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ARTICLES

Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success

HANSJOERG P. KUNC*, VALENTIN AMRHEIN† & MARC NAGUIB*
*Department of Animal Behaviour, University of Bielefeld
†Research Station Petite Camargue Alsacienne, University of Basel

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Song overlapping in birds is used and perceived as a signal of aggression, and evidence suggests that eavesdropping females base their extrapair mating decisions on the performance of males in vocal contests. In our study population of nightingales a large proportion of territorial males remain unpaired throughout the breeding season. A comparison between subsequently mated males and unpaired males may reveal whether females could use singing performance during vocal interactions in their choice of a social mate. We investigated how males that differed in their subsequent pairing status overlapped a noninteractive playback during the period of mate attraction, and how males used specific structural song components in response to playback. Subsequently mated males overlapped more playback songs than did males that remained unpaired throughout the breeding season. Males also adjusted the use of specific song components and decreased song rate during playback, suggesting that the flexible use of structural song components is more important in vocal contests than increasing song output. Because song overlapping is thought to be a signal of aggression, more aggressive males seem to have greater pairing success.

There is growing evidence that song overlapping is used and perceived as a signal of immediate aggression. Males of different bird species either respond more aggressively when their songs are overlapped by playback than when playback songs are alternated with the males' songs (e.g. Dabelsteen et al. 1997; Naguib 1999; Mennill & Ratcliffe 2004a; but see Osiejuk et al. 2004) or stop singing when overlapped (Langemann et al. 2000). Furthermore, simulations of vocal interactions between two males using two-speaker designs have shown that eavesdropping males respond more strongly to speakers playing songs that started while the other speaker was playing a song, that is, to the speaker that simulated a male that was actively using its songs to overlap the songs of its counterpart (Naguib & Todt 1997; Naguib et al. 1999; Peake et al. 2001; Mennill & Ratcliffe 2004b). Evidence suggests that females extract information on relative differences between males by listening to their singing interactions (eavesdropping) and may base their choice of an extrapair mate on the performance of males in vocal contests (Otter et al. 1999; Mennill et al. 2002, 2003).

These studies used interactive playbacks to manipulate female choice after pair formation. It remains to be shown, however, whether individual differences in performance between unpaired males during vocal interactions are correlated with subsequent pairing status. Attracting a social female might be more relevant to male reproductive success than attracting extrapair females to sire additional extrapair young (Whittingham & Dunn 2005). If performance of males during male–male interactions is linked to female choice of a social mate, we predict differences between males in their singing strategies during such interactions. Nightingales show striking variation in their vocal performance during natural interactions (Hultsch & Todt 1981). Some males consistently overlap more songs than other males, suggesting that these singing strategies reflect social status (Hultsch & Todt 1982). Thus, females could use male singing performance to assess a potential partner and might base their choice of a social mate on which males are more or less aggressive or dominant during a vocal contest. If so, singing performance during male–male interactions might

Correspondence: H. P. Kunc, Verhaltensbiologie, Zoologisches Institut, Universität Zürich-Irchel, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland (email: kunc@gmx.at). V. Amrhein is at the Research Station Petite Camargue Alsacienne, Rue de la Pisciculture, 68300 Saint-Louis, France. M. Naguib is at the Department of Animal Behaviour, University Bielefeld, PO Box 100 131, 33501 Bielefeld, Germany.

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be an indicator of male quality relative to other males in the population. Furthermore, females could also base their mating decisions on other singing patterns, such as the relative use of songs with specific structural characteristics during vocal contests. Male nightingales, for instance, respond differently to songs that contain a series of mostly unmodulated whistles (Fig. 1) than to songs without these whistles (Naguib et al. 2002). Another song component that may be salient during vocal interactions are the rapid, broadband trills that are common in the songs of many species (e.g. Podos 1997; Kopuchian et al. 2004), including the nightingale (Fig. 1). Such trills may be constrained by physiological limits and may thus serve as an indicator of male quality (Vallet & Kreutzer 1995; Suthers & Goller 1997; Draganoiu et al. 2002). Furthermore, an interacting male may reply to an opponent's song with the same song, that is, match the type of the opponent's song (Todt & Naguib 2000). Such vocal matching can also be interpreted as a directed and threatening singing strategy (Krebs et al. 1981; Vehrencamp 2001).

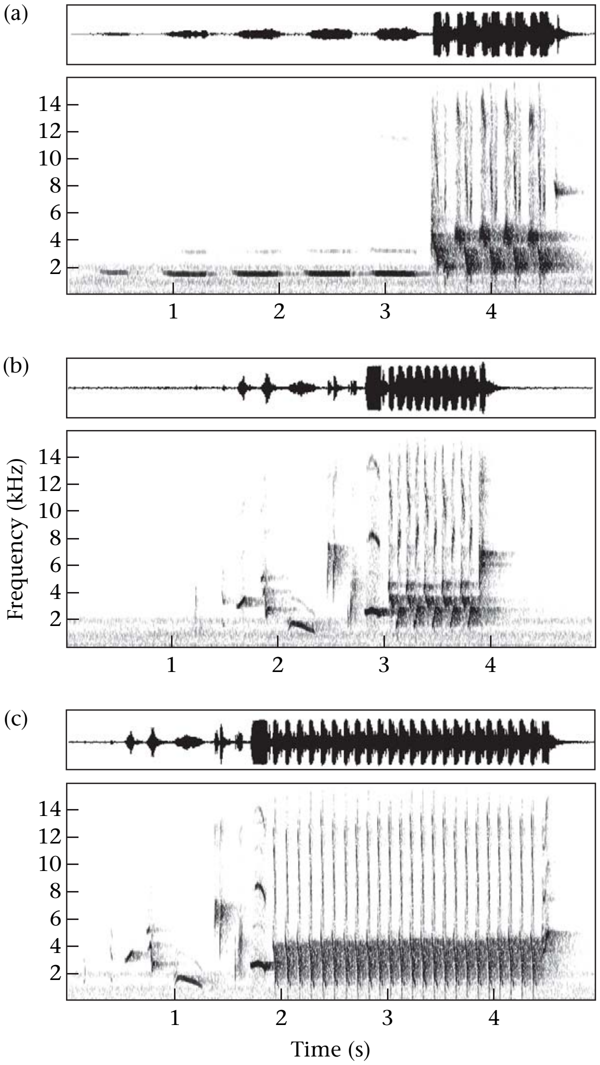

Figure 1. Oscillograms (above) and spectrograms (below) of songs of male nightingales: (a) a whistle song, (b) a nonwhistle song and (c) a nonwhistle song containing a rapid broadband trill.

In our study population, up to 49% of territorial male nightingales remain unpaired throughout the breeding season (Amrhein et al. 2004). This provides the opportunity during the period of mate attraction to compare the singing behaviour of territorial males that are successful in attracting a social mate and those that remain unpaired throughout the season. A comparison between successful and unsuccessful males in their response to a simulated rival's songs may reveal whether singing strategies during vocal interactions predict subsequent mating status.

We simulated unfamiliar males singing near the territory boundaries of resident males. We investigated how males that differed in their subsequent pairing status responded to a noninteractive playback during the period of mate attraction. Because females are likely to base their choice of a social mate on nocturnal song (Amrhein et al. 2002), we initiated the song contests at night. If overlapping an opponent's songs is a signal of male quality, we predicted that males that are able to attract a female should overlap more songs than males that remain unpaired. We also examined whether pairing success was correlated with the use of whistle songs, with songs with rapid, broadband trills and with song matching during nocturnal contests with simulated strangers.

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 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. Since only unmated males sing regularly at night for a prolonged period (Amrhein et al. 2002), we surveyed nocturnal singing activity of all males throughout the breeding season to assess their pairing status. We use the term 'bachelors' for males that remained unpaired throughout the breeding season and the term 'mated males' for males that subsequently attracted a female. During the time when the playback experiment was performed, none of the males had attracted a female, but each defended a territory.

Birds with territories at the Petite Camargue Alsacienne were caught and ringed. Mist-netting sessions were distributed throughout the field season and were done in the mornings until both members of a pair were captured or until we were sure no female was present in the territory. Mist nets were usually opened before sunrise and stayed open for about 2 h; birds were ringed in their territory and released within 15 min of capture. Permission for catching and ringing birds was granted by H. Jenn and by the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris.

Playback Stimuli

We created stimulus tapes from clear recordings made in our study area. Songs were recorded with a Sennheiser ME

66/K6 microphone, which was connected to either a Sony TC-D5M or a Sony WM-D6C cassette recorder. We digitized recordings on a PC with Cool Edit 2000 (Syntrillium Software, Scottsdale, AZ, U.S.A.; sample frequency: 44.1 kHz; resolution: 16 bit). We used Avisoft SASLab Pro 3.5 (R. Specht, Berlin, Germany) for selecting nonwhistle songs and whistle songs from each recording. Whistle songs contain a series of mostly unmodulated whistles in the beginning and can therefore be identified and distinguished clearly from nonwhistle songs (Fig. 1a, b; Hultsch & Todt 1996). Each male has a repertoire of different whistle songs with whistles at different carrier frequencies (Naguib et al. 2002).

To avoid pseudoreplication, we created a new stimulus tape for each subject. We recorded 25 birds, constructed 25 playback tapes and conducted 25 playbacks to a new set of birds, making all trials independent. Stimulus tapes were created to simulate an average singing male nightingale (10 songs/min, approximately 80% nonwhistle songs and 20% whistle songs; Kunc et al. 2005). Therefore, each playback consisted of 40 nonwhistle songs and 10 whistle songs. The 50 songs were randomly merged into one wave file in Cool Edit and normalized simultaneously to the peak amplitude. For all tapes we used a standardized recording level.

Playback Protocol

Playback trials were conducted from outside the territories of unmated males, during the time when females started to arrive and began to settle in the area. Trials were conducted on nocturnal song between 0000 and 0330 hours CEST. As a prerequisite for each playback we only used males as subjects that were singing before the trial started. We recorded the singing males for 5 min before a trial. Trial duration was 5 min, and after playback we continued to record the singing subject for another 5 min. As stimuli, we used songs that had been recorded from males that held territories several hundred metres away from the subjects. Singing behaviour of subjects was observed during the days before the playback trials to estimate territory sizes and territory boundaries. We placed the loudspeaker (Canton Plus X passive loudspeaker) outside a subject's territory at a side where a neighbour had not yet been observed but close to its territory boundary, to simulate a newly arriving neighbour. The loudspeaker was positioned at a height of 0.5–2 m, depending on the male's singing position, and approximately 30–50 m from the subject's song post, depending on the habitat structure. At these distances, nightingales respond to nocturnal playbacks by countersinging and do not usually approach the loudspeaker (Naguib 1999). Songs were broadcast from a SONY WMD 6M tape recorder connected to a Blaupunkt MPA 2 amplifier, 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, with a second Sennheiser ME 66/K6 directional microphone, we recorded the songs broadcast by the loudspeaker. The volume of broadcast songs was adjusted before playback to 88 dB at 1 m, measured with a Brüel & Kjær 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 the percentage of songs that males overlapped during the playback and recorded whether males responded immediately with whistle songs to playback of whistle songs, that is, whether they matched the broadcast whistle song. We considered a song of the playback as overlapped by the focal bird if the bird started to respond at least 300 ms after onset of a broadcast song, to avoid confounding effects of the slow speed of sound (Dabelsteen 1992). We considered a whistle song as matched if subjects immediately produced a whistle song after we played a whistle song. Since we used 10 whistle songs in every stimulus we calculated the number of whistle songs that were matched.

We measured the following song parameters for each of the three 5-min periods (before, during and after playback): song rate (number of songs/min), percentage of whistle songs and percentage of songs that included rapid broadband trills (Fig. 1c).

Statistical Analyses

We applied repeated measures ANOVA using SPSS version 11.0 (SPSS Inc., Chicago, IL, U.S.A.). The within-subjects factor was one of the particular song parameters, measured at the three times (before, during and after playback), and the between-subjects factor was the males' subsequent pairing status (mated male or bachelor). Our sample consisted of 14 mated males and 11 bachelors. Means are given ± SE; all reported tests are two tailed.

RESULTS

Males that attracted a social mate later in the season overlapped playback songs significantly more often than males that remained unpaired throughout the breeding season (Student's *t* test: $t_{23} = 2.67$, $P = 0.014$; Fig. 2). Males altered the use of structurally different songs over the course of the experiment by varying the use of whistle songs and the use of songs with rapid broadband trills in opposite directions: the percentage of whistle songs decreased significantly during playback (ANOVA: $F_{2,46} = 11.69$, $P < 0.001$; Fig. 3a), but did not differ between subsequently mated males and bachelors ($F_{1,23} = 0.08$, $P = 0.77$). We found no significant interaction between the three periods of the playback experiment and subsequent pairing success ($F_{2,46} = 2.62$, $P = 0.08$), indicating that the patterns of change of the percentage of whistle songs over the course of the experiment were similar in subsequently mated males and bachelors.

In contrast to whistle songs, the proportion of songs containing trills increased significantly during playback (ANOVA: $F_{2,46} = 13.52$, $P < 0.001$; Fig. 3b), but did not

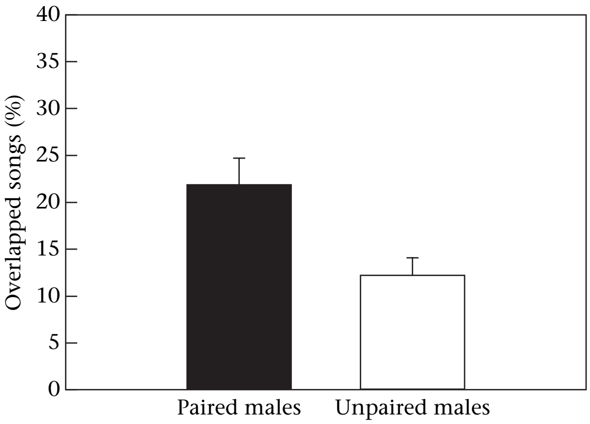

Figure 2. Mean percentage + SE of playback songs overlapped by males with respect to their subsequent pairing status (paired males: $N = 14$; unpaired males: $N = 11$).

differ between subsequently mated males and bachelors ($F_{1,23} = 0.20$, $P = 0.66$). Again, there was no significant interaction between the three periods of the playback experiment and mating status ($F_{2,46} = 0.25$, $P = 0.93$), indicating that the responses of subsequently mated males and bachelors with respect to the use of songs with rapid trills were similar.

Song rate decreased significantly during playback (ANOVA: $F_{2,46} = 3.60$, $P = 0.036$; Fig. 3c), but did not differ significantly between subsequently mated males and bachelors ($F_{1,23} = 1.24$, $P = 0.28$). There was no significant interaction between the periods of the playback and mating status ($F_{2,46} = 0.70$, $P = 0.5$), suggesting that the patterns in song rate variation were similar in subsequently mated males and bachelors, even though bachelors seemed to reduce their song rate during playback more than mated males (Fig. 3c).

Eight of 14 mated males (57%) and eight of 11 unpaired males (72%) matched a whistle song at least once. Mated males and bachelors did not differ significantly in the number of whistle songs that they matched during the playback (Mann–Whitney *U* test: $U = 56$, $N_1 = 14$, $N_2 = 11$, $P > 0.27$).

DISCUSSION

Before settlement of females, male nightingales that subsequently attracted a social mate overlapped playback songs more often than males that remained unpaired throughout the breeding season. Thus, differences in subsequent pairing success were reflected in the vocal performance during male–male interactions during the period of mate attraction.

There is increasing evidence that song overlapping is used and perceived as an immediate signal of aggression (Brindley 1991; Dabelsteen et al. 1996, 1997; Naguib 1999; Mennill & Ratcliffe 2004a). In our study, territorial males that attracted a social mate were those males that, before pairing, overlapped more songs of the playback, that is, they responded more aggressively to playback. Hultsch & Todt (1982) suggested that, in the nightingale, song overlapping may indicate male social status, since individual males seem to have specific roles, that is, they were overlappers, alternators or autonomous singers (males that could not be assigned to either of the two singing strategies) and those findings were confirmed in a playback experiment (Naguib 1999). In the present study, we found that subsequent pairing success was related to the frequency of song overlapping in male–male interactions during the time of mate attraction, which suggests that

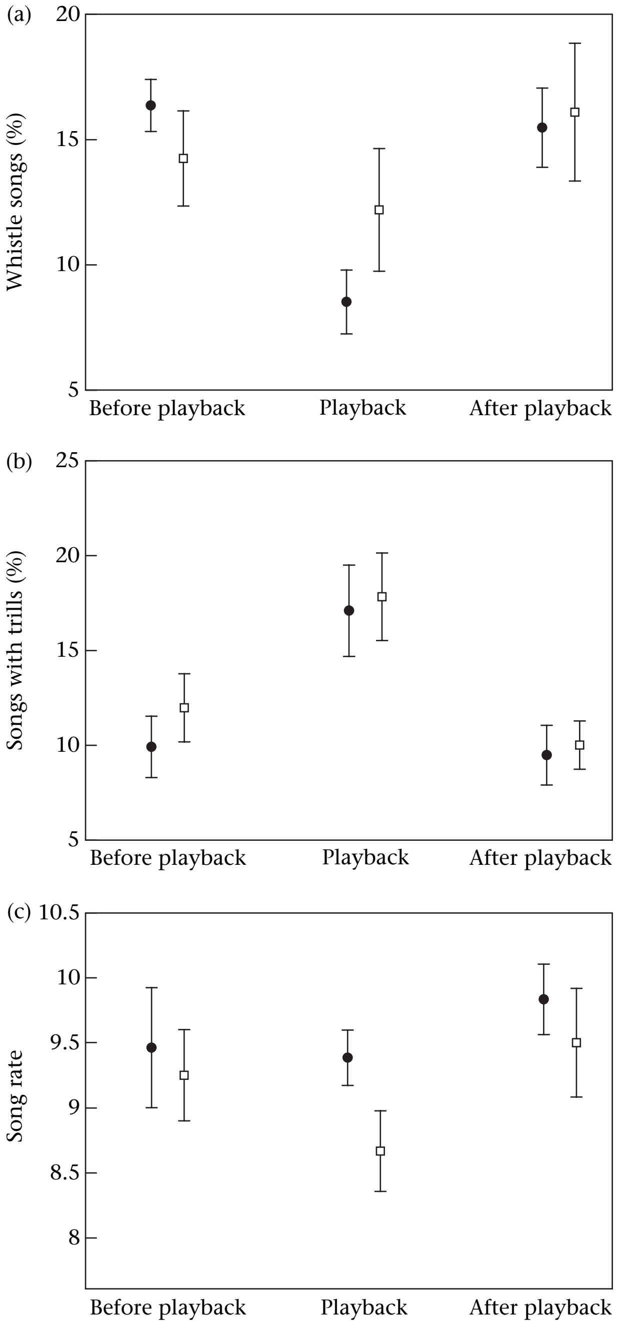

Figure 3. Mean ± SE of (a) the percentage of whistle songs, (b) the percentage of songs with trills and (c) song rate, before, during and after playback in relation to the males' subsequent pairing status (●: males that later attracted a female, $N = 14$; □: males that remained unpaired throughout the breeding season, $N = 11$).

overlapping during vocal contests is a singing strategy that signals aspects of male quality.

Nocturnal song in the nightingale may function in mate attraction (Amrhein et al. 2002), so overlapping the songs of other males during nocturnal contests could influence the choice of a social mate by eavesdropping females, as has been shown for extrapair mating decisions in other species (great tits, *Parus major*: Otter et al. 1999; black-capped chickadees, *Poecile atricapillus*: Mennill et al. 2002, 2003). Female choice that is based on the performance of males during vocal male–male interactions may have influenced the evolution of these singing strategies. Further evidence that females eavesdrop on overlapping during male–male interactions comes from little blue penguins, *Eudyptula minor*, in which females preferred speakers that started while the other speaker was playing a vocalization, that is, that simulated active overlapping of vocalizations, to speakers that started earlier than the other speaker, that is, whose vocalizations were overlapped (Miyazaki & Waas 2002); similar effects have been reported in anurans (e.g. Grafe 1996; Schwartz et al. 2002) and insects (e.g. Snedden & Greenfield 1998).

Independently of the subsequent pairing status of the males, the proportion of whistle songs was significantly lower during than before and after playback, but the proportion of songs containing rapid broadband trills was higher during playback. Furthermore, matching of whistle song was not correlated with subsequent pairing status. The finding that the proportion of whistle songs was lower during playback suggests that whistle songs may be less important in short-range male–male interactions but rather may function as a long-range signal. Unmodulated whistles are well designed for long-range transmission because they suffer less from frequency-dependent degradation (Wiley & Richards 1982; Slabbekoorn et al. 2002) than do more complex song components such as broadband trills (Naguib 2003). Thus the higher percentage of response songs that contained rapid broadband trills during playback suggests that these trills are more important in short-range interactions with other males. Similarly, trills are also important in male–male interactions in chaffinches *Fringilla coelebs* (Leitao & Riebel 2003). We found that the song rate of our subjects was also lower during playback, suggesting that the flexible use of structural components is more important in vocal contests than increasing song output. The decrease in song rate is likely be caused by males listening to the broadcast song during playback and then switching back to their natural song rate after the playback ended.

In conclusion, we found that in nocturnal playback during the period of mate attraction, male nightingales responded by increasing the proportion of songs that included trills but decreased the proportion of whistle songs and song rate. Remarkably, males that attracted a female later in the breeding season overlapped more songs during playback than males that remained unpaired. Because song overlapping is thought to be a signal of aggression in male–male vocal interactions, males that interact more aggressively may be more likely to find a mate and thus to have high reproductive success.

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