

# Is song-type matching a conventional signal of aggressive intentions?

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Song-type matching is a singing strategy found in some oscine songbirds with repertoires of song types and at least partial sharing of song types between males. Males reply to the song of a rival male by subsequently singing the same song type. For type matching to serve as an effective long-distance threat signal, it must be backed up by some probability of aggressive approach and impose some type of cost on senders that minimizes the temptation to bluff. Western subspecies of the song sparrow exhibit moderate levels of song-type sharing between adjacent males and sometimes type match in response to playback of song types they possess in their repertoires. Interactive playback experiments were used in order to examine the subsequent behaviour of type-matching birds and to quantify the responses of focal birds to type-matching versus non-matching stimuli. Birds that chose to type match the playback of a shared song type subsequently approached the speaker much more aggressively than birds that did not type match. Moreover, birds approached a type-matching stimulus much more aggressively than a non-matching stimulus. These results and consideration of alternatives suggest that type matching in song sparrows is a conventional signal in which honesty is maintained by a receiver retaliation cost against bluffers.

**Keywords:** interactive playback; song matching; receiver retaliation; threat signals

## 1. INTRODUCTION

Conventional signals (sense 2 of Guilford & Dawkins 1995) are communication signals of arbitrary form that are associated with specific contexts by convention. Cost-free conventional signals may evolve and remain stable against cheaters if there is no conflict of interest between sender and receiver, i.e. they agree about the optimal receiver response to the signal in the given context (Maynard Smith 1994). Possible examples might include bee dances, group coordination signals and human language. However, some degree of conflict between sender and receiver is likely for most communication exchanges in animals and in this case there must be a stabilizing cost that prevents invasion by cheaters (Zahavi 1993). A receiver retaliation or punishment rule is the postulated cost for this class of signal. This type of cost is the key feature that distinguishes conventional signals from other kinds of signals (Maynard Smith & Harper 1988, 1995; Hasson 1997; Vehrencamp 2000). Strategic handicap signals are stabilized by signal production costs (Grafen 1990), increased exposure to predators or increased vulnerability to injury by opponents caused by the postures and movements of displays (Enquist *et al.* 1985; Waas 1991; Adams & Mesterton-Gibbons 1995). Index or assessment signals are physically or physiologically constrained in order to reveal honest information (Maynard Smith & Harper 1995).

Conventional signal game models for agonistic contexts have been developed by Enquist (1985, model 1), Johnstone & Norris (1993), Hurd (1997), Hurd & Enquist (1998) and Enquist *et al.* (1998). A critical assumption of these models is the presence of two competitors who each know their own willingness or ability to fight, but not that of the opponent. In most models, both opponents give one of two alternative signals, A or B, and then base their responses on the joint result. The evolutionarily stable decision policy is to use signal A when strong or

highly motivated and signal B when weak or not motivated, then immediately attack opponents who signal an equal strength, flee from opponents who signal a stronger state and pause before attacking opponents who signal a weaker state (giving them a chance to flee). Such a policy implies that competitors frequently test each other, particularly those competitors giving equal-strength signals. Honesty is maintained by the high retaliation cost of signalling a strong state when actually weak, e.g. other truly strong competitors will frequently test or attack such cheaters. When the two contestants differ sufficiently in motivation or fighting ability both benefit from avoiding the cost of a fight.

The models also predict that one could switch around the meaning of signals A and B and still maintain an honest signalling system. This prediction confirms the arbitrariness of signal form for conventional signals, in contrast to the obligate linkage between signal form and information content for other types of signals that are stabilized by production costs, vulnerability risk, physical constraints or intention movement precursors. Conventional signals therefore do not need to be excessively costly to produce, but the weak versus strong signals should be easily distinguishable and, thus, antithetical in form (Hurd *et al.* 1995). Signals are likely to consist of either a set of two alternative discrete signals or a graded signal set that varies along one easily distinguished axis.

In order to qualify as a conventional signal, all individuals should be capable of producing the A and B signals and there should not be any differential energetic cost or vulnerability risk associated with the production or execution of the two signals. When a sender signals a strong threat, they should be subsequently more likely to approach and attack their opponent and they should be at greater risk of receiving an attack if their opponent also signals a strong threat. Arbitrariness of signal form could be demonstrated by showing that the same signal structure serves as the A and B signal in different contexts

or that different species using a particular signal set vary in their assignment of the A versus B signal to the more aggressive context.

Most conventional signals described to date are colour patch badges of status in birds and lizards (Rohwer 1982; Studd & Robertson 1985; Møller 1987; Maynard Smith & Harper 1988; Lemel & Wallin 1993; Qvarnström 1997; Pärt & Qvarnström 1997). The colour patch can be any colour, but is often either a white patch against a dark field or a black patch against a white field. The production cost of the colour patch itself is believed to be trivial. The size of the patch is correlated with the signaller's dominance status and/or willingness to escalate. Large-badged individuals usually win against small-badged individuals. Moreover, large-badged individuals receive frequent aggressive tests from other large-badged individuals and pay significant retaliation costs compared with small-badged individuals. Simultaneous evidence for large badge size as both a predictor of subsequent aggressive behaviour by the signaller and a stimulus for a strong receiver's retaliation was most clearly shown in the study of yellow warblers by Studd & Robertson (1985).

No auditory signals have as yet been designated as conventional signals, yet it is highly likely that many of the variable elements of passerine bird song used in male–male counter-singing interactions meet the requirements. An auditory conventional signal would be able to convey short-term information about aggressive intentions as opposed to status, condition and general willingness to attack, as in the case of colour signals that are always 'on'. For example, the switching rate between song types is a good candidate for a conventional signal. The switching rate in the song sparrow both predicts a singer's subsequent aggressive approach and elicits differential approach responses in receivers when given as a stimulus (Kramer *et al.* 1985; Stoddard *et al.* 1988; Nielsen & Vehrencamp 1995; Searcy *et al.* 1995, 1999).

Type matching, in which counter-singing males sharing at least some of the same song types reply to each other with the same song type, was first argued to be a method of directing an otherwise omnidirectional signal to a specific rival singing male (Brémond 1968). A signal that 'points' to another signaller by immediately copying him may qualify as an index signal, which is honest by physical constraint and needs no other cost in order to maintain honesty. Since then, type matching has also been proposed as a signal of aggressive intentions (Krebs *et al.* 1981). Type matching is associated with escalated encounters and early-season territorial establishment and predicts subsequent approach in several species, for example chaffinches (Hinde 1958), great tits (Krebs *et al.* 1981), cardinals (Lemon 1968) and song sparrows (Beecher *et al.* 2000). In order to prevent bluffing in this case, some additional type of cost must be paid by senders. Tests of the approach response to type-matching stimuli have been more difficult to conduct because such experiments require interactive playback techniques. Here I ask whether type matching meets the conditions of a conventional signal in the song sparrow *Melospiza melodia cooperi*. Playback experiments were used for testing the two key predictions, i.e. are receivers more likely to approach a type-matching stimulus compared with a non-matching stimulus, and are senders that choose to

type match subsequently more likely to approach a stimulus than senders that choose not to match?

## 2. METHODS

Playback experiments for assessing subsequent sender responses following matching versus non-matching song choices were conducted in the spring of 1998 and 1999 on a population of song sparrows in a freshwater marsh habitat adjacent to an urban park in Escondido, California. Males defended territories in the bullrushes surrounding pools of open water and each male had from two to four adjacent neighbours. All males were banded and recorded during the previous two years (for details see Wilson *et al.* 2000). Only adjacent male pairs that shared two or more song types were used in these experiments. A shared neighbour song type was broadcast to each focal male from the appropriate boundary with that neighbour. In order to reduce the incidence of neighbour interference during experiments, I mounted the speaker in front of a parabola in order to reduce backward sound transmission. In some problematic cases the speaker was moved 1 m into the territory of the focal male or the neighbour was lured away from the boundary with a tape-loop playback from another part of his territory. I did not begin a playback experiment until the focal bird was known to be present in the approximate centre of his territory and had been quiet for 1 min. I played the song stimulus at *ca.* 10-s intervals for 3 min. Playback was run interactively in order to avoid overlapping the focal bird's songs. During the playback and for 3 min post-playback I noted the amount of time that the focal bird spent in five distance zones from the speaker (0–2, 2–5, 5–10, 10–20 and < 20 m) and recorded the entire trial in order to determine which song types were sung. The eight subjects were tested several times with different neighbours and in different years until each had given at least one matching and one non-matching response.

I also present a reanalysis of playback experiments conducted in 1992–1993 on a different population of song sparrows in San Diego county but residing in a similar type of habitat (Nielsen & Vehrencamp 1995). In these experiments, focal males were presented with stranger (i.e. non-neighbour) songs from other males in the same population. Song stimuli were broadcast interactively from the side of the male's territory away from the marsh where there was no neighbouring territorial male. The duration of playback in these experiments was 10 min and the post-playback monitoring period was 6 min. Identical approach distance measurements were made and all trials were recorded, as in the 1998–1999 experiments. Six treatments were presented to each focal male consisting of three different song-type switching regimes (no switching, synchronized switching with the focal bird and rapid unsynchronized switching) using two different artificial song repertoires (song types shared with the focal male and song types not present in the focal male's repertoire). In the treatment with synchronized switching and shared song types, we type matched every song sung by the focal bird for the duration of the playback period. I made use of the different treatments in order to examine both receiver responses to matching versus non-matching stimuli and subsequent sender actions following matching versus non-matching song choice, as explained in the results below.

Experiments for assessing receiver responses to type-matching versus non-matching neighbour songs were conducted by Burt (1999) on a different subspecies of song sparrow (*Melospiza melodia morphna*) with similar song-sharing levels among

neighbours to those found in *M. m. cooperi*. Burt (1999) also used a 3-min playback duration with song stimuli delivered interactively at 10-s intervals. His response measurements included the closest approach to the speaker, the number of close-distance threat displays (wing waves and soft songs) and the number of flights that were less than 1 m during the playback period.

### 3. RESULTS

Figure 1*b* shows the results of the 1998–1999 playbacks of shared neighbour song types. Males could either type match the stimulus song type, sing another song type that they shared with that neighbour (called repertoire matching) (Beecher *et al.* 1996) or sing a song type that was not shared with that neighbour. The response variable is the amount of time spent within 2 m of the speaker during the post-playback period, which is the response component that is most consistently associated with different treatments in all of the 3-min experiments we have conducted on this species. Males that chose to type match subsequently spent significantly more time close to the speaker than males that did not type match. Close-approaching males often stopped singing or produced soft songs, gave wing-waving displays and searched on the ground for the ‘invader’. Figure 1*a* shows the results of the equivalent type of experiment from the 1992–1993 experiments with shared stranger songs using only those treatments in which the playback did not match the focal bird. Half of the males chose to type match the playback at some point during the 10-min trial and half did not type match. As in the neighbour stimulus trials, matching males spent significantly more time close to the speaker than non-matching males. Note that focal males were more likely to match the stranger playback than the neighbour playback (50 versus 39% of trials), as was also found by Stoddard *et al.* (1992). Regardless of whether the stimulus is a shared song from a neighbour or stranger, type matching consistently signals the strong likelihood that the singer will approach the speaker aggressively.

Figure 2*a* shows the approach responses of focal birds to a type-matching stimulus versus a non-matching stimulus. These results are derived from the 1992–1993 stranger playback trials with synchronized switching, delivered once with shared song types that immediately matched the focal bird and then again on another day (random order) with unshared song types. Focal birds approached the type-matching stimulus more aggressively than the non-matching stimulus. This difference in response could have been caused by the shared versus unshared song types in these two treatments rather than by the type matching itself in the shared song treatment and, indeed, we found stronger responses to shared versus unshared song types in our other switching regime treatments as well. Burt’s (1999) experiment using only shared neighbour song types (broadcast from the appropriate boundary) represents a more definitive test of receiver responses to type matching. Treatments either type matched the current song of the focal bird or delivered a different but shared neighbour song type (i.e. a repertoire match). Males responded significantly more aggressively to the type-matching stimulus than to the repertoire-matching stimulus (figure 2*b*). Together, these results lend strong support to the idea that a type-matching opponent

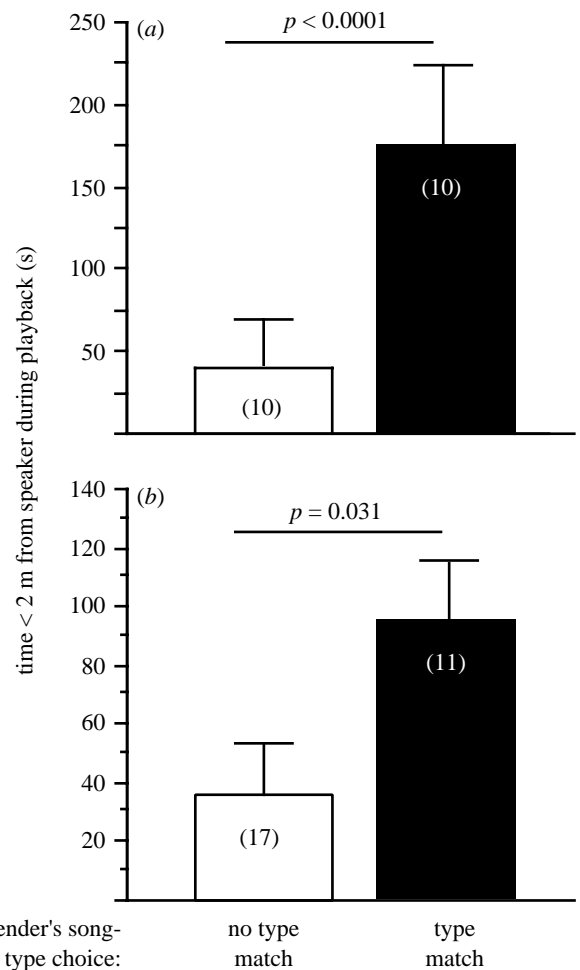


Figure 1. A sender's subsequent approach to the speaker as a function of his singing response to playback of a shared song type. Males that chose to type match the stimulus song subsequently approached the speaker more aggressively than males that did not type match. Bars indicate means  $\pm$  s.e. The number of trials is given in parentheses. (a) Playback of shared songs from a non-neighbouring bird broadcast from a boundary unoccupied by another song sparrow (based on Nielsen & Vehrencamp 1995). ANOVA on log-transformed data,  $F_{1,18} = 23.05$  and  $p < 0.0001$ . (b) Playback of shared songs from an adjacent neighbour broadcast from the boundary with that neighbour (1998–1999 experiments). Repeated-measures ANOVA,  $F_{1,5} = 8.89$  and  $p = 0.031$ . Bars show least-squares treatment means, which have been corrected for bird differences.

will be treated with a strong aggressive retaliatory response.

### 4. DISCUSSION

Type matching is clearly a signal of aggressive intentions in the song sparrow. Burt (1999) obtained an equivalent result in his study of the same species in that males who continued to type match a type-matching stimulus throughout the 3-min playback trial gave a stronger aggressive approach response compared with males who stopped type matching. An association between type matching and subsequent aggressive approaches has also been demonstrated in chaffinches, great tits and cardinals, as mentioned earlier. Does type matching qualify as a

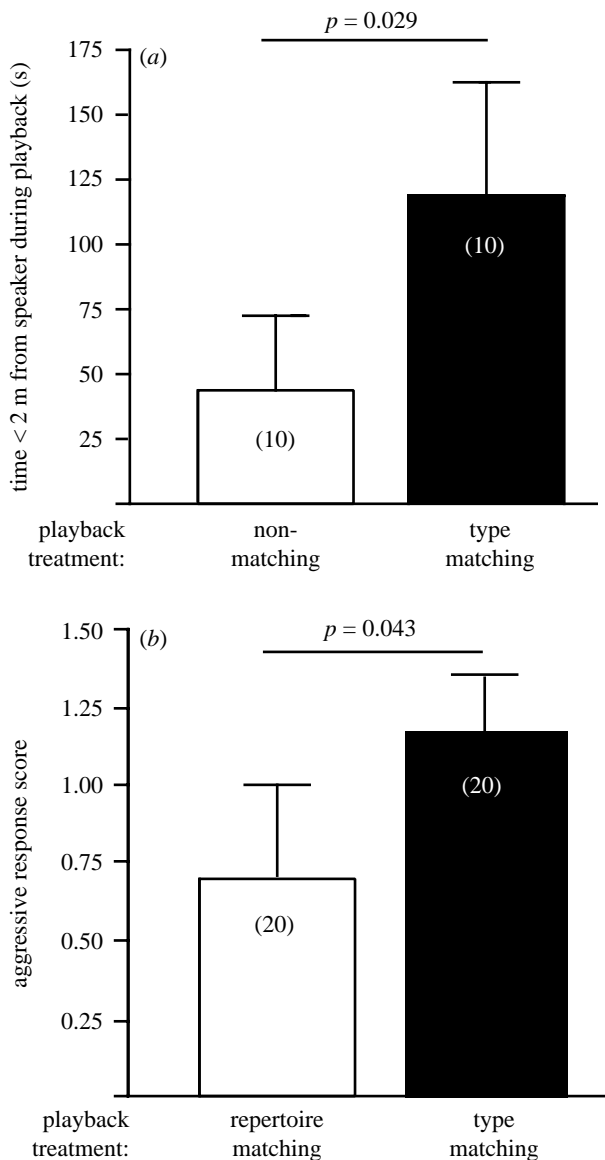


Figure 2. A receiver's approach response to a type-matching playback treatment versus a non-matching playback treatment. Type matching elicited the stronger approach response. (a) Playback of stranger (non-neighbour) songs broadcast from a boundary unoccupied by another song sparrow (based on Nielsen & Vehrencamp 1995). The non-matching treatment involved the use of song types that were not present in the focal bird's repertoire. Paired *t*-test on log-transformed data,  $n = 10$  and  $p = 0.029$ . (b) Playback of shared neighbour songs from the appropriate boundary (based on Burt 1999). The non-matching treatment involved the use of neighbour song types that were present in the focal bird's repertoire but not currently being sung by the focal bird (i.e. repertoire matching). The response score, which combines the closest approach, the number of threat displays and the number of flights from a principal components analysis, is entirely analogous to my measure of time spent close to the speaker. Paired *t*-test on transformed data,  $n = 20$  and  $p = 0.043$ .

conventional signal? In the discussion below, I evaluate the requirements for conventional signals: a retaliation cost as opposed to a production or vulnerability cost and arbitrariness of signal form.

Interactive playback studies on the song sparrow show that type matching elicits a strong aggressive approach in

receivers, which is a necessary requirement for a conventional signal (Nielsen & Vehrencamp 1995; Burt 1999). A type-matching stimulus also appears to be a precursor for subsequent escalation in the great tit (McGregor *et al.* 1992). Many students of bird song might conclude that this response is the expected one, i.e. that territorial birds respond more aggressively to the signal representing the greater intruder threat, but that this is not sufficient evidence to classify the signal as conventional. This expectation (of approach response proportional to degree of threat) is fostered by studies investigating species recognition of song and neighbour-stranger discrimination, where stronger responses are generally found for conspecific (versus modified or non-conspecific) and stranger (versus neighbour) song stimuli (Stoddard 1996). However, studies designed for investigating the relative threat signal value of subtle singing strategies tend to use signals so threatening that even a successful territorial bird may sometimes refrain from attacking (Dabelsteen & Pedersen 1990; Langemann *et al.* 2000). Most such studies are run interactively in some way, either by varying what song types are played relative to what the bird is singing or by varying what signals are played relative to the approach distance of the focal male. Investigators sometimes find that focal birds approach the stronger threat signal, as in this study, but in other species subjects retreat from the stronger threat signal. The observed disparity in response to playback has led some investigators to denounce this type of experiment as a tool for investigating the territorial function of song (Searcy & Nowicki 2000). I suggest that the nature of the response to very strong threats is indicative of different signal classes: strong approach responses imply that the signal imposes a retaliation cost and is therefore conventional, whereas frequent retreating responses imply that the signal is either an unbluffable index of fighting ability or a strategic handicap signal with a production or vulnerability risk cost. A very strong signal of this latter category is expected to cause even the most territorial of birds to pause.

For the few studies that have examined movement responses to song features that vary with agonistic context, this separation into conventional versus handicap/index signals is consistent with what we know about the production cost/risk and arbitrariness of signal form. Threat signals that result in significant retreating responses include type A songs in the willow warbler (Järvi *et al.* 1980), type I songs in Cetti warblers (Luschi & Del Seppia 1996), 'strangled songs' in the European blackbird (Dabelsteen & Pedersen 1990), song overlapping in European blackbirds and great tits (Tödt 1981; Otter *et al.* 1999), high song amplitude in the European blackbird (Tödt 1981) and low whistle-note frequency in chickadees (Shackleton & Ratcliffe 1994; D. Mennill, personal communication). High song amplitude and low-note frequency are likely to be more costly or difficult to perform (Lambrechts 1996), overlapping while type matching must require rapid neural integration and soft song and the 'strangled song' of the blackbird must be performed at short distances to the opponent and, therefore, entails a vulnerability risk of opponent attack. In these examples and others, specific song structures are associated with more versus less aggressive threat signals

(Smith 1996). With type matching, on the other hand, there is no specific structure associated with an aggressive versus non-aggressive threat, since a particular song type that is used as a type match towards one neighbour may not be shared with another neighbour and, therefore, used as a non-matching signal of lowered aggressive intentions. Type matching therefore meets the arbitrariness criterion at the level of an individual bird.

A male must share at least one song type with a neighbour in order to type match him. Some adjacent male song sparrows do not share any whole song types with each other (Wilson *et al.* 2000). We noticed that males in this situation would use half matches, and Burt (1999) demonstrated that non-sharing males would respond with 'cadence' matches of the introductory notes. However, these cruder matches may be less effective and males sharing few or no songs with adjacent males had more aggressive interactions and lower territorial survival than males sharing two or more songs (Wilson *et al.* 2000; Wilson & Vehrencamp 2001). Song sharers may therefore be able to deliver more effective threats that resolve most conflicts by song, whereas non-sharers must resort to direct confrontation.

Type matching may not qualify as a conventional signal in all species. For example, in the great tit type matching does predict subsequent aggressive approaches, but birds do not respond more strongly to type matching than to non-matching interactive playback. Instead, type matching occurs at a fairly early stage of escalation and appears to be necessary for facilitating the strophe-length matching and song-overlapping strategies of highly escalated vocal contests in this species (McGregor *et al.* 1992; Otter *et al.* 1999; Langemann *et al.* 2000). In the wood thrush, males do not possess fixed song types but compose each song with a mix of different A, B and C parts. Birds strongly avoid matching any element of a playback song with a B or C element that they share, but matching does occur in the field and is performed more often by certain birds (Whitney & Miller 1983; Whitney 1991). It may be extremely difficult to compose a matching song rapidly in this species and the ability to do so could reflect a male's repertoire size, age or condition, as expected of a handicap or index signal.

As mentioned above, the switching rate may also qualify as a conventional signal. In the song sparrow, an increase in the switching rate is associated with subsequent aggressive approaches and receivers approach a switching stimulus more strongly than a non-switching stimulus. The switching rate does not seem to entail any differential production cost and, in fact, Lambrechts (1996) suggested that more rapid switching is less tiring than repeated singing of the same song type. The switching rate also exhibits different coding rules in different species: some species use high switching as the default non-aggressive signal and reduce their switching rate in agonistic encounters, whereas other species increase their switching rate in agonistic encounters (Vehrencamp 2000). Both type matching and the rate of switching involve the strategic use of apparently interchangeable song types. Since there is no constraint on production, differential energetic cost or vulnerability risk the evolution of these signals as threats in male-male counter-singing contests may require the concurrent

evolution of a receiver retaliation rule in order to stabilize signal honesty.

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