



Forum article

Continued scepticism that song overlapping is a signal

William A. Searcy^{a,*}, Michael D. Beecher^{b,c,1}^a Department of Biology, University of Miami^b Department of Psychology, University of Washington^c Department of Biology, University of Washington

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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

* Correspondence: W. A. Searcy, Department of Biology, University of Miami, Coral Gables, FL 33124, U.S.A.

E-mail address: wsearcy@miami.edu (W.A. Searcy).

¹ M. D. Beecher is at Box 351525, University of Washington, Seattle, WA 98195, U.S.A.

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.

(2001, 2002) and Mennill & Ratcliffe (2004b). Nevertheless, we feel that most studies of response to overlapping are unconvincing, and that a compelling case that overlapping is a signal in any species requires evidence of above random levels of overlapping in at least some circumstance, together with evidence of a nonrandom association of overlapping with some characteristic of the signaller or its environment.

OVERLAPPING AS AN AGGRESSIVE SIGNAL

In our review, we suggested three criteria for establishing that a signal is aggressive (in the sense of threatening): (1) a demonstration that the signal increases in aggressive contexts, (2) a demonstration that the signal predicts aggressive escalation, and (3) a demonstration that receivers respond to the signal. We concluded that there was little evidence that overlapping met either the first or the second criterion (Searcy & Beecher 2009), and we do not see much in the compilation of studies presented by Naguib & Mennill (2010) to change our minds. Instead, most of the studies presented by Naguib & Mennill (2010) bear on the third criterion, that of receiver response.

We have already argued above that many of the receiver response studies find responses to overlapping songs that might be given to any loud sound, which does not constitute convincing evidence that overlapping is a signal. Again we concede that a few studies give more convincing evidence of the sorts of responses that one would expect to be given only to within-species signals. Even in these cases, however, it is difficult to maintain that receiver response alone demonstrates that a signal is threatening. If receivers show a strong aggressive response to a signal, that response can be used to argue that the signal is especially aggressive, with the receiver showing a strong response because the threat is serious; conversely, if receivers show a weak aggressive response, that can also be used to argue that the signal is especially aggressive, with the receiver showing a weak response because it is intimidated. If both outcomes can be used to argue that a signal is aggressive, then the test cannot be regarded as convincing.

THE WAY FORWARD

Although we remain highly sceptical about existing evidence that overlapping is an aggressive signal or even a signal at all, we readily admit that new evidence might someday be found that would change our minds, at least with respect to particular species and contexts. Therefore it seems valuable to end by stipulating what evidence we would consider most convincing. To show that overlapping is a signal, it is first critical to show that overlapping occurs at higher than random levels under some circumstances. Again, these circumstances might be rather narrow. For example, it is clear that in black-capped chickadees, overlapping does not consistently occur at above random levels in aggressive interactions as a whole, and that dominant individuals do not consistently overlap others at above random levels (Fitzsimmons et al. 2008; Foote et al. 2008). Nevertheless, it still is possible that overlapping might occur at above chance levels in the subset of aggressive interactions that are most intense, or when the most dominant individuals are interacting with the least dominant, or when the most dominant individuals are just on the point of attacking the least dominant, and so forth. Whether or not above chance levels of overlapping are ever found, it is important to provide an estimate of a random level of overlapping whenever an observed level is given; this is a rule that has rarely been followed to date in the overlapping literature, although it has been widely followed in the matching literature.

Second, more studies need to be done in which the information content of overlapping is assessed. Again, such assessments cannot be made using experimental designs in which researchers overlap subjects via playback, but rather require studies that either examine natural interactions or that allow subjects to overlap fixed-rate playback. Such studies might investigate associations of overlapping frequency with characteristics of the singer (dominance, size, age, etc.) or context (close interaction versus distant, territorial intrusion versus no intrusion, etc.). As a test of whether overlapping is specifically an aggressive signal, experiments that examine whether overlapping predicts aggressive escalation would be particularly valuable (Searcy & Beecher 2009). Such studies should either control for song rates or use a measure of overlapping that does not depend on song rate (Searcy & Beecher 2009), and should provide estimates of random expectations for overlapping as argued above.

Finally, once some signal value of overlapping is established for a species, interactive playback can be used to test for response to being overlapped. Here it seems important to use a control treatment (in addition to the normal control of nonoverlapping playback) in which subjects are overlapped with another sound of the same amplitude and similar frequency characteristics as the conspecific songs used for overlap. Such a control would allow researchers to discriminate between aggressive responses and jamming avoidance.

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References

- Amy, M., Sprau, P., de Goede, P. & Naguib, M. In press. Effects of personality on territory defence in communication networks: a playback experiment with radio-tagged great tits. *Proceedings of the Royal Society B*.
- 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.
- Ballentine, B., Searcy, W. A. & Nowicki, S. 2008. Reliable aggressive signalling in swamp sparrows. *Animal Behaviour*, **75**, 693–703.
- Brumm, H. 2006. Signalling through acoustic windows: nightingales avoid inter-specific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A*, **192**, 1279–1285.
- 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.
- Evans, C. S., Evans, L. & Marler, P. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, **46**, 23–38.
- Falls, J. B. 1985. Song matching in western meadowlarks. *Canadian Journal of Zoology*, **63**, 2520–2524.
- 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.
- Hultsch, H. & Todt, D. 1982. Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos* B.). *Behavioral Ecology and Sociobiology*, **11**, 253–260.
- 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.
- Kunc, H. P., Amrhein, V. & Naguib, M. 2007. Vocal interactions in common nightingales (*Luscinia megarhynchos*): males take it easy after pairing. *Behavioral Ecology and Sociobiology*, **61**, 557–563.
- 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.

- 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. & Mennill, D. J.** 2010. The signal value of birdsong: empirical evidence suggests song overlapping is a signal. *Animal Behaviour*, **80**, e11–e15.
- Otte, D.** 1974. Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics*, **5**, 385–417.
- 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.
- 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.
- Searcy, W. A. & Beecher, M. D.** 2009. Song as an aggressive signal in songbirds. *Animal Behaviour*, **78**, 1281–1292.
- Seyfarth, R. M. & Cheney, D. L.** 1980. The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift für Tierpsychologie*, **54**, 37–56.
- 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.
- Templeton, C. N., Greene, E. & Davis, K.** 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, **308**, 1934–1937.
- Williams, G. C.** 1966. *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.
- Zuberbühler, K.** 2000. Referential labelling in Diana monkeys. *Animal Behaviour*, **59**, 917–927.