

Vocal interactions in common nightingales (*Luscinia megarhynchos*): males take it easy after pairing

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Abstract Seasonal patterns of bird song have been studied intensively with a focus on individual males. However, little is known about seasonal patterns of singing during vocal interactions between males. Vocal interactions have been shown to be important in sexual selection as males may signal aspects of motivation or quality. Here, we investigated in nightingales (*Luscinia megarhynchos*) whether a male's behaviour in vocal interactions at different stages of the breeding season is influenced by its mating status. We examined how males that differ in their subsequent mating success respond to a non-interactive, nocturnal playback presented during the period of mate attraction and subsequently during the egg-laying period. We found that mated males overlapped fewer songs and had a lower song rate during the egg-laying period compared to their responses during the mate-attraction period, whereas unpaired males did not vary in their responses between the two periods. Our results suggest that mating status is a key factor affecting singing behaviour in vocal interactions and that a time-specific singing pattern like song overlapping is used

flexibly during vocal interactions. Because song overlapping is thought to be a signal of aggression in male–male vocal interactions, it seems that males vary the level of aggression in vocal interactions according to their mating status and to the stage in the breeding season.

Keywords Sexual selection · Eavesdropping · Nightingale · Bird song · Nocturnal song · Male–male interactions

Introduction

During agonistic vocal interactions, such as the song contests of territorial song birds, animals exchange information by varying the timing of a signal (e.g. by overlapping an opponent's signal) or by changing the signal type (e.g. by matching the type of an opponent's signal). Both the type of signal and the timing of a signal may carry information about the signaller's quality, status or motivation level (Todt and Naguib 2000; Vehrencamp 2000). There is growing evidence that song overlapping is used and perceived as a signal of immediate aggression. Males of several bird species respond more aggressively when overlapped by playback than when playback songs are alternated with their songs (Dabelsteen et al. 1997; Naguib 1999; but see Osiejuk et al. 2004), or stop singing when overlapped (Langemann et al. 2000). Such interactions are not only important for the competing individuals but also for other individuals eavesdropping on such vocal interactions that are able to make immediate comparisons between the two contestants on the basis of their relative performance during the interaction (McGregor and Dabelsteen 1996; McGregor and Peake 2000; Naguib 2005). It has been shown that eavesdropping individuals use information from interactions both in female choice and male–male competition

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(Naguib and Todt 1997; Mennill et al. 2002, 2003; Leboucher and Pallot 2004; Miyazaki and Waas 2002; Naguib et al. 2004; Oliveira et al. 1998; Peake et al. 2001, 2002).

Studies investigating the impact of vocal interactions on a male's reproductive success have either focused on the period of social pair formation (Leboucher and Pallot 2004) or on times during which females engage in extra-pair copulations (Otter et al. 1999; Mennill et al. 2002). However, it is well known that patterns of bird song vary over the breeding season (e.g. Møller 1991; Gil et al. 1999; Leitner et al. 2001; Forstmeier and Balsby 2002). Thus, to understand the possible impact of vocal interactions on reproductive success, we need to know if and how individuals seasonally change their behaviour during vocal interactions and what information is available for interacting and eavesdropping individuals.

In nightingales (*Luscinia megarhynchos*), females are likely to base their choice of a social mate on nocturnal song because males cease nocturnal song after successful mate attraction; males then resume nocturnal song for a few days when their social mates lay eggs (Amrhein et al. 2002, 2004a). Nightingales show striking variation in their vocal behaviour during natural interactions (Hultsch and Todt 1981, 1982) and their songs can be grouped into different song categories (Kunc et al. 2005a). In a playback experiment, we found that males adjust the use of different song categories during a nocturnal vocal interaction (Kunc et al. 2006). During playback, males reduced the proportion of whistle songs produced and increased the proportion of songs containing trills (Kunc et al. 2006). These data were consistent with the hypothesis that whistle songs are more important in female attraction, and also suggest that trills are particularly important in short-range male–male vocal interactions. Furthermore, male nightingales that overlapped more songs of a nocturnal playback during the mate attraction period were more likely to attract a female, suggesting that the performance of contestants during vocal interactions reflects information that could be used in female choice (Kunc et al. 2006). Based on these findings, we here investigated if a male's singing strategy during vocal interactions changes over the breeding season corresponding to changes in its mating status.

Our aim was to examine whether the differential responses to playback among males during mate attraction (Kunc et al. 2006) still persist after mating when mated males resume nocturnal song during egg laying of their females. In our study population, up to 49% of territorial male nightingales remain unpaired throughout the breeding season (Amrhein et al. 2004b), providing the opportunity to compare singing behaviour of males that are successful in attracting a social mate with males that remain unpaired throughout the breeding season. We investigated how males

that differ in their subsequent mating status respond to a non-interactive nocturnal playback during the period of mate attraction and during the egg-laying period of their social mate. The function of nocturnal song during egg laying is unclear, but could be to encourage the female to increase the investment in the brood according to male quality (Sheldon 2000; Amrhein et al. 2002). Alternatively, nocturnal song during egg laying may serve to protect paternity, either by repelling rival males or by stimulating the female to solicit copulations (Pinxten and Eens 1998). If aggressive signalling, i.e. overlapping a high proportion of an opponent's song, is mainly important during mate attraction, we expect that paired males should decrease the percentage of an opponent's songs that they overlap. In contrast, if aggressive signalling is important over the entire breeding season, perhaps to repel rival males or as a signal to their own mate or potential extra-pair mates, we expect both mated and unmated males to overlap similar proportions of songs in both periods of the breeding cycle. We also examined if the use of whistle songs and songs with trills varies between the stages of the breeding cycle and between males differing in their mating success, as these song traits might have specific signal values in intra- and intersexual communication.

Materials and methods

Study site and study species

The study was carried out from April to June 2002 and 2003 at the Petite Camargue Alsacienne (France) and in adjacent areas. The first males were observed on 12 April in 2002 and 13 April in 2003, and the first females were observed on 20 April in both years. Nightingales form socially monogamous seasonal pair bonds, and only unmated males sing regularly at night for prolonged periods (Amrhein et al. 2002, 2004a). Diurnal singing behaviour of subjects was observed throughout the breeding season to determine territory boundaries. We also surveyed the nocturnal singing activity of all males each day throughout the breeding season to assess their mating status. Males that remained unpaired throughout the breeding season are referred to henceforth as bachelors, and males that were able to attract females are referred to as mated males. When the first round of playbacks was performed during the mate-attraction period, none of the males had yet attracted a female, but each defended a territory.

Playback stimuli

We created stimuli tapes from clear recordings of nocturnal song made in our study area. Songs were recorded with a

Sennheiser ME66/K6 microphone (Sennheiser Electronic GmbH, Wedemark, Germany), which was connected either to a Sony TC-D5M or a Sony WM-D6C cassette recorder (Sony, Tokyo, Japan). We digitised recordings on a PC with Cool Edit 2000 (Syntrillium Software, Phoenix, USA; sample frequency: 44.1 kHz, resolution: 16 bit). We generated spectrograms of recordings using Avisoft SAS-Lab Pro 3.5 (R. Specht, Berlin, Germany), and selected non-whistle songs and whistle songs from each recording. Whistle songs contain a series of mostly unmodulated whistles in the beginning of a song and can therefore be identified and distinguished clearly from non-whistle songs (Hultsch and Todt 1996; Kipper et al. 2004; Kunc et al. 2005a). To avoid pseudoreplication, we generated a new set of stimuli for each playback by using the songs of each recorded male only once. Stimuli tapes were created to simulate an average nocturnally singing male nightingale (10 songs per minute, approximately 80% non-whistle songs and 20% whistle songs; Kunc et al. 2005a). Each playback consisted of 5 min of song playback; each playback song consisted of 40 non-whistle songs and 10 whistle songs. The 50 songs were randomly merged into one wave file in Cool Edit and normalised at once to the peak amplitude. All tapes ($N=21$) were then created using a standardised recording level.

Playback protocol

Nocturnal playbacks were conducted twice on the same individuals: first during the mate-attraction period and then 14.7 ± 0.8 days later during the laying period. Each individual received the same set of stimuli twice. For the mate-attraction period, the responses of the subjects were reanalysed from a subsample of males that were examined in a previous study (Kunc et al. 2006). To allow comparisons of responses of mated males and bachelors during the egg-laying period, we performed playbacks with bachelors when their immediate neighbouring mated males had resumed nocturnal singing for a few nights during egg laying (Amrhein et al. 2002, 2004a). Playbacks were conducted on nocturnally singing males between 0000 and 0330 hours Central European Summer Time. As a prerequisite for each playback, we used males that had been singing before the playback started as subjects. As stimuli, we used songs that were recorded from males out of a subject's hearing range. We placed the loudspeaker (Canton Plus X passive loudspeaker; Canton Elektronik GmbH, Weilrod, Germany) outside a subject's territory at a side where no neighbour had been observed, but close to the subject's territory boundary. The loudspeaker was positioned at the same place during both playbacks, at a height of 0.5 to 2 m, depending on the focal male's singing position, and at a distance of approximately 30 to 50 m

from the subject's song post, depending on the habitat structure. Songs were broadcast from a Sony WMD 6M tape recorder connected to a Blaupunkt MPA 2 amplifier (Blaupunkt GmbH, Hildesheim, Germany), which was connected to the Canton loudspeaker. Singing responses of focal males were recorded with a Sennheiser ME 66/K6 directional microphone on one channel of a Sony TCD 5M stereo tape recorder. On the other channel, we recorded the songs broadcast by the loudspeaker with a second Sennheiser ME 66/K6 directional microphone. Volume of broadcast songs was adjusted prior to playback to 88 dB at a 1-m distance, measured with a Brüel & Kjær (Nærum, Denmark) precision SPL meter 2233 (C-weighting, fast response). This sound pressure level lies within the range of naturally singing nightingales (Brumm 2004).

Measures of response

We calculated (a) the percentage of songs that males overlapped during the playback. We considered a song of the playback as being overlapped by the focal bird if the bird started to vocalise within 300 ms of the onset of a broadcast song, to avoid confounding effects of the relatively slow speed of sound (Dabelsteen 1992). Furthermore, we measured the following song parameters during the playback: (b) song rate (number of songs per minute), (c) percentage of whistle songs and (d) percentage of songs including rapid broadband trills (cf. Kunc et al. 2006). We also noted (e) whether a bird changed its song post during and after a playback or not. During the 42 nocturnal playbacks that we conducted, only two birds changed their song post: one male during and one male after the playback. We therefore excluded the post change parameter from any further analysis.

Statistical analyses

For all response variables, the baseline assumptions for the use of parametric statistics, i.e. normally distributed errors and homoscedasticity, were met. We applied repeated-measures ANOVA using SPSS 11.0. The within-subjects factors were the particular song parameters measured during the mate-attraction period and the egg-laying period, and the between-subjects factor was mating status (two levels: mated male or bachelor). Our sample consisted of 11 mated males and 10 bachelors. Results are given as mean \pm SE; all reported tests are two-tailed.

Results

The proportion of broadcast songs overlapped by the subjects differed significantly between the mate-attraction and egg-

laying periods (Fig. 1; $F_{1,19}=4.70$, $p=0.043$), but not between mated males and bachelors ($F_{1,19}=0.38$, $p=0.85$). However, the interaction between the periods of the breeding season and male mating status was significant ($F_{1,19}=17.01$, $p=0.001$). Mated males reduced the proportion of overlapping songs significantly during the egg-laying period (Fig. 1; paired t test: $t_{10}=4.10$, $p=0.002$), whereas bachelors kept the proportion of songs they overlapped at similar levels (paired t test: $t_9=-1.57$, $p=0.15$) during both periods.

Song rate during the playback differed significantly between the mate-attraction and egg-laying periods (Fig. 2a; $F_{1,19}=11.65$, $p=0.003$) and between mated males and bachelors ($F_{1,19}=8.90$, $p=0.036$). During the period of egg laying, mated males decreased their song rates during the playback, whereas the song rates of bachelors remained consistent (interaction between the periods of the breeding cycle and male mating status: $F_{1,19}=13.65$, $p=0.002$).

Neither the percentage of whistle songs (Fig. 2b; $F_{1,19}=0.41$, $p=0.53$) nor the percentage of songs containing trills (Fig. 2c; $F_{1,19}=0.26$, $p=0.61$) during the playback differed significantly between the mate-attraction and egg-laying periods, and neither measure differed significantly between mated males and bachelors (whistle songs: $F_{1,19}=1.2$, $p=0.28$; trills: $F_{1,19}=0.39$, $p=0.53$). Furthermore, we found no significant interactions between the two periods and male mating status, indicating that the seasonal patterns of whistle song use ($F_{1,19}=0.11$, $p=0.74$) and songs containing trills ($F_{1,19}=0.06$, $p=0.81$) were similar in mated males and bachelors.

Discussion

Male nightingales that attracted females showed diminished responses to playback, both in terms of song overlap and

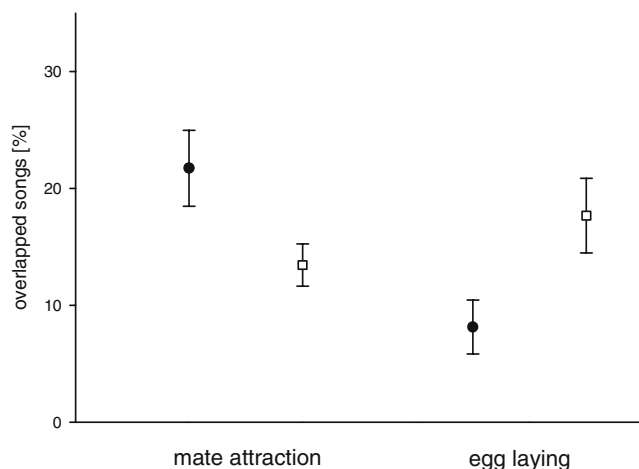


Fig. 1 Changes in mean±SE percentage of playback songs that were overlapped by male nightingales at different stages of the breeding cycle for mated males (filled circles; $N=11$) and bachelors (open squares; $N=10$; see also Kunc et al. 2006)

song rates, from the mate-attraction period to the period of egg laying. Unmated males, by contrast, retained similar levels of responses to song playback during the same intervals. These results indicate that in nocturnal interactions in nightingales, song overlapping and singing at high song rates are important during mate attraction but are less important after attracting a mate. However, the use of different song categories remained constant. Neither the use of whistle songs nor the use of songs containing trills differed between the mate-attraction and egg-laying periods, and neither measure differed between mated males and bachelors. Furthermore, we did not find seasonal changes in singing behaviour during vocal interactions in territorial males that remained unpaired throughout the breeding season.

There is increasing evidence that song overlapping is used and perceived as an immediate signal of aggression (Brindley 1991; Dabelsteen et al. 1997; Naguib 1999; Mennill and Ratcliffe 2004) which even has persisting effects over several hours or days (Hall et al. 2006; Schmidt et al. 2006). Thus, one might expect that males, once mated, should maintain a high level of aggression, i.e. the proportion of songs they overlap, as well as song rate constant during egg laying, because this time has been interpreted to be part of the fertile period of females (Birkhead and Møller 1992). A possible explanation for the decreased response to playback observed here in mated males is that the functions of song in the nightingale differ at least partly between times of the day: nocturnal song in unpaired males seems to serve primarily to attract nocturnally migrating females, given that males cease nocturnal song after mating (with the exception of a few nights during egg laying; Amrhein et al. 2002, 2004a), whereas dawn song may be important in territory defence, given that dawn singing activity remains high throughout the breeding season in both mated and unmated males (Amrhein et al. 2004a; Kunc et al. 2005b). A high level of song output at dawn after attracting a mate is a common pattern in many bird species, whereas song output at other times of the day often decreases after mating (Kunc et al. 2005b). Thus, like song output, performance during a vocal interaction might not only vary between different stages of the breeding season, as shown here, but also between different times of the day. Also, as in other species (Staicer et al. 1996; Liu 2004), the audience to which signals are directed might change during the course of the breeding season and with the time of day. Hence, male nightingales might still overlap a high percentage of songs after mate attraction at other times of the day.

The decrease in response in mated males during egg laying in our study is consistent with findings in male song sparrows (*Melospiza melodia*; Nowicki et al. 2002; but see Hyman et al. 2004), wherein males decreased their

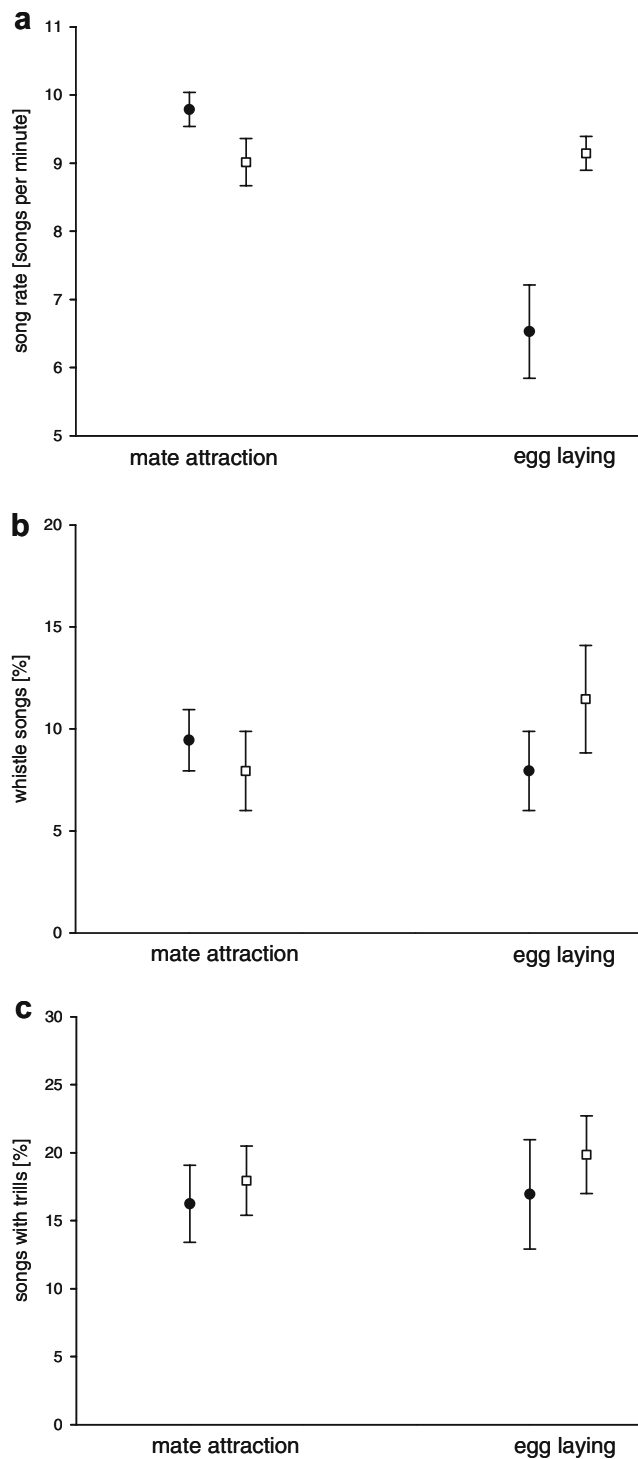


Fig. 2 Changes in mean \pm SE of **a** song rate, **b** the percentage of whistle songs and **c** the percentage of songs with trills in male nightingales during playbacks at different stages of the breeding cycle for mated males (filled circles; $N=11$) and bachelors (open squares; $N=10$)

responses to diurnal playback when their social mate was laying eggs. Nowicki et al. (2002) argued that mated males might respond to playback by approaching and guarding

their social mate rather than by approaching the simulated intruder. However, this argument does not apply for our study because we conducted our playbacks at night and males usually did not change their song posts during and after the playback. Thus, it seems unlikely that males guard their mates at night. In contrast to mated males, bachelors changed neither the proportion of overlapped songs nor their song rates significantly over the breeding season, which can be explained by the fact that unmated males still try to attract females (Amrhein et al. 2002).

The proportional use of whistle songs and the use of songs containing trills did not vary during the breeding season nor between bachelors and mated males. It thus seems that structural components, such as whistle songs and trills, are used less flexibly in vocal interactions over the breeding season than time-specific patterns (overlapping and song rate). A possible explanation is that the use of structural song components varies less across the breeding season because the same components retain equal importance during a vocal interaction. For example, if a specific song component (i.e. trills) functions as a deterrent signal to other males in a vocal interaction, it should be constantly used at a high and similar level if it has the same importance during egg-laying as during mate attraction. Given that the proposed function of trills and song overlapping is similar, it remains to be shown why both traits varied independently from each other. Male nightingales reduce the use of whistle songs in vocal interactions in contrast to when singing alone (Kunc et al. 2006), suggesting that whistle songs are more important for long-range communication to attract females (Kunc et al. 2005a) than in short-range male–male interactions. Therefore, the use of whistle songs in vocal interactions might not vary between the stages of the breeding season because, in male–male vocal interactions, whistle songs may be less important and, thus, less frequently used.

In conclusion, our study showed, by comparing responses to a playback at different stages of the breeding cycle, that a time-specific singing pattern like song overlapping was used more flexibly than structural traits during vocal interactions and was linked to the mating status of males. Because song overlapping is thought to be a signal of aggression in male–male vocal interactions, it seems that males vary the level of aggression in vocal interactions according to their mating status and depending on the period of the breeding cycle, indicating that performance during vocal interactions is not a seasonally and individually static trait. Future studies investigating vocal interactions and their possible impacts on eavesdropping individuals should take into account variations in vocal interactions over the breeding cycle, as this seasonally varying behaviour may affect the information that is available for interacting and eavesdropping individuals.

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References

- Amrhein V, Komer P, Naguib M (2002) Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Anim Behav* 64:939–944
- Amrhein V, Kunc HP, Naguib M (2004a) Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121:110–117
- Amrhein V, Kunc HP, Naguib M (2004b) Non-territorial nightingales prospect territories during the dawn chorus. *Proc R Soc Lond B* 271:S167–S169 (Suppl)
- Birkhead TR, Møller AP (1992) Sperm competition in birds: evolutionary causes and consequences. Academic, London
- Brindley EL (1991) Response of European robins to playback of song: neighbour recognition and overlapping. *Anim Behav* 41:503–512
- Brumm H (2004) The impact of environmental noise on song amplitude in a territorial bird. *J Anim Ecol* 73:434–440
- Dabelsteen T (1992) Interactive playback: a finely tuned response. In: McGregor PK (ed) *Playback and studies of animal communication*. Plenum, New York, pp 97–109
- Dabelsteen T, McGregor PK, Holland J, Tobias JA, Pedersen SB (1997) The signal function of overlapping singing in male robins. *Anim Behav* 53:249–256
- Forstmeier W, Balsby TJS (2002) Why mated dusky warblers sing so much: territory guarding and male quality announcement. *Behaviour* 139:89–111
- Gil D, Graves JA, Slater PJ (1999) Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Anim Behav* 58:995–1000
- Hall ML, Illes A, Vehrencamp SL (2006) Overlapping signals in banded wrens: long-term effects of prior experience on males and females. *Behav Ecol* 17:260–269
- Hultsch H, Todt D (1981) Repertoire sharing and song-post distance in nightingales (*Luscinia megarhynchos*). *Behav Ecol Sociobiol* 8:183–188
- Hultsch H, Todt D (1982) Temporal performance roles during vocal interactions in nightingales (*Luscinia megarhynchos*). *Behav Ecol Sociobiol* 11:253–260
- Hultsch H, Todt D (1996) Rules of parameter variation in homotype series of birdsong can indicate a “sollwert” significance. *Behav Processes* 38:175–182
- Hyman J, Hughes M, Searcy WA, Nowicki S (2004) Individual variation in the strength of territory defense in male song sparrows: correlations of age, territory tenure, and neighbor aggressiveness. *Behaviour* 141:15–27
- Kipper S, Mundry R, Hultsch H, Todt D (2004) Long-term persistence of song performance rules in nightingales (*Luscinia megarhynchos*): a longitudinal field study on repertoire size and composition. *Behaviour* 141:371–390
- Kunc HP, Amrhein V, Naguib M (2005a) Acoustic features of song categories and their possible implications for communication in the common nightingale (*Luscinia megarhynchos*). *Behaviour* 142:1083–1097
- Kunc HP, Amrhein V, Naguib M (2005b) Seasonal variation of dawn song characteristics in the common nightingale. *Anim Behav* 70:1265–1271
- Kunc HP, Amrhein V, Naguib M (2006) Vocal interactions in common nightingales: more aggressive males have higher pairing success. *Anim Behav* 72:25–30
- Langemann U, Tavares JP, Peake TM, McGregor PK (2000) Response of great tits to escalating patterns of playback. *Behaviour* 137:451–471
- Leboucher G, Pallot K (2004) Is he all he says he is? Intersexual eavesdropping in the domestic canary, *Serinus canaria*. *Anim Behav* 68:957–963
- Leitner S, Voigt C, Gahr M (2001) Seasonal changes in the song pattern of the non-domesticated island canary (*Serinus canaria*), a field study. *Behaviour* 138:885–904
- Liu W-C (2004) The effect of neighbours and females on dawn and daytime singing behaviours male chipping sparrows. *Anim Behav* 68:39–44
- McGregor PK, Dabelsteen T (1996) Communication networks. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY, pp 409–425
- McGregor PK, Peake TM (2000) Communication networks: social environments for receiving and signalling behaviour. *Acta Ethol* 2:71–81
- Mennill DJ, Ratcliffe LM (2004) Overlapping and matching in the song contests of black-capped chickadees. *Anim Behav* 67:441–450
- Mennill DJ, Ratcliffe LM, Boag PT (2002) Female eavesdropping on male song contests in songbirds. *Science* 296:873
- Mennill DJ, Boag PT, Ratcliffe LM (2003) The reproductive choices of eavesdropping female black-capped chickadees, *Poecile atricapillus*. *Naturwissenschaften* 90:577–582
- Miyazaki M, Waas JR (2002) “Last word” effects of male advertising calls on female preference in little blue penguins. *Behaviour* 139:1413–1423
- Møller AP (1991) Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *Am Nat* 138:994–1013
- Naguib M (2005) Singing interactions in song birds: implications for social relations, territoriality and territorial settlement. In: McGregor PK (ed) *Animal communication networks*. Cambridge University Press, Cambridge, pp 300–319
- Naguib M (1999) Effects of song overlapping and alternating on nocturnally singing nightingales. *Anim Behav* 58:1061–1067
- Naguib M, Todt D (1997) Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Anim Behav* 54:1535–1543
- Naguib M, Amrhein V, Kunc HP (2004) Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behav Ecol* 6:1011–1015
- Nowicki S, Searcy WA, Krueger T, Hughes M (2002) Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *J Avian Biol* 33:253–259
- Oliveira RF, McGregor PK, Latruffe C (1998) Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc R Soc Lond Ser B Biol Sci* 265:1045–1049
- Osiejuk TS, Ratynska K, Cygan JP (2004) Signal value of alternating and overlapping singing in the Yellowhammer *Emberiza citrinella*. *J Ethol* 22:55–61
- Otter K, McGregor PK, Terry AMR, Burford FRL, Peake TM, Dabelsteen T (1999) Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proc R Soc Lond Ser B Biol Sci* 266:1305–1309

- Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2001) Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proc R Soc Lond Ser B Biol Sci* 268:1183–1187
- Peake TM, Terry AMR, McGregor PK, Dabelsteen T (2002) Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proc R Soc Lond Ser B Biol Sci* 269:1925–1929
- Pinxten R, Eens M (1998) Male starlings sing most in the late morning, following egg-laying: a strategy to protect their paternity? *Behaviour* 135:1197–1211
- Schmidt R, Amrhein V, Kunc HP, Naguib M (2006) The day after: Effects of vocal interactions on territory defence in nightingales. *J Anim Ecol* (in press)
- Sheldon BC (2000) Differential allocation: tests, mechanisms and implications. *Trends Ecol Evol* 15:397–402
- Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, London, pp 426–453
- Todt D, Naguib M (2000) Vocal interactions in birds: the use of song as a model in communication. *Adv Study Behav* 29:247–296
- Vehrencamp SL (2000) Handicap, index, and conventional signal elements of bird song. In: Espmark Y, Amundsen T, Rosenqvist G (ed) *Animals signals: signal design in animal communication*. Tapir, Trondheim, pp 227–300