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# Continued scepticism that song overlapping is a signal

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In our recent review of aggressive signalling via song in songbirds (Searcy & Beecher 2009, pp. 1286 and 1290), we concluded that 'existing evidence that overlapping is a threatening signal is… minimal' and that 'overlapping may not be a signal at all'. Overlapping here refers to a behaviour in which one singer begins a song while another is singing. Naguib & Mennill (2010) have contested both these conclusions, maintaining (1) that overlapping is a signal and (2) that it is more specifically an aggressive signal. Below, we consider their arguments on these two points in turn.

## OVERLAPPING AS A SIGNAL

To assess the more general hypothesis, that overlapping is a signal, it is helpful to start by specifying a definition of signals. In our review, we cited Otte's (1974, page 385) definition of signals as 'behavioral, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms'. Following Williams (1966), Otte (1974, page 385) further noted that 'a common and critical difficulty in treatments of communicative systems centers on the failure to distinguish between evolved functions and incidental effects'. Our major criticism of overlapping studies is that they have often failed to address the problem that overlapping may occur incidentally, as a chance effect of two birds independently singing at the same time. We argue, therefore, that the first step in considering whether overlapping is a signal is to establish by comparison to a null model that overlapping has not occurred only by chance. The use of null models is of course a standard procedure in animal behaviour, and a good example is close at hand: song type matching (replying to a bird with the same song type he has just sung) is routinely compared against a null model before consideration of whether it is an aggressive (or some other kind of) signal. Generally the null expectation is simply the reciprocal of the bird's repertoire size (the probability that the bird would select that song type by chance). In cases where matching exceeds the random expectation, it is concluded that the birds intentionally match (e.g. Krebs et al. 1981; Falls 1985; Stoddard et al. 1992; Rogers 2004; Anderson et al. 2005; Burt & Vehrencamp 2005; Gammon et al. 2008); in cases where matching does not exceed random expectations, it is concluded that the species does not use this tactic (Ballentine et al. 2008). In several songbirds it has been found that birds song match (at greater than chance levels) their own song or a stranger's song but not a neighbour's song, and this contrast can then lead to a fruitful consideration of the function of song matching (Falls 1985; Stoddard et al. 1992). We have simply suggested that this same standard approach be taken with song overlapping.

Given the lack of evidence that overlapping ever occurs at above chance levels, Naguib & Mennill (2010, page E14) express

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dissatisfaction with the use of random interaction as a null model for song overlapping, saying, ‘If signal timing is not random in the first place, as we understand to be true for song matching and song type switching, then any calculations based on random song timing may produce misleading conclusions’. It is a truism, of course, that a null model will be wrong if the phenomenon is not random. As an alternative to a random model, Naguib & Mennill (2010, page E14) suggest ‘a null model calculated on the basis of no overlapping whatsoever’. This of course is not a null model at all, but rather an alternative hypothesis, that birds avoid overlapping, for which evidence needs to be provided. That is, the investigator needs to provide evidence first that birds generally avoid overlapping, second, that under some special circumstances they do not, and, finally, that these special circumstances cannot be explained by other hypotheses (such as the birds do not hear one another, or simply are not interacting). Use of no overlap as a null model or baseline would lead to the conclusion that two singers were intentionally overlapping even if they were actually both seeking to alternate, but were doing so with some level of error in execution. Any two singers that were actually ignoring each other would also be concluded to be overlapping. The dangers of such a null model are obvious.

Naguib & Mennill (2010) argue that even rare behaviours can have a signal value, giving alarm calls as an example. By signal value they presumably mean information content, which is a necessary but not sufficient part of Otte’s (1974) definition. To have information content, a behaviour must have a nonrandom association with some attribute of the actor or its environment. Although alarm calls are rare when a predator is absent, they are common when the predator is present, as has been shown rigorously in a number of instances (e.g. Seyfarth & Cheney 1980; Evans et al. 1993; Zuberbühler 2000; Templeton et al. 2005). Comparable evidence, showing that overlapping is relatively more common in agonistic contexts, is scant for overlapping. Most studies of overlapping have used designs in which researchers have deliberately overlapped their subjects via interactive playback (see Table 1 in Naguib & Mennill 2010), an approach that allows measurement of response to overlapping but does not allow assessment of the association of overlapping with context or with the subject’s phenotype or future behaviour. To assess the information content of overlapping, it is necessary to study either natural interactions between singers or overlapping responses to noninteractive playback.

Naguib & Mennill (2010) discuss three studies that have examined overlapping in natural interactions, each of which we also examined in our review (Searcy & Beecher 2009). Hultsch & Todt (1982) studied nocturnal singing interactions between male nightingales, *Luscinia megarhynchos*, and found that overall overlapping occurred at lower than random levels (Searcy & Beecher 2009). The most thorough studies of overlapping in natural interactions have examined black-capped chickadees, *Poecile atricapillus*, using multimicrophone acoustic location systems (Fitzsimmons et al. 2008; Foote et al. 2008). In these studies, overlapping occurred at chance or below chance levels, and no associations were found between overlapping and singer attributes such as dominance or external conditions such as distance between singers. Again, neither intentional overlapping nor a signal value for overlapping was supported.

Naguib & Mennill (2010) discuss five studies that have examined overlapping by subjects of noninteractive playback. We discussed four of these in our review (Searcy & Beecher 2009) and stand by our conclusion that these as a whole provide no evidence that overlapping is intentional and little evidence that overlapping conveys aggressive intent. The fifth study, which we did not discuss in our review, illustrates some of the ambiguities of these studies as a whole. Kunc et al. (2007) presented nightingales at night with a fixed-rate playback, and found that males that eventually mated overlapped more of the playback songs during the premating period than during incubation. Males that remained bachelors showed no such pattern over equivalent time periods. Kunc et al. (2007) concluded that males vary the level of aggression in their vocal interactions according to the stage in the breeding season. With their measure of overlap, however, levels of overlapping expected by chance depend directly on song rates, which in their study dropped substantially between the premating and incubation periods in mated males but not in bachelors. Thus the seasonal patterns of overlapping found in this study can be explained at least in part as the consequence of the well-known phenomenon of a drop in song rate after pairing. No evidence was provided that levels of overlapping were higher than chance in either mated or bachelor males during either part of the season, and comparison with figures in Kunc et al. (2006) suggests that all levels were substantially below chance values (see calculations in Searcy & Beecher 2009). Finally, even if it could be shown that intentional overlapping by mated males decreased after pairing, this would not constitute evidence that overlapping is aggressive, since it has not been shown that male nightingales are more aggressive before than after pairing.

The bulk of the empirical studies adduced by Naguib & Mennill (2010) as evidence that overlapping is an aggressive signal examine responses of subjects to being overlapped. The most common response in these studies is for males to interrupt their songs when overlapped by playback. For example, Mennill & Ratcliffe (2004a) compared the responses of male black-capped chickadees to playback that either did or did not overlap them. Subjects did not respond to overlapping with higher song rates, greater agitation or closer approach. Instead, the effects of playback were on song length and song timing: overlapped males sang shorter songs with more variable time intervals between songs. Similarly, the most consistent response of male nightingales to overlapping is to interrupt more of their songs (Naguib 1999; Naguib & Kipper 2006; Schmidt et al. 2006). None of these effects could be said to show a ‘stronger’ or ‘more intense’ response to overlapping. Instead, effects on song interruptions and intervals between songs are just what would be expected if males are seeking to avoid being jammed, and might be produced by any loud sound in the nearby environment. In fact, songbirds (including nightingales) have been shown to adjust the timing of their songs to avoid being overlapped by the songs of other species in natural interactions (Ficken et al. 1974) and playback experiments (Brumm 2006).

Because adjustments in the timing of singing are so likely in response to any overlapping sound, singing responses have to be interpreted with particular care in the case of overlapping playbacks. For example, song rate might increase in response to overlapping treatments because subjects are interrupting more of their songs and starting over more often, without actually increasing the overall amount of song they produce. We would interpret a recent study by Amy et al. (in press) in just this way: in response to overlapping playback, great tits, *Parus major*, increased their song rate but sang shorter songs with fewer elements, while showing no change in approach behaviour.

Because of the ambiguity of interpreting singing responses to overlapping, it is safer to assess aggressive response to overlapping playback using approach or retreat from the loudspeaker, attack on a mount, or use of other vocalizations or visual displays known to be aggressive. Responses to overlapping on these types of measures have been negative in most studies (Searcy & Beecher 2009; Naguib & Mennill 2010).

We acknowledge (as we did in Searcy & Beecher 2009) that a few studies have shown more convincing evidence of response to overlapping, notably the eavesdropping experiments of Peake et al.