Aggressive responses to broadband trills are related to subsequent pairing success in nightingales

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In sexually selected signals, distinct components often have specific signal value in mate choice or male–male competition. In songbirds, structural song traits such as trills, that is, a series of repetitive notes, can be important in female choice. However, little is known about their signal value in male–male interactions. Here, we investigated the hypothesis that males assess the competitive abilities of rivals based on the use and performance of rapid broadband trills produced within songs. Using a 2-speaker playback experiment, we exposed territorial male nightingales, *Luscinia megarhynchos*, that differed in their subsequent pairing success, to a simulated vocal interaction between 2 unfamiliar rivals. The singing of the 2 simulated rivals differed in the number of songs containing rapid broadband trills. Subjects responded significantly more strongly to the loudspeaker that broadcast songs containing such trills than to the loudspeaker that broadcast exclusively songs without such trills. Moreover, responses also depended on the fine structure of trills. Males that became paired later in the season significantly increased their response intensity with increasing trill performance, whereas males that remained unpaired responded in the opposite way and decreased their response intensity with increasing trill performance. These results indicate that rapid broadband trills are a signal of aggression and that the nature of the response in vocal interactions reflects aspects of the challenged male's fitness. *Key words:* birdsong, *Luscinia megarhynchos*, male–male interaction, sexual selection, song structure, trill. *[Behav Ecol 19:635–641 (2008)]*

A nimal communication is an essential component of all social behavior, as strategies used in communication can determine or reflect an individual's social status, its access to resources, and, thereby, its fitness (Searcy and Nowicki 2005). Specifically, sexually selected elaborate signals and complex signaling behavior have been investigated intensively. Birdsong has been a key model in the study of sexual selection, and a variety of song components as well as different singing patterns have been shown to be linked to a male's short-term motivation and to his fitness (Searcy and Nowicki 2005). By focusing on pattern-specific singing behavior (song type matching or switching, McGregor et al. 1992; Todt and Naguib 2000; Burt et al. 2001; Vehrencamp 2001) or time-specific singing patterns (song overlapping vs. alternating, Dabelsteen et al. 1996; Naguib 1999; Langemann et al. 2000; Todt and Naguib 2000; Mennill and Ratcliffe 2004; Schmidt et al. 2007), studies on the function of song in male–male competition have revealed that males assess rivals on the basis of their singing performance in vocal interactions. In contrast, structural song traits, such as song complexity or repertoire size (e.g., Lambrechts and Dhondt 1986; Lampe

and Epsmark 1994; Catchpole and Leisler 1996; Hasselquist et al. 1996), are well documented to be important in female choice (Gil and Gahr 2002). Regarding the functional significance of structural song traits in male rivalry, previous experiments have revealed that intruders are less likely to invade territories where males have larger repertoires (Krebs et al. 1978; Yasukawa 1981) or sing complex songs with large syllable repertoires (Mountjoy and Lemon 1991). However, surprisingly little is known of the effects of song structure in male–male singing interactions (McGregor and Horn 1992; Slabbekoorn and ten Cate 1997; ten Cate et al. 2002; Illes et al. 2006).

One conspicuous structural song component used by many songbird species is the trill, that is, a song section consisting of rapidly repeated almost identical short notes (Podos and Nowicki 2005). The production of trills appears to be constrained by a trade-off between how quickly a bird can repeat the trill units and the frequency bandwidth each unit can span (Podos 1996; Podos and Nowicki 2005) because repetitive note production requires a precise coordination of vocal tract movement and airflow (Hartley and Suthers 1990; Westneat et al. 1993; Podos 1996; Hoese et al. 2000). This trade-off between trill rate and bandwidth is assumed to result in a performance limit (Podos 1996). Thus, the production of these physically challenging trills may reflect male quality. Indeed, females have been shown to prefer males that perform trills close to the production limit (Vallet and Kreutzer 1995; Draganoiu et al. 2002; Ballentine et al. 2004).

Recently, Illes et al. (2006) showed that male banded wrens, *Thryothorus pleurostictus*, that were allowed to choose between a fast and a slow trill stimulus in a 2-speaker playback experiment approached the fast trill stimulus first. This suggests

that banded wren males attend to the fine structure of trills and perceive faster trills as being more threatening than slower trills. However, an additional analysis of trill performance as a graded signal revealed that males spent less time close to the fast stimulus when the performance score of the stimulus trill was higher. Illes et al. (2006) concluded that the highest performance trills posed a threat so extreme that they effectively repelled the resident male.

One important variable determining whether more threatening signals repel territorial animals or induce approach and attack is the resource holding potential or quality of the challenged male. In other words, the response of a male during an agonistic interaction will not only depend on the level of threat signaled by the rival but also on the male's own condition or quality. The responses of black-capped chickadee, *Poecile atricapilla*, males to a simulated song overlapping opponent, for instance, differ with their dominance status (Mennill and Ratcliffe 2004). Similarly, in nightingales, *Luscinia megarhynchos*, the way males sing during vocal interactions with rival males early in the breeding season predicts their subsequent pairing success, which also may reflect male resource holding potential or quality (Kunc et al. 2006; Schmidt et al. 2006).

Previous studies found that male nightingales include rapid broadband trills in a greater proportion of songs when they are confronted with a countersinging rival compared with the spontaneous song (Kunc et al. 2006; Schmidt et al. 2006). This suggests that rapid broadband trills are important in close-range male–male communication. To address the question of whether rapid broadband trills are perceived as aggressive signal components, we here exposed unmated male nightingales to simulated vocal interactions in which one male sang rapid broadband trills in 50% of its songs and another male sang only songs without rapid broadband trills. We conducted these playbacks on diurnal song early in the breeding season during the period of mate attraction. We predicted that subjects would respond preferentially to the loudspeaker from which songs with trills were presented. Furthermore, we also predicted that responses to trills would differ in relation to the subjects' subsequent pairing success.

METHODS

Subjects and study site

At the beginning of the breeding season in 2005 (between 23 April and 6 May), we conducted 2-speaker playback experiments on diurnal song of male territorial nightingales in the vicinity of the Petite Camargue Alsacienne in France, about 10 km north of Basel (Switzerland). In this agricultural area of the Upper Rhine Valley, nightingales settle in patches of dense bushes and woods along roads, rivers, or fields. Playbacks were conducted on 21 male nightingales holding territories that were sufficiently isolated by clear territory boundaries to avoid interference with neighbors. Because nightingales have been shown to cease regular nocturnal song on attracting a social mate (Amrhein et al. 2002; 2004), we determined nocturnal singing activity of subjects every night over the entire breeding season to assess their pairing success as a measure of male quality. All subjects had been singing for at least 2 nights before they received playback and thus were considered to be unmated at the time of playback. Subjects sang during at least the first 2 nights after playbacks, but later in the season, 10 males ceased nocturnal song indicating that they attracted a social mate ("subsequently mated males"), whereas the other 11 males were considered to remain unmated because they were singing at night throughout the breeding season ("bachelors"). Subjects were different from those used in another study conducted in the same year (Schmidt et al. 2006).
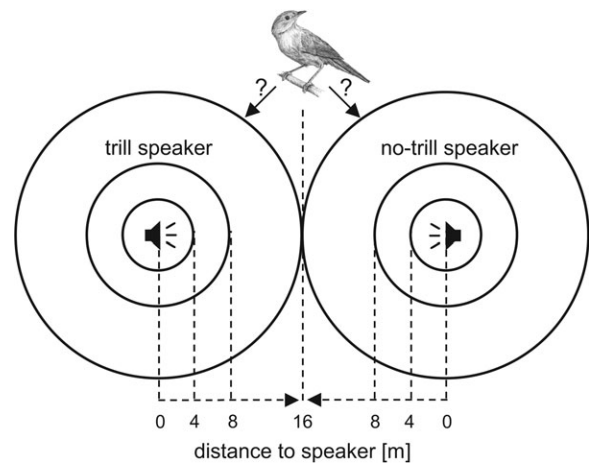

Figure 1
Schematic map of the 2-speaker playback setup. Speakers were 32 m apart; circles represent the flagged radii around the 2 speakers; dashed lines show distances to the corresponding speaker.

Playback design and stimuli

We used a 2-speaker playback design to simulate a vocal interaction between 2 males (Figure 1). On one channel, we presented one male singing 10 songs containing rapid broadband trills and 10 songs without rapid broadband trills ("trill speaker" in Figure 1) in a randomized order. On the other channel, another male singing 20 songs without rapid broadband trills was presented ("no-trill speaker"). Both types of sequences were within the range of naturally singing nightingales (Kunc et al. 2006, 2007). With a trill being a song section in which notes are repeated, most nightingale songs contain trills and there is much variation in the rate of element or syllable repetition as well as in the range of frequencies expressed within trills (Figure 2). However, previous studies have shown that nightingales sing a higher proportion of songs containing very rapid and broadband trills (Figure 2a) during close-range interactions with rival males compared with their spontaneous song (Kunc et al. 2006; Schmidt et al. 2006). In the present study, we used such rapid broadband trills with a rate of at least 7 elements/s and a frequency bandwidth of at least 3 kHz (threshold = −20 dB below frequency at peak amplitude) that can clearly be distinguished from slower and/or narrow trills (Figure 2b), which usually are sung during spontaneous song at night and during the day (see below for details on structure of rapid broadband trills that were used).

Stimulus songs were derived from nocturnal song recordings of 22 color-banded male nightingales made between 2002 and 2005 in the study population. Nocturnal song was recorded on a Sony TCD-5M tape recorder (SONY Ltd., Tokyo, Japan) with a Sennheiser ME66/K6 microphone (Sennheiser electronic GmbH, Wedemark, Germany) and digitized using Cool Edit 2000 (Syntrillium Software Cooperation, Scottsdale, AZ, sample frequency: 44.1 kHz, resolution: 16 bit). From each of 20 of these recordings, 2 sets of 20 different song types were selected randomly but considering the quality of the recording and the song duration (Kunc et al. 2005) to construct both the trill and the no-trill stimulus (Avisoft SASLab Pro 4.31, R. Specht, Berlin, Germany, http://avisoft.com) according to the criteria mentioned above. These sets were grouped in pairs of stimulus songs with a trill stimulus (20 songs of one male, 10 of which contained a rapid broadband trill) and a no-trill stimulus (20 songs of another male without rapid broadband trills). From each of the remaining 2 recordings,
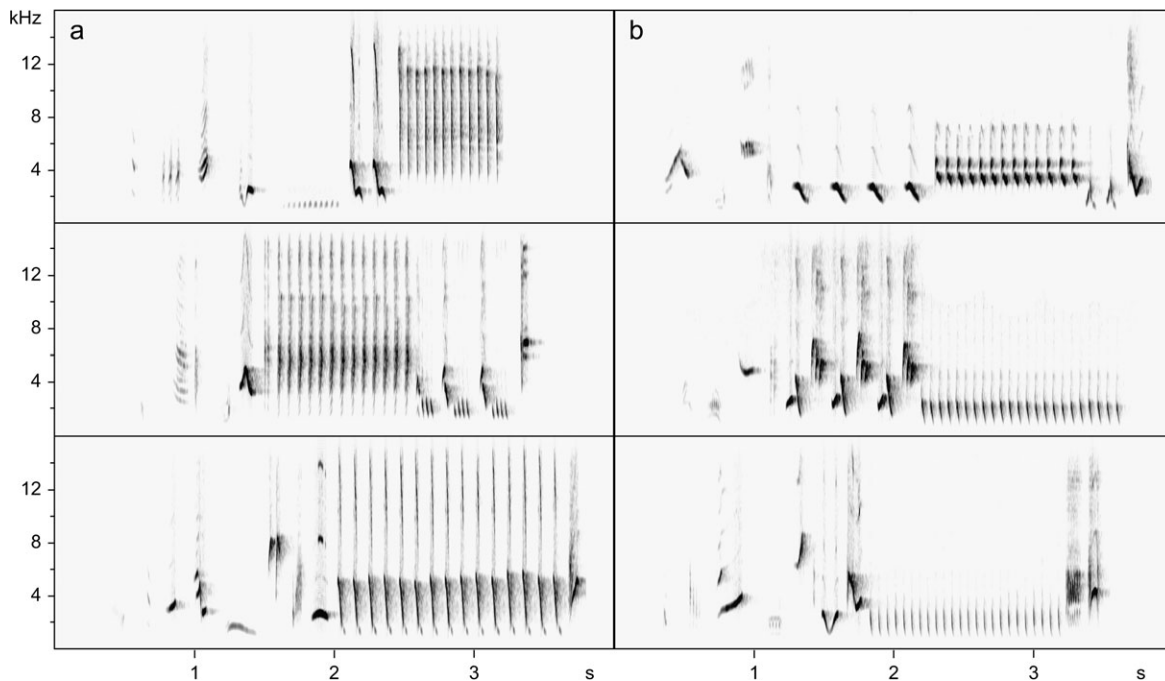
Figure 2
Examples of nightingale song types containing elaborate trills of different repetition rates and frequency ranges. Broadband trills that span a large frequency range (a) can easily be distinguished from trills with narrow frequency range (b).

only 1 set of 20 different song types were selected to build the last pair of stimulus songs. One recording was used to build the trill stimulus and the other one to build the no-trill stimulus. This resulted in 21 pairs of stimulus songs from 22 different source males. Across the stimuli, song duration did not differ considerably between the sets of songs that contained rapid broadband trills (2.96 ± 0.2 s, mean $\pm$ standard deviation [SD]) or did not contain such trills (2.93 ± 0.2 s). There was also no significant difference in song duration within each pair of stimulus songs (paired t-test, $n = 21$, $T = 0.66$, $P = 0.52$).

Across the 21 trill stimulus sets, the trills consisted of 17.1 ± 2.1 elements (mean $\pm$ SD), ranging from 14 to 23 elements, and trill duration was 1.6 ± 0.2 s (range: 1.3–2.1 s) as measured from sonograms and oscillograms using SASLab Pro 4.31 software (Fast Fourier transformation [FFT] size = 1024, window function = Hamming). These measures resulted in a mean $\pm$ SD trill rate of 11.0 ± 0.6 elements/s (range: 10.0–12.3 elements/s). Power spectra generated from spectrograms in SASLab (FFT size: 512, window function = FlatTop, and FFT overlap = 50%, resulting in a frequency resolution of 86 Hz and a temporal resolution of 5.8 ms) were used to identify minimum and maximum frequencies (threshold = -20 dB below frequency at peak amplitude). Trills covered a frequency bandwidth of 6.5 ± 1.8 kHz (range: 4.3–10.3 kHz), ranging from a minimum frequency of 1.8 ± 0.2 kHz to a maximum of 6.8 ± 0.7 kHz (mean $\pm$ SD).

To build the stereo files, we used Cool Edit 2000 to copy the songs of 2 different males into the separate channels and to normalize the peak amplitude across the file, which was done to maintain natural variety in song amplitude. The order of songs was randomized with the exception of the first song, which was always a song without a rapid broadband trill. We arranged alternating renditions of the 2 stimulus males' songs with a pause of 0.5 s between consecutive songs so that there was no song overlap between the 2 channels. The leading stimulus was balanced between trials. Because we used 20 of the 22

stimulus males twice (as the trill stimulus in one trial and, with a different set of songs, as the no-trill stimulus in another trial), we also balanced the leading stimulus according to individual source males. The complete files were then recorded on tapes with a standardized record level.

Playback procedure

All playbacks were conducted during the day, between 0830 and 1100 h CEST. Grüll (1981) found that more than 75% of male nightingales return to the same territory they occupied in the preceding year or to a directly neighboring one. For each subject, we thus constructed a stimulus built of recordings that were made in nonneighboring territories at least several 100 m away. This minimized the possibility that subjects were familiar with the songs heard during playback. We only used males that were singing already when the playback started.

The 2 loudspeakers (Canton Plus X passive loudspeakers, Canton Elektronik GmbH, Weilrod, Germany) were placed 32 m apart (Figure 1) well within the subjects' territories. We flagged radii of 4, 8, and 16 m around each experimental loudspeaker to measure subjects' approaches. The sound pressure level was calibrated to natural nightingale song amplitudes of 90 dB at 1 m distance (Brumm 2004), measured with a Brüel & Kjær precision SPL meter 2233 (C-weighting, fast response). Songs were played from a Sony WM-D6C tape recorder, which was connected to a Blaupunkt MPA 2 amplifier (Blaupunkt GmbH, Hildesheim, Germany).

Subjects' singing responses and their distance from the loudspeakers after each subject's song were recorded on the left channel of a Sony TCD-5M stereo tape recorder with a Sennheiser ME66/K6 directional microphone. On the right channel, we recorded the songs broadcast by the loudspeaker to measure the on- and offset of playback. Subjects' responses were recorded on tape during playback and for an additional period of 10 min after the playback had terminated.

Response measures and statistical analysis

We extracted the following behavioral parameters: 1) the closest song post to each loudspeaker (m), 2) the latency to this closest song post (s), 3) the latency to sing within 4 m of each loudspeaker (s). We further calculated 4) the number of songs sung within the 4-m radius around each loudspeaker and 5) the number of songs sung on each side (i.e., within 16 m around each loudspeaker).

We conducted a principal component (PC) analysis on these 5 parameters (SPSS 14.0.1) to summarize male responses to one composite response variable. We then applied a repeated-measures analysis of variance (ANOVA) using the PC scores with 2 levels of the within-subject factor (responses to trill and no-trill speaker) and with 2 between-subject factors: the speaker initiating the simulated interaction (to control for a possible preference toward the speaker that initiated the playback) and the subjects' subsequent mating status (mated male or bachelor). The initial model also included as a covariate the initial distance of subjects to the speaker from which songs with trills were presented at onset of playback. Because the initial distance did not significantly affect the responses ($P = 0.95$), this covariate was removed in the final model. At the onset of playback, subjects were singing at mean ± standard error distances of 23 ± 4 m to the loudspeaker from which trills were broadcast and 22 ± 2m to the other loudspeaker.

We also investigated how the subjects' responses were affected by the vocal performance of stimuli trills. Therefore, we conducted an analysis of covariance (ANCOVA) on the response intensity (PC score) at the loudspeaker from which rapid broadband trills were presented with the subjects' subsequent pairing success as fixed factor and 2 covariates, the rate and bandwidth of stimuli trills. The stimuli trill rate was excluded in the final model as this variable did not significantly affect the responses of subsequently mated and unmated males ($P = 0.4$).

RESULTS

Four males made their first approach before the first song with trill had been played and therefore were excluded from the analysis of first approach. Of the remaining 17 subjects that heard songs from both loudspeakers and at least one rapid broadband trill before approaching, 14 made their first approach to the loudspeaker from which songs with trills were presented and 3 subjects approached first the speaker that presented only songs without trills (binomial test, $P = 0.013$).

The PC analysis we applied to the responses of all 21 subjects generated one PC with an eigenvalue >1.0 that explained 62.6% of the variation in subjects' responses (Kaiser–Meyer–Olkin measure of sampling adequacy: 0.638; Bartlett test of sphericity: $\chi^2 = 113.8$, $P < 0.001$). Measures of approach behavior loaded negatively on this first PC (closest approach: -0.85; latency to closest approach: -0.43; latency to approach up to at least 4 m: -0.90), indicating a very close and rapid approach (small values of the approach variables), whereas loadings of singing responses were positive (number of songs within 16 m: 0.85; number of songs within 4 m: 0.82), indicating a large number of songs given in response to playback. A pairwise comparison with the scores of the first PC as a composite measure of responses indicated significantly stronger responses toward the loudspeaker from which songs with trills were broadcast than toward the loudspeaker that broadcast songs without trills (repeated-measures ANOVA: $F_{1,18} = 6.6$, $P = 0.019$, Table 1; Figure 3). Subjects approached the speaker broadcasting songs with rapid broadband trills more quickly and closer than the speaker from which songs without

Table 1

Mean ± standard error responses of 21 nightingales during a 2-speaker playback experiment, separately shown for the 2 loudspeakers that differed in the proportion of rapid broadband trills of broadcast songs

Response variable	Response at trill speaker	Response at no-trill speaker
Latency to closest approach	115 ± 28 s	272 ± 45 s
Latency to approach $\leq$ 4 m	283 ± 74 s	618 ± 55 s
Closest approach	4 ± 1 m	12 ± 2 m
Number of songs within 16 m	64 ± 12	35 ± 10
Number of songs within 4 m	30 ± 10	11 ± 5

trills were presented (Table 1). Furthermore, subjects sang more songs on the side with the loudspeaker that broadcast trills (i.e., within 16 m of the trill speaker) and also sang closer to this speaker (i.e., within 4m) than to the speaker that broadcast songs without trills. Subjects' responses were not notably affected by the speaker that initiated the simulated interaction ($F_{1,18} = 0.006$, $P = 0.95$). Subsequently mated males and bachelors did not show significant differences in their responses to the 2 experimental loudspeakers during the playback trials ($F_{1,18} = 0.016$, $P = 0.90$).

Frequency bandwidth and the rate of repetitive elements of broadcast trills were positively correlated, although not significantly so, that is, faster repeated trill elements tended to cover a broader frequency range than did trills of a slower rate ($r = 0.42$, $n = 21$, $P = 0.057$, Figure 4). However, the stimulus trill rate was excluded in the final ANCOVA model as this variable did not significantly affect the responses of subsequently mated and unmated males ($F_{2,15} = 0.7$, $P = 0.5$). In order to test the intensity of response with respect to the fine structure of broadcast trills, we then analyzed responses only at the loudspeaker that broadcast these songs. This analysis revealed that the response intensity at this loudspeaker was significantly different for subsequently mated and unmated males (ANCOVA, pairing success: $F_{1,17} = 9.1$, $P = 0.008$). Also, the interaction between the stimuli trills' bandwidth and
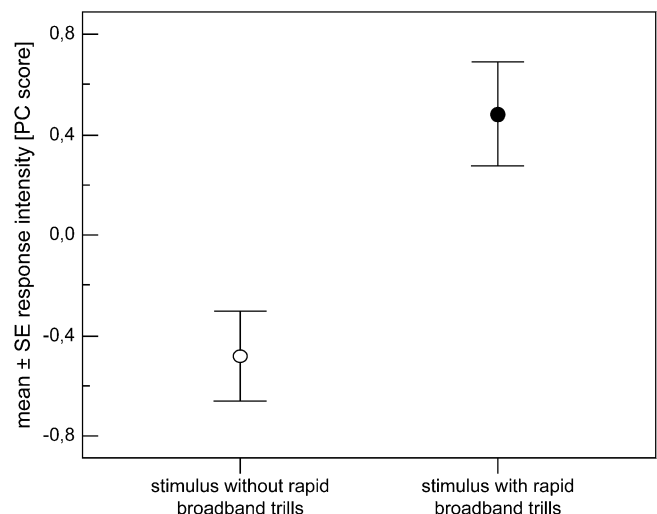
Figure 3
Mean ± standard error (SE) response intensity (PC scores as a composite measure of 5 variables) of 21 nightingales at the 2 experimental loudspeakers from which either exclusively songs without rapid broadband trills (open circle) or songs that contained such trills (filled circle) were presented.
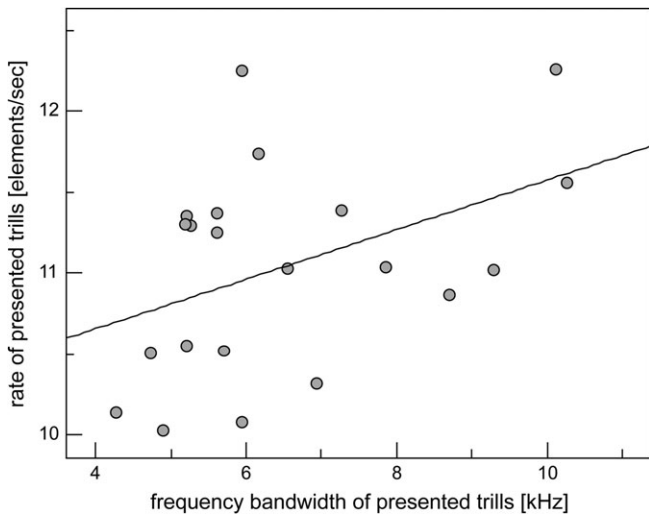
Figure 4
Relationship between mean frequency bandwidth and mean element repetition rate in 21 sets of 10 rapid broadband trills derived from recordings of nocturnal song of 21 different nightingales ($r = 0.42$, $P = 0.057$, see Methods section for details).

subjects' pairing success was significant (ANCOVA, $F_{1,17} = 10.7$, $P = 0.005$), indicating that subjects responded differently to variation in the stimuli trill bandwidth: Males that remained unmated throughout the breeding season decreased their response intensity significantly with increasing frequency bandwidth of presented trills ($r = -0.67$, $n = 11$, $P = 0.024$, Figure 5). In contrast, subsequently mated males responded in the opposite direction and tended to increase their response intensity with increasing frequency bandwidth of presented trills ($r = 0.56$, $n = 10$, $P = 0.094$, Figure 5).
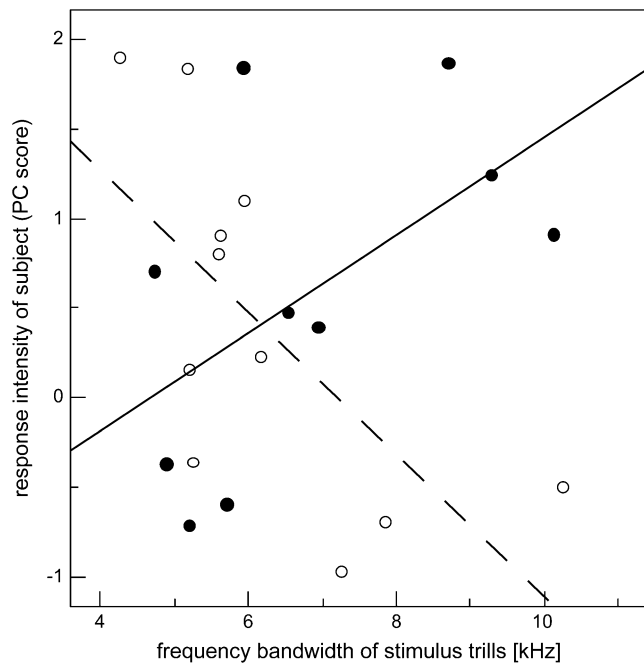

Figure 5
Response intensity (PC scores) of subsequently mated (filled circles and solid line) and unmated (open circles and dashed line) male nightingales in relation to the frequency range of presented trills.

DISCUSSION

Our results demonstrate that male nightingales discriminated between simulated rivals that differed in the percentage of songs containing rapid broadband trills and responded more strongly to simulated rivals that sang a high proportion of such trills. Generally, strong responses toward a simulated singing intruder, such as a quick approach (e.g., Mennill and Ratcliffe 2004) or a high song output (e.g., Peake et al. 2002; Hyman 2003) are interpreted as reflecting male arousal and thereby also indicate the level of aggression of the intruder (reviewed in Naguib 2005). Therefore, strong responses toward those simulated rivals that sang a high proportion of rapid broadband trills in our study can be taken as evidence that songs with such trills are perceived as aggressive signals. This suggests that a territorial male's immediate response to being challenged is based on a general assessment of the rival. The presence or absence of conspicuous song traits such as specific song elements (this study), incomplete songs (Leitao and Riebel 2003), or frequency jumps (Slabbekoorn and ten Cate 1997; ten Cate et al. 2002) can easily be detected and thus can be used as a first approximation of the level of threat.

Subsequently, mated males and bachelors responded significantly differently toward the speaker that presented rapid broadband trills. In particular, the response intensity in relation to the fine structure of trills appears to be a predictor of the males' future pairing success. Males that remained unpaired throughout the breeding season decreased their territorial defense behavior with increasing trill performance of the simulated opponent. In contrast, males that became paired later in the season increased their response intensity with increasing trill performance of the simulated intruder. In contrast to previous studies on constraints in trill production (Podos 1996, 1997; Ballentine et al. 2004), we found a tendency for the frequency range of broadband trills to be positively correlated with the element repetition rate. This finding could be explained by our focus on those trills that were already at the upper boundary of the performance range (i.e., rapid and broadband). Podos (1997) analyzed a much wider range of repeated song elements, including also slow and narrow trills, in song recordings of 34 different Emberizidae species.

Illes et al. (2006) found that banded wren males in a 2-loudspeaker playback experiment discriminated between fast-trilled and slow-trilled songs. Males approached the fast stimulus first but subsequently spent less time close to the fast stimulus if it was a higher performance type. Our results are consistent with this previous study with respect to the first approach toward the higher performed stimulus. On the other hand, by highlighting the subsequent pairing success as source of variation in territorial defense behavior, our study expands on these previous findings. Similar to the banded wrens in the study by Illes et al. (2006), bachelor males in our study showed a strong response only when trills of lower performance were broadcast. This may be an adaptive response strategy as it will not pay an individual to signal its willingness to escalate a contest in response to an opponent of presumably higher resource holding potential or quality. In contrast, strong responses by subsequently mated males only in response to high-performance trills suggest that they are willing to escalate contests only when the opponent signals a high level of threat. The response to interindividual variation in structural components of song has rarely been investigated in male birds (ten Cate et al. 2002; Leitao and Riebel 2003; Illes et al. 2006), and different responses by males to such structural variants in relation to the males' subsequent pairing success have not been described previously.

So far, the signal function of song performance has been investigated predominantly in an intersexual context; for

example, both canary, *Serinus canaria* (Draganoiu et al. 2002), and swamp sparrow, *Melospiza georgiana*, females have been shown to prefer high-performance songs (Ballentine et al. 2004). Songs in these 2 species consists mainly of trilled note types or syllables that differ in the number of elements and repetition rate (Vallet and Kreutzer 1995; Ballentine et al. 2004), so these song features may act as powerful drivers in sexual selection. In contrast, only about 10 to 20% of a nightingale's songs contain rapid broadband trills, and the percentage of such songs is upregulated during agonistic interactions (Kunc et al. 2006; Schmidt et al. 2006). Therefore, physically challenging broadband trills can be seen as a signal indicating the motivation to engage in a close-range interaction. Additionally, using trills to signal aggression or motivation during a close-range interaction limits the probability of a long-range transfer of this information to conspecifics not directly involved in that interaction due to effects of reverberation that increase with trill duration and repetition rate and due to frequency-dependent attenuation affecting signal bandwidth (Wiley and Richards 1982; Naguib 2003).

In conclusion, our study shows that male nightingales discriminate between rivals based on the presence or absence of rapid broadband trills. An increase in the use of trills during male–male interactions as well as the signal value of high-performance trills for males described here indicates that rapidly repeated frequency-modulated song components are perceived and used as a signal of aggression in intrasexual contexts. Most interestingly, we showed that responses to the fine structure of trills differed among males according to their subsequent pairing success, indicating that response to the fine structure of signals correlate with fitness components.

FUNDING

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