



The signal value of birdsong: empirical evidence suggests song overlapping is a signal

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ARTICLE INFO

Article history:

Received 12 February 2010

Initial acceptance 19 March 2010

Final acceptance 31 May 2010

Available online 5 July 2010

MS. number: 10-00110

Keywords:

aggressive signalling
animal communication
birdsong
signal timing
song overlapping
vocal interaction

Birdsong is among the most well-studied communication systems in vertebrates and provides many textbook examples in animal behaviour, ecology and evolution. Owing to the substantial body of research dealing with this topic, and the numerous research groups focusing on different aspects of birdsong, it is often difficult to maintain an overview across the discipline. An increasing number of reviews on various aspects of birdsong provide important syntheses (Todt & Naguib 2000; Vehrencamp 2000; Gil & Gahr 2002; Beecher & Brenowitz 2005; Catchpole & Slater 2008). The recent review by Searcy & Beecher (2009) makes a valuable contribution by bringing together a substantial body of research on the territorial function of birdsong with a specific focus on singing contests. The review covers a large body of research and critically discusses the evidence that certain components of singing contests act as aggressive signals. Furthermore, it places many ideas in a context that will stimulate researchers to conduct more advanced studies and to plan carefully which behavioural responses to measure.

While reviewing the literature on the signal value of various communication strategies, Searcy & Beecher (2009) discuss song overlapping, a well-studied component of singing contests. They conclude that song overlapping may not be a signal at all, despite a large body of research which argues to the contrary. Here we complement the valuable review of Searcy & Beecher (2009) by providing a different view on how to evaluate the traits that are components of animal signalling interactions. We focus on song overlapping because it is among the best studied traits in the territorial interactions of songbirds, because it is well studied in other taxa including anurans and insects (Grafe 1999; Gerhardt & Huber 2002), and because Searcy & Beecher (2009) discuss overlapping from a perspective we do not share.

THE OCCURRENCE OF SONG OVERLAPPING

The term 'song overlapping' is used to refer to vocal signalling in which the song of one individual starts before the song of another individual has finished. The term is often used in species with a singing pattern consisting of discrete songs separated by silent intervals that are usually longer than a song. In species that use this singing style, including many well-studied temperate songbirds, animals can engage in interactions without overlapping each other's songs, or by overlapping them. Overlapping can occur in many different ways: (1) by chance because of haphazard or

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random timing of songs; (2) when two individuals sing at different rates so that their songs periodically coincide; (3) when a singer does not correctly anticipate the end of another individual's song and initiates a song too early; (4) because of the limitations of acoustic space (e.g. when many animals are singing in close proximity) so that an individual must produce an overlapping song or no song at all; or (5) when a singer intentionally adjusts the timing of a song so that it occurs at the same time as some portion of the opponent's song. Song overlapping might convey information in several of these cases. For example, haphazard timing of songs could indicate a singer's disinterest in communicating interactively with an opponent. Intentional overlapping may be a directed signal, whereby an individual deliberately conveys information to the overlapped singer. Most studies on the signal value of song overlapping have focused on intentional overlap in dyadic interactions, usually by using playback to overlap or avoid overlapping a subject's song, by evaluating whether birds overlap a fixed-stimulus playback, or by testing how birds respond to two-speaker stimuli that differ only in their degree of overlap (Table 1).

SONG OVERLAPPING AS A SIGNAL

Searcy & Beecher (2009) review most studies on song overlapping and conclude first that 'existing evidence that overlapping is a threatening signal is minimal' (page 1286) and state as a final conclusion that 'overlapping may not be a signal at all' (abstract and page 1290). We disagree with this conclusion and we present four arguments to support our position: (1) a substantial body of literature shows that animals behave differently in an overlapping versus nonoverlapping context and most studies show a strong vocal or physical response to song overlap; (2) no compelling or widely accepted null model exists for comparison with realized levels of song overlap, so that it is difficult to evaluate whether overlapping occurs at levels that exceed expectation; (3) even if overlapping occurs less often than expected by chance, it may nevertheless have signal value; and (4) there are multiple methods for assessing animals' responses to different signalling strategies, and these methods may be instructive for understanding song overlapping behaviour.

Searcy & Beecher (2009) highlight three criteria that should be met to establish that a signal trait is aggressive: a context criterion, a predictive criterion and a response criterion. We agree that these criteria provide a valuable framework for studying aggressive signalling. Given that not all studies on song overlapping were designed to address all three criteria, evidence for overlapping supporting the three criteria varies across studies. Some criteria, such as the response criterion, are more thoroughly studied than others. Yet the research on song overlapping does provide some support for all three criteria, offering evidence that song overlapping has not only a signal value in general, but also an aggressive signal value.

Birds Respond Differently to Overlapping

Searcy & Beecher (2009) acknowledge that 'demonstrating that subjects respond differently to two categories of signals is useful in showing that the difference between the two categories is salient to the receiver' (page 1283). We reviewed every published study we are aware of that features a focus on song overlapping in birds. We found more than 30 studies of song overlapping, including studies that evaluate overlapping from the signaller's perspective (i.e. whether an individual overlaps), the receiver's perspective (i.e. how an individual responds to being overlapped) and the eavesdropper's perspective (i.e. how an individual responds to hearing overlap between two others; terminology from Hall et al. 2006). The vast majority of studies (more than 90%) show that birds vary

their overlapping behaviour in different contexts (context criterion), that they respond differently to being overlapped (response and predictive criteria), or that they change their behaviour after hearing two other individuals involved in an overlapping interaction (Table 1). Furthermore, most of these studies show changes towards more intense singing and/or approach to the overlapping treatment (Table 1). Therefore, the conclusion that song overlapping may not be a signal at all contradicts most empirical studies on this topic. The conclusion that song overlapping is not a threatening signal does not match the behavioural evidence from many empirical studies.

The many published studies on song overlapping have reported different strengths of effect on birds' vocal and spatial behaviour. This variation does not diminish the conclusion that overlapping is a signal during singing contests, and such variation may even be expected given the range of species studied and the range of contexts and experimental designs used. Even though the strength of evidence for overlapping as a signal varies across studies and species, the majority of published studies found that animals change their behaviour in response to overlap. We recognize that most of the published studies on overlapping (Table 1) have not defined the term aggressive as indicating the readiness to escalate towards a stage of physical attack, as Searcy & Beecher (2009) do; many studies use the terms 'aggressive', 'threatening', 'agonistic' or even 'aroused' interchangeably or in a loose sense or do not use the term aggressive at all. Searcy & Beecher's (2009) review is very constructive in reminding researchers to be more specific with their terminology.

Null Models of Overlapping Lack Consensus

One central argument made by Searcy & Beecher (2009) is that song overlapping does not appear to occur more often than expected by chance during naturally occurring song contests or in responses to playback, and therefore overlapping may not be a signal at all. This conclusion is based on an assumption that the patterning and timing of contributions to vocal interactions are random, and that the value of a trait will be defined by its deviation from randomness. Few studies have quantified the timing of songs during natural interactions (e.g. Wasserman 1977; Gochfeld 1978; Naguib & Kipper 2006; Fitzsimmons et al. 2008a; Foote et al. 2008). Most have found that overlapping does not exceed levels, or occurs less often than, expected by chance. However, the natural interactions that have been examined to date were primarily long-range encounters with lower levels of escalation (e.g. Naguib & Kipper 2006; Fitzsimmons et al. 2008a) than the close-range territorial conflicts that have been the focus of most experimental studies on overlapping (e.g. Mennill & Ratcliffe 2004b; Schmidt et al. 2007). Future studies that carefully quantify overlapping during natural interactions during escalated close-range disputes will provide a valuable contribution to our understanding of song contests, particularly where various singing contexts are evaluated (e.g. black-capped chickadees, *Poecile atricapillus*, show different levels of overlap during dawn chorus singing versus daytime singing; Fitzsimmons et al. 2008b; Foote et al. 2008) or where counter-singing interactions are assessed at different distances from territorial boundaries.

How do we establish null models to compare with realized levels of overlapping? By comparing the timing of songs with frequencies of overlapping that are expected by chance, as Searcy & Beecher (2009) propose, can we develop a better understanding of the information encoded in the timing of birds' songs? Searcy & Beecher (2009) review several methods that have been used to establish chance levels of overlapping in the literature, including calculating 'duty cycle' (this involves calculations based on a bird's

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