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Review

Song as an aggressive signal in songbirds

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Birdsong is often regarded as an aggressive signal. More specifically, particular singing behaviours are hypothesized to be threatening, including song type matching, frequency matching, song overlapping, song type switching and low-amplitude song. The term aggressive signal should be reserved for behaviours that are associated with, and, in that sense, signal aggressive escalation. Three criteria are relevant to whether a signal should be classified as aggressive: (1) whether the signal increases in aggressive contexts (the context criterion); (2) whether the signal predicts aggressive escalation by the signaller (the predictive criterion); and (3) whether receivers respond to the signal (the response criterion). Adequate evidence on all three criteria is not available for most putative aggressive signals. The evidence that is available suggests that low-amplitude song and perhaps frequency matching are strongly aggressive signals in some species; that type matching is not a signal of attack but may be a signal of lower levels of aggressive escalation; that type switching can be either a signal of escalation or of de-escalation; and that overlapping may not be a signal at all. Song performance is probably mainly a signal of male quality, but may additionally signal aggressive escalation in some cases. We propose that more attention be devoted to testing the predictive criterion: an aggressive signal should either predict attack, or if not, it should predict escalation to the next higher level of aggressive signalling, and each higher level of signalling should more reliably predict the ultimate response of actual attack.

A number of singing behaviours have been suggested to be aggressive signals in songbirds; notable examples include song type matching, frequency matching, song type switching, overlapping and low-amplitude 'soft song'. The evidence that such behaviours are aggressive varies widely from signal to signal and from study species to study species. Here we hope to establish some criteria for demonstrating that a singing behaviour is an aggressive signal, and to compare existing evidence to those criteria.

Otte (1974, page 385) defined signals as 'behavioral, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms'. A broad definition of 'aggressive signal', then, would be any characteristic that meets Otte's definition and that is associated with aggressive contexts, that is, with conflict situations that may lead to physical fights. Scott & Fredericson (1951), however, pointed out that conflict situations lead not only to fighting, but also to defensive behaviour, passivity and escape. Signals associated with aggressive contexts thus will include signals associated with escape as well as those associated with attack, and as Huntingford & Turner (1987, page 9) remark, 'it seems an abuse of language to include escape under the heading of aggression'. To avoid this sort of abuse, Scott & Fredericson (1951) coined the term 'agonistic' to describe the entire gamut of behaviour, from fighting to escape, that occurs in conflicts. 'Aggressive' behaviour can then be restricted to the subset of agonistic behaviour that is associated with escalation towards physical fighting.

We use the term 'agonistic signals' to designate all signals used in aggressive contexts, including signals associated with attack, submissiveness and escape. We reserve the term 'aggressive signals' for the subset of agonistic signals associated with attack or escalation towards attack. A signal that predicts escalation towards attack can also be termed a 'threat' or a 'threatening signal', and we use these terms interchangeably with 'aggressive signal'.

Many aggressive signalling systems are graded, meaning that the sender has a hierarchy of signals of increasing 'threat value'. Call this hierarchy of signals, in order of escalation, X, Y and Z, with attack being the final step. Each step in the series may be contingent on the behaviour of the receiver; for example, the signaller may escalate to the next step only if the receiver does not de-escalate. In such cases,

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signals at the end of the graded series (such as Z) will be better predictors of overt aggression than will signals at the start (such as X), because a smaller number of contingencies intervene between the signal and attack. Signals at the start of the series may be better viewed as predicting the next level of signals (e.g. X predicts Y) rather than as predicting attack, although even here the prediction will still often be contingent on factors such as receiver response. A display then should qualify as an 'aggressive signal' or 'threat' if it predicts any step higher up the chain of escalation, whether or not it reliably predicts actual attack.

CATEGORIES OF SIGNALS

Signalling is worthwhile to signallers only if receivers respond to their signals, and receivers should respond only if the signals contain information important to them. In aggressive contests, two kinds of information are important to a receiver: information on the signaller's willingness to escalate and on its fighting ability. We have defined aggressive signals in terms of the former kind of information, that is, as signals associated with attack or escalation towards attack. Therefore, by our definition, a signal that contained information on fighting ability but not on willingness to escalate would not be an aggressive signal. In practise, however, signals of fighting ability are very likely to convey information on aggressive escalation, if only because individuals of high fighting ability are more likely to escalate than individuals of low fighting ability (Enquist 1985).

Agonistic signals can also be categorized by the mechanisms that maintain variation in signalling at evolutionary equilibrium (Hurd & Enquist 2005). A first distinction is between 'free strategic signals', which are available for use by all signallers, and 'performance signals', whose use is constrained to a subset of signallers. Use of performance signals may be limited by a physical constraint, meaning that only a subset of signallers are physically capable of performing some signal variants; a signal of this type is termed an 'index' (Maynard Smith & Harper 1995, 2003). Alternatively, performance signals may be limited by an 'information constraint', meaning that only a subset of signallers have the information needed to produce the signal (Hurd & Enquist 2005). Song type matching, for example, is subject to two information constraints, one in that matching requires that the signaller has paid attention to what another bird has just sung, and two in that matching requires that the signaller has previously learned the appropriate song type and stored it in memory. Strategic signals, those available to all signallers, may be either 'classic handicaps' or 'conventional signals' (Hurd & Enquist 2005). Classic handicaps have some inherent cost, independent of receiver response, and variation in the level of cost experienced by different individuals produces different optimum signalling levels (Grafen 1990). An example from birdsong may be song output, which has some energy cost and perhaps a greater cost in time taken from other activities such as foraging. Conventional signals are again stabilized by costs, but in this case the costs stem from the responses of receivers to the signals (Enquist 1985; Guilford & Dawkins 1995). Song type switching has been proposed to be a conventional signal in birdsong, with either an increase or decrease in switching conveying higher aggressiveness, depending on convention (Vehrencamp 2000).

Understanding how a signal fits into this taxonomy can be helpful in deciding whether a given signal communicates fighting ability or aggressiveness. Fighting ability often depends on physical properties of the animal, such as body size, strength and coordination, and thus is often conveyed by index signals that are tied to the same physical properties. An index signal, then, can be expected to convey aggressiveness only to the extent that willingness to escalate is associated with fighting ability. Index signals, however, can sometimes be modulated within limits (Wagner 1989; Reby & McComb 2003), with the effect of exaggerating fighting ability, and the degree of modulation may itself become an aggressive signal (Wagner 1992). Willingness to escalate, by contrast, is in general a choice open to all, and thus may most often be communicated by a free strategic signal. Within the free strategic signal category, conventional signals may most often be used to communicate aggressive intentions, because receiver-dependent costs through receiver retaliation or increased vulnerability are so likely in aggressive contests (Vehrencamp 2000).

METHODS FOR ESTABLISHING AGGRESSIVENESS

How can one establish that an agonistic signal is 'associated with attack or escalation towards attack'? Evidence relevant to this question can be gathered from either the 'sender's perspective' or the 'receiver's perspective' (Vehrencamp et al. 2007). The sender's perspective represents what the signal means to the signaller, and can be investigated by examining either how external context influences production of the signal or how production of the signal is correlated with other aspects of the signaller's behaviour. The receiver's perspective represents what the signal means to the receiver, and can be investigated by examining the responses of receivers to the signal (Vehrencamp et al. 2007).

One method of investigating the sender's perspective is to measure the association between a singing behaviour and either natural variation in context or experimentally manipulated context. Thus, one might measure how a particular signal changes as individuals enter natural aggressive interactions or confront an experimentally produced threatening stimulus. Results from this approach are somewhat ambiguous, because of a problem mentioned earlier: signals produced in an aggressive context might signal intention either to escalate or to de-escalate, and signals of de-escalation cannot be considered aggressive.

The second approach to investigating the sender's perspective is to measure whether the signal predicts subsequent aggressive escalation. Data may be obtained either by observing natural aggressive interactions or by experimentally confronting subjects with a stimulus that elicits aggression, such as territorial playback or a taxidermic mount. The researcher records both the signals given and any overt aggression, and then tests statistically how well signals predict aggressive escalation. When analysing natural interactions, it may be important to control for the receiver's behaviour. A signal can be accepted as aggressive if it predicts either attack or some smaller step in aggressive escalation. Thus, if there is evidence that approach to a mount predicts subsequent attack, one can demonstrate that signal Z is aggressive by demonstrating that Z predicts approach, and once signal Z has been demonstrated to be aggressive, one can demonstrate signal Y is aggressive by showing it predicts Z.

Although interpreting results from this approach is fairly straightforward, one caveat is in order. Receivers are interested in what a signaller is going to do, not in what it has already done. For this reason, it makes more sense to determine the aggressive meaning of a signal by measuring the association between the signal and the signaller's subsequent behaviour, rather than between the signal and the signaller's prior behaviour. In practise, however, what has been done most often is to measure signalling behaviour and aggressive behaviour during the same time period, so that some of the signalling occurs before and some after the aggressive behaviour. This problem is critical only if signalling changes in a nonrandom way through the course of the chosen time period. Given that we typically do not know whether such changes occur, it seems prudent to maintain the correct temporal sequence when possible, with signalling behaviour measured first and aggressive behaviour second.

The aggressive context in which song is produced in most songbirds is territory defence. A classic method for measuring receiver response in this context is territorial playback: song is played from a speaker placed on a territory and the response of the territory owner is observed. A problem with using this method to determine the aggressiveness of a signal is in deciding how to interpret a strong response, one in which the territory owner approaches the stimulus closely and displays vigorously (Searcy & Nowicki 2000). A common interpretation is that a strong response indicates that the signal communicates a high level of aggressiveness or fighting ability (Nelson & Croner 1991; Dabelsteen et al. 1996; Slabbekoorn & ten Cate 1996; Otter et al. 2002), the logic being that owners should react more strongly the greater the threat to their territories. In other cases, however, a weak response to a playback stimulus is interpreted as indicating a highly aggressive signal (Järvi et al. 1980; Catchpole 1983; Hall et al. 2006), with the logic that a weak response is produced when the territory owner has been intimidated. Both interpretations may even be maintained within a single paper (Mennill & Ratcliffe 2004a).

The problem is not that one of these interpretations is always correct and the other always wrong. On the contrary, good cases exist in which there is independent evidence that one signal is more aggressive than another and the more aggressive signal produces a stronger response in territorial playback, as well as good cases in which exactly the opposite pattern is found. In some species of songbirds, for example, a certain song type or category of song is used preferentially in aggressive contexts. In field sparrows, *Spizella pusilla*, territorial playback of the aggressive song category produces a stronger aggressive response than other songs (Nelson & Croner 1991), whereas in willow warblers, *Phylloscopus trochilus*, and great reed warblers, *Acrocephalus arundinaceus*, playback of the aggressive song category produces a weaker response (Järvi et al. 1980; Catchpole 1983). Because both patterns occur, we have no way of knowing (in the absence of other evidence) whether a strong response indicates a threatening signal or a nonthreatening signal, so measuring response in this way advances us little towards determining how threatening the signal is. Nevertheless, demonstrating that subjects respond differentially in territorial playback to two categories of signals is useful in showing that the difference between the two categories is salient to the receivers.

Speaker occupation provides a second means of measuring receiver response (Göransson et al. 1974; Krebs et al. 1978; Yasukawa 1981). This design involves removing a territory owner and then measuring how well songs broadcast from his territory function in keeping out intruders. If one song pattern functions better in warding off intruders than does a second, this suggests that the first pattern is more threatening. Unfortunately, speaker occupation experiments are cumbersome to perform (Searcy & Nowicki 2000), and consequently very few have been done that examine more than the effects of presence versus absence of song.

To synthesize these possible lines of evidence, three criteria should be met to establish that a given singing behaviour is aggressive.

(1) A demonstration that the signal increases in aggressive contexts ('context criterion').

(2) A demonstration that the signal predicts aggressive escalation by the signaller ('predictive criterion').

(3) A demonstration of receiver response to the signal, by demonstrating differential response to the signal versus a proper control ('response criterion').

The first and second criteria represent the sender's perspective, and the third represents the receiver's perspective. The context criterion alone is sufficient only to establish that the signal is agonistic, not that it is aggressive. The predictive criterion can establish that the signal is aggressive, but not that it is salient to receivers. The response criterion, if demonstrated using territorial playback, tells us that the signal is salient to receivers but not whether it is aggressive. Establishing both the predictive and the response criteria, or better yet all three criteria, makes a strong case that a given signal is aggressive.

Song Type Matching

Song type matching is a behaviour in which one bird replies to another with the same song type that the other bird just sang. Matching in this sense is only possible if the two individuals share song types that are sufficiently similar. If two individuals do share song types, some level of matching will occur by chance alone; thus, to establish that matching is a signal, it is important to show that matching occurs, at least in some circumstances, at above-chance levels. Above-random levels of matching have been rigorously demonstrated for a number of species, both in natural interactions (e.g. rufous bristlebirds, *Dasyornis broadbenti*: Rogers 2004; banded wrens, *Thryothorus pleurostictus*: Burt & Vehrencamp 2005; black-capped chickadees, *Poecile atricapillus*: Gammon et al. 2008) and in response to playback (e.g. great tits, *Parus major*: Krebs et al. 1981; western meadowlarks, *Sturnella neglecta*: Falls 1985; song sparrows, *Melospiza melodia*: Stoddard et al. 1992). In song sparrows, males match at above-random levels using songs that are not identical but instead are similar only in particular characteristics, such as in tempo or in the form of the introduction (Burt et al. 2002; Anderson et al. 2005). Finally, Beecher et al. (1996) found that song sparrows sometimes reply to a neighbour, not with the same song that the neighbour has just sung, but with another shared song. Such 'repertoire matching' also occurs at above-chance levels under some circumstances (Beecher et al. 1996).

One way that the context criterion has been tested for matching is by comparing matching levels in response to neighbours and strangers. Territorial songbirds are generally less aggressive towards familiar neighbours than they are towards strangers (Falls 1982; Stoddard 1996). If type matching is aggressive, then it should be more likely to occur in response to stranger song than in response to neighbour song when playback is from the boundary of the neighbour and subject (i.e. where that neighbour would often sing naturally). This prediction has been met in western song sparrows (Stoddard et al. 1992) and western meadowlarks (Falls 1985). Although the matching rate was found to be higher to neighbour than stranger song in great tits (Falls et al. 1982), the neighbour matching songs were more similar to a subject's songs than were stranger matching songs, and when neighbour and stranger stimulus songs were equated for similarity, type matching was higher as predicted to stranger song. Two studies have also found that type matching is more common early in the season when new neighbours presumably have not yet worked out their territorial boundaries (Krebs et al. 1981; Beecher et al. 2000). Overall then there is good evidence in support of the context criterion for song type matching.

Evidence on the value of song matching in predicting aggressive escalation is mixed. Falls et al. (1982) studied matching to self, neighbour and stranger song in great tits and found no correlation between type matching and conventional measures of aggressive response over a 10 min trial consisting of 2 min of playback followed by 8 min of silence. In a study of western meadowlarks, Falls (1985) also found no correlation between matching and aggressive response measured over a 5 min trial consisting of 2 min of playback followed by 3 min of silence. By contrast, in a study of western song sparrows, Vehrencamp (2001) found that birds that type-matched playback of neighbour or stranger song also responded more aggressively in the 3 min period after the playback concluded. In a similarly designed study of western song sparrows, Beecher et al. (2000) found no correlation between type matching and aggressive response in response to neighbour shared song during the 3 min playback, but they did not measure postplayback aggressive response. In a third study of song sparrows, of an eastern population in which neighbours do not share whole song types, Anderson et al. (2005) found that if the playback stimulus was the subject's own song ('self song'), birds that type-matched did not respond more strongly, either during the 3 min trial or in the 2 min postplayback period. However, if the playback stimulus was a half-match (first half self song, second half stranger song), matchers did respond more strongly during the 3 min playback but not in the 2 min postplayback trial. Finally, in studies of eastern song sparrows (Searcy et al. 2006) and swamp sparrows, *Melospiza georgiana* (Ballentine et al. 2008), in which subjects were presented with a taxidermic mount of a conspecific, type matching failed to predict whether a subject would subsequently attack the mount. These 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.

Several studies have measured response to matching. In an interactive playback study of western song sparrows, when a subject sang a song he shared with a particular neighbour, the experimenters replied with either the neighbour's version of that song (a type match) or another shared song of that neighbour (a 'repertoire match') (Burt et al. 2001). Subjects responded more aggressively when type-matched than when repertoire-matched. Moreover, subjects that 'stayed on type' (did not switch to a new type when matched) also responded more aggressively than did subjects that switched off type or stopped singing. In contrast, in a similar study of eastern song sparrows, Anderson et al. (2008a) found that birds did not respond more aggressively to partial-matching songs than they did to nonmatching songs. Moreover, birds that stayed on type did not respond more aggressively than those that did not. The difference in response patterns between eastern and western populations of song sparrows may reflect a greater salience of type matching in western populations, where song-learning strategies seem to have been shaped to produce type sharing between neighbours (Beecher et al. 1994; Nordby et al. 1999) and where type-sharing levels (Hill et al. 1999) are substantially higher than in eastern populations (Hughes et al. 1998). In another interactive playback study using neighbour songs, Molles & Vehrencamp (2001) found that banded wrens responded more strongly to a 'retreating' playback speaker (moved from 15 m within the territory to the territory boundary) when it continued to type-match than when it switched to another shared song (a repertoire match).

In summary, type matching is more likely in aggressive contexts, but the evidence is mixed as to whether subjects respond aggressively when type-matched. The bulk of the evidence indicates that type matching does not predict conventional measures of aggressive response. A possible explanation of the general failure of type matching to satisfy the predictive criterion is that matching (1) may predict aggressive response only if the receiver escalates and (2) may represent a lower level of aggressive signal (i.e. one that only predicts the next level of aggressive signalling rather than aggression per se). With respect to the first point, the experimental paradigms used in the studies we have reviewed usually simulate a weakly aggressive challenge without escalation. The challenger song is played at or near the territory boundary, and the challenge is never escalated. Moreover, as discussed earlier, the strongest prediction is that type matching at one point in time (e.g. during the playback period) will predict aggressive response at a later point in time (e.g. during the postplayback period), yet the design just described is inherently a de-escalation, for the simulated bird simply 'disappears' when the playback ends. The only way around this is to maintain the challenge, say by leaving a mount on the territory (Searcy et al. 2006). In this case, we might expect type matching to predict the next level of aggressive signalling, rather than outright attack. Future work should test directly the possibility that song type matching predicts intermediate steps in aggressive escalation short of outright attack, such as increased levels of other aggressive signals.

Frequency Matching

Frequency matching is a behaviour in which a bird adjusts the frequency (or pitch) of its song to resemble that of a rival's song. Morton & Young (1986) described Kentucky warblers, *Oporornis formosus*, as frequency matching by shifting the frequency characteristics of their single song type without otherwise changing its acoustic form. Harris's sparrows, *Zonotrichia querula*, frequency-match in another way, by choosing from their repertoire the song type most similar in frequency to the song a rival has just sung (Shackleton et al. 1991). This latter style of frequency matching is equivalent to song type matching. In this section, we restrict ourselves to cases in which a bird matches by shifting the frequency of a given song type, rather than by choice of song type.

Evidence for deliberate frequency matching is available for two species. First, Morton & Young (1986) showed that four of six Kentucky warblers sang at significantly higher frequencies in response to playback of high-frequency songs than in response to playback of low-frequency songs. Second, in black-capped chickadees, Horn et al. (1992) found a significant positive relationship between the frequency of playback songs and the frequency of songs given by subjects in reply. In addition, Foote et al. (2008) found that males of this species frequency matched each other significantly more during the dawn chorus than expected by chance. Other studies of black-capped chickadees found random levels of frequency matching, both in natural interactions (Shackleton & Ratcliffe 1994; Fitzsimmons et al. 2008) and in response to playback (Shackleton & Ratcliffe 1994).

Evidence on whether frequency matching meets our criteria for a threatening signal is available only for black-capped chickadees. Foote et al. (2008) found no relationship between amount of matching and distance between opponents. Shackleton & Ratcliffe (1994) found a strong association between the occurrence of frequency matching and subsequent aggressive escalation in natural encounters between chickadees, providing good support for the predictive criterion. Fitzsimmons et al. (2008), however, found no significant relationship between frequency matching and approach in a second, larger sample of natural interactions. With respect to receiver response, Otter et al. (2002) found evidence of stronger approach to playback of songs that frequency-matched their subjects, whereas Mennill & Ratcliffe (2004a) found the opposite pattern. Both studies indicate that receivers respond differentially to frequency matching, supporting the response criterion. Overall, the evidence is at present not yet sufficient on whether frequency matching functions as a threat, although the results of Shackleton & Ratcliffe (1994) are suggestive. Additional work is needed in black-capped chickadees, especially on the context criterion, and it would also be valuable to extend investigations of this behaviour to other species.

Song Overlapping

Song overlapping is a behaviour in which one individual starts to sing while another is in mid-song. Overlapping has been hypothesized to be an aggressive signal (Todt 1981; Naguib & Todt 1997; Todt & Naguib 2000; Mennill & Ratcliffe 2004a; Naguib & Kipper 2006) in just the same sense that we define the term. For example, Kunc et al. (2006, page 25) state 'there is growing evidence that song overlapping is used and perceived as a signal of immediate aggression'. Another timing pattern that has been suggested to be aggressive is countersinging, in which a focal male replies after rather than during a rival's song (Hyman 2003), but little research has been done on this behaviour.

Overlapping, like matching, is a pattern that can occur by chance alone, even if two singers ignore each other completely. Thus it seems important to ask whether overlapping occurs at frequencies greater than chance. A simple method for addressing this question was formulated by Ficken et al. (1974). Suppose that bird B sings with a mean song length of S_{on} and a mean pause length between songs of S_{off}. B thus spends a proportion $S_{\mathrm{on}}/(S_{\mathrm{on}}+S_{\mathrm{off}})$ of the time in song, a proportion that can be termed D (for duty cycle). If bird A sings one song and begins it without reference to what B is doing, then the chance that A's song starts while B is singing is equal to D. Wasserman (1977) used this approach to calculate expected levels of overlapping between neighbouring male white-throated sparrows, *Zonotrichia albicollis*, and found that they consistently overlapped each other at below-chance levels. Using another method, Gochfeld (1978) found that male lesser skylarks, *Alauda gulgula*, also avoid overlapping each other. Fitzsimmons et al. (2008) estimated chance levels of overlapping for black-capped chickadees singing during the day using a randomization procedure, and found no difference between observed and chance levels. In a similar analysis of natural singing during the dawn chorus, black-capped chickadees overlapped slightly, but significantly, less than chance (Foote et al. 2008). Singers have also been found in some cases to avoid overlapping the songs of other species (Ficken et al. 1974; Brumm 2006).

As far as we know, no one has demonstrated that singers consistently overlap each other at above-chance levels in any species in any context. The closest approach to such a demonstration is provided by Hultsch & Todt (1982). These authors recorded natural interactions between nightingales, *Luscinia megarhynchos*, singing at night, and found five cases in which one male overlapped another more often than by chance, six in which one male overlapped another less often than by chance, and five in which overlapping occurred at chance levels. Combining data across birds, overlapping was considerably under chance levels. Nightingales sing with such a high duty cycle ($\mathrm{mean} = 0.45$) that mutual avoidance of overlapping by both members of a dyad becomes very difficult. Hultsch & Todt (1982) also played to the same males bouts of songs with a natural sequence of pauses, and found that three males overlapped the playback at chance levels, three at below-chance levels, and just one at above-chance levels.

Although these findings provide little evidence that overlapping levels are above chance overall, one might still be convinced that overlapping is a nonrandom signal in nightingales if it could be shown that the minority of males that overlap at above-chance levels are a special subset in some other respect, for example, the most aggressive or the most dominant males. No such evidence is provided by Hultsch & Todt (1982), but a second study of nightingales is suggestive. Kunc et al. (2006) confronted nocturnally singing nightingales with playback during the prebreeding period, and then observed whether their subjects later succeeded in pairing. Males that subsequently paired overlapped 22% of the playback songs, significantly more than the 12% overlapped by males that did not pair. Thus the males that overlapped more were a particular subset: they were the males that succeeded in pairing, perhaps because they were more attractive to females, or perhaps because they were better able to defend attractive territories. It is again interesting to ask whether these successful males overlapped playback more than expected by chance. The duty cycle used by Kunc et al. (2006) for playbacks was quite high, 0.45 by our calculation, which is the same as in the natural singing bouts observed by Hultsch & Todt (1982). Successful males sang about 9.3 songs per minute on average, so that $9.3 \times 0.45 = 4.2$ songs per minute would be expected to overlap playback songs by chance. Since the playback rate was 10 songs per minute, the random expectation of overlapping was 4.2/10 or 42%, compared to the observed 22%. Thus, even successful males overlapped playback at frequencies substantially lower than chance. Rather than deliberately overlapping their rivals, successful males may have simply been less careful than unsuccessful males in avoiding overlapping others.

Even when overlapping occurs less often than expected by chance, the occasional occurrence of overlapping might none the less have a signal value; therefore, we will still address whether overlapping meets our criteria for an aggressive signal. Before we do so, however, it is important to note that some measures of overlapping are dependent on a focal male's song rate. The random expectation for number of overlaps between A's songs and B's songs is $N_{\mathrm{A}}(D_{\mathrm{B}})$, where N_{A} is the number of songs sung by A and D_{B} is B's duty cycle. One measure of A's propensity to overlap is the proportion of A's songs that overlap B's songs; here the random expectation is $N_{\mathrm{A}}(D_{\mathrm{B}})/N_{\mathrm{A}} = D_{\mathrm{B}}$. Note that N_{A} cancels out of this expression, so this measure is not dependent on A's song rate. A second measure of A's propensity to overlap is the proportion of B's songs that are overlapped by A; here the random expectation is $N_{\mathrm{A}}(D_{\mathrm{B}})/N_{\mathrm{B}}$, where N_{B} is the number of songs sung by B. Note that this measure is dependent on A's song rate, so that changes in this measure with context or signaller behaviour may be due to changes in signaller's song rate rather than to its tendency to overlap.

Two studies have investigated overlapping from the sender's perspective. Foote et al. (2008) found that overlapping does not vary with distance between interactants in black-capped chickadees. Brindley (1991) examined overlapping of neighbour and stranger song in European robins, *Erithacus rubecula*, which show the typical pattern of lower aggressiveness towards neighbours at the appropriate boundary (Brindley 1991). Brindley (1991) reported that overlapping was higher in response to stranger song than in response to neighbour song, but what measure of overlap did she use? In the figure legends (page 509), she reports on the 'proportion of total songs given by subject bird found to overlap those of either neighbour or stranger playback', which corresponds to our first measure of overlapping, the one not dependent on subject's song rate. In the text (page 506), she reports the same results as showing that 'the songs of a strange bird were more likely to be overlapped than those of a neighbouring individual', which corresponds to our second measure, the one that is dependent on subject's song rate. As song rates of subjects were about 60% higher and overlapping about 50% higher for stranger songs than for neighbour songs, the increase in song rate could explain entirely the increase in overlapping if the latter measure was the one actually used.

Several studies have tested whether overlapping is associated with escalation (the predictive criterion). van Dongen (2006) simulated territorial intrusions in golden whistlers, *Pachycephala pectoralis*, using song playback coupled with a caged male, and found that territory owners were on average closer to the simulated intruder when they overlapped the speaker's song than when they did not overlap. Song rate was not controlled, so the result could be due to males singing at higher rates near the stimulus. The duty cycle of the playback was approximately 0.11 (W. F. D. van Dongen, personal communication), so the observed level of 3.8% overlapping was lower than expected by chance. Vehrencamp et al. (2007) presented territorial male banded wrens with playback of conspecific songs, and calculated overlapping as the proportion of the subject's songs that overlapped the playback songs (a measure that does control for song rate). High overlapping was associated with earlier retreat from the speaker. This result, then, is consistent with overlapping being a signal of de-escalation rather than escalation. Fitzsimmons et al. (2008) analysed natural interactions between black-capped chickadees and found no association between overlapping and singer's dominance as measured in winter flocks or between overlapping and approach to an opponent. Fitzsimmons et al. (2008) did find evidence of a positive association between overlapping and frequency matching, although no such association was found by Foote et al. (2008) in another analysis of the same population. An association between overlapping and frequency matching would indicate that overlapping is aggressive if frequency matching is also aggressive, but evidence for the latter is at present incomplete.

A number of studies have evaluated overlapping from the receiver's perspective, that is, have measured how subjects respond to being overlapped. The clearest effect is on the subjects' own singing: males shorten their songs or interrupt them more when overlapped by playback in black-capped chickadees (Mennill & Ratcliffe 2004a), nightingales (Naguib 1999; Naguib & Kipper 2006; Schmidt et al. 2006) and banded wrens (Hall et al. 2006). The simplest interpretation of these effects is that males stop singing when jammed, which makes sense if jamming prevents others from hearing their songs. Avoidance of jamming is also consistent with the strong tendency found in many species for birds to avoid overlapping others of the same or different species (see above), and with the avoidance by male nightingales of singing from perches where they have been overlapped (Todt 1981). Effects of being overlapped on aggressive behaviour are less consistent. Yellowhammers, *Emberiza citrinella*, showed a higher latency to approach overlapping playback (Osiejuk et al. 2003), thus showing a less aggressive response to overlapping. Male European robins started to sing aggressive, low-amplitude twitter songs sooner in response to overlapping, thus indicating a stronger aggressive response to overlapping (Dabelsteen et al. 1997). Male nightingales responded with faster and closer approach to playback of a rival's songs that had overlapped their own songs during the previous night than to songs that had alternated with theirs (Schmidt et al. 2007). The majority of results, however, indicate no difference in aggressive response: great tits (Dabelsteen et al. 1996), European robins (Dabelsteen et al. 1997), black-capped chickadees (Mennill & Ratcliffe 2004a) and banded wrens (Hall et al. 2006) all showed equal approach responses to overlapping and alternating playbacks.

Overlapping has also been investigated in the context of 'eavesdropping', a behaviour in which one individual attends to signals passed between two others (McGregor & Dabelsteen 1996). The eavesdropping studies have been designed under the assumption that overlapping is aggressive, rather than as a test of that assumption; nevertheless, the results cast some light on receiver response to overlapping. Peake et al. (2001) used playback from two loudspeakers to simulate a singing interaction between two great tits just off a subject male's territory, and then simulated an intrusion by one of the two interacting males onto the subject's territory. Subjects gave fewer songs in response to intrusions by interactants that had been overlapped than in response to interactants that had not been overlapped. Mennill & Ratcliffe (2004b) used two loudspeakers both placed on a subject's territory to simulate an interaction between black-capped chickadees; subjects preferred to approach the speaker broadcasting songs that overlapped the other speaker's songs. These and similar studies (Peake et al. 2002) indicate that receivers are responsive to overlapping, but eavesdropping studies are as ambiguous as territorial playback as to which stimuli are more threatening.

In conclusion, existing evidence that overlapping is a threatening signal is in our opinion minimal. The fact that most species overlap at levels lower than those expected by chance suggests that overlapping, when it does occur, may be accidental rather than deliberate. We strongly suggest that all future studies of overlapping relate observed levels to chance levels. It is still possible that the occasional occurrence of overlapping is a signal, but there is little or no evidence that this behaviour is associated with aggressive escalation, and evidence based on males' responses to being overlapped by playback is even more ambiguous than that based on males' responses to other signals. The single most positive result is that of Brindley (1991), showing that overlapping in European robins increases in more aggressive contexts, but even this result may be explained by changes in song rates. More studies are needed investigating both the context and predictive criteria, using measures of overlapping that are independent of subject's song rate.

Low-amplitude Song

Song that is produced at amplitudes that are markedly lower than normal has been termed 'soft song' (Nice 1943), 'strangled song' (Snow 1958), 'quiet song' (Dabelsteen et al. 1998), or 'whisper song' (Morton 2000). Low-amplitude songs sometimes have the same acoustic structure as normal broadcast song, whereas in other cases their acoustic structure is quite distinctive. Song sparrows, for example, produce both 'crystallized soft songs', which are identical to song types from the normal broadcast repertoire, and 'warbled soft songs', which are not in the normal repertoire, meaning they are never sung at high amplitude, and which have distinctive acoustic features such as a broader-frequency bandwidth (Anderson et al. 2008b). In other species, such as redwings, *Turdus iliacus*, and European blackbirds, *Turdus merula*, males produce distinctive loud and soft phrases, which are sometimes put together in a single song and are sometimes sung separately (Lampe & Espmark 1987; Dabelsteen & Pedersen 1990).

Many anecdotal reports suggest that use of soft song increases in aggressive contexts, for example, in song sparrows (Nice 1943), European blackbirds (Snow 1958), redwings (Lampe & Espmark 1987), and various species of wood warblers (Morton 2000). Few studies, however, have tested quantitatively whether use of the signal increases in aggressive contexts. An exception is a study by Lampe (1991), which showed that male redwings increase the mean duration of the quiet 'twitter' phrases of their songs during territorial playback relative to that before playback. In contrast, Ripmeester et al. (2007) found that the proportion of European blackbird songs made up of low-amplitude twitter phrases did not change following playback.

Soft song has been shown to predict aggression in two species. Searcy et al. (2006) provoked aggressive signalling from male song sparrows by playing songs on their territories, and after recording their displays, gave the subjects an opportunity to attack a stuffed male conspecific. Of a variety of displays, including type matching and type switching, only numbers of soft songs differed significantly between the males that attacked and those that did not. In a discriminant function analysis, the number of soft songs given before attack correctly classified 74% of males as attacker or nonattackers. Ballentine et al. (2008) tested swamp sparrows using a similar procedure and measured similar behaviours. Again, soft song was the display that differed most between attackers and nonattackers, although in this species, wing waving, a visual display, also differed. In a forward, stepwise discriminant function analysis, soft song was the first variable to enter, and together with wing waves correctly classified 85% of the subjects as attackers or nonattackers. These two studies of song and swamp sparrows, then, satisfy the predictive criterion. One caution is that because soft song is given almost exclusively in close proximity to a receiver, it may be that proximity is the real predictor of attack and that low-amplitude song is used for another reason, such as avoiding eavesdropping (McGregor & Dabelsteen 1996; Searcy & Nowicki 2006). In song sparrows, however, soft song enters a stepwise discriminant function predicting attack in preference to proximity (Searcy et al. 2006).

Dabelsteen & Pedersen (1990) tested European blackbirds for differential response to territorial playbacks of strangled song and high- and low-intensity versions of normal song. To ensure that subjects would notice playback of the low-amplitude strangled songs, some of the trials were started with playback of normal song, with playback switching to strangled song or continuing with normal song once the subject had started to respond. No difference in response was found to strangled song versus high-intensity normal songs, while response was stronger to strangled song than to low-intensity song on one of five measures. Similarly, Anderson et al. (2007) lured male song sparrows to within 4 m of a speaker using playback of normal song, and then switched playback to either another normal song or to a crystallized soft song. Response to soft song was no different than that to normal song. More recently, however, R. C. Anderson, W. A. Searcy & S. Nowicki (unpublished data) repeated this experiment using warbled soft song rather than crystallized soft song, and found significantly greater approach to warbled soft song than to normal song.

The results showing that low-amplitude song predicts attack in song and swamp sparrows provide strong evidence that low-amplitude song satisfies the predictive criterion, at least in these two species. The case for soft song as a threat could be strengthened by additional investigation of the context and response criteria in song and swamp sparrows and by investigation of all three criteria in additional species reported to use low-amplitude song.

Song Type Switching

Song type switching refers to the frequency with which a singer changes song types, measured, for example, as the number of switches per opportunity to switch (Searcy et al. 2000). Switching can be considered to be a means of displaying the singer's repertoire size. Repertoire size may be a signal of male quality (Spencer et al. 2004; Reid et al. 2005) and thus of fighting ability, and indeed has been shown to have an intimidating effect on opponents in speaker occupation experiments with great tits (Krebs et al. 1978) and red-winged blackbirds, *Agelaius phoeniceus* (Yasukawa 1981). The frequency of song type switching has been proposed to be a graded signal of aggressiveness, originally under the assumption that increased switching is the more threatening signal (Kramer & Lemon 1983). This assumption is logical: if repertoire size is a signal of fighting ability, then increasing switching frequency might at first be favoured as a means of exaggerating apparent fighting ability in aggressive contexts and then secondarily become a signal of aggressive arousal. Vehrencamp (2000), however, pointed out that switching may well be a conventional signal, and that it is characteristic of conventional signals that their meaning is arbitrary with respect to their structure. Thus, it would be consistent with this idea if threat was in some cases signalled by an increase in switching frequency and in others by a decrease.

Switching has been found to increase in aggressive contexts in some species. In natural interactions between song sparrows, for example, switching frequencies were lowest in solo singing, higher in countersinging, and highest of all during fights (Kramer & Lemon 1983). Furthermore, song sparrows increased switching in response to playback on their territories (Kramer et al. 1985; Searcy et al. 2000), and increased switching even more when playback was accompanied by a song sparrow mount (Kramer et al. 1985). Switching also increases in aggressive contexts in eastern meadowlarks, *Sturnella magna* (Falls & D'Agincourt 1982), western meadowlarks (Horn & Falls 1991), Carolina wrens, *Thryothorus ludovicianus* (Simpson 1985) and golden whistlers (van Dongen 2006).

The opposite pattern, of switching frequencies decreasing in aggressive contexts, has been demonstrated in at least two species. In red-winged blackbirds, territorial males lowered switching rates when confronted with a caged male intruder on their territories (Searcy & Yasukawa 1990). In banded wrens, switching rate was lower in natural countersinging interactions than in solo singing, and was lower still immediately after male–male aggressive interactions (Molles & Vehrencamp 1999).

Data on behaviour associated with switching has been gathered for a few species. In red-winged blackbirds, males that attacked a stuffed male had significantly lower switching frequencies than males that did not attack (Searcy & Yasukawa 1990). In banded wrens, by contrast, males that sang with high versatility (which combines switching frequency with song type diversity) spent longer close to a simulated intruder (Vehrencamp et al. 2007). In both song sparrows and swamp sparrows, switching frequency was not higher in males that attacked a simulated intruder than in males that did not attack (Searcy et al. 2006; Ballentine et al. 2008).

In terms of receiver's perspective, high switching evokes a stronger approach response in song sparrows (Nielsen & Vehrencamp 1995) and tropical mockingbirds, *Mimus gilvus* (Botero & Vehrencamp 2007), whereas low switching evokes a stronger response in banded wrens (Molles 2006). In plain wrens, *Thryothorus modestus*, playback switching frequency has no effect on approach responses (Marshall-Ball & Slater 2004).

Synthesizing evidence on switching across multiple lines of evidence produces inconsistent patterns in some species. In song sparrows, for example, switching increases in aggressive contexts, and high switching elicits strong aggressive responses but does not predict attack. In banded wrens, high versatility is associated with prolonged approach, but switching is lower in aggressive contexts than in nonaggressive contexts and low switching evokes a stronger aggressive response. Only in red-winged blackbirds is there good consistency so far: switching decreases in aggressive contexts and is lower in males that attack than in males that do not attack. Receiver response to switching has not, however, been investigated in red-winged blackbirds; such a study would be valuable, as would be coordinated investigations of all three criteria in additional species.

Vocal Performance

Vocal performance is the ability to produce physically challenging songs (Podos & Nowicki 2004). One method of estimating vocal performance is as the deviation of a song from an upper bound regression of frequency bandwidth on trill rate (Podos 2001). This measure is applied to trills, that is, songs or parts of songs consisting of rapidly repeated syllables. For biomechanical reasons, birds should not be able to maximize trill rate and syllable bandwidth simultaneously (Westneat et al. 1993). Bandwidth is therefore traded off against trill rate, and the limit imposed by this trade-off can be estimated by an upper bound regression between maximum observed bandwidths and trill rates (Podos 1997; Ballentine et al. 2004; Illes et al. 2006; Cramer & Price 2007; Janicke et al. 2008). Deviation from the upper bound provides an estimate of performance, with low deviation indicating high performance (Podos 2001).

Vocal performance is an index signal, that is, a signal limited by physical constraints, and as such is likely to be primarily a signal of fighting ability rather than of aggressive intentions. Fighting ability and aggressive intentions, however, may be correlated, simply because strong individuals are more likely to escalate aggressive encounters than are weak ones (Enquist 1985). In addition, it is possible in some cases for performance signals to be modulated in aggressive contexts, and for that modulation itself to become an aggressive signal. In frogs and toads, for example, dominant frequency of male advertisement calls is negatively correlated with body size for biomechanical reasons (Martin 1971), and body size is in turn strongly associated with fighting ability. In some species of frogs, males lower the dominant frequency of their calls in aggressive contexts (Wagner 1989; Bee & Perrill 1996), and in cricket frogs, *Acris crepitans*, the magnitude of the frequency shift is correlated with likelihood of attack (Wagner 1992; Burmeister et al. 2002). In other words, modulation of an index signal becomes an aggressive signal. By analogy, then, it is possible for either modulation of vocal performance or vocal performance per se to be an aggressive signal in songbirds.

If males sing a single song type whose performance level is strictly determined by physical constraints, then there may be no possibility for performance to increase in aggressive contexts. If, on the other hand, males sing multiple song types that differ in their degree of biomechanical difficulty, those males might increase performance in aggressive contexts by choosing to produce their highest performance song types. There is evidence against this kind of differential use of song types for red-winged blackbirds (Cramer & Price 2007) and swamp sparrows (DuBois et al. 2009), but for nightingales there is supporting evidence: males produce a greater proportion of songs with rapid broadband trills during simulated intrusions on their territories than they do during control contexts (Kunc et al. 2006). Additionally, DuBois et al. (2009) found that male swamp sparrows sing particular song types with higher performance in aggressive contexts than in neutral contexts, manipulating performance by increasing both bandwidth and trill rate. This result indicates that vocal performance must be constrained only within limits, leaving the signaller some opportunity to modulate performance adaptively. Again, a pattern of adaptive modulation within limits imposed by physical constraints is also found in other index signals (Wagner 1989; Bee et al. 1999; Reby & McComb 2003; Reby et al. 2005).

Several studies have investigated receiver response to vocal performance. Illes et al. (2006) presented male banded wrens with two speakers, one playing a song of higher vocal performance than the other. Males preferentially approached the high-performance songs. Cramer & Price (2007) found the opposite pattern in red-winged blackbirds: males showed a stronger aggressive response to songs of low vocal performance than to songs of high performance. A second experiment with banded wrens suggests a way of reconciling these results. de Kort et al. (2009) manipulated vocal performance in the songs of banded wrens by increasing or decreasing bandwidth, creating songs that were at the population median for performance or just above or just below the population extremes. In single-speaker playbacks, subjects gave a stronger aggressive response to

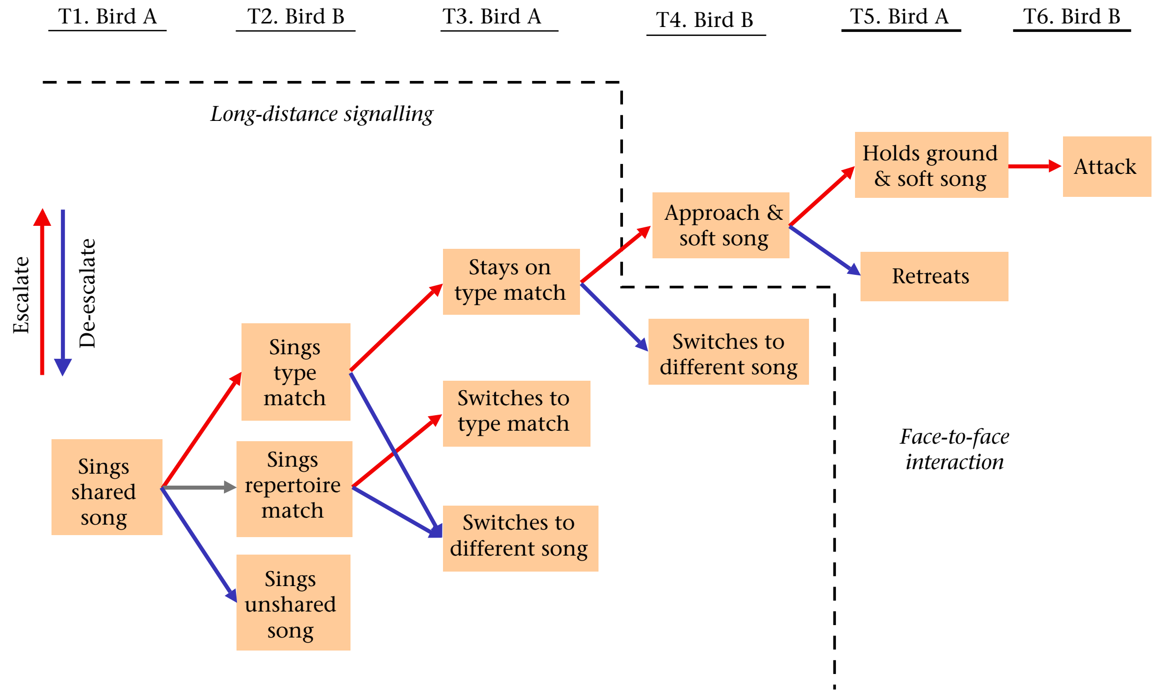

Figure 1. Schematic diagram of an interaction between two neighbouring song sparrows. Birds A and B interact during six time periods (T1–T6), each of which contains a change of state. Aggressive escalations are indicated with upward red arrows, and de-escalations with downward blue arrows. For simplicity the diagram focuses on escalations. The interaction begins when the two birds are at a distance, on their own territories, and probably out of visual contact, but as the interaction escalates, the birds approach one another and are presumed to be within a few metres of one another to the right of the dotted line. The signal and response alternatives of each bird are indicated vertically, with more aggressive alternatives above less aggressive ones. The song sparrow signalling system depends on the fact that two territorial neighbours will share some of their 7–10 song types and not others. At T1, bird A engages his neighbour by singing a shared song. At T2, the neighbour (bird B) can escalate by replying to that shared song with a 'type match' (the same song type), de-escalate by singing an unshared song, or reply at an intermediate level with a 'repertoire match' (a different song type they share). If bird B repertoire-matches (the most common reply for established neighbours), then at T3, bird A can escalate by type matching, or de-escalate by singing a different song type (either an unshared song type, or a different shared type; i.e. another repertoire match). If bird B instead type-matches at T2, then at T3, bird A can either maintain escalation by staying with the type match or de-escalate by switching song types. At T4, the birds should be close, and bird B can escalate by switching to soft song. Bird A can meet the escalation by switching to soft song, or he can retreat (T5). Soft song is the strongest aggressive signal in the hierarchy, and at this point (T6), soft song is most likely followed by attack. In this system, the type matching is a poor predictor of attack, because several layers of contingency intervene between B's initial decision on whether to type-match and his final decision on whether to attack. Type matching can still be viewed as an aggressive signal, however, because it does predict escalation in the interaction. This model is based primarily on Beecher et al. (1996, 2000), Burt et al. (2001), Beecher & Campbell (2005) and Searcy et al. (2006).

the songs of median performance than to the songs of high and low performance. These results are compatible with there being a peaked relationship between response and threat intensity (Collins 2004; de Kort et al. 2009), with males responding most strongly to opponents whose quality is perceived as similar to their own, and responding less strongly to opponents of higher or lower quality. Another interpretation is that subjects show less recognition of songs the more they are manipulated.

A recent study of nightingales provides further support for the peaked response interpretation. Schmidt et al. (2008) found that on average territorial male nightingales gave stronger aggressive responses to songs with rapid broadband trills than to songs without such trills. The response of males that failed to pair, however, declined as the frequency bandwidth of the playback song increased. These results suggest that males generally respond more aggressively to high performance songs, but that low-quality individuals can be intimidated by songs of too high performance.

All the results on receiver response to vocal performance are compatible with this parameter signalling a singer's quality. The evidence that males of some species change vocal performance with aggressive context (Kunc et al. 2006; DuBois et al. 2009) suggests that either vocal performance or modulation of performance might also be used to communicate aggressive intentions. Settling this question will require data on whether either vocal performance or its modulation predicts aggressive escalation.

Hierarchical Signalling

Most tests of the predictive value of song in aggressive signalling have investigated the association between particular singing behaviours and measures of overt aggression such as approach or attack. If, however, song functions as part of a hierarchical system of aggressive signalling, then signals low in the hierarchy might be better predictors of escalated levels of signalling, rather than of overt aggression. Figure 1 shows a model of how one such system may work in western song sparrows (Beecher & Campbell 2005), synthesizing across some of the singing behaviours that we have already reviewed. The diagram indicates that as the interaction escalates, progressively stronger signals come into play: singing a shared song, type matching, staying on type, and soft song. In this system, type matching should be a relatively poor predictor of attack because several layers of contingency intervene between bird B's initial decision on whether to type-match and bird B's final decision on whether to attack, whereas soft song should be a better predictor (Searcy et al. 2006). Type matching can still be viewed as an aggressive signal, however, because it does predict escalation in the interaction.

Conclusions

Singing behaviours such as type matching, frequency matching, overlapping, type switching and low-amplitude song have traditionally been viewed as aggressive signals in songbirds. Table 1 summarizes existing evidence on whether each of these behaviours meets the three criteria for aggressive signals. In our view, the evidence that these behaviours actually function as aggressive signals, in the sense of signals of impending aggressive escalation, is in most cases relatively weak. What evidence there is suggests that low-amplitude song is at least in two instances a strongly aggressive signal; that type matching is usually a signal of low-level escalation; that frequency matching may be an aggressive signal in at least one

Table 1

Summary of evidence on the three criteria for aggressive signals for the singing behaviours proposed to be aggressive signals

Singing behaviour	Context criterion*	Predictive criterion†	Response criterion‡
Song type matching	**Positive:** western meadowlarks[1]; song sparrows[2]; great tits[3]	**No effect:** great tits[3]; western meadowlarks[1]; swamp sparrows[4]; **Mixed:** song sparrows[5, 6, 7, 8]	**Mixed:** song sparrows[9, 10]; **Positive:** banded wrens[11]
Frequency matching	**No effect:** black-capped chickadees[12]	**Mixed:** black-capped chickadees[13, 14]	**Mixed:** black-capped chickadees[15, 16]
Overlapping	**No effect:** black-capped chickadees[12]; **Equivocal:** European robins[17]	**Equivocal:** golden whistlers[18]; **Negative:** banded wrens[19]; **No effect:** black-capped chickadees[14]	**Negative:** yellowhammers[20]; **Positive:** European robins[21]; nightingales[22]; **No effect:** great tits[23]; black-capped chickadees[16]; banded wrens[24]
Low-amplitude song	**Positive:** redwings[25]; **No effect:** European blackbirds[26]	**Positive:** song sparrows[8]; swamp sparrows[4]	**Equivocal:** European blackbirds[27]; song sparrows[28]
Song type switching	**Positive:** song sparrows[29, 30, 31]; eastern meadowlarks[32]; western meadowlarks[33]; Carolina wrens[34]; golden whistlers[18]; **Negative:** red-winged blackbirds[35]; banded wrens[36]	**Positive:** red-winged blackbirds[35]; **Negative:** banded wrens[19]; **No effect:** song sparrows[8]; swamp sparrows[4]	**Positive:** song sparrows[37]; tropical mockingbirds[38]; banded wrens[39]; **No effect:** plain wrens[40]
Vocal performance	**No effect:** red-winged blackbirds[41]; **Positive:** nightingales[42]; swamp sparrows[43]	**No evidence**	**Positive:** banded wrens[44, 45]; **Negative:** red-winged blackbirds[41]

[1]Falls (1985); [2]Stoddard et al. (1992); [3]Falls et al. (1982); [4]Ballentine et al. (2008); [5]Vehrencamp (2001); [6]Beecher et al. (2000); [7]Anderson et al. (2005); [8]Searcy et al. (2006); [9]Burt et al. (2001); [10]Anderson et al. (2008a); [11]Molles & Vehrencamp (2001); [12]Foote et al. (2008); [13]Shackleton & Ratcliffe (1994); [14]Fitzsimmons et al. (2008); [15]Otter et al. (2002); [16]Mennill & Ratcliffe (2004a); [17]Brindley (1991); [18]van Dongen (2006); [19]Vehrencamp et al. (2007); [20]Osiejuk et al. (2003); [21]Dabelsteen et al. (1997); [22]Schmidt et al. (2007); [23]Dabelsteen et al. (1996); [24]Hall et al. (2006); [25]Lampe (1991); [26]Ripmeester et al. (2007); [27]Dabelsteen & Pedersen (1990); [28]Anderson et al. (2007); [29]Kramer & Lemon (1983); [30]Kramer et al. (1985); [31]Searcy et al. (2000); [32]Falls & D'Agincourt (1982); [33]Horn & Falls (1991); [34]Simpson (1985); [35]Searcy & Yasukawa (1990); [36]Molles & Vehrencamp (1999); [37]Nielsen & Vehrencamp (1995); [38]Botero & Vehrencamp (2007); [39]Molles (2006); [40]Marshall-Ball & Slater (2004); [41]Cramer & Price (2007); [42]Kunc et al. (2006); [43]DuBois et al. (2009); [44]Illes et al. (2006); [45]de Kort et al. (2009).

[*] Singing behaviour in aggressive contexts increased ('Positive'), decreased ('Negative'), or did not change (No effect).

[†] Putatively aggressive singing behaviour and aggressive escalation were positively correlated ('Positive'), negatively correlated ('Negative'), or not correlated ('No effect').

[‡] Evidence is noted only for aggressive responses (attack, approach, known aggressive signals); 'Positive' = stronger response for the putative aggressive signal; 'Negative' = weaker response for the putative aggressive signal; 'No effect' = no difference in response.

species; that type switching can be either a signal of escalation or of de-escalation; and that overlapping may not be a signal at all. Rather than reiterating our criticisms of the existing evidence, we prefer to end with suggestions for future work. First, it seems important, in cases where a signal might occur by chance, to demonstrate that it in fact occurs at levels higher than chance, at least in certain individuals or under certain circumstances. This prescription applies in particular to cases, such as matching and overlapping, in which the signal arises out of the interaction of two individuals, and might be mistakenly ascribed to one individual when that individual is signalling without reference to the other. Second, it is important to recognize that the aggressive response of territorial individuals to any signal is an ambiguous guide to whether the signal is itself aggressive, so that the response criterion alone can never be sufficient to establish that a signal is aggressive. Third, the most direct way to demonstrate that a signal is aggressive is to demonstrate that it regularly precedes and thus predicts ('signals') that aggressive escalation of some level is about to occur. Thus, more attention should be devoted to testing the predictive criterion for putatively aggressive signals. Finally, given that many aggressive signalling systems seem to be hierarchical, an aggressive signal may predict an escalation to the next higher level of signalling, rather than to outright attack, and research should be designed with this possibility in mind.

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References

Anderson, R. C., Searcy, W. A. & Nowicki, S. 2005. Partial song matching in an eastern population of song sparrows, *Melospiza melodia*. *Animal Behaviour*, **69**, 189–196.

Anderson, R. C., Nowicki, S. & Searcy, W. A. 2007. Soft song in song sparrows: response of males and females to an enigmatic signal. *Behavioral Ecology and Sociobiology*, **61**, 1267–1274.

Anderson, R. C., Searcy, W. A. & Nowicki, S. 2008a. Testing the function of song-matching in birds: responses of eastern male song sparrows *Melospiza melodia* to partial song-matching. *Behaviour*, **145**, 347–363.

Anderson, R. C., Searcy, W. A., Peters, S. & Nowicki, S. 2008b. Soft song in song sparrows: acoustic structure and implications for signal function. *Ethology*, **114**, 662–676.

Ballentine, B., Hyman, J. & Nowicki, S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, **15**, 163–168.

Ballentine, B., Searcy, W. A. & Nowicki, S. 2008. Reliable aggressive signalling in swamp sparrows. *Animal Behaviour*, **75**, 693–703.

Bee, M. A. & Perrill, S. A. 1996. Responses to conspecific advertisement calls in the green frog (*Rana clamitans*) and their role in male–male communication. *Behaviour*, **133**, 283–301.

Bee, M. A., Perrill, S. A. & Owen, P. C. 1999. Size assessment in simulated territorial encounters between male green frogs (*Rana clamitans*). *Behavioral Ecology and Sociobiology*, **45**, 177–184.

Beecher, M. D. & Campbell, S. E. 2005. The role of unshared songs in singing interactions between neighbouring song sparrows. *Animal Behaviour*, **70**, 1297–1304.

Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 1450–1454.

Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. L. 1996. Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, **51**, 917–923.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000. Song-type matching between neighbouring song sparrows. *Animal Behaviour*, **59**, 21–27.

Botero, C. A. & Vehrencamp, S. L. 2007. Responses of male tropical mockingbirds (*Mimus gilvus*) to variations in within-song and between-song versatility. *Auk*, **124**, 185–196.

Brindley, E. L. 1991. Response of European robins to playback of song: neighbour recognition and overlapping. *Animal Behaviour*, **41**, 503–512.

Brumm, H. 2006. Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A*, **192**, 1279–1285.

Burmeister, S. S., Ophir, A. G., Ryan, M. J. & Wilczynski, W. 2002. Information transfer during cricket frog contests. *Animal Behaviour*, **64**, 715–725.

Burt, J. M. & Vehrencamp, S. L. 2005. Dawn chorus as an interactive communication network. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 320–343. Cambridge: Cambridge University Press.

Burt, J. M., Campbell, S. E. & Beecher, M. D. 2001. Song type matching as threat: a test using interactive playback. *Animal Behaviour*, **62**, 1163–1170.

Burt, J. M., Bard, S. C., Campbell, S. E. & Beecher, M. D. 2002. Alternative forms of song matching in song sparrows. *Animal Behaviour*, **63**, 1143–1151.

Catchpole, C. K. 1983. Variation in the song of the great reed warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. *Animal Behaviour*, **31**, 1217–1225.

Collins, S. 2004. Vocal fighting and flirting: the functions of birdsong. In: *Nature's Music: the Science of Birdsong* (Ed. by P. Marler & H. Slabbekoorn), pp. 39–79. San Diego: Elsevier.

Cramer, E. R. A. & Price, J. J. 2007. Red-winged blackbirds *Agelaius phoeniceus* respond differently to songs types with different performance levels. *Journal of Avian Biology*, **38**, 122–127.

Dabelsteen, T. & Pedersen, S. B. 1990. Song and information about aggressive responses of blackbirds, *Turdus merula*: evidence from interactive playback experiments with territory owners. *Animal Behaviour*, **40**, 1158–1168.

Dabelsteen, T., McGregor, P. K., Shepherd, M., Whittaker, X. & Pedersen, S. B. 1996. Is the signal value of overlapping different from that of alternating during matched singing in great tits? *Journal of Avian Biology*, **27**, 189–194.

Dabelsteen, T., McGregor, P. K., Holland, J., Tobias, J. A. & Pedersen, S. B. 1997. The signal function of overlapping singing in male robins. *Animal Behaviour*, **53**, 249–256.

Dabelsteen, T., McGregor, P. K., Lampe, H. M., Langmore, N. E. & Holland, J. 1998. Quiet song in birds: an overlooked phenomenon. *Bioacoustics*, **9**, 89–105.

van Dongen, W. F. D. 2006. Variation in singing behaviour reveals possible functions of song in male golden whistlers. *Behaviour*, **143**, 57–82.

DuBois, A. L., Nowicki, S. & Searcy, W. A. 2009. Swamp sparrows modulate vocal performance in an aggressive context. *Biology Letters*, **5**, 163–165.

Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour*, **33**, 1152–1161.

Falls, J. B. 1982. Individual recognition by sounds in birds. In: *Acoustic Communication in Birds. Vol. 2* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 237–278. New York: Academic Press.

Falls, J. B. 1985. Song matching in western meadowlarks. *Canadian Journal of Zoology*, **63**, 2520–2524.

Falls, J. B. & D'Agincourt, L. G. 1982. Why do meadowlarks switch song types? *Canadian Journal of Zoology*, **60**, 3400–3408.

Falls, J. B., Krebs, J. R. & McGregor, P. K. 1982. Song matching in the great tit (*Parus major*): the effect of similarity and familiarity. *Animal Behaviour*, **30**, 997–1009.

Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science*, **183**, 762–763.

Fitzsimmons, L. P., Foote, J. R., Ratcliffe, L. M. & Mennill, D. J. 2008. Frequency matching, overlapping and movement behaviour in diurnal countersinging interactions of black-capped chickadees. *Animal Behaviour*, **75**, 1913–1920.

Foote, J. R., Fitzsimmons, L. P., Mennill, D. J. & Ratcliffe, L. M. 2008. Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behavioral Ecology*, **19**, 1192–1199.

Gammon, D. E., Hendrick, M. C. & Baker, M. C. 2008. Vocal communication in a songbird with a novel song repertoire. *Behaviour*, **145**, 1003–1026.

Gochfeld, M. 1978. Intraspecific social stimulation and temporal displacement of songs of the lesser skylark, *Alauda gulgula*. *Zeitschrift für Tierpsychologie*, **48**, 337–344.

Göransson, G., Högstedt, G., Karlsson, J., Källander, H. & Ulfstrand, S. 1974. Sångensroll för revirhållandet hos näktergal *Luscinia luscinia*: några experiment med play-back-teknik. *Vår Fågelvärld*, **33**, 201–209.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Guilford, T. & Dawkins, M. S. 1995. What are conventional signals? *Animal Behaviour*, **49**, 1689–1695.

Hall, M. L., Illes, A. & Vehrencamp, S. L. 2006. Overlapping signals in banded wrens: long-term effects of prior experience on males and females. *Behavioral Ecology*, **17**, 260–269.

Hill, C. E., Campbell, S. E., Nordby, J. C., Burt, J. M. & Beecher, M. D. 1999. Song sharing in two populations of song sparrows (*Melospiza melodia*). *Behavioral Ecology and Sociobiology*, **46**, 341–349.

Horn, A. G. & Falls, J. B. 1991. Song switching in mate attraction and territory defense by western meadowlarks (*Sturnella neglecta*). *Ethology*, **87**, 262–268.

Horn, A. G., Leonard, M. L., Ratcliffe, L., Shackleton, S. A. & Weisman, R. G. 1992. Frequency variation in songs of black-capped chickadees (*Parus atricapillus*). *Auk*, **109**, 847–852.

Hughes, M., Nowicki, S., Searcy, W. A. & Peters, S. 1998. Song-type sharing in song sparrows: implications for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, **42**, 437–446.

Hultsch, H. & Todt, D. 1982. Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos* B.). *Behavioral Ecology and Sociobiology*, **11**, 253–260.

Huntingford, F. A. & Turner, A. 1987. *Animal Conflict*. London: Chapman & Hall.

Hurd, P. L. & Enquist, M. 2005. A strategic taxonomy of biological communication. *Animal Behaviour*, **70**, 1155–1170.

Hyman, J. 2003. Countersinging as a signal of aggression in a territorial songbird. *Animal Behaviour*, **65**, 1179–1185.

Illes, A. E., Hall, M. L. & Vehrencamp, S. L. 2006. Vocal performance influences male receiver response in the banded wren. *Proceedings of the Royal Society B*, **273**, 1907–1912.

Janicke, T., Hahn, S., Ritz, M. S. & Peter, H. U. 2008. Vocal performance reflects individual quality in a nonpasserine. *Animal Behaviour*, **75**, 91–98.

Järvi, T., Radesäter, T. & Jakobsson, S. 1980. The song of the willow warbler *Phylloscopus trochilus* with special reference to singing behaviour in agonistic situations. *Ornis Scandinavica*, **11**, 236–242.

de Kort, S. R., Eldermire, E. R. B., Cramer, E. R. A. & Vehrencamp, S. L. 2009. The deterrent effect of bird song in territory defense. *Behavioral Ecology*, **20**, 200–206.

Kramer, H. G. & Lemon, R. E. 1983. Dynamics of territorial singing between neighboring song sparrows (*Melospiza melodia*). *Behaviour*, **85**, 198–223.

Kramer, H. G., Lemon, R. E. & Morris, M. J. 1985. Song switching and agonistic stimulation in the song sparrow (*Melospiza melodia*): five tests. *Animal Behaviour*, **33**, 135–149.

Krebs, J., Ashcroft, R. & Webber, M. 1978. Song repertoires and territory defence in the great tit. *Nature*, **271**, 539–542.

Krebs, J. R., Ashcroft, R. & Van Orsdol, K. 1981. Song matching in the great tit *Parus major* L. *Animal Behaviour*, **29**, 918–923.

Kunc, H. P., Amrhein, V. & Naguib, M. 2006. Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success. *Animal Behaviour*, **72**, 25–30.

Lampe, H. M. 1991. The response of male redwings *Turdus iliacus* to playback of conspecific songs with or without the terminating twitter. *Ornis Scandinavica*, **22**, 137–142.

Lampe, H. M. & Espmark, Y. O. 1987. Singing activity and song pattern of the redwing *Turdus iliacus* during the breedng season. *Ornis Scandinavica*, **18**, 179–185.

McGregor, P. K. & Dabelsteen, T. 1996. Communication networks. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 409–425. Ithaca, New York: Cornell University Press.

Marshall-Ball, L. & Slater, P. J. B. 2004. Duet singing and repertoire use in threat signalling of individuals and pairs. *Proceedings of the Royal Society of London, Series B, Supplement*, **271**, S440–S443.

Martin, W. F. 1971. Mechanics of sound production in toads of the genus *Bufo*: passive elements. *Journal of Experimental Zoology*, **176**, 273–293.

Maynard Smith, J. & Harper, D. G. C. 1995. Animal signals: models and terminology. *Journal of Theoretical Biology*, **177**, 305–311.

Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. Oxford: Oxford University Press.

Mennill, D. J. & Ratcliffe, L. M. 2004a. Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour*, **67**, 441–450.

Mennill, D. J. & Ratcliffe, L. M. 2004b. Do male black-capped chickadees eavesdrop on song contests? A multi-speaker playback experiment. *Behaviour*, **141**, 125–139.

Molles, L. E. 2006. Singing complexity of the banded wren (*Thryothorus pleurostictus*): do switching rate and song-type diversity send different messages? *Auk*, **123**, 991–1003.

Molles, L. E. & Vehrencamp, S. L. 1999. Repertoire size, repertoire overlap, and singing modes in the banded wren (*Thryothorus pleurostictus*). *Auk*, **116**, 667–689.

Molles, L. E. & Vehrencamp, S. L. 2001. Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. *Proceedings of the Royal Society B*, **268**, 2013–2019.

Morton, E. S. 2000. An evolutionary view of the origins and functions of avian vocal communication. *Japanese Journal of Ornithology*, **49**, 69–78.

Morton, E. S. & Young, K. 1986. A previously undescribed method of song matching in a species with a single song 'type', the Kentucky warbler (*Oporornis formosus*). *Ethology*, **73**, 334–342.

Naguib, M. 1999. Effects of song overlapping and alternating on nocturnally singing nightingales. *Animal Behaviour*, **58**, 1061–1067.

Naguib, M. & Kipper, S. 2006. Effects of different levels of song overlapping on singing behaviour in male territorial nightingales (*Luscinia megarhynchos*). *Behavioral Ecology and Sociobiology*, **59**, 419–426.

Naguib, M. & Todt, D. 1997. Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Animal Behaviour*, **54**, 1535–1543.

Nelson, D. A. & Croner, L. J. 1991. Song categories and their functions in the field sparrow (*Spizella pusilla*). *Auk*, **108**, 42–52.

Nice, M. M. 1943. Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerines. *Transactions of the Linnean Society of New York*, **6**, 1–328.

Nielsen, B. M. B. & Vehrencamp, S. L. 1995. Responses of song sparrows to song-type matching via interactive playback. *Behavioral Ecology and Sociobiology*, **37**, 109–117.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 1999. Ecological correlates of song learning in song sparrows. *Behavioral Ecology*, **10**, 287–297.

Osiejuk, T. S., Ratynska, K. & Cygan, J. P. 2003. Signal value of alternating and overlapping singing in the yellowhammer *Emberiza citrinella*. *Journal of Ethology*, **22**, 55–61.

Otte, D. 1974. Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics*, **5**, 385–417.

Otter, K. A., Ratcliffe, L., Njegovan, M. & Fotheringham, J. 2002. Importance of frequency and temporal song matching in black-capped chickadees: evidence from interactive playback. *Ethology*, **108**, 181–191.

Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2001. Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proceedings of the Royal Society B*, **268**, 1183–1187.

Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceedings of the Royal Society B*, **269**, 1925–1929.

Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, **51**, 537–551.

Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, **409**, 185–188.

Podos, J. & Nowicki, S. 2004. Performance limits on birdsong. In: *Nature's Music: the Science of Birdsong* (Ed. by P. Marler & H. Slabbekoorn), pp. 318–342. San Diego: Academic Press.

Reby, D. & McComb, K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, **65**, 519–530.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T. & Clutton-Brock, T. H. 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceeding of the Royal Society B*, **272**, 941–947.

Reid, J. M., Arcese, P., Cassidy, A. L. E. V., Marr, A. B., Smith, J. N. M. & Keller, L. F. 2005. Hamilton and Zuk meet heterozygosity? Song repertoire size indicates inbreeding and immunity in song sparrows (*Melospiza melodia*). *Proceedings of the Royal Society B*, **272**, 481–487.

Ripmeester, E. A. P., de Vries, A. M. & Slabbekoorn, H. 2007. Do blackbirds signal motivation to fight with their song? *Ethology*, **113**, 1021–1028.

Rogers, D. 2004. Repertoire size, song sharing and type matching in the rufous bristlebird (*Dasyornis broadbenti*). *Emu*, **104**, 7–13.

Schmidt, R., Kunc, H. P., Amrhein, V. & Naguib, M. 2006. Responses to interactive playback predict future pairing success in nightingales. *Animal Behaviour*, **72**, 1355–1362.

Schmidt, R., Amrhein, V., Kunc, H. P. & Naguib, M. 2007. The day after: effects of vocal interactions on territory defence in nightingales. *Journal of Animal Ecology*, **76**, 168–173.

Schmidt, R., Kunc, H. P., Amrhein, V. & Naguib, M. 2008. Aggressive responses to broadband trills are related to subsequent pairing success in nightingales. *Behavioral Ecology*, **19**, 635–641.

Scott, J. P. & Fredericson, E. 1951. The causes of fighting in mice and rats. *Physiological Zoology*, **24**, 273–309.

Searcy, W. A. & Nowicki, S. 2000. Male–male competition and female choice in the evolution of vocal signaling. In: *Animal Signals: Signalling and Signal Design in Animal Communcation* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 301–315. Trondheim: Tapir Academic Press.

Searcy, W. A. & Nowicki, S. 2006. Signal interception and the use of soft song in aggressive interactions. *Ethology*, **112**, 865–872.

Searcy, W. A. & Yasukawa, K. 1990. Use of the song repertoire in intersexual and intrasexual contexts by male red-winged blackbirds. *Behavioral Ecology and Sociobiology*, **27**, 123–128.

Searcy, W. A., Nowicki, S. & Hogan, C. 2000. Song type variants and aggressive context. *Behavioral Ecology and Sociobiology*, **48**, 358–363.

Searcy, W. A., Anderson, R. C. & Nowicki, S. 2006. Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology*, **60**, 234–241.

Shackleton, S. A. & Ratcliffe, L. 1994. Matched counter-singing signals escalation of aggression in black-capped chickadees (*Parus atricapillus*). *Ethology*, **97**, 310–316.

Shackleton, S. A., Ratcliffe, L., Horn, A. G. & Naugler, C. T. 1991. Song repertoires of Harris' sparrows (*Zonotrichia querula*). *Canadian Journal of Zoology*, **69**, 1867–1874.

Simpson, B. S. 1985. Effects of location in territory and distance from neighbours on the use of song repertoires by Carolina wrens. *Animal Behaviour*, **33**, 793–804.

Slabbekoorn, H. & ten Cate, C. 1996. Responses of collared doves to playback of coos. *Behavioural Processes*, **38**, 169–174.

Snow, D. W. 1958. *A Study of Blackbirds*. Dorchester: Dorset Press.

Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. & Catchpole, C. K. 2004. Developmental stress, social rank and song complexity in the European starling (*Sturnus vulgaris*). *Proceedings of the Royal Society B, Supplement*, **271**, S121–S123.

Stoddard, P. K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 356–374. Ithaca, New York: Cornell University Press.

Stoddard, P. K., Beecher, M. D., Campbell, S. E. & Horning, C. L. 1992. Song-type matching in the song sparrow. *Canadian Journal of Zoology*, **70**, 1440–1444.

Todt, D. 1981. On functions of vocal matching: effects of counter-replies on song post choice and singing. *Zeitschrift für Tierpsychologie*, **57**, 73–93.

Todt, D. & Naguib, M. 2000. Vocal interactions in birds: the use of song as a model in communication. In: *Advances in the Study of Behavior* (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon & T. J. Roper), pp. 247–296. New York: Academic Press.

Vehrencamp, S. L. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal Signals: Signalling and Signal Design in Animal Communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 277–300. Trondheim: Tapir Academic Press.

Vehrencamp, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions? *Proceedings of the Royal Society B*, **268**, 1637–1642.

Vehrencamp, S. L., Hall, M. L., Bohman, E. R., Depeine, C. D. & Dalziel, A. H. 2007. Song matching, overlapping, and switching in the banded wren: the sender's perspective. *Behavioral Ecology*, **18**, 849–859.

Wagner, W. E. 1989. Fighting, assessment, and frequency alteration in Blanchard's cricket frog. *Behavioral Ecology and Sociobiology*, **25**, 429–436.

Wagner, W. E. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Animal Behaviour*, **44**, 449–462.

Wasserman, F. E. 1977. Intraspecific acoustical interference in the white-throated sparrow (*Zonotrichia albicollis*). *Animal Behaviour*, **25**, 949–952.

Westneat, M. W., Long, J. H., Hoese, W. & Nowicki, S. 1993. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. *Journal of Experimental Biology*, **182**, 147–171.

Yasukawa, K. 1981. Song repertoires in the red-winged blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Animal Behaviour*, **29**, 114–125.