



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

Marc Naguib^{a,*}, Daniel J. Mennill^{b,*}

^a Netherlands Institute of Ecology (NIOO-KNAW), Department of Animal Ecology

^b Department of Biological Sciences, University of Windsor

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

* Correspondence: M. Naguib, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 40, 6666 ZG Heteren, The Netherlands and D. J. Mennill, Biology Building, 401 Sunset Avenue, Windsor, Ontario N9B3P4, Canada.

E-mail addresses: m.naguib@nioo.knaw.nl (M. Naguib), dmennill@uwindsor.ca (D.J. Mennill).

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

Table 1

Studies of overlapping in birds, organized by species, with a brief summary of whether the result indicates that birds behave differently during overlapping interactions

Species	Type of study	Summary of result	Response category	Source
Blackbird	Interactive playback, aviary setting	Males avoided song posts where they were overlapped	1	Todt 1981
Banded wren	Interactive playback	Males altered songs when overlapped; males behaved differently when re-encountering a bird that had previously overlapped them	1	Hall et al. 2006
Banded wren	Fixed-stimulus playback	Males that overlapped playback retreated sooner from the site of playback	x	Vehrencamp et al. 2007
Black-capped chickadee	Interactive playback	Females changed to a mixed reproductive strategy after hearing their partner overlapped and matched in a song contest	4	Mennill et al. 2002
Black-capped chickadee	Two-speaker playback	Males preferentially approached an overlapping loudspeaker rather than overlapped loudspeaker	2	Mennill & Ratcliffe 2004a
Black-capped chickadee	Interactive playback	Males overlapped by playback shortened songs and increased song timing variability	1	Mennill & Ratcliffe 2004b
Black-capped chickadee	Multichannel recording of daytime song contests	Overlapping in natural daytime song contests was not more common than expected by chance; overlapping preceded song matching in such song contests	x	Fitzsimmons et al. 2008a
Black-capped chickadee	Multichannel recording of two-speaker playback	Neighbourhood song output increased more after simulated song contests that included overlapping and matching	3	Fitzsimmons et al. 2008b
Black-capped chickadee	Multichannel recording of dawn chorus	Overlapping was less common than expected by chance during the dawn chorus; no relationship between distance and overlapping	x	Foote et al. 2008
Blue tit	Interactive playback	Males behaved differently and sang at higher rate when overlapped	3	Poesel & Dabelsteen 2005
Canary	Two-speaker playback, aviary setting	Females preferred overlapping song unless the two songs contained 'sexy syllables'	4	Leboucher & Pallot 2004
Canary	Two-speaker playback, aviary setting	Females preferred overlapping songs	4	Amy et al. 2008
Canary	Two-speaker playback, aviary setting	Males decreased calling in response to playback simulating a bird previously heard overlapping an opponent	x	Amy & Leboucher 2009
Canary	Two-speaker playback, aviary setting	Females invested more yolk in eggs from males whose song was heard as overlapping than when heard as overlapped	4	Garcia-Fernandez et al. 2010
Corn bunting	Interactive playback	Males that were overlapped approached the loudspeaker more slowly	x	Osiejuk et al. 2007
Golden whistler	Fixed-stimulus playback	Males overlapped when closer to loudspeaker and used different types of songs to overlap	5	van Dongen 2006
Great tit	Interactive playback	Variation in male song length and song timing increased when they were overlapped	1	Dabelsteen et al. 1996
Great tit	Interactive playback	Males sang at high rate, with shorter songs and fewer song type switches to overlapping playback	3	Amy et al., in press
Great tit	Interactive playback	Males increased overlapping when territorial intruder escalated song contests, or stopped singing when overlapped*	5	Langemann et al. 2000
Great tit	Two-speaker playback	Males sang fewer songs in response to previously overlapped songs in a two-loudspeaker setting	3	Peake et al. 2001
Great tit	Two-speaker playback	Males sang fewer songs in response to a known loser in an overlapping interaction	3	Peake et al. 2002
European robin	Fixed-stimulus playback	Males overlapped more stranger than neighbour songs and overlapped more when playback was nearby	5	Brindley 1991
European robin	Interactive playback	Males sang with shorter latency to aggressive calls (the twitter call) in response to overlapping playback	3	Dabelsteen et al. 1997
Little blue penguins	Two-speaker playback	Females approached overlapping loudspeaker	4	Miyazaki & Waas 2002
Nightingale	Descriptive, playback, nocturnal song	Males demonstrated different roles in interactions ('inserters', 'overlappers', 'autonomous singers'); 'inserters' and 'overlappers' increased song rate in response to song overlap	3	Hultsch & Todt 1982
Nightingale	Two-speaker playback, daytime song	Males showed closer approach to overlapping speaker	2	Naguib & Todt 1997
Nightingale	Interactive playback, nocturnal song	Males exhibited more singing interruptions to overlapping playback	1	Naguib 1999
Nightingale	Interactive playback, nocturnal song	Males exhibited more singing interruptions to overlapping playback	1	Naguib & Kipper 2006
Nightingale	Interactive playback, nocturnal song	More singing interruptions to overlapping by males that remained unpaired	1	Schmidt et al. 2006
Nightingale	Interactive playback	Males sang at higher rate to overlapping playback and to playback with (aggressive trills) compared to alternating playback	3	Sprau et al., in press
Nightingale	Fixed-stimulus playback, nocturnal song	Subsequently mated males overlapped more songs than males that remained unpaired	5	Kunc et al. 2006
Nightingale	Fixed-stimulus playback, nocturnal song	Mated males overlapped fewer songs after mating than before mating; bachelors did not vary overlap at corresponding times	5	Kunc et al. 2007
Nightingale	Interactive playback, daytime song	Closer approach to fixed playback when male had received an overlapping playback the previous night	2	Schmidt et al. 2007
Yellow hammer	Interactive playback	Males that were overlapped approached the loudspeaker more slowly	x	Osiejuk et al. 2004

Most interactive playback experiments used song overlapping and song alternating as different treatments for assessing the responses of territorial males; in most two-speaker experiments, songs of one speaker overlapped songs of the other speaker and the subjects' responses to the two loudspeakers were compared; in most fixed-stimulus experiments, overlapping of the noninteractive playback stimulus by the subject was evaluated. We categorize different responses to overlapping into four groups: (1) subjects responded with irregular singing or some other singing style consistent with the idea of overlapping avoidance; (2) subjects physically approached overlapping playback; (3) subjects increased song rate or another trait in response to overlapping playback; (4) females exhibited preference for overlapping song; (5) males responded more strongly in an escalating playback design, responded closer to the loudspeaker, or males that were found to be successful in mate attraction were found to overlap more. Studies not falling in these categories, and studies with results that revealed weaker responses to overlapping are marked as 'x'. Almost all studies revealed a different response to song overlapping versus alternating, and most studies showed a stronger vocal or physical response to overlapping (categories 1–5). The few studies showing weaker responses to overlapping could reflect a different 'less aggressive' interpretation of the signal value in those contexts but often are interpreted as cautious responses to stronger threats (see de Kort et al. 2009).

* In the study by Langemann et al. (2000), overlapping playback was always presented after an alternating treatment so that differences in response to the two treatments cannot be separated from order effects.

typical song length and intersong interval; Ficken et al. 1974), or using a randomization procedure (this involves comparisons of the singing behaviour of birds recorded at different times or locations; e.g. Fitzsimmons et al. 2008a). Another alternative still would be a null model calculated on the basis of no overlapping whatsoever. The timing of songs, including the avoidance of overlap, has been well studied in chorusing contexts as well as in more direct vocal interactions (e.g. Ficken et al. 1974, 1985; Popp et al. 1985; Greenfield 1994). Signalling space is limited along the time axis and any signal will be easier to detect and to recognize when it is not masked by other sounds, whether conspecific signals or background noise (Aubin & Jouventin 1998; Wiley 2006; Brumm & Naguib 2009). Because an unmasked signal will have a larger signal range, and because overlapping may impair mutual listening, the default strategy of signallers may be to avoid overlap. Each of these null models leads to very different predictions concerning the occurrence of overlap. 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. Further work on the development of appropriate null models is badly needed to integrate and compare different techniques for establishing baseline levels of overlap.

Even Rare Events Can be Signals

Even if overlapping is a rare event, even if it is rarer than predicted by a randomization or duty cycle model, it may nevertheless have signal value. Many events involving interactions between two individuals are rare, but very important in animal behaviour. Some signals may have a signal value specifically because they are rare and consequently catch the attention of a receiver (e.g. alarm calls). Conversely, song alternating appears to occur at greater-than-chance levels in several species, but does not automatically qualify as having signal value merely because it is common. Even when empirical studies show that song overlapping occurs less often than predicted by chance, this is not a sufficient reason to argue that it may not be a signal at all.

Alternative Aggressive Response Measures Provide Insight

Searcy & Beecher (2009) make an important point that studies designed to investigate whether song overlapping predicts a physically aggressive response (their second criterion of aggressive signalling) will be valuable. Birds rarely physically attack a loudspeaker, and other behavioural measures aid in interpreting an animal's motivation during a song contest, such as physical approach towards a loudspeaker, aggressive postures towards the loudspeaker or certain vocal responses. These alternative ways in which animals vary their behaviour can provide insight into how animals perceive different traits during song interactions.

One commonly used measure of response is to evaluate a focal animal's pattern of vocal behaviour during an interaction. Animals may change their pattern of vocal behaviour in response to overlapping exchanges during a song contest, and they may do so without approaching physically. For example, birds have been shown to vary song rate or intersong intervals, to produce more interrupted songs, or to use specific song patterns more frequently during overlapping interactions (e.g. Naguib 1999; Mennill & Ratcliffe 2004b). Each of these changes in vocal behaviour indicates that birds are responding to song overlapping, and such changes are interpreted to reflect internal changes in the singer consistent with the idea that overlapping is a threatening signal. A physical approach may appear as directed aggressive behaviour, but changes in singing pattern may also reflect readiness to escalate

a song contest. Consequently, we do not agree that it is justified to conclude that the majority of results show no difference in aggressive response to overlapping versus nonoverlapping treatments (Searcy & Beecher 2009, page 1286) based solely on equivalent approach responses to these two playback treatments; the vocal behaviour of the interacting animals may also offer important insight into their aggressive responses as also acknowledged elsewhere in their review.

A second alternative measure of response, recognized by Searcy & Beecher (2009), is to evaluate the behaviour of the animals after an interaction has concluded. To take such effects into account, several studies have analysed separately the responses of animals during and immediately after playback. Even long-term effects of playbacks have been the focus of several playback experiments (Mennill et al. 2002; Amrhein & Erne 2006; Erne & Amrhein 2008; Amrhein & Lerch 2010) including some studies testing specifically for long-term effects of song overlapping (Hall et al. 2006; Schmidt et al. 2007). The latter two studies were specifically designed to separate the period of vocal overlapping from the period when animals' responses were assessed (the predictive criterion). For example, Schmidt et al. (2007) used nocturnal song in nightingales, *Luscinia megarhynchos*, as a standardized context to overlap or avoid overlapping territorial males from outside their territories, and then evaluated birds' responses to simulated territorial intrusions the following morning. Males that had received overlapping playback at night had a stronger territorial response the next day, showing that overlapping leads to subsequent escalation by the receiver, fulfilling the second (predictive) and third (response) criteria put forward by Searcy & Beecher (2009).

CONCLUSION

Further research on the signals involved in song contests will allow behaviourists to understand better how animals communicate territorial aggression. We feel that any understanding of vocal interactions using randomness as a null model may miss important components of animal signalling systems. Arguing that traits are not signals, or that they are not aggressive signals, when they are less common than expected by chance ignores existing empirical data that rare events have important consequences; even rare events may have a specific signal value. We recommend that behaviourists should assess multiple responses of animals to variation in interactive communication strategies, including physical approaches but also including changes in vocal behaviour and changes in behaviour that may be evident only after the signalling interaction has finished.

We applaud Searcy & Beecher's attempt to provide a coherent review of behaviours that are involved in the complex song contests of birds. Yet we disagree with one of their conclusions; that overlapping may not be a signal within these song contests. Evidence from many studies demonstrates that overlapping influences bird behaviour during and after male–male song contests. The evidence clearly supports the idea that overlapping is a signal, and the results of most studies are consistent with the idea that overlapping functions as a threatening signal (Table 1). The responses to overlapping playback, across multiple species and different experimental designs, can best be interpreted as 'a step up the chain of escalation, whether or not it reliably predicts actual attack' (Searcy & Beecher, page 1282). To what extent overlapping functions as an aggressive signal, in the sense defined by Searcy & Beecher in terms of predicting actual physical aggression, and how overlapping relates to other traits in signalling contests (including matching, use of trills, quiet song, etc.) remains an important area for research. Future research should focus on clarifying the function of overlapping through studies that carefully control for other

aspects of counter-singing behaviour to understand overlapping on its own. The context of the three criteria provided by Searcy & Beecher (2009), together with the context of the signaller/receiver/eavesdropper perspective provided by Hall et al. (2006), the time-specific/pattern-specific perspective provided by Todt & Naguib (2000), and the considerations we present here, will help to guide these future studies.

We thank Mathieu Amy, David Logue, William Searcy and David Wilson for constructive comments on the manuscript. M.N.'s research programme is supported by the German Research Foundation. D.J.M.'s research programme is supported by the Natural Sciences and Engineering Research Council of Canada.

References

- Amrhein, V. & Erne, N. 2006. Dawn singing reflects past territorial challenges in the winter wren. *Animal Behaviour*, **71**, 1075–1080.
- Amrhein, V. & Lerch, S. 2010. Differential effects of moving versus stationary territorial intruders on territory defence in a songbird. *Journal of Animal Ecology*, **79**, 82–87.
- Amy, M. & Leboucher, G. 2009. Effects of eavesdropping on subsequent signalling behaviours in male canaries. *Ethology*, **115**, 239–246.
- Amy, M., Monbureau, M., Durand, C., Gomez, D., Thery, M. & Leboucher, G. 2008. Female canary mate preferences: differential use of information from two types of male–male interaction. *Animal Behaviour*, **76**, 971–982.
- 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*. doi:10.1098/rspb.2010.0598.
- Aubin, T. & Jouventin, P. 1998. Cocktail-party effect in king penguin colonies. *Proceedings of the Royal Society B*, **265**, 1665–1673.
- Beecher, M. D. & Brenowitz, E. A. 2005. Functional aspects of song learning in songbirds. *Trends in Ecology & Evolution*, **20**, 143–149.
- Brindley, E. L. 1991. Response of European robins to playback of song: neighbour recognition and overlapping. *Animal Behaviour*, **41**, 503–512.
- Brumm, H. & Naguib, M. 2009. Environmental acoustics and the evolution of bird song. *Advances in the Study of Behavior*, **40**, 1–33.
- Catchpole, C. K. & Slater, P. J. B. 2008. *Bird Song: Biological Themes and Variation*. New York: Cambridge University Press.
- 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.
- van Dongen, W. F. D. 2006. Variation in singing behaviour reveal possible functions of song in male golden whistlers. *Behaviour*, **143**, 57–82.
- Erne, N. & Amrhein, V. 2008. Long-term influence of simulated territorial intrusions on dawn and dusk singing in the winter wren: spring versus autumn. *Journal of Ornithology*, **149**, 479–486.
- Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science*, **183**, 762–763.
- Ficken, R. W., Popp, J. W. & Matthiae, P. E. 1985. Avoidance of acoustic interference by ovenbirds. *Wilson Bulletin*, **97**, 569–571.
- Fitzsimmons, L. P., Foote, J. R., Ratcliffe, L. M. & Mennill, D. J. 2008a. Frequency matching, overlapping and movement behaviour in diurnal countersinging interactions of black-capped chickadees. *Animal Behaviour*, **75**, 1913–1920.
- Fitzsimmons, L. P., Foote, J. R., Ratcliffe, L. M. & Mennill, D. J. 2008b. Eavesdropping and communication networks revealed through playback and an acoustic location system. *Behavioral Ecology*, **19**, 824–829.
- 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.
- Garcia-Fernandez, V., Amy, M., Lacroix, A., Malacarne, G. & Leboucher, G. 2010. Eavesdropping on male singing interactions leads to differential allocation in eggs. *Ethology*, **116**, 662–670.
- Gerhardt, H. C. & Huber, F. 2002. *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions*. Chicago: University of Chicago Press.
- Gil, D. & Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, **17**, 133–141.
- Gochfeld, M. 1978. Intraspecific social stimulation and temporal displacement of songs of the lesser skylark, *Alauda gulgula*. *Zeitschrift für Tierpsychologie*, **48**, 337–344.
- Grafe, T. U. 1999. A function of synchronous chorusing and a novel female preference shift in an anuran. *Proceedings of the Royal Society B*, **266**, 2331–2336.
- Greenfield, M. D. 1994. Synchronous and alternating choruses in insects and anurans: common mechanisms and diverse functions. *American Zoologist*, **34**, 605–615.
- 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.
- Hultsch, H. & Todt, D. 1982. Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos*). *Behavioral Ecology and Sociobiology*, **11**, 253–260.
- de Kort, S. R., Eldermire, E. R., Cramer, E. R. & Vehrencamp, S. L. 2009. The deterring function of bird song. *Behavioral Ecology*, **20**, 200–206.
- 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.
- Langemann, U., Tavares, J. P., Peake, T. M. & McGregor, P. K. 2000. Response of great tits to escalating patterns of playback. *Behaviour*, **137**, 451–471.
- Leboucher, G. & Pallot, K. 2004. Is he all he says? Intersexual eavesdropping in the domestic canary, *Serinus canaria*. *Animal Behaviour*, **68**, 957–963.
- Mennill, D. J. & Ratcliffe, L. M. 2004a. Do male black-capped chickadees eavesdrop on song contests? A multi-speaker playback experiment. *Behaviour*, **141**, 125–139.
- Mennill, D. J. & Ratcliffe, L. M. 2004b. Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour*, **67**, 441–450.
- Mennill, D. J., Ratcliffe, L. M. & Boag, P. T. 2002. Female eavesdropping on male song contests in songbirds. *Science*, **296**, 873.
- Miyazaki, M. & Waas, J. R. 2002. 'Last word' effects of male advertising calls on female preference in little blue penguins. *Behaviour*, **139**, 1413–1423.
- 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.
- Osiejuk, T. S., Ratynska, K. & Cygan, J. P. 2004. Signal value of alternating and overlapping singing in the yellowhammer *Emberiza citrinella*. *Journal of Ethology*, **22**, 55–61.
- Osiejuk, T. S., Ratynska, K. & Cygan, J. P. 2007. Corn bunting (*Miliaria calandra*) males respond differently to alternating and overlapping playback of song. *Journal of Ethology*, **25**, 159–168.
- 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**, 925–929.
- Poesel, A. & Dabelsteen, T. 2005. Territorial responses of male blue tits to simulated dynamic intrusions: effects of song overlap and intruder location. *Animal Behaviour*, **70**, 1419–1427.
- Popp, J. W., Ficken, R. W. & Reinartz, J. A. 1985. Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk*, **102**, 744–748.
- Schmidt, R., Kunc, H. P., Amrhein, V. & Naguib, M. 2006. Responses to interactive playback predict future mating status in nightingales. *Animal Behaviour*, **72**, 1355–1362.
- Schmidt, R., Kunc, H. P., Amrhein, V. & Naguib, M. 2007. The day after: effects of vocal interactions on territory defence in nightingales. *Journal of Animal Ecology*, **76**, 168–173.
- Searcy, W. A. & Beecher, M. D. 2009. Song as an aggressive signal in songbirds. *Animal Behaviour*, **78**, 1281–1292.
- Sprau, P., Roth, T., Schmidt, R., Amrhein, V. & Naguib, M. In press. Communication across territory boundaries: distance dependent responses in nightingales. *Behavioral Ecology*. doi:10.1093/beheco/arq097.
- 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. *Advances in the Study of Behavior*, **29**, 247–296.
- Vehrencamp, S. L. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal Signals* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 277–300. Trondheim: Tapir Academic Press.
- 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 and Sociobiology*, **18**, 849–859.
- Wasserman, F. E. 1977. Intraspecific acoustical interference in the white-throated sparrow (*Zonotrichia albicollis*). *Animal Behaviour*, **25**, 949–952.
- Wiley, R. H. 2006. Signal detection and animal communication. *Advances in the Study of Behavior*, **36**, 217–247.