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Song type matching is an honest early threat signal in a hierarchical animal communication system

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Aggressive encounters between animals often involve significant amounts of signalling before or in lieu of physical fights. When, as is often the case, these apparent threat signals are neither inherently costly nor inherently indicative of fighting ability, we should ask whether they are in fact honest signals, i.e. do they predict that escalation is imminent? While signalling theories have indicated that such 'conventional' threat signals can honestly predict escalation, attempts to gather supporting empirical evidence have mostly failed. For example, recent studies in songbirds of song type matching (replying to an opponent's song with the same song type he has just sung) have failed to confirm that it predicts an eventual attack by the signaller. In the present study of song sparrows (*Melospiza melodia*), we tested the hypothesis that song type matching is an early threat signal in a hierarchical signalling system. We used an improved model-playback design that simulated an escalating intrusion onto the subject's territory: the simulated opponent first sang in hiding from the boundary before moving to the centre of the territory, where he revealed himself and continued to sing. We found that type matching beginning in the boundary phase and continuing into the escalation phase, or beginning immediately after the escalation, reliably predicted both subsequent escalated signalling (soft songs and wing waves) and subsequent attack on the model, supporting the hypothesis that type matching is a reliable early threat signal.

1. Introduction

The threat signals of animals have intrigued researchers since the early days of the study of animal behaviour. Some threat signals are costly or inherently non-bluffable, such as parallel walking and roaring bouts in red deer, and permit the assessment of the size or strength of the opponent [1]. However, many threat signals are neither costly nor directly related to a trait critical to the outcome of the aggressive interaction, and thus they appear easy to bluff, i.e. they are not inherently honest signals. The existence of such signals thus raises the question of how their honesty is maintained [2]. These signals are called 'conventional signals' because the relationship between signal design and signal message is arbitrary, thus requiring a convention as to what the signal means [3].

In a major theoretical breakthrough in the late 1980s and early 1990s, it was shown that honest signalling is possible even in competitive contexts [4–8]. In the years since, however, it has proved difficult to demonstrate that honest threat signals actually occur in nature. What must be demonstrated is that the putative threat signal actually predicts subsequent escalation. This prediction was initially tested by observing whether, in natural interactions between individuals, putative threat signals were indeed followed by escalation by the signaller. Such tests have failed to confirm the hypothesis in most cases [9], possibly because in observational studies the behaviour of the receiver of the signal is uncontrolled. To control for receiver (opponent) behaviour, researchers in recent studies have presented a model of the opponent (e.g. a taxidermic

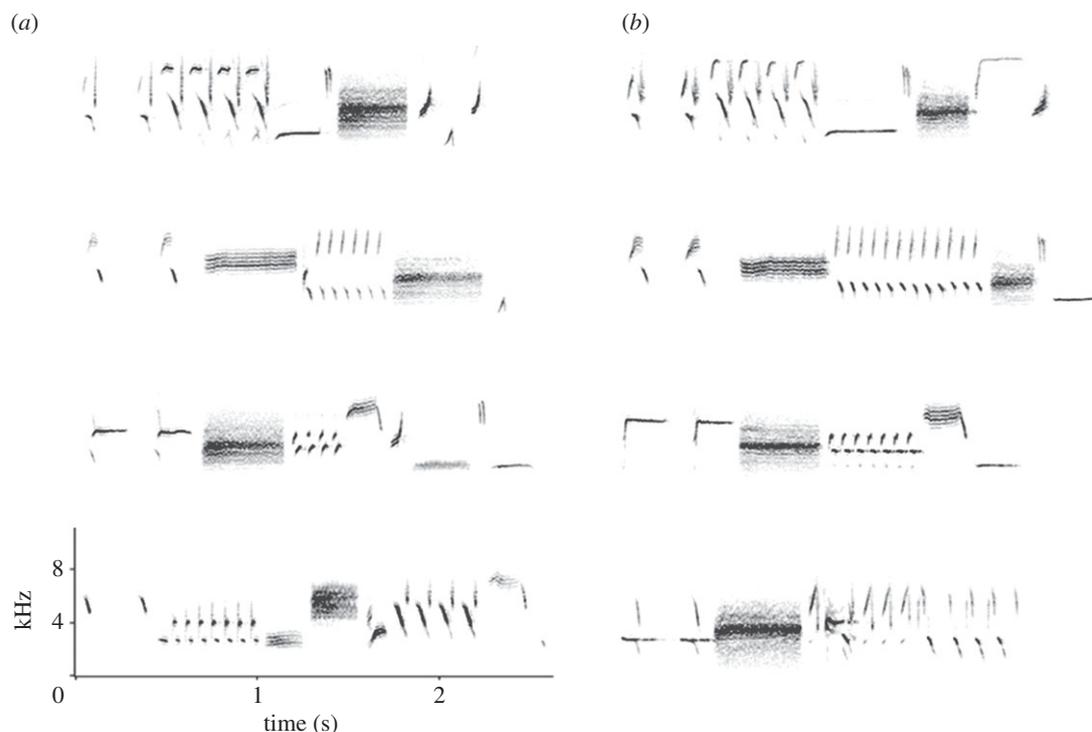


Figure 1. Partial song repertoires of two song sparrows. The birds ‘share’ the song types in the three top rows, but not the two types in the bottom row, or any of the other of their eight or nine song types each (not shown). Thus, if bird 1 (*a*) sings any one of the top three songs, bird 2 (*b*) could type match him. We generally use 50% similarity as the criterion for ‘matching’ between the song types of different birds. Note that in the present study, determining matching was simple because the stimulus song was the bird’s own song.

mount) to the subject, usually along with an experimental stimulus such as playback of song. The researchers can then measure the occurrence or rate of the subject’s signals to the model and ask whether a particular signal is reliably followed by further escalation and, ultimately, attack. Using this approach a number of recent studies [10–14] have attempted to identify signals that reliably predict attack. Some signals have been found to be reliable, but in general these cases have been the exception rather than the rule. In the most thoroughly studied system to date—the signals used by many songbird species in territorial defence—most putative threat signals have failed to predict escalation or attack by the signaller [15]. For instance, Searcy *et al.* [11] found that of several putative aggressive signals in song sparrows (*Melospiza melodia*), only a single signal, low amplitude (soft) song, reliably predicted attack.

Perhaps the most notable of these failures has been song type matching, first hypothesized to be a threat signal by Krebs *et al.* [16] in 1981 and so characterized in many reviews and secondary sources since then [17]. Song type matching is possible in any species in which individuals have multiple song types (‘song repertoires’), as is true of most songbirds, and where neighbours share some of their song types, as is also true of many songbirds. In these circumstances, a bird will often have the option of replying to a song his neighbour has just sung with the same song type (also called simply type matching or song matching) [16,18–21]. Examples are shown in figure 1. Song type matching has been shown to occur at above chance levels for numerous species (see review in [15]) suggesting that it has some sort of a social signalling function in male–male interaction, yet as noted, attempts to show that it predicts escalation (is a threat signal) have repeatedly failed since the original study [16].

Indeed, in a recent review Searcy & Beecher [15] concluded that the ‘mostly negative results indicate that type matching usually does not consistently predict the conventional measures of aggressive response such as close approach to the playback speaker, much less unequivocal measures such as attack’ (p. 1284).

A possible reason for this failure to confirm the reliability of song matching and most other putative threat signals may be the hierarchical nature of many animal communication systems. By a hierarchical signalling system, we mean one in which different signals are arranged such that lower-threat signals are used earlier in an aggressive encounter than higher-threat signals. In such a system, two individuals in a signalling interaction would hypothetically signal first using lower-level threat signals, and proceed to higher-level threat signals if neither backs down. In their review, Searcy & Beecher [15] concluded that most attempts to demonstrate that song type matching is a threat signal may have failed precisely because it is an early-stage threat signal (usually given at a distance) which precedes the late-stage threat signals (such as soft song) that are given when the opponents are face to face. If it is true that song type matching is an early conventional signal of aggressive intent, then the experimental paradigms to date, which have used only a single high-level threat stimulus [15,19,22], will have been inadequate for determining whether song type matching reliably predicts subsequent escalation. What is needed is a design that begins with an initial low-level threat, allowing subjects to use song type matching as an early-stage threat, followed by an experimental escalation designed to see whether subjects will follow through on their initial threat. The current experiment incorporates such a design (originally proposed by Beecher *et al.* [19]).

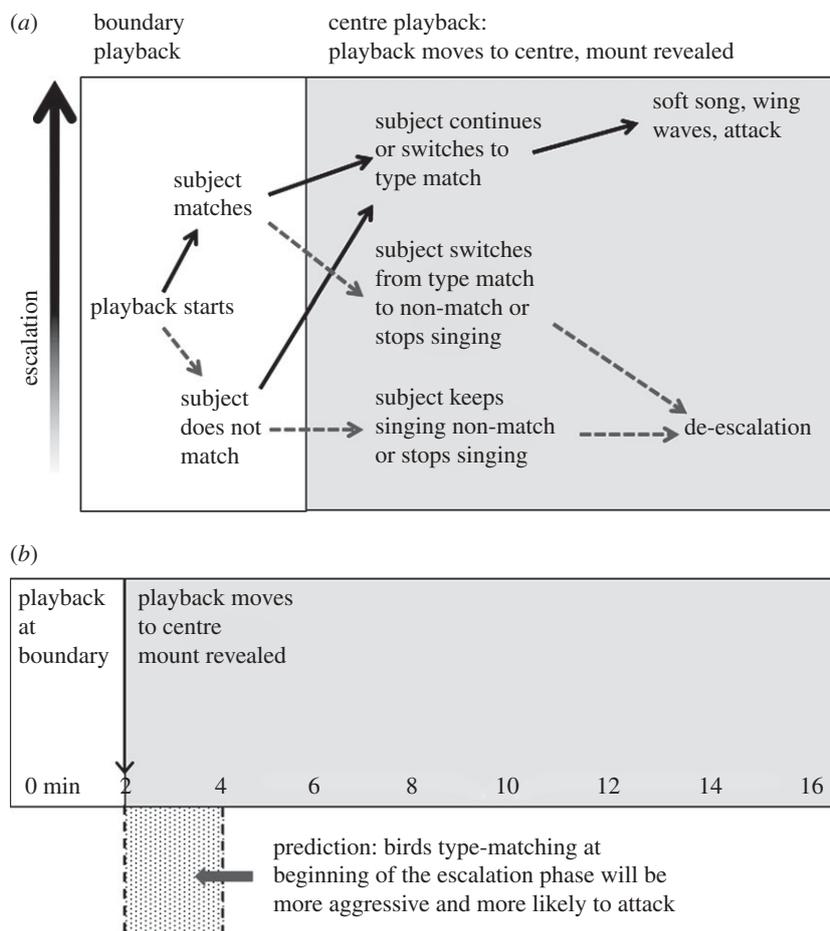


Figure 2. (a) The hierarchical signalling hypothesis (based on [15,18,23]) in the context of the present experimental design. The design has two phases. In the first phase, song is played from the subject's territory boundary. In the second phase, the playback switches to the centre of the territory and the mount is revealed. When the bird hears a song from his territory boundary, he may or may not consider it seriously threatening. If he does consider it threatening, according to the hierarchical signalling hypothesis he should type match and he should continue to type match once the escalation occurs (breaking off the type match is considered a de-escalation). If the bird does not consider song from the boundary threatening enough to warrant a type match, by hypothesis he will certainly consider the escalation into his territory threatening, and he should type match at this point, i.e. soon after the escalation. The common denominator of these two patterns is that the bird should type match in the short period following escalation. (b) The experimental design, shown to scale: phase 1 was 2 min long, phase 2 was 15 min long (but shorter if the subject attacked the mount). Birds that were type matching during the 2 min period following the escalation from phase 1 to phase 2 were predicted to be more aggressive subsequently and be more likely to attack the mount. Type matches that occurred later in phase 2 were not expected to be correlates or predictors of aggression because according to the hierarchical hypothesis, type matching is an early warning signal, and because later matches are increasingly likely to be 'chance' matches (see text).

A second key feature of the present design derives from earlier research on our study population [18]. In an interactive playback experiment, we found that although type matching might not predict attack [11,22], song sparrows nevertheless perceived being type matched as a threat: they responded more aggressively when a simulated neighbour at their mutual boundary replied to their song with a type match rather than with a non-matching song. Moreover, subjects who continued to type match ('stayed on the type') responded more aggressively than did subjects who switched off type or stopped singing [18]. These results have been incorporated in a model of type matching [18,19,23] that guides the present study. In this model, initiating a type match is an aggressive escalation signal, staying on type maintains the threat intensity, and switching off type (or stopping singing) is a de-escalation signal. Given that a bird can type match initially but switch off (and de-escalate) once the opponent escalates, the critical predictor of further escalation is not the bird's initial type match, but whether or not he stays on type as the opponent escalates.

Figure 2 presents the model, the design of the experiment, and the predictions derived from the hierarchical signalling hypothesis. Each trial started with playback at the boundary of the subject's territory, using a song from the subject's own repertoire (self-song). We then escalated the interaction by switching to a speaker near the centre of the subject's territory, revealing a taxidermic mount of a song sparrow and continuing with playback of the same song type. We predicted that subjects who type matched the simulated intruder at the boundary and stayed on type match when the opponent escalated would be more likely to escalate to higher-level signals, such as soft songs and wing waves, and ultimately to attack. We realized that exactly how threatening the subject perceived the boundary playback to be would be determined by other, uncontrolled factors, including recent aggressive interactions the bird may have had at that boundary, whether or not the subject was busy feeding nestlings at the time, the personality of the subject (some subjects are consistently more or less aggressive than others [24,25]), and so forth. Therefore, birds that did not type

match boundary playback, perhaps because they did not consider it threatening enough to merit a type match, but did so immediately after the escalation, were included in the 'early matcher category'. Thus, we defined 'early matchers' as birds that were matching in the first two minutes after the escalation from boundary to centre.

By contrast, we predicted that subjects who failed to type match during the boundary playback or in the centre playback would be less aggressive towards the centre intruder. Finally, based on our model, we predicted that subjects who type matched at the boundary but switched off to a non-match when the centre escalation occurred ('bluffers'), would also be less aggressive towards the centre intruder.

2. Material and methods

(a) Subjects and study population

We tested 48 territorial male song sparrows in Discovery Park, Seattle, WA, USA, between 8 April and 30 May 2011. All males were colour-banded and mated at the time of testing. We recorded the repertoire of each male (see details of repertoire recording in [26]) before the experiment using a solid-state recorder (Marantz PMD 660) and a shotgun microphone (Sennheiser ME66/K6). The frequency response of the recording system was flat within 3 dB from 500 to 10 000 Hz. We also mapped the territory boundaries of each subject based on observation of singing posts and boundary interactions. We refrained from testing immediate neighbours on the same day.

(b) Stimuli

For each subject, as the playback stimulus we used a song from his own repertoire ('self-song'). Self-song is probably perceived as stranger song, and previous experiments have shown that song sparrows type match self-song at high levels [20] and also that there is no voice recognition in this species [27]. The stimulus tape for a given subject was made from a single rendition of that bird's song, selected from his repertoire based on the quality of recording, using Syrinx (John Burt, www.syrinxpc.com). We created a 10 s loop including the song (approx. 3 s) and a silent period (approx. 7 s), and presented these stimuli during the experiment using an Apple iPod Touch (Apple Inc.).

(c) Design and equipment

As our design included playbacks from two locations (boundary and centre), we used an iMainGo2 (Portable Sound Laboratories, Inc.) loudspeaker for the boundary playbacks and an x-Mini II (black, Xmi Pte Ltd, Singapore) loudspeaker for the centre playback. The frequency response of the playback systems was flat within 6 dB from 200 to 18 000 Hz. A small speaker was chosen for the centre playback to be inconspicuous and thus to make the model-speaker set-up as natural-appearing as possible. Playback amplitude from both speakers was approximately 80 dB SPL measured at 1 m with a Radio Shack 33-2055 sound meter, which is normal broadcast singing amplitude for song sparrows. Each speaker was connected to the iPod via a 20 m cable.

We placed the speaker for the boundary playback on a branch just inside the territory of the subject, within 1–2 m of the boundary to avoid interference from the neighbours. The speaker for the centre playback was placed near the centre of the territory of the subject, which on average was about 15–20 m inside the boundary. This speaker was coupled with a taxidermic mount (model) of a song sparrow in the singing position. The mount was fixed to a dowel which was taped on a natural perch of the sort that song sparrows favour. The speaker

was hung from the perch so that it was only a few centimetres away from the mount. We placed the mount on a natural perch, because in earlier experiments by our group and others a mount placed on top of a loudspeaker or mounted on a pole has been found to elicit a surprisingly low level of attack (20–25%) [11,22]. In pilot experiments, we discovered that birds who declined to attack the mount when it was sitting on the loudspeaker, would usually attack when it was put on a tree branch or a bush. We concluded that the unnatural placement of the mount had been inhibiting attack in many birds. Therefore, in the present experiment we placed the mount on a natural perch, and this indeed increased the attack frequencies significantly (see §3). The model-speaker set-up was covered with a shroud until the start of the centre playback.

We started each trial with the boundary playback, which lasted 2 min (12 repetitions of the stimulus song). In the cases where the subject did not appear within the 2 min, we waited a minute and repeated the boundary playback. If the subject appeared but did not sing, we aborted the trial and repeated it on another day (this happened just one time). At the end of the boundary playback, one experimenter removed the shroud from the model and retreated to 20 m, at which point we started the centre playback (this always took less than a minute, during which time the other observer kept track of the subject). The centre playback lasted 15 min or until the subject attacked the mount and consisted of the same 10 s loop stimulus tape that was used at the boundary. Two or three observers standing at different angles from the speaker ran each trial to make sure the subject was in view during the entire trial. One of the observers recorded the whole trial using the same recording equipment as above, narrating the behaviours of the subject, while the other observers relayed their observations to the recordist.

(d) Response measures

Response measures were extracted separately for the centre and boundary playback (boundary playback data are reported in the electronic supplementary material). We calculated the proportion of the time spent within 1 m of the model for the centre playback and noted the latency of first approach to the model. We also counted the number of loud songs, soft songs, wing waves and flights (any movement during which the bird became airborne). The distinction between loud and soft songs was made in the field by one experienced observer (C.A.); this method has been shown to produce an accurate cut-off point separating soft and loud songs on the amplitude continuum [28]. We converted the counts of behaviours into rates to account for unequal durations of observation. We calculated the rates of behaviour from the first sighting to the last boundary playback song for the boundary playback period, and from the first centre playback song to the end of the 15 min trial or the time of attack for the centre playback period. We counted the number of song types the subject sang during centre playback and calculated the switching frequency as the number of switches/number of total songs – 1 (if the total number of songs—soft and loud—during centre playback was 1, the subject was assigned a score of zero). Switching frequency was considered because of previous research suggesting it might be an aggressive signal as well [29]. Most subjects sang only one song type during the boundary playback owing to its short duration.

We noted whether any of the songs given during boundary or centre playback was a type match to the playback song (self-song). As in prior studies using self-song as stimulus [11,22,30] type matches were determined visually in Syrinx by two observers (C.A. and M.E.T.). Because we used self-song and because within-type variation is much smaller than between type variation in song sparrows [31], visual matching of a rendition of a song type to a type in the bird's recorded repertoire was straightforward.

Table 1. Loading coefficients in PCA analysis.

	coefficients
rate of flights	0.82
time spent less than 1 m	0.74
latency to approach	−0.78

Subjects were classified as ‘early matchers’, ‘non-matchers’ or ‘off-switchers’. Early matchers (i) matched the stimulus song during the 2 min boundary phase and continued matching (for at least one more song) into escalation phase, or (ii) began matching the stimulus song during the first two minutes of the escalation phase. The 2 min cut-off was an *a priori* criterion that we deemed long enough to elicit one type switch but short enough that we could be certain the type switch was in response to the playback. ‘Non-matchers’ (i) never matched the stimulus song, or (ii) matched it only late in the escalation phase (during minutes 3–15); the basis for treating late matchers as non-matchers is explained below. ‘Off-switchers’ matched during the boundary phase but ceased matching or ceased singing altogether following the escalation. Our hierarchical signalling hypothesis predicts that ‘matchers’ will be more likely to show increased aggressive behaviour (including high-level threat signals soft song and wing waves) during the remainder of the escalation phase and, ultimately, attack. Non-matchers are predicted to show lower levels of aggression and lower rates of attack. Because off-switchers back off their threat when escalation occurs, they are also predicted to show lower levels of aggression and lower rates of attack. Note that because playback of the same song continues throughout the trial (up to 15 min in the centre phase if there is no attack), birds classified as non-matchers may have still type matched the playback at some later point. However, according to our hierarchical signalling hypothesis, type matching later in the interaction is not an escalation signal. Furthermore, there is a much higher likelihood that a late type match may be a chance match, since song sparrows (eventual-variety singers) tend to cycle through the eight to nine songs in their repertoire and given enough singing, will eventually sing that song type. In other words, singing a type match by chance alone is far more probable later in the trial when the bird has already cycled through several non-matching types. For these two reasons, we classified these late (or chance) matchers ($n = 7$) as non-matchers.

We considered a subject to have attacked when the subject either physically landed on the model, or flew very close to (within approx. 10 cm) the model but pulled away without or just barely touching it (it is difficult to distinguish these two categories).

(e) Data analyses

Our measures of aggression were correlated with each other, so we carried out a principal component analysis (PCA) to extract a single measure of aggression. The PCA included time spent within 1 m, rate of flights and latency to approach the model. The first component in the PCA analysis (unrotated) explained 60.9 per cent of the variance and was taken as the measure of aggression, with higher scores indicating higher aggression (see table 1 for coefficients).

We first asked whether early type matching predicted attack by carrying out a χ^2 -test comparing rates of attack for early matchers, non-matchers and off-switchers. In addition, we compared the aggression scores at the centre for these groups using a one-way ANOVA. The second question we asked was whether

Table 2. Type matchers were significantly more likely to attack than non-matchers and switchers. (Numbers of subjects in each category (expected numbers).)

	type matchers	non-matchers	off-switchers
non-attackers	2 (6.02)	11 (8.14)	4 (2.83)
attackers	15 (10.98)	12 (14.85)	4 (5.17)

signalling was hierarchical. We carried out two analyses to address this question. First, we carried out discriminant function analyses (DFAs) with each signalling variable from centre playback (soft songs, loud songs, wing waves, switching) as an independent variable and attack/no-attack as the classification variable. For those aggressive signals identified by the DFA analyses as predictive of attack, we asked whether they in turn were predicted by type matching early in the trial using Kruskal–Wallis tests (signalling rates were not normally distributed). Second, we asked whether type matching tended to precede higher intensity signals in the temporal sequence as predicted by the hierarchical signalling model. For this analysis, we included all trials where the bird sang at least one type match. To be conservative, we included all birds that type matched at any time during the trial, including off-switchers as well as late type matchers described above. Although we classified off-switchers and late matchers as ‘non-matchers’ for the prior analyses, it would be ‘stacking the deck’ for the temporal hypothesis if we did not include them here. We carried out binomial tests on whether type matching preceded the other signal, assuming a chance level of 0.5 that one signal would precede the other.

3. Results

The majority of subjects, 31 out of 48 (65%), attacked the model. This attack frequency is substantially higher than the attack frequencies (approx. 20–25%) observed in earlier experiments [11,22], a difference we attribute to the natural placement of the mount. Not surprisingly, aggression scores of attackers were significantly higher than those of non-attackers ($t_{46} = 8.37$, $p = 8.4 \times 10^{-11}$). About a third of the subjects, 17 out of 48, were early type matchers: 11 of them type matched at the boundary and stayed on type following the escalation, while six type matched shortly after the escalation (average latency 31.5 s). An additional eight birds type matched at the boundary but did not continue to do so when the escalation occurred, and so were included in the ‘off-switcher’ category rather than the ‘early type matcher’ category. In the crucial test, attack frequencies were significantly higher for early type matchers (15 of the 17, 88.2%) compared with non-matchers (12 out of 23, 52.2%) and off-switchers (four out of eight, 50%, $\chi^2 = 6.45$, $p = 0.04$; table 2). In addition, early type matchers had higher aggression scores than non-matchers and off-switchers (one-way ANOVA, $F_{2,45} = 5.81$, $p = 0.006$; figure 3a).

We carried out separate DFAs on the four other signalling variables, namely rates of soft song, loud songs, wing waves and song-type switching, to determine which of these signals were associated with attack. Only the rates of soft song (Wilks’ Lambda = 0.79, $F_{1,46} = 11.96$, $p = 0.001$) and rates of wing waves (Wilks’ Lambda = 0.88, $F_{1,46} = 6.41$, $p = 0.015$)

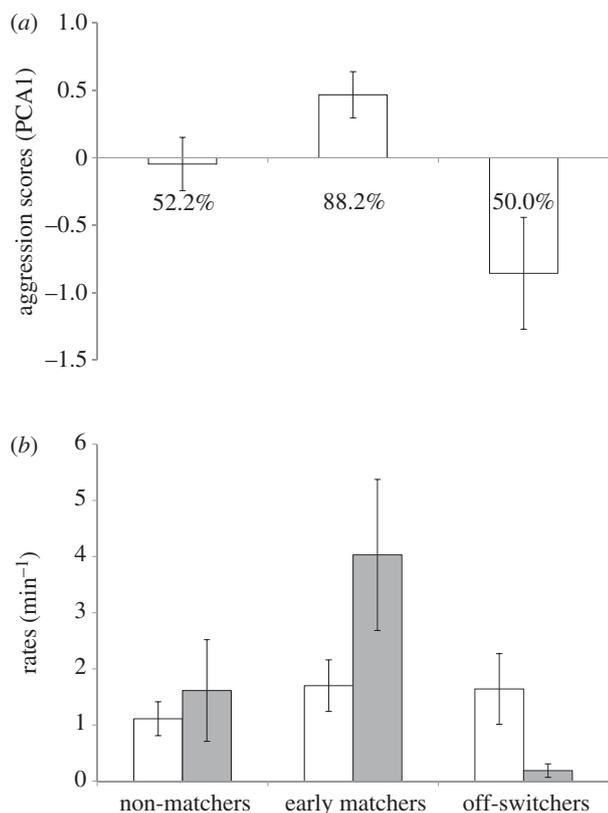


Figure 3. (a) Aggression scores and rates of soft song and (b) wing waves during the centre playback. Error bars represent ± 1 s.e. The percentages in (a) represent the percentage of attackers for each group. (b) White bars, soft song rates; grey bars, wing wave rates.

significantly predicted attacks and non-attacks, classifying the subjects correctly 66.7 and 62.5 per cent of the time, respectively. On average, attackers had higher rates during centre playback than non-attackers in both soft songs (mean \pm s.d.: 1.97 ± 1.78 versus 0.41 ± 0.63) and wing waves (3.42 ± 5.42 versus 0.07 ± 0.15). Interestingly, most of the classification errors were as a result of classifying attackers as non-attackers. Rate of soft songs was able to predict 88.2 per cent of non-attacks but only 54.8 per cent of the attacks. Rate of wing waves predicted 100 per cent of non-attacks but only 41.9 per cent of attacks. Neither rate of loud songs, nor switching rates differed significantly between attackers and non-attackers (see the electronic supplementary material, table S3).

Next, we asked whether early type matching was associated with the signals that we had identified as being associated with attack, namely soft songs and wing waves. Although rates of soft songs did not differ significantly between early type matchers, non-matchers and off-switchers (Kruskal–Wallis test, $\chi^2 = 1.70$, $p = 0.43$; figure 3b), rates of wing waves did (Kruskal–Wallis test, $\chi^2 = 6.60$, $p = 0.04$; figure 3b), with early type matchers wing-waving at highest levels. In pairwise comparisons between each group, early type matchers gave significantly more wing waves than both non-matchers (Mann–Whitney test, $z = 2.09$, $p = 0.04$) and off-switchers ($z = 2.20$, $p = 0.03$).

Finally, we asked whether type matching preceded soft songs or wing waves, as one would expect for a hierarchical signalling system where type matching serves as an early threat signal. Note that in this test, type matching at any point in the trial, early or late, was counted as type matching. In 26 cases, the subject sang at least one type match and at

least one soft song. In 19 of these cases, the first type match preceded the first soft song. In the remaining trials, soft song preceded type match ($n = 6$) or the first soft song was also the first type match ($n = 1$). Assuming a chance level of 0.5, type matching preceded soft songs significantly more often than expected by chance (binomial test: $p = 0.005$, excluding the one trial where both signals were given simultaneously). There was a similar trend for type matching preceding wing waves: in 13 out of 21 trials in which both a type match and a wing wave was given, type matching preceded wing waves, although the effect did not reach significance (binomial test, $p = 0.09$).

4. Discussion

In this experiment, we tested the hypothesis that type matching is an early-stage signal given in an agonistic encounter that predicts that the signaller will escalate—give higher intensity threat signals and eventually attack—if his opponent fails to de-escalate in response to this early-stage threat signal. We simulated an escalating intrusion sequence and found that subjects who type matched early in the sequence and in the face of escalation were in fact more likely to escalate their signalling and ultimately attack. Strikingly, close to 90 per cent of subjects (15 out of 17) who type matched early, ultimately attacked the model. In comparison, the attack frequencies of non-matchers, and those who type matched at the boundary but switched off type when the opponent escalated (off-switchers), were significantly lower, around 50 per cent. These results indicate that song type matching early in the encounter and in the face of an escalating intruder is an honest signal of aggressive intent. These results, to our knowledge, are the first direct evidence that type matching, long assumed to be an aggressive signal, does in fact predict that the bird will escalate in response to an escalation by an intruder. It is also, to the best of our knowledge, the first implementation of an escalation design in a field experiment, and we believe that the design will be very fruitful in future studies of complex animal signalling systems. In the present study, we also obtained clear evidence that this signalling system is hierarchical, with type matching occurring earlier in the escalation sequence, and wing waves and soft song generally occurring later in the sequence, closer to the ultimate attack. We found that when type matching, soft song and wing waves all occurred in a trial, type matching typically preceded the close-range signals. Moreover, type matchers tended to show higher rates of wing waving than did non-type matchers.

How can song type matching, an early threat signal that does not seem costly to produce, be a reliable signal of subsequent escalation? As discussed in §1, song type matching probably has a cost in terms of increased aggression from the receiver. In fact song sparrows in our population approach the playback speaker more readily when they are type matched by it [18]. Furthermore, as a long-range signal, song type matching may be eavesdropped on by other males [32,33]. We have previously found that song sparrow males will increase aggression towards their aggressive neighbours [34,35], which would introduce a second layer of social cost of type matching: if a male type matches a neighbour instead of repertoire matching, the norm between established neighbours [36], he may deal with increased aggression from other

Table 3. Post hoc categorization of response types.

<i>a priori</i> category	boundary response	centre response	<i>N</i>	attacks	%	comment (see §4)
'matchers'	match	match	11	9	82	these two sub-groups may differ only in how threatening they considered the initial boundary playback
	non-match	match (early)	6	6	100	
'off-switchers'	match	soft songs	4	4	100	reach high aggressive level (soft song) early in centre
	match (1 song only)	stop singing	4	0	0	'bluffers'?
'non-matchers'	non-match	non-match or late match	23	12	52	about half of these birds attacked and were 'undersignallers'

neighbours which in turn may be more costly to bluffers than truly aggressive signallers.

Although we found type matching to be a reliable early warning signal, this effect was diluted somewhat by two interesting departures from expectations (summarized in table 3). First, a relatively large number of birds type matched but switched off once the simulated opponent escalated. We classified these birds all as 'off-switchers', but two very distinct groups become apparent when we look at them closer. In one group were the 'bluffers', who type matched the boundary playback but then switched off or stopped singing once the simulated opponent escalated (four birds). These birds sang a single type match in response to the boundary playback, and did not attack. We note again that we are using 'bluffer' in a purely functional, non-mentalistic sense, as for all we know the four apparent bluffers may have been 'intending' to escalate at the boundary, but 'changed their minds' when the simulated opponent escalated. The four other birds from the 'off-switcher' class responded in a very different way: to begin with they sang at a higher rate than the rest of the off-switchers during the boundary phase (3.3 songs per minute) and then switched immediately to giving soft songs and/or wing waves at a high rate immediately after the playback moved to the centre; these birds all ended up attacking the model, and thus actually did act on their initial threat. This subgroup of 'off-switchers' is thus essentially the same as our 'matchers'—they match early, escalate to soft song and wing waves, then attack. It was only our *a priori* classification—matching in the boundary playback but not in the centre playback—that landed them in the same group as the bluffers. It would appear that these birds simply escalated from type matching to soft song more quickly than most of the matchers (see table 3). In short, we observed only four of the 48 subjects who could reasonably be classified as 'bluffers' in that they did not back up their initial threat signal with action.

The second kind of exception was the group of non-matchers who attacked: while type matchers attacked at close to 90 per cent, a substantial portion of the attackers (12 out of 31, 38.7%) were non-matchers. A similar pattern was seen for wing waves and soft songs: seven of the attackers sang no soft song before attacking, 10 attackers gave no wing waves and several more signalled only at low levels as seen in the results of the DFA (see the electronic supplementary material). This surprising pattern indicates that some birds did not bother to signal, or signal much, before

attacking [11,37]. More specifically, it seems that while the signalling system may start with type matching and proceed to soft songs and wing waves, individual birds can start signalling from any point in the hierarchy, forsaking earlier signalling steps. Note that skipping signalling steps is not deceptive in the usual sense of the word, as the subjects are not 'exaggerating' their aggressive intentions, but 'understating' them. Theoretical models of deceptive signalling have always focused on exaggeration [38–41] and we are not aware of any model that predicts the high levels of under-signalling that we found in the present study. Whether natural interactions also contain significant amounts of under-signalling is not known. Therefore, future studies of honest signalling will need to take into account not just the possibility of deceptive signalling which was (potentially) present at low levels in this system, but also under-signalling, which seems far more prevalent in song sparrows and potentially other species.

In summary, we found that type matching in song sparrows in the face of an escalated challenge was a reliable signal that predicted attack. We identified two types of exception that reduced, but did not eliminate, the overall correlation between this threat signal and escalation: 'bluffers' type matched but did not escalate, while 'undersignallers' did the opposite—attacked but did not type match (and in some cases did not give higher-level threat signals either). Finally, we found that the signalling systems appear to be hierarchical, in that type matching generally preceded the close-range soft songs and wing waves, and early type matchers generally gave higher rates of wing waves during the escalation phase of the challenge. The hierarchy is an imperfect one in which individuals can skip earlier steps in the hierarchy and in extreme cases, skip signalling altogether. Future studies should focus on why individuals skip signalling their aggressive intentions, when in theory it would always appear to be advantageous to make use of cheap signals before attacking. We believe that the escalation design presented here will be helpful in furthering our understanding of complex signalling systems.

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