



CURRENT ISSUES – PERSPECTIVES AND REVIEWS

It Takes All Kinds in Acoustic Communication: A New Perspective on the Song Overlapping Phenomenon

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Abstract

Over the last few decades, research into song overlapping produced many – often conflicting – interpretations of its function and culminated in the current debate about the usefulness of this concept. To avoid a deadlock in song overlapping research, we present a new approach to existing evidence and offer several novel hypotheses that might help enhance future experiments. Our analysis offers both a theoretical perspective and specific predictions of each testable hypothesis. We present a detailed analysis of important questions. First, what information does song overlapping convey (is it a signal of aggressive intent or of male quality)? Second, what evolutionary mechanism stabilizes honesty of song overlapping as a signal (is it an index signal, handicap, proximity risk, conventional signal or a modifier)? Additionally, we offer some alternative explanations of the phenomenon (song overlapping as a mask or an incidental phenomenon). We hope to encourage future researchers not only to gather high-quality experimental data, but also to make more careful interpretations, as we believe that no all-encompassing explanation of song overlapping will be formulated any time soon. Focused comparative approaches will be necessary, as song overlapping might have different functions in different species.

Introduction

Song overlapping (SO) is a behaviour of singing birds in which one individual starts signalling before the song of another (within hearing range) has not yet terminated. SO should be differentiated from duetting, that is overlapping bouts of vocalization given by paired individuals (Hall 2004). Over the last 30 yr, the concept of SO went from a promising assumption of being a functionally significant phenomenon in vocal interactions between male songbirds (Hultsch & Todt 1982) to an object of intense scepticism (Searcy & Beecher 2011) with many – often conflicting – interpretations in between (Naguib & Mennill 2010).

Instead of arguing in favour of yet another bold claim about SO, we would like to adopt a more pragmatic approach and – by carefully reviewing the

available empirical data – offer several new working hypotheses that could help enhance future research on SO (Table 1). We understand that a working hypothesis is a statement that is not yet scientifically established and can serve only as a tool in guiding scientific progress. Nevertheless, it can be a very useful tool, leading to new important discoveries (Dewey 1938).

The inspiration for establishing our working hypotheses stems from two fundamental questions. The first one is: 'What information does SO convey?' (Table 2) SO is often interpreted as a signal of aggressive intent. Some studies, however, presented SO rather as signal of male quality (review in Naguib & Mennill 2010). Both explanations assume that SO conveys some important information. After all, senders produce signals to change behaviour of the

receivers; hence, one should expect that the information encoded in the signal will be useful and that a mechanism stabilizing honesty of SO as a signal would exist. We believe that any real progress in understanding functions of SO will be possible only after specific costs associated with SO become well understood. Thus, the second question we would like to offer is: 'What kinds of costs stabilize honesty of SO as a signal (Table 2)?' Here, we consider five essential cost-based signal categories: index signal, handicap signal, proximity risk signal, conventional signal and modifier (after Bradbury & Vehrencamp 2011). We are aware that alternative classifications of these signal categories exist, and in real-world settings, signal values are influenced by the level of escalation between rivals (Higham 2014).

Aggressive intent signals are usually cheap to produce (each individual is able to signal) and more likely to be evolutionarily stabilized by retaliation or injury cost through the proximity risk or conventional signalling mechanism. For a proximity risk signal, retaliation is more likely when the opponents are closer to each other (vulnerable posture or attack preparation posture can serve as an example) and when injury risk is a cost that guarantees honesty (Számádó 2008). A conventional signal indicates an 'agreement' between the sender and the receiver about what the signal means. The signal itself is more or less arbitrary and is stabilized by a possible retaliation from the receiver (Guilford & Dawkins 1995). Colour patches of low production cost that are connected with dominance status in many bird species are a good example (Studd & Robertson 1985). Importantly, auditory signals can be conventional as well (Vehrencamp 2001; Ręk & Osiejuk 2010).

Production costs of male quality signalling are higher, and the signals are stabilized by individual constraints (index signals) or by a handicap mechanism. An index signal is an honest type of signal, because of some physical or physiological constraint, which is costly to produce during development (Dawkins & Guilford 1991; some further subcategories of index signals will be briefly discussed later). A handicap signal is also costly to produce, but for a different reason. It often worsens the situation of the signaller and therefore can be viewed as another honest indicator of quality. What distinguishes it from an index signal is that individuals of different overall quality are influenced differently by its production costs. An individual of higher quality or in a better condition can take a heavier burden of signalling than an individual of relatively lower quality. Thus, if a signaller is able to survive and stay in a good physical

condition despite being burdened with a handicap, he must have a higher intrinsic quality than a non-handicapped individual (Zahavi 1975). Contrary to index signals, each individual is able to produce handicap signals, but the optimal level of signalling (benefit-to-cost ratio) is different for individuals of different quality (Johnstone 1997).

Finally, modifiers are signals constrained by some sender attributes, but they are only improving or hindering assessment of these attributes. Therefore, in terms of function, they may be involved in both aggressive signalling and presenting quality-related attributes or behaviours (Bradbury & Vehrencamp 2011).

As mentioned earlier, some researchers have questioned whether SO is an aggressive signal or a signal at all (Searcy & Beecher 2009, 2011). One of the primary concerns is that SO may occur by chance whenever two or more signallers sing or call within same acoustic space. Searcy & Beecher (2009) present a valuable theoretical background about what aggressive signals are and how to discriminate them from other meaningful signals. At the end of this review, we consider some alternative hypotheses for the existence of SO as a non-signal phenomenon.

Song Overlapping as a Signal or What Information Does it Convey?

Already at the dawn of SO research, it was commonly thought that it is an antagonistic signal indicating territorial status (Brindley 1991; Dabelsteen et al. 1996, 1997; Naguib & Todt 1997; McGregor et al. 1999; Naguib 1999; Naguib et al. 1999; Lange-mann et al. 2000; Todt & Naguib 2000). Many more recent findings reached similar conclusions (Mennill & Ratcliffe 2004b; Kunc et al. 2006; Naguib & Kipper 2006). However, as new studies emerged, the big picture started to slowly change, due to evidence for less aggressive responses to SO (Osiejuk et al. 2003, 2007) or no rank-related differences associated with this pattern of signalling (Fitzsimmons et al. 2008). Around that time, some authors expressed their urge for better explanations (Laidre & Vehrencamp 2008; de Kort et al. 2009). Nowadays, the view that SO is an aggressive signal seems to still dominate (Naguib & Mennill 2010), but it has been authoritatively questioned by Searcy & Beecher (2009, 2011). They argue that in the majority of species, songs overlap at a lower frequency than expected by chance and that there is no or minimal evidence that SO is a threatening signal. Without repeating the detailed concerns that were already

expressed (for a review, see Searcy & Beecher 2009, 2011), we present an additional caveat.

The vast majority of SO experiments involve the use of interactive playback, which is a challenging technique for studying aggressive signalling. To be sure that a signal carries information about aggressive intent, it should be a good predictor of an eventual physical attack (or at least lead to a next level of escalation). Paradoxically, however, there is virtually nothing to attack in case of interactive playback experiments (Laidre & Vehrencamp 2008); thus, physical attack is typically not possible in such experiments. The loudspeaker itself is attacked very rarely [Corn crane (*Crex crex*) attacks the speaker, see Ręk & Osiejuk 2010, 2011a,b; but this is an exception to the general trend]. To overcome this problem, taxidermic mounts are sometimes used (Hof & Podos 2013), but to our knowledge, they were used only once in SO experiments (Baker et al. 2012). Moreover, the use of artificial birds probably generates as many methodological problems as it solves, because birds would react not only to the acoustic signal, but to the visual one as well. In addition, the artificiality of the bird undoubtedly complicates the analysis of the behavioural response, given that we do not know how the artificiality influences the bird's behaviour under non-SO situations. That is not to say that visual stimuli should be avoided. On the contrary, if carefully used, they might offer unique insight into acoustic communication. After all, some of the most aggressive signals might be switched on only when a visual contact with the opponent is established.

The idea that SO is an aggressive signal is an influential hypothesis, but, in the light of current evidence, its importance seems somewhat overinflated. Although our goal is not to discourage potential investigators from following its lead, we believe that the concept of aggressive signal is best understood as a *working* hypothesis, rather than a rigid paradigm determining interpretation of the results. That is why we would like to outline a few alternatives and, by doing so, spark interest and shift attention towards new promising directions.

Song Overlapping as a Proximity Risk Signal

Let us go back to the interpretation that SO does not have to be costly to produce (or at least not in the short run), and hypothesize that it can be a signal stabilized by the proximity risk mechanism. In that case, we should expect that the frequency of such signals would change with the distance between the opponents, so that at a closer distance these signals are

more likely to occur and lead to an aggressive behaviour (Bradbury & Vehrencamp 2011). Some studies seem to support such a concept. Brindley (1991) found that male European robins (*Erithacus rubecula*) can discriminate between songs of neighbours and strangers and that unfamiliar songs are more likely to be overlapped by the territory holder, regardless of the distance. Importantly, both unfamiliar and familiar songs were significantly more overlapped when the distance between opponents was smaller. This suggests that territorial intrusion (closer distance) is more likely associated with SO. In a study of Montezuma oropendolas (*Psarocolius montezuma*), SO was present only at the colony tree when the distance between males was smaller than five metres (Price et al. 2006). In contrast to these findings, a study of black-capped chickadees (*Poecile atricapillus*) (Foote et al. 2008) and nightingales (*Luscinia megarhynchos*) (Sprau et al. 2010b) found no effect of distance for SO.

It has to be noted that proximity risk signals are problematic with respect to honesty. The range of acoustic signals, as opposed to visual signals, is at least potentially much larger. As has been shown for threat displays, there is always a border outside which the honest use of proximity risk signals will no longer be evolutionary stable, such that a mixture of honest and dishonest strategies will be used (Számadó 2008). In a network of communicating males, SO may sometimes happen by chance and do not affect behaviour of the overlapped individual. However, in a short-distance communication, SO is much more likely to be an intentional aggressive signal directed towards a particular receiver. This looks somewhat analogous to human behaviour: while speaking at the same time as somebody else in a crowd of people is irrelevant, interrupting our direct interlocutor often reflects negative emotions or overt aggression. The observation that SO among European robins changes with the distance seems to support this interpretation (Brindley 1991). In addition to that, in some birds, the proximity risk signals are also relatively quiet, which suggest that senders limit the signal range to reach only a specific receiver and avoid eavesdropping by any other (see Ręk & Osiejuk 2010 for a review).

It is important to note that proximity risk signals may also work in some different ways, and consequently, it has been argued that SO is a 'defensive threat' or an 'intention-to-retreat signal' that *both holds receivers at distance and predicts sender withdrawal* (Vehrencamp et al. 2007, p. 857). Or, conversely, that it is *so threatening that it inhibits aggression* (Hall et al. 2006, p. 266).

Table 1: Summary of working hypotheses, predictions and hints for future studies

Working hypothesis	Predictions	Hints for future studies
proximity risk signal	SO should be more frequent when opponents are at a closer distance SO should be followed by a more aggressive behaviour with a physical attack at the end	Focus on spatial relationships between singing opponents, associations between signalling strategies, distance between signallers and their behaviour Useful technique: acoustic location systems, robotic artificial birds
conventional signal	SO should be accompanied by a specific vulnerable or attack preparation postures Each individual should be able to perform SO SO should occur more frequently or less frequently than expected by chance depending on a specific context (e.g. territorial intrusions of neighbours vs. strangers) SO should be more frequently followed by an aggressive behaviour of the sender and the increase in aggressiveness should be highest when both opponents exhibit a similar level of motivation SO vs. non-SO signalling should code different information in different species and should sometimes be influenced by learning a new association between a specific version of a signal and its meaning Quality index: only high-quality males should be able to perform SO (in practice: to overlap intensively). Such males should be preferred by females Pointing index: a bird whose song was overlapped at the beginning of the experiment should respond differently to subsequent playback (e.g. song alternating) than his neighbours whose songs were not overlapped at the beginning of the experiment	There might be no direct costs of SO for a bird singing from a distance and the convention of SO vs. non-SO would indicate only motivation for territory defence It is possible that in a greater distance, SO works because of an agreement about its meaning and at a closer distance because of a direct risk of being attacked
Index signal (quality or pointing index)		It might be hard to classify a given signal as an index or a handicap – in some contexts and species, SO could look like an index signal, in others – as a handicap Control responses of both sexes to SO Pointing index: experiments with microphone array set-up inside a communicating network of territorial birds might prove useful Pointing indices and conventional signals might be hard to differentiate. Any interpretation should be based on a firm knowledge of the species in question
Handicap	SO should increase with male quality and females should favour the higher-quality individuals Less developed (or poorer quality) individuals should signal with a lower intensity but nevertheless be able to produce SO.	Test whether SO is associated with increased environmental threats and female preferences Check whether nightingales (<i>Luscinia megarhynchos</i>) use more SO before mating to handicap themselves and signal higher quality to females
Modifier	SO should place the same signal in a modified perspective for the potential direct or third party receivers.	Link overlapping vs. non-overlapping patterns of singing with other song characteristics.
Mask	SO should disturb other individuals and be pronounced in species with second part of the song particularly rich in information, like European thrushes (<i>Turdus spp.</i>)	Use observational studies and masking experiments in different species, with different parts of the song simply masked or overlapped by opponents song
Incidental phenomenon	SO should occur below chance level SO should only be a side effect of differences in song duration and song rate	Remember that is the nature of some signals to occur less frequently than expected by chance Use null models to establish chance levels for SO

Table 2: Summary and description of signal categories divided by the type of information they convey

Type of information	Cost-based signal categories	Description
Signal of aggressive intent	Proximity risk signal	Retaliation is more likely when the opponents are closer to each other. Injury risk is a cost that guarantees honesty
	Conventional signal	There is an 'agreement' between the sender and the receiver about what the signal means. The signal itself is more or less arbitrary and is stabilized by receiver response
	Modifier (amplifier or attenuator)	Is constrained by some sender attributes, but they are only improving or hindering assessment of these attributes Amplifier improves assessment of sender attributes, but this improvement depends on the physical parameters of the signaller Attenuator has exactly the same features but works in the opposite direction
Signal of male quality	Index signal	Is an honest type of signal because of some physical or physiological constraint which is costly to produce during development
	Handicap signal	Worsens situation of the signaller and therefore can be viewed as an honest indicator of quality. Individuals of higher quality can take a heavier burden of signalling
	Modifiers	See above

Future studies could focus on spatial relationships between singing opponents, preferably using techniques like acoustic location systems (Mennill et al. 2006), to determine whether there are any associations between the signalling strategies (overlapping vs. non-overlapping), the distance between signallers and their behaviour. If SO is an aggressive signal in which honesty is maintained by a proximity risk mechanism, one should expect that (i) SO should be more frequent when opponents are at a closer distance, (ii) SO should be followed by a more aggressive behaviour with a physical attack at the end and (iii) SO will be accompanied by a specific vulnerable or attack preparation postures.

Song Overlapping as a Conventional Signal

Vehrencamp (2001) provided a few criteria that an acoustic signal should fulfil to be classified as conventional. It should: *convey short-term information about aggressive intentions as opposed to status, condition and general willingness to attack* (p. 1638). Existing evidence speaks against such classification. Some authors argue that SO can convey long-term information, as some birds can use it after a time delay (Hall et al. 2006; Schmidt et al. 2007). Others maintain that SO transmits information about social status and dominance (Hyman 2003; Mennill & Ratcliffe 2004a,b) and the willingness to escalate (Dabelsteen et al. 1997). That is why it is crucial to understand the costs of conventional signalling. Such signals are honest not because of the costs paid during the production (e.g. energy necessary to sing) but because of receiver response (Guilford & Dawkins 1995). The receiver-dependent costs may belong to one of two categories: receiver retaliation or vulnerability handicap. However, they

are not mediated by distance as in case of proximity risk signals (Enquist 1985; Adams and Mesterton-Gibbons 1995, Bradbury & Vehrencamp 2011). For example, in corncrake (*Crex crex*), the information coded in the rhythm of calling has conventional character, which was shown in a set of experiments with natural, rhythm-modified and artificial calls (Ręk & Osiejuk 2010). The observed long-distance SO in European robin (Brindley 1991) could be also interpreted as a conventional signal. It is likely that there are no direct costs of SO for a bird singing from a distance, but the convention of overlapping vs. non-overlapping indicates motivation for territory defence, which is different in case of neighbours than strangers. Moreover, this is not inconsistent with the earlier interpretation of SO as a proximity risk signal. In a greater distance, SO works because of the agreement about its meaning among singing individuals, while at a closer distance, it works because of a direct risk of being attacked. Again, in corncrake, the level of motivation is signalled from a distance and provided by the rhythm, whereas in direct encounters, males produce specific soft calls preceding physical attack (Ręk & Osiejuk 2011a,b). In the light of the corncrake study, it is also clear that it is possible to test cost-related hypotheses of SO. However, the experimental design should be very carefully crafted. If SO is a conventional signal of aggressive intent one should expect that each individual would be able to perform SO and that SO will occur more frequently or less frequently than expected by chance depending on a specific context. For example, SO could be more frequent when a stranger is entering the territory compared to a neighbour's intrusion. SO should be (on average) more frequently followed by an aggressive behaviour of the sender, and the increase in aggressiveness (or

probability of physical fight) should be highest when both opponents exhibit a similar level of motivation (i.e. both are trying to overlap songs of the opponent; compare discussion in Ręk & Osiejuk 2010). We should also expect that the meaning of SO vs. non-SO signalling would code different information in different species or could even be influenced by learning a new association between a specific version of a signal and its meaning (Ręk 2013).

Song Overlapping as a Male Quality Signal

The idea that SO may be related to male quality does not appear in earlier research as directly as the aggressiveness hypothesis (Naguib & Mennill 2010). However, a more careful look at some of the results clearly suggest that a link between SO and sender quality may exist. Even though the theoretical distinctions between index and handicap signals seem clear, in practice, it is very hard to classify a given signal as an index or a handicap (Maynard Smith & Harper 2003). Often a decision comes down to subjective preferences of an interpreter (Searcy & Nowicki 2006). It is perfectly possible to imagine that in some contexts and species, SO could look like an index signal, whereas in others, it would appear as a handicap. Therefore, we present some examples of studies linking SO with male quality, but we do not force the issue of categorizing costs as index signals or handicaps. Nevertheless, we will go back to this topic later on when presenting specific predictions of these working hypotheses.

As index signals can be divided into two or three groups (depending on the authors), we selected only these examples that fit into the least questionable categories, that is quality and pointing indices (Bradbury & Vehrencamp 2011). The vast majority of these examples can be considered handicap signals.

How could SO be linked with male quality? Song in songbirds is a secondary sexually selected trait (Darwin 1871) and an honest indicator of many different aspects of quality or condition (Gil & Gahr 2002). For example, it has been argued that such elaborate sexually selected traits may reflect resistance to parasites (Buchanan et al. 1999). Hamilton & Zuk (1982) argue that females should choose males according to traits, indicating parasite resistance in order to pass this adaptation on their offspring. As mentioned earlier, the production of a quality index signal depends on physiological and/or physical constraints of the signaler. For example, when the conditions during early life are not optimal, the vocal equipment cannot appropriately develop. In case of handicap signals,

one should expect that less developed (or poorer quality) individuals will signal with a lower intensity but nevertheless will be able to produce these signals. Presence of parasites is a typical factor negatively influencing development. Male great tits (*Parus major*) raised in the presence of ectoparasitic hen fleas (*Ceratophyllus gallinae*), which suck blood from the nestlings, used significantly less SO in adult life than birds from parasite-free nests. Crucially, SO and song duration were the only two factors influenced by these experimental conditions (Bischoff et al. 2009). In nightingales, the frequency of SO during time of mate attraction is positively correlated with pairing success (Kunc et al. 2006). In blue penguins (*Eudyptula minor*), females prefer speakers broadcasting overlapping calls to speakers playing overlapped calls or control speakers (Miyazaki & Waas 2002). In some bird species, females invest more yolk in eggs from overlapping than from overlapped males (Garcia-Fernandez et al. 2010). Leboucher & Pallot (2004) found that the female domestic canary (*Serinus canaria*) preferred the overlapping song, as opposed to overlapped one, because it elicited a greater number of copulation solicitation displays. Lastly, Kunc et al. (2007) found that SO is more important during the period of mate attraction than during the time after this period. However, one should remember that male singing can serve two masters at the same time: mate attraction and maintaining antagonistic interactions for the sake of territorial defence (Catchpole & Slater 1995). When a song is functioning in such a dual role, it is necessary to control responses of both sexes to SO. For example, males respond with fewer songs when the intruder is overlapped compared to when he is not (Peake et al. 2001) and prefer to approach the overlapping (and not the overlapped) loudspeaker (Mennill & Ratcliffe 2004b). Todt (1981) found that males avoided singing on perches where their own songs were temporally overlapped by playback songs.

There are also other quite simple mechanisms that may link SO with male quality and female choice. For example, one could test whether the preference of females for an overlapping as opposed to overlapped signals (Miyazaki & Waas 2002; Leboucher & Pallot 2004; Kunc et al. 2006; Garcia-Fernandez et al. 2010) is associated with increased environmental threats for the frequent overlappers. A possible mechanism could be very simple: frequent overlapping of many rivals demands more singing and singing is costly to produce (Vehrencamp et al. 1989; Eberhardt 1994). Perhaps nightingales – a species with especially loud, long and frequently repeated song phrases – use more SO

before mating (Kunc et al. 2006, 2007) to handicap themselves, thus signalling a higher quality?

Taken together, these studies suggest that SO may signal male quality and be stabilized by handicap principles as usually all senders are able to overlap songs of others, but with different intensity. It is worth repeating that to experimentally differentiate between different types of costs, one has to be very careful about the design.

In all examples mentioned so far, male quality was defined by some physical or physiological constraint. However, some signals work because of information constraints, namely pointing index signals (Bradbury & Vehrencamp 2011). For example, directing a signal towards a particular receiver is possible only when the sender is able to localize the receiver among many other individuals. With regard to the pointing index, SO would seem to be the simplest (requiring no repertoire) and most efficient mechanism for getting the target rival's attention, by directing the signal at him.

Testing hypotheses based on the assumption that SO is a signal of male quality would not be easy. If SO is a quality index signal, one should expect that only high-quality males are able to perform SO (in practice, to overlap intensively) and that such males will be preferred by females. If SO is a handicap signal, the level of SO should increase with male quality and again females should favour the higher-quality individuals. Although a number of studies shows that SO correlates with male quality attributes, much more detailed understanding of this hypothetical mechanism that makes SO an honest indicator of quality is necessary.

Testing SO as a possible pointing index seems to be easier. What first comes to mind are relatively simple experiments with microphone array set-up inside a communicating network of territorial birds. One should expect that a bird whose song was overlapped at the beginning of the experiment would respond differently to subsequent playback (e.g. song alternating) than his neighbours whose songs were not overlapped at the beginning of the experiment. It is important to note that pointing indices may have a lot in common with conventional signals. Therefore, we admit that a precise differentiation between these explanations may prove difficult and thus should always be based on a firm knowledge of the species in question.

Song Overlapping as a Modifier

Bradbury & Vehrencamp (2011) distinguished two kinds of modifiers: amplifiers and attenuators. An

amplifier index signal has many commonalities with a quality index and sometimes is considered as a category of quality indices. The difference is subtle: using an amplifier, a signaller can improve assessment of sender attributes, but this improvement depends on the physical parameters of the signaller anyway (ruffling the feathers for presenting their colours can serve as example). Attenuators have exactly the same features but work in the opposite direction.

Is it possible that SO is a modifier? In Montezuma oropendolas, the production of the lowest peak frequency (LPF) is constrained by body size (larger individuals produce lower LPFs than smaller ones) and is significantly lower during SO compared to singing alone (Price et al. 2006). The results of studies on two bunting species (Osiejuk et al. 2003, 2007), where one of the main differences between response to alternating and overlapping stimuli was a delay in approaching when focal male song was overlapped, suggest that SO may hinder assessment of the sender attributes (e.g. the singing position). There are many examples indicating that contextual factors might significantly influence communication. In fact, it was found that SO can be altered by the presence of other signals: a combination of SO and rapid broadband trill has an enhancing effect on song agonistic function (Sprau et al. 2010a). Individual strategies and differences might also play a role. A list of potentially relevant factors includes level of aggressiveness (Nowicki et al. 2002), motivation or estimation of resource's value (Enquist 1985), mating status and the stage in breeding season (Kunc et al. 2006, 2007), age and dominance rank (Hyman 2003; Mennill & Ratcliffe 2004a,b; Kiefer et al. 2011), quality of habitat (Grava et al. 2013) or even memory (Geberzahn et al. 2013) and personality traits (Naguib et al. 2010).

Testing SO as a potential modifier signal should therefore link overlapping vs. non-overlapping patterns of singing with other song characteristics. One should expect that SO would place the same signal in a modified perspective for the potential direct or third party receivers.

Alternative Explanations for Song Overlapping

Song Overlapping as a Mask

Some researchers suggested that SO may not be a signal *per se* but a behaviour used to mask signals of other individuals (Hultsch & Todt 1982). Such a strategy would be quite understandable in the case of many European thrushes (*Turdus spp.*), for the second part of their songs is particularly rich in information

(Todt & Hultsch 1978; Naguib & Todt 1997). Starting after the opponent would be then similar to a sacrifice manoeuvre in chess: spending a little to gain a lot. There are many examples of singing behaviour where signallers respond to ambient noise or signals of other species by avoiding them in time or changing characteristics of own songs (e.g. Planque & Slabbekoorn 2008; Goodwin & Podos 2013). However, intentional masking has to be considered a special kind of behaviour that evolved in order to disturb other individuals. Overlapping playback in experiments with buntings works in a similar way (Osiejuk et al. 2003, 2007), but a real support for the intentional masking hypothesis would have to come from observation of birds (and not a playback loudspeaker) overlapping songs of their opponents to change their behaviour or behaviour of eavesdropping individuals (e.g. females).

There are several hints indicating how masking may work. For example, the overlapping songs might be preferred to the overlapped ones because the important aspects are received without interference. On the one hand, Brumm & Naguib (2009) found that signals without interference are recognized more easily. On the other hand, however, European starlings (*Sturnus vulgaris*) and male canaries (*Serinus canaria*) are able to recognize songs that were presented together with a very loud noise (Hulse et al. 1997; Appeltants et al. 2005). If we go as far as to interpret this as suggesting that some species may listen to two songs at the same time, then perhaps the basic function of SO is simply to give eavesdroppers a chance to directly compare songs of two competing males? Such a hypothesis was proposed by Logue and Forstmeier (2008) for song-type matching singers. These authors suggested that higher-performance singers benefit from matching song types of opponents. However, if SO works similarly, it should be considered to be an amplifier, rather than a mechanism of incidental masking. Careful masking experiments in different species with different parts of the song simply masked or overlapped by opponents song could lead to new interesting results.

Song Overlapping as an Incidental Phenomenon

Recently, a debate developed around the question whether SO is an aggressive signal or a signal at all (Searcy & Beecher 2009, 2011; Naguib & Mennill 2010). Surprising as it might seem after three decades of research, this debate cannot be ignored because it raises important methodological issues that future SO researchers would have to consider. The core of this debate revolves around the fact that

in many studies, SO occurs below chance level (Naguib & Mennill 2010). According to Searcy & Beecher (2009), this might indicate that SO is only a side effect of differences in song duration and song rate. For example, when songs are shorter, SO decreases because the probability of random temporal overlap is reduced. Of course, it does not mean that this is always the case, but it shows that song rates should be controlled in SO experiments. In addition to that, relating observed levels of SO to chance levels might be useful. However, one should not forget that it is the nature of some signals to occur less frequently than expected by chance (Naguib & Mennill 2010).

Even though these issues are worth considering when designing SO experiments, one should realize that calculating chance levels of SO using simple methods (for example Ficken et al. 1974; as suggested by Searcy & Beecher 2009) will be useful only in case of simple interactions. Think of people talking in a cube farm. There is more overlapping and a vast majority of it is random, but when you speak, a single rude interruption from your boss will still ruin your whole day. In fact, Burt & Vehrencamp (2005) suggested that accidental and deliberate SO can be distinguished and, when controlling for song rates, they identified a pattern suggesting occasional deliberate SO.

No matter how controversial, the positive impact of this debate can already be spotted in the newest SO experiments employing null models to establish chance levels. Two such experiments confirmed that SO avoidance is a non-random phenomenon in male long-tailed manakins (*Chiroxiphia linearis*) (Maynard et al. 2012) and Eurasian wrens (*Troglodytes troglodytes*) (Yang et al. 2014).

Song Overlapping and Song Learning

Could SO play a role in song learning? If it really signals status and dominance, then a youngster could use it as an indicator of which song is worth learning. Indeed, there is evidence from the African village indigobird (*Vidua chalybeata*) that youngsters can learn the song of the dominant bird from the neighbourhood (Payne 1985).

Song Overlapping and Song Alternating

Yet another approach would be to compare SO with another pattern of signalling. Song alternating is an accompanying experimental condition in many SO studies and often serves as such a comparison point.

Many studies found SO to be a stronger threat than song alternating (Amy et al. 2008; Brindley 1991; Dabelsteen et al. 1997; McGregor et al. 1999; Naguib 1999; Naguib et al. 1999; Todt & Naguib 2000; Schmidt et al. 2007); however, this is not the case in some species such as the yellowhammer (*Emberiza citrinella*) (Osiejuk et al. 2003) and corn bunting (*Emberiza calandra*) (Osiejuk et al. 2007).

Conclusion

In this study, we adopted an exploratory approach to existing data, trying sketch some working hypotheses (Dewey 1938) and their predictions about the function of SO (Tables 1 and 2).

Undoubtedly, SO is still a very attractive topic for future research. However, new studies should be designed in a way that would enable to clearly demonstrate that SO is a signal. In case of the aggressive signalling hypothesis, the specific context, predictive and response criteria presented by Searcy & Beecher (2009) will be very useful. Even if in some species SO will turn out not to be a signal, it could still be an acoustic tool used for modifying behaviour of opponents or opponents' signal assessment by masking. We hope that the framework of signal costs presented in this study would serve as a valuable guide for studying possible functions of SO as it helps to formulate clear hypotheses with testable predictions and specific experimental designs (we present them at the end of each section and summarize in Table 1).

No all-encompassing explanation of SO exists and probably will not be formulated any time soon. Nevertheless, it is now clearer than ever that more high-quality experimentation is required to buttress current theorizing on this subject. In all the articles concerning SO cited throughout this study, a total number of fifteen bird species were investigated. This is one reason why identifying the function of SO is such a challenge. Moreover, SO might simply have different functions in different species, and thus, careful comparative approaches will be necessary.

The other reason why it might be particularly hard to reach any final conclusion about SO is that we cannot simply assume (without carefully testing this assumption) that the relationship between the intensity of SO and any response to it is linear. In fact, why not assume something more like bell-curve with peak response intensity for the medium signal values (Collins 2004)? After all, when conflict arises in some species, opponents with similar fighting abilities behave most aggressively (Ręk & Osiejuk 2010, 2011a,b).

Again, special attention should be devoted not only to designs, but to interpretations as well.

As signalling is not black or white (Szalai & Számadó 2009), we are convinced that SO will continue to inspire future researchers and believe that the most insightful findings still lay ahead.

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