identified during playback trials using previously applied colour bands ($N = 10$), or by using spectrograms to determine whether whole songs given during trials were found in our prior recordings ($N = 27$). A small subset ($N = 3$) did not have identities confirmed by either method, but in this population territories remain stable during the height of the breeding season (Hughes & Hyman 2011), so territorial males can also reliably be identified by location.

We tested males with a two-part playback design in which they were first presented with a short bout of song playback at the edge of their territories, providing an opportunity to song type match, followed by playback at the centre of the territory, providing an opportunity to produce soft song and other aggressive behaviours. The design simulated an intrusion by one male onto another's territory; such intrusions are fairly common in song sparrows (Akçay et al. 2012) and often involve the intruder singing both before and during the intrusion (Kramer & Lemon 1983; Bower 2000). The first part of the playback trial consisted of a single song type from the male's own repertoire broadcast repeatedly from just outside the subject's territory: the 'edge playback'. Male song sparrows typically sing with 'eventual variety', repeating one song type many times before switching to another (Nowicki et al. 1994). The playback stimulus was recorded from the subject male to guarantee that the subject could potentially type match the edge playback. Response to self songs in song sparrows is similar to response to stranger song both in terms of matching (Stoddard et al. 1992) and aggression (Searcy et al. 1981), and self songs have been used extensively in prior experiments on matching in song sparrows (Stoddard et al. 1992; Anderson et al. 2005; Akçay et al. 2011, 2013). Playback songs were stored as WAV files and broadcast at a rate of six songs/min at 83–87 dB SPL (measured with a B&K Precision 32A sound level meter) using an iPod Touch and an iMainGo X portable speaker. During playback the speaker was housed in an open box lined with polyurethane composite foam (Acoustical Surfaces, Inc., Chaska, MN, U.S.A.), with the open end directed towards the subject's territory. This set-up reduced the amplitude of the playback behind and to the sides of the speaker, lowering responses by males other than the subject. If the subject did not

sing in response to the edge playback, he was given a 1 min period of silence, after which the edge playback was repeated (up to two additional times). Subjects met the response criterion for the edge playback after having been played a mean of nine songs (range 2–36). If no song was given after three edge playbacks, the trial was abandoned. If a trial was abandoned, a second attempt was made to test the subject on a subsequent day. A second attempt to test a subject failed once.

If the subject sang in response to the edge playback (a minimum of two songs), then the edge playback was immediately stopped, and the 'centre playback' began. During the 5 min centre playback portion of the trial, song was broadcast from an iPod Touch connected by cable to a Nagra DSM loudspeaker situated near the centre of the subject's territory (six songs/min, again at 83–87 dB SPL). Subjects were thus played an edge and a centre playback together, for a mean of 38 songs of one song type. A bout of 38 songs is longer than the mean natural bout length (Kramer & Lemon 1983; Nowicki et al. 1994) but within the natural range we have observed in this population (S. Peters & S. Nowicki, unpublished data). Two observers stood 15–20 m from the speaker. One observer (W.A.S.) narrated the subject's behaviour and location. Spoken narration and subject songs were recorded by the second observer (again with a Marantz 660 digital recorder, Realistic omnidirectional microphone, and Sony Parabolic Reflector-330). Behaviours noted included broadcast songs, soft songs and wing waves. Wing waving is the visual display most closely associated with aggression in song sparrows (Searcy et al. 2006; Akçay et al. 2013). Our accuracy in classifying songs as soft in the field has been confirmed previously by playback of songs at known amplitudes (Searcy et al. 2006) and by amplitude measurements of naturally produced song (Anderson et al. 2008). The observer also estimated the subject's distance from the speaker (henceforth approach distance) and noted the subject's latency to approach within 8 m. Flagging markers set at 2 m, 4 m and 8 m in either direction from the speaker facilitated estimation of approach distance.

Recordings were subsequently reviewed and the narration transcribed onto data sheets divided into 10 s intervals. To calculate approach distance, we assumed males in the 0–2 m range were 1 m from the speaker, in the 2–4 m range 3 m, in the 4–8 m range 6 m, in the 8–16 m range 12 m, and in the >16 m range 24 m (see Peters et al. 1980). Distances were averaged over the centre playback period. Spectrograms produced in SYRINX (J. M. Burt, www.syrinxpc.com) were used to determine whether subjects had matched the edge playback and, if so, whether they had stayed on the match during centre playback.

Each male was tested twice with both edge and centre playbacks, with 6–20 days between the first and second trials. Part of the rationale for testing subjects twice was to give each subject two opportunities to match, in order to allow a test of individual consistency in matching (Anderson et al. 2005) and in aggressive behaviours. Using two trials also allowed within-subjects comparisons of behaviour after matching and after not matching for those individuals whose matching behaviour was not consistent. During their second trials, males received a different playback song, again from their own repertoire.

To test whether matching occurred more frequently than expected by chance, we compared observed frequency of matching separately for first and second trials to the expected chance frequency using chi-square tests. As the chance frequency, we used 0.125, which is the frequency that males replied with a target song type in control playback trials in a previous matching experiment in our population (Anderson et al. 2005) and which approximates the inverse of the mean repertoire size (Peters et al. 2000). To test for consistency in matching, we compared the number of males

matching on both trials, matching on one trial and not the other, and not matching on both to the expected numbers calculated using the observed frequency of matching on first and second trials. Consistency in soft song production and approach distance across the two trials per individual was tested with Spearman correlation coefficients (r_s).

We used linear mixed models to test associations between matching in response to edge playback and five measures of response to centre playback: number of soft songs, number of broadcast songs, number of wing-waving bouts, mean approach distance and latency to approach to within 8 m. The first three variables are count data, with distributions that are approximately Poisson. We analysed these three variables with generalized linear mixed models in the R package lmer4, using a Poisson distribution, a logarithmic link and LaPlace estimation (Bolker et al. 2008). The distance and latency variables were continuous, and for these we used linear mixed effects models in the R package nlme, which assume a normal distribution. In all cases, matching (matching versus nonmatching) was entered as a fixed effect and subject identity as a random effect. To control for trial order, order was entered as a fixed effect. Some previous work (Burt et al. 2001; Akçay et al. 2013) has suggested that the threatening aspect of matching is staying on the match when the encounter escalates. Accordingly, we performed a second analysis splitting males that matched the edge playback into those that stayed on the match for at least the first song given in reply to the centre playback and those that switched off the match at or before this point. In these analyses we used the same statistical models, but expanded the matching variable to three categories: nonmatchers, matchers who stayed on match for the centre playback, and matchers who switched off the match at the start of the centre playback. All tests were two tailed. Following the advice of Zuur et al. (2009), we are cautious in interpreting *P* values from generalized linear mixed models that were near 0.05.

RESULTS

In first trials, 21 of 40 males matched the edge playback. The frequency of matching (0.525) significantly exceeded chance levels ($\chi^2 = 58.5$, $P < 0.0001$). In second trials, 13 of 39 males matched the edge playback. The frequency of matching (0.333) was lower than in first trials, but was still significantly above chance levels ($\chi^2 = 15.5$, $P < 0.0001$). Individuals were not consistent in matching across their two trials: of the 39 males tested successfully twice, eight matched on both trials, 18 matched on one trial but not the other, and 13 matched on neither trial. These numbers were not significantly different from random expectations (6.8, 19.8 and 12.4) calculated assuming that a male that matches on the first trial is equally likely as a nonmatcher to match on the second trial ($\chi^2 = 0.404$, $P = 0.82$). In contrast, males were consistent across their two trials in soft song production ($r_s = 0.71$, $N = 39$, $P < 0.0001$), wing waves ($r_s = 0.52$, $N = 39$, $P < 0.001$) and approach distance ($r_s = 0.48$, $N = 39$, $P = 0.002$).

Matching the edge playback was not associated with greater production of soft song at the centre. The distribution of the number of soft songs given when males matched was very similar to the distribution of soft songs given when they did not match (Fig. 1a). In the GLMM analysis the effect of matching on soft song went very slightly in the direction counter to prediction (i.e. fewer soft songs by matchers), but was very close to 0, with a *P* value very close to 1 (Table 1). Males gave fewer broadcast songs when they matched than when they did not match (Fig. 1b), but the *P* value in the GLMM analysis was somewhat marginal (Table 1). Subjects also gave fewer wing waves when they matched than when they did not

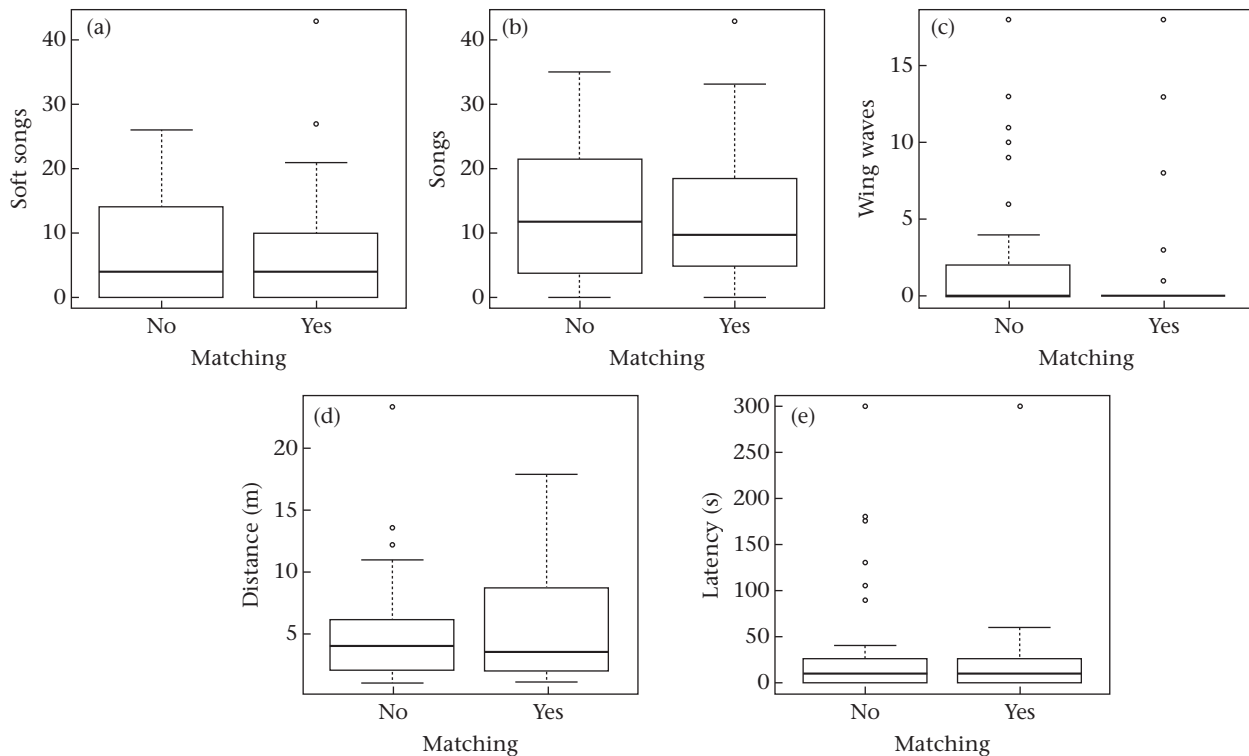


Figure 1. Male song sparrows that did and did not match the edge playback compared for five behaviours in response to centre playback: (a) soft songs, (b) broadcast songs, (c) wing waves, (d) distance and (e) latency. Dark lines are medians, boxes show 25th and 75th percentiles, the whiskers are defined by 1.5X the interquartile range, and circles are points that lie outside the whiskers.

match (Fig. 1c), and here the statistical analysis strongly supported the difference.

Matching the edge playback also was not associated with non-signalling measures of aggressive response. The effect of matching on distance to the speaker was slightly in the direction opposite to prediction, with a greater distance and thus lower aggressive response when males matched, but the effect was not significant (Fig. 1d, Table 1). Matching had virtually no association with latency to respond (Fig. 1e, Table 1).

Splitting the matchers into those that stayed on the match and those that switched off the match did not change the results. Matching and staying on the match was not associated with greater production of soft songs (Fig. 2a, Table 2), nor with greater production of broadcast songs (Fig. 2b, Table 2). Matching and staying on the match was associated with significantly lower production of wing waves (Fig. 2c, Table 2). Matching and staying on the match had no significant association with distance to the speaker (Fig. 2d, Table 2) and also no association with latency to respond (Fig. 2e, Table 2).

Table 1
Effects of song type matching in response to edge playback on behaviours of song sparrows during centre playback

	Estimate	Test statistic	<i>P</i>
Soft song	-0.004±0.142	<i>z</i> =-0.026	0.979
Broadcast song	-0.0198±0.088	<i>z</i> =-2.263	0.024
Wing waves	-1.017±0.290	<i>z</i> =-3.502	0.0005
Distance	1.027±0.916	<i>t</i> =1.121	0.270
Latency	-0.009±12.67	<i>t</i> =-0.001	0.999

Sample sizes for each dependent variable are 40 subjects and 79 trials. Trial order was controlled by entering order as a covariate.

DISCUSSION

In the hierarchical model of aggressive signalling in song sparrows (Searcy & Beecher 2009), song type matching is hypothesized to lead to soft song, and soft song to attack. The model generates two predictions with regard to type matching: type matching should be a strong predictor of soft song and a weak predictor of attack. The first prediction was not supported in this study: matching the edge playback did not predict soft song production in response to the centre playback. Matching also did not predict production of wing waving, the other signal that can be interpreted as a reliable threat. In addition, we found no individual consistency in tendency to type match: males that matched on one trial were no more likely than nonmatchers to match on a second trial. Anderson et al. (2005) also found no individual consistency in matching in the same population. In contrast, we found that individuals were consistent in the number of soft songs given on first and second trials, and earlier evidence showed consistency in the proportional use of soft song in successive playback trials (Searcy & Nowicki 2006). Given that eastern males show no consistency in their type matching response and yet are individually consistent in their use of soft song, a consistent association between matching and soft song seems logically unlikely.

The second prediction of the model is that song type matching should be a weaker predictor of attack than is soft song, but nevertheless should be associated with aggression. We took two measures of aggressive response in addition to soft song: distance to the speaker and wing waves. Distance to the speaker is an excellent predictor of attack in song sparrows (Searcy et al. 2006), while wing waving is weakly associated with attack in eastern song sparrows (Searcy et al. 2006) and more strongly associated with attack in western song sparrows (Akçay et al. 2013). Song type

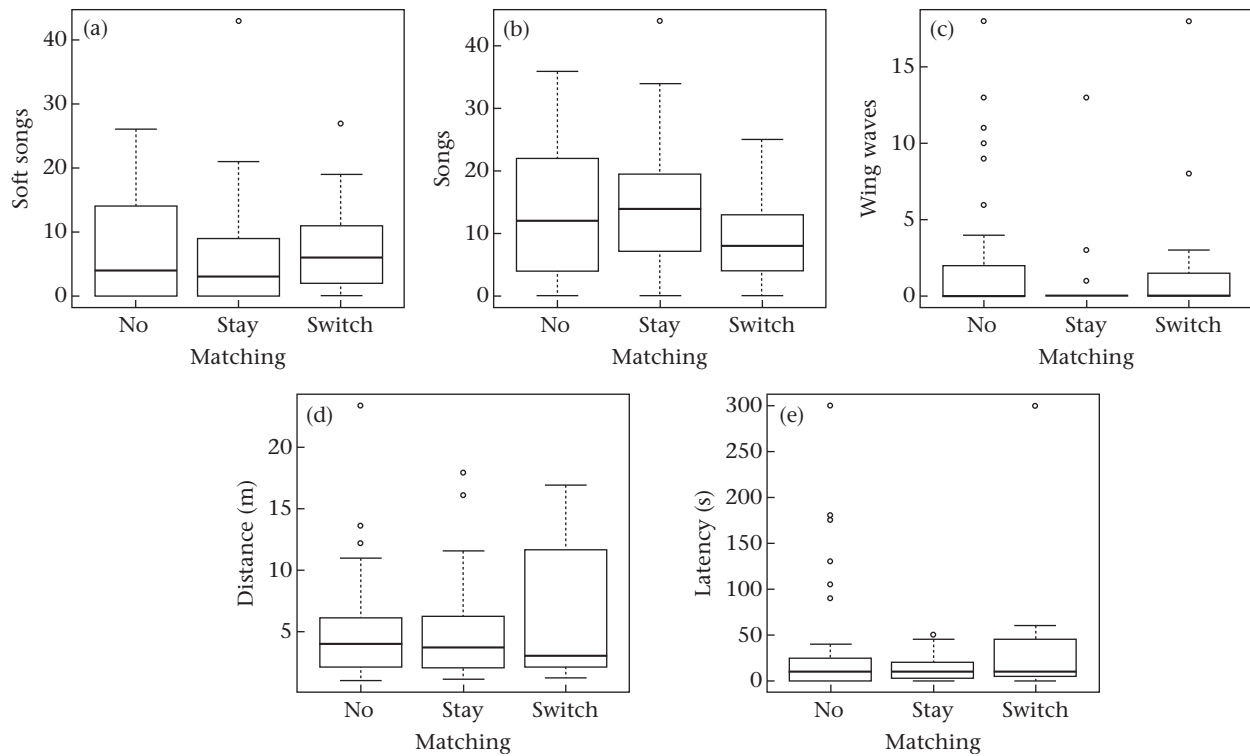


Figure 2. Male song sparrows that did not match (no), that matched and stayed on match (stay) and that matched but switched off the match (switch) compared for five behaviours in response to centre playback: (a) soft songs, (b) broadcast songs, (c) wing waves, (d) distance and (e) latency. Dark lines are medians, boxes show 25th and 75th percentiles, the whiskers are defined by 1.5X the interquartile range, and circles are points that lie outside the whiskers.

matching in our results was associated with neither approach nor wing waves. Thus the second prediction of the model was also negated.

Some evidence from western song sparrows suggests that staying on a type match as an encounter escalates is a more threatening signal than simply type matching in the first place (Burt et al. 2001; Akçay et al. 2013). In our data, however, males that matched and then stayed on the match did not give more soft songs and were not more aggressive on other measures than were males that matched and switched off the match, or than males that never matched at all. Thus focusing on individuals that stayed on a match does not rescue the hierarchical signalling hypothesis.

Akçay et al. (2013) performed a similar experiment in a western population of song sparrows, with one major difference in experimental design: centre playback was coupled with presentation of a taxidermic mount, so that subjects could actually attack. In their results, matching at the boundary and staying on the match at the centre predicted attack on the mount and was also significantly associated with aggressive behaviours such as approach. Neither matching nor matching and staying on match was predictive of soft

songs, but matching and staying on match was predictive of wing waves. The results on western song sparrows are thus more supportive of the hierarchical signalling model in two respects: in the western population, matching and staying on the match is (1) associated with aggression and (2) predicts performance of a more reliable threat. Neither of these results held for our eastern population. The important difference then is that matching appears to function as an intermediate level of threat in the western population but not in the eastern population.

What Is the Function of Matching?

Male song sparrows type match other singers or song playback at far above chance levels (Stoddard et al. 1992; Burt et al. 2002; Anderson et al. 2005; this study). A nonrandom behaviour such as this seems likely to have some function. The most widely held hypothesis on the function of matching in songbirds in general is that it represents a threat (Krebs et al. 1981; Burt et al. 2001; Vehrencamp 2001) and thus functions as do other aggressive signals in intimidating conspecifics. Evidence from the western population of song sparrows studied by Beecher and colleagues suggests that type matching is threatening there (Burt et al. 2001; Akçay et al. 2013). In our eastern study population, however, matching does not predict attack on a taxidermic mount (Searcy et al. 2006), and neither matching nor staying on a match is associated with aggressive response measures such as approach to playback (this study). Approach to playback is consistent within individuals when they are tested multiple times within a season (Nowicki et al. 2002; Hyman et al. 2004; this study). As with soft song, if aggressive approach is consistent within individuals and matching is inconsistent, then it seems unlikely that aggressive approach and matching could be strongly associated.

Table 2
Effects of matching and staying on the match on behaviours of song sparrows during the centre playback

	Estimate	Test statistic	<i>P</i>
Soft song	0.050±0.157	<i>z</i> =0.319	0.750
Broadcast song	-0.177±0.097	<i>z</i> =-1.820	0.07
Wing waves	-0.935±0.365	<i>z</i> =-2.561	0.01
Distance	0.969±1.028	<i>t</i> =0.943	0.352
Latency	-10.20±14.01	<i>t</i> =-0.728	0.471

Sample sizes for each dependent variable are 40 subjects and 79 trials. Trial order was controlled by entering order as a covariate.

Another hypothesis for the function of type matching is that it serves as a signal of attention directed to the particular rival being matched (Searcy et al. 2006; Searcy & Beecher 2009). An elegant feature of this hypothesis is that such a signal is inherently uncheatable: an individual cannot match at above chance levels unless it is in fact paying attention to what the rival is singing. In the context of competition for territory between rival males, a signal of attention can very likely be interpreted as a threat, so the signal of attention hypothesis is not necessarily distinct from the aggressive signal hypothesis. If the signal of attention hypothesis makes any prediction not made by the aggressive signal hypothesis, it might be that an individual that matches another should respond to the other's behaviour more quickly than an individual that does not match. To test this prediction, we took data on latency to approach the speaker in the centre playback. Males that type matched the edge playback did not show a lower latency to respond to the centre playback than males that did not type match. Thus our results also do not support the signal of attention hypothesis.

Thus, song type matching has a solid function in aggressive signalling in the best-studied western population but no such function in the best-studied eastern population. Other functions for matching are possible. Logue & Forstmeier (2008), for example, proposed that matching is directed at individuals that are eavesdropping on the interaction, rather than at the opponent in the interaction. Males that are able to sing a higher-performance version of the song type a rival has sung reply with a match in order to impress their superiority on eavesdroppers, either male or female. Another possibility is that matching has a function in solidifying relationships with long-term, territory-owning neighbours, rather than in brief interactions with intruders. A third possibility is that matching in our population is currently functionless, and exists as a holdover from a common ancestor with western song sparrows, a common ancestor in which the behaviour had a function as a threat.

Hierarchical Aggressive Signalling

Although our results do not support hierarchical aggressive signalling for our population, our study does illustrate an approach that can be used to test hierarchical signalling in other systems. Suppose that two signals, X and Y, are hypothesized to form an aggressive signalling hierarchy, either in whole or part, with escalation occurring in the progression $X \rightarrow Y \rightarrow \text{attack}$. Then to support this hypothesis, it is necessary to show that signal X predicts signal Y strongly but it predicts attack weakly, and that signal Y predicts attack, and does so better than X. In our study, the hypothesized X and Y are song type matching and soft songs, respectively, and although signal Y (soft songs) does predict attack, signal X (matching) predicts neither signal Y nor attack. In western song sparrows (Akçay et al. 2013), support is much stronger, especially if wing waving is substituted for soft song as signal Y: signal X (matching) predicts signal Y (wing waving), and signal Y predicts attack and does so better than signal X. Other examples in which support is good include the little blue penguin case ($X = \text{growl}$, $Y = \text{hiss}$) and the fallow deer case ($X = \text{groan}$, $Y = \text{parallel walk}$) discussed previously (Waas 1991a; Bartos et al. 2007). Many other cases are known in which multiple threat displays are given, and in which it would be valuable to apply these tests to assess the generality of hierarchical signalling models across diverse groups of organisms.

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