



Responses to interactive playback predict future pairing success in nightingales

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Birdsong is a sexually selected trait that serves in territory defence and mate choice. Individual song traits can be affected by the body condition of the male and thus may reflect his quality. Such relations between male quality and general singing performance raise the question whether differences in male quality also affect response strategies used in dyadic interactions. To address this question, we studied the relation between pairing success of male common nightingales, *Luscinia megarhynchos*, and their responses to rivals posing different levels of threat. Using interactive playback, we exposed males prior to mating to either aggressively or moderately singing rivals (by song overlapping and song alternating, respectively). Males that remained unpaired throughout the season (bachelors) interrupted their singing significantly more often after being overlapped than after alternating playback, whereas subsequently mated males kept the number of singing interruptions more constant across playback treatment. This suggests that subsequently paired males are less discriminative than are bachelors when challenged by rivals varying in aggressiveness. Regardless of playback treatment, males that later became paired responded significantly more strongly than did bachelor males. Thus, an increase in singing after a vocal interaction prior to mating predicted future mating success.

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Elaborate animal signals serve in the acquisition and defence of resources, and thus provide important models in studies on sexual selection. Among the various signalling modalities, acoustic signals have been investigated most intensely in several taxa to assess principles in communication (Greenfield 1994; Catchpole & Slater 1995; Grafe 2005). Birdsong and its striking variation within and across species is among the most complex communication systems in vertebrates. It has evolved under both inter- and intrasexual selection, as an individual's song may function in territory defence as well as in mate choice (Kroodsma & Byers 1991; Catchpole & Slater 1995). Individual song traits, such as song rate (Alatalo et al. 1990), or specific song elements, such as trills (Vallet & Kreutzer 1995; Ballentine et al. 2004; Leboucher & Pallot 2004), can be affected by constraints in production or by

male body condition and thus may advertise the quality or condition of a singer. Furthermore, dyadic singing interactions can provide information on relative differences in motivation or social status between rival males to the interacting singers themselves as well as to eavesdropping conspecifics in a communication network (McGregor & Dabelsteen 1996; Peake 2005). Males of various songbird species have been shown to extract information from vocal interactions to assess rivals (Naguib et al. 1999, 2004; Peake et al. 2001, 2002; Mennill & Ratcliffe 2004a), and females also use information obtained from interactions in mate choice (Otter et al. 1999; Mennill et al. 2002, 2003; Leboucher & Pallot 2004).

In such intrasexual interactions males use dynamic singing strategies by varying the pattern of the signal or the timing of the signal in relation to that of the opponent (Todt & Naguib 2000). By varying the timing of song delivery, a male can either alternate his songs with those of an opponent or overlap the opponent's songs. Several studies support the hypothesis that song overlapping is perceived as a signal of aggression during vocal interactions, as males sing more irregularly during overlapping than during alternating playback (Dabelsteen et al. 1996; Naguib 1999; Mennill & Ratcliffe 2004b; Naguib & Kipper

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2006) or stop singing when their songs are overlapped (Langemann et al. 2000).

Given the possible relations between male quality and general singing performance in 'undirected' territorial song and the importance of song in territory defence, differences in male quality or condition can also be predicted to affect response strategies used in male–male interactions occurring in territorial conflicts (see also Poessel et al. 2004). For instance, the singing performance of common nightingales, *Luscinia megarhynchos*, during interactions conveys information that may be used in female choice (Kunc et al. 2006): males that are successful in attracting a social mate overlap more songs of a noninteractive playback during mate attraction than males that remain unpaired throughout the breeding season ('bachelors'). Such findings and the above considerations raise the question whether males that differ in their subsequent pairing success respond differentially to rivals varying in aggressiveness (see also Mennill & Ratcliffe 2004b).

If males that are attractive to females are more aggressive or have a higher resource-holding potential than males that remain unpaired throughout the season, then we predict that these attractive males should also be less likely to lose a contest against aggressive unfamiliar rivals. Therefore, we expect subsequently paired males to respond similarly regardless of the threat posed by an unfamiliar rival. In contrast, we predict bachelor males to be more discriminative because although they may succeed against moderate rivals they are less likely to succeed against aggressive rivals.

To study the relation between pairing success of males and their responses to rivals posing different levels of threat, we simulated unfamiliar rivals singing near the territory boundaries of subsequently mated and unmated nightingales as being either aggressive (by song overlapping) or moderate (by song alternating). Playbacks were conducted with nocturnal song during which nightingales interact intensively, with communication being restricted to acoustic signalling. We predicted that subsequently mated and unmated males would respond differently to playback treatments. Nightingales form socially monogamous seasonal pair bonds, but in our study population up to 49% of territorial males remain unpaired throughout the breeding season (Amrhein et al. 2004a), which gave us the opportunity to compare singing behaviour of males with respect to their future success in attracting a female. To investigate changes in singing behaviour elicited by playback, we compared singing behaviour before and after playback. We analysed singing behaviour by quantifying temporal singing patterns and structural song components.

METHODS

Subjects and Study Site

We conducted playbacks on 42 nocturnally singing nightingales in the vicinity of the Petite Camargue Alsacienne (France) within a population of about 240 singing males in an area of 18 km² in the Upper Rhine

Valley north of Basel, Switzerland (Amrhein & Zwygart 2004). Here, nightingales usually settle in patches of woods and dense bushes along rivers or footpaths. In addition, territories often border grasslands or fields, resulting in clear territory boundaries. For playback, we chose territories that were sufficiently isolated that playbacks did not interfere with responses from neighbours. Thus, our subjects were individually recognizable by territory location. Song posts of subjects were mapped on at least 2 days and nights prior to playback to determine territory boundaries. Playbacks were conducted at the beginning of the breeding period in 2004 (20 playbacks between 18 April and 3 May) and 2005 (22 playbacks between 19 April and 2 May). Grüll (1981) found that 76% of males return to the same territory of the preceding year or to a directly neighbouring one. Since we used different, non-neighbouring territories in both years, it is unlikely that we used the same subject twice.

Male nightingales sing regularly at night for a prolonged period only until a female has settled in their territory (Amrhein et al. 2002, 2004b). Thus, we monitored nocturnal singing activity of all subjects after playback every second night throughout the breeding season to assess their mating status. All subjects had been singing during the nights before they received playback and they sang during at least 2 nights after playback. Later in the season, 20 males ceased nocturnal song indicating that they became paired, whereas the other 22 males sang at night throughout the breeding season indicating that they remained unpaired.

Playback Stimuli

We created stimuli from nocturnal recordings of 42 male nightingales made between 2002 and 2005 in the study population. These males were different from those used as subjects in the present study. Nocturnal song was recorded on a Sony TC-D5M or WM-D6C cassette recorder with a Sennheiser ME66/K6 microphone and digitized using Cool Edit 2000 (Syntrillium Software, Scottsdale, AZ, U.S.A.; sample frequency: 44.1 kHz; resolution: 16 bits). To generate stimuli, we selected 22 songs from each recording (Avisoft SASLab Pro 3.5, R. Specht, Berlin, Germany). In line with the natural proportion of different song categories in nocturnal song (Kunc et al. 2005), each set of 22 songs consisted of three whistle songs, i.e. songs starting with a series of mostly unmodulated whistles (Hultsch & Todt 1996), and 19 nonwhistle songs (Fig. 1a). Three of these 19 nonwhistle songs contained a rapid broadband trill (Fig. 1b). Male nightingales have been shown to vary these song traits during vocal interactions with rival males (Todt & Naguib 2000; Kunc et al. 2006). We generated a new set of stimulus songs for each playback and used the songs of each source male only once. The 22 songs were randomly merged into one wave-file in Cool Edit and normalized at once to the peak amplitude to standardize playback amplitude across trials. Then, we arranged the 22 single songs in one file of SyrinxPC version 2.3s (J. Burt, <http://www.syrinxpc.com>), on a Toshiba Satellite notebook (S2210CDT), to enable the experimenter

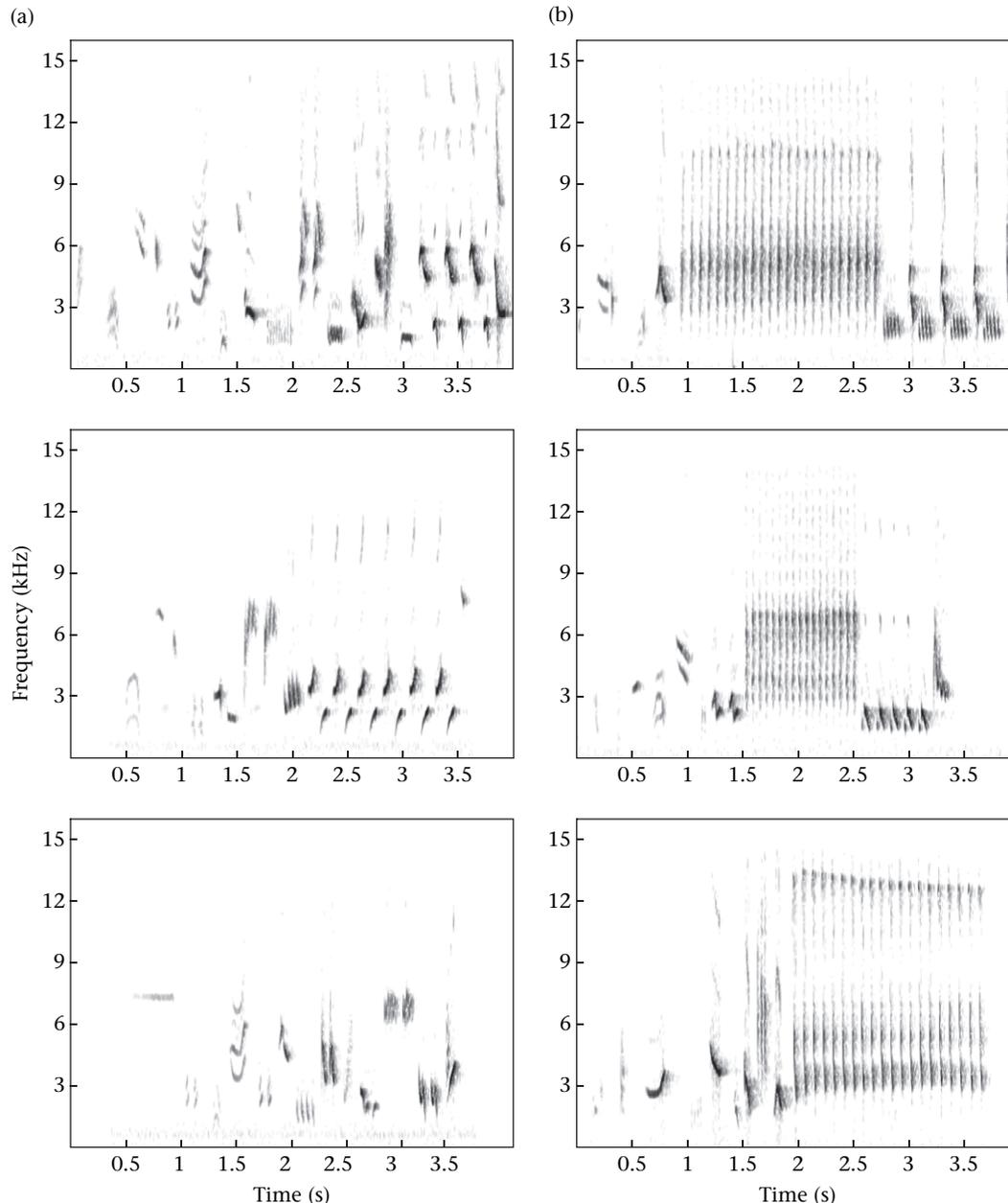


Figure 1. Spectrograms of six different song types of male nightingales' song: (a) nonwhistle songs without rapid broadband trills and (b) non-whistle songs containing such trills.

to play each song separately during playback. Thereby, each song could be played on demand, but no song was played twice during a playback trial.

Playback Protocol

All nocturnal playbacks were conducted between 2345 and 0330 hours CEST. We only used males that were already singing when the playback started. The subjects received either an overlapping playback ($N = 21$), in which a mean \pm SD of $86.0 \pm 11.1\%$ of playback songs overlapped the subjects' songs, or an alternating playback ($N = 21$) in which we avoided song overlapping

($0.4 \pm 1.3\%$ of playback songs overlapped the subjects' songs). The order of playback treatments was alternated systematically across the males. To simulate a newly arrived rival singing near the subject males' territory boundaries, we positioned the loudspeaker outside the males' territories at distances of 30–40 m from their nocturnal song posts.

The notebook used for playback was connected to a Blaupunkt MPA 2 amplifier and a Canton Plus X passive speaker. The sound pressure of broadcast songs was adjusted before playback to 90 dB at 1 m distance, 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). Singing of focal males was 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 with another microphone of the same kind. Before we started playbacks, we recorded the subjects' nocturnal song for 10 min, and we continued recordings for 10 min after playbacks terminated.

Response Measures and Statistical Analysis

To investigate influences of playback treatment, we focused on the changes in singing after playback compared to the singing before playback. Therefore, we first measured the song parameters for the 10-min intervals before and after playback separately. Then, we calculated the difference between these two measures for each subject to assess the change in singing behaviour elicited by the playback treatment.

Our subjects occasionally interrupted their regular nocturnal singing, leading to between-song intervals that differed markedly from the mean intersong intervals \pm SD of 3.2 ± 3.7 . As the occurrence of such nonvocalizing elicited by playback confounds the analysis of regular intersong intervals, we analysed these interruptions separately. By defining a singing interruption as a silent interval exceeding 10 s (Fig. 2), we followed previous studies which showed such interruptions to be characteristic responses to overlapping playback (Naguib 1999; Mennill & Ratcliffe 2004b).

We measured (1) the number of singing interruptions (number of silent intervals longer than 10 s) and (2) the total duration of these interruptions (s). Measures unaffected by singing interruptions were (3) the percentage of songs containing trills, (4) the percentage of whistle songs and (5) the song duration (s). Furthermore, for the effective signalling time, i.e. after excluding the duration of interruptions, we measured (6) the pause duration (duration of intersong intervals < 10 s) and (7) the song rate (number of songs/min).

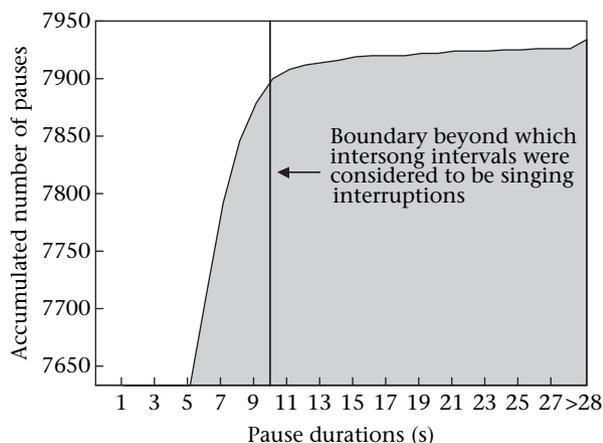


Figure 2. Distribution of silent intersong intervals of all male nightingales during 10 min before and 10 min after playback. We defined a singing interruption to be a silent interval of more than 10 s.

We applied a multivariate general linear model (SPSS 12.0, SPSS Inc., Chicago, IL, U.S.A.) with the seven song parameters as dependent variables, measured as changes after playback in comparison to before playback (i.e. the difference between them). The initial model included three fixed factors: the playback treatment (song alternating or song overlapping), the males' subsequent pairing status (mated male or bachelor) and the year of study (2004 or 2005). Since the year of study did not have a significant influence in the MANOVA ($P > 0.2$), this factor was removed in the final model. The influence of playback treatment on each song parameter and the relation between subsequent mating status and song parameters were then assessed with univariate general linear models. Data on the number of singing interruptions were log transformed to meet requirements for parametric statistics. In our sample, 13 of 21 males in the song-alternating treatment group and nine of 21 males in the song-overlapping group remained unpaired throughout the season. Results are given as mean \pm SE; all reported tests are two tailed.

RESULTS

With all measures taken together, the subjects' singing was influenced by playback treatment, although not quite significantly so (MANOVA: $F_{7,32} = 2.23$, $P = 0.058$), and responses differed significantly between subsequently mated males and bachelors ($F_{7,32} = 2.95$, $P = 0.017$). The interaction between treatment and pairing success overall was significant ($F_{7,32} = 3.28$, $P = 0.010$), indicating that subsequently mated males and bachelors responded differently to overlapping and to alternating playback.

Effects of Playback Treatment

Across subsequently mated and unmated males, subjects whose song had been overlapped interrupted their singing for significantly longer than subjects that had received the song-alternating treatment (Fig. 3a, Table 1). Playback treatment did not significantly affect the number of singing interruptions across all males, but the interaction between playback treatment and mating status was significant (Table 1). In other words, bachelors interrupted their singing more often after the overlapping treatment than after the alternating treatment, whereas subsequently mated males kept the number of interruptions at similar levels in both treatments (Fig. 3b).

The structural song components (whistle songs and trills) and the three measures of singing activity (song duration, pause duration and song rate) did not differ significantly in response to the two types of interactive playback; nor did we find significant interactions between playback treatment and pairing success with regard to these five variables (Table 1).

Effects of Subsequent Pairing Success

Males that later in the season attracted a female sang at significantly higher rates (Fig. 4) and increased the

proportion of trills after playback, although not significantly so (Fig. 5, Table 1), regardless of playback treatment. These males increased their song rate by shortening the intersong intervals significantly by about 14% (Fig. 4), whereas song duration remained similar in subsequently mated males and bachelors (Fig. 4). Pairing success was not significantly related to the duration or number of singing interruptions, nor to the use of whistle songs (Table 1).

DISCUSSION

The singing behaviour of male nightingales in response to playback suggests an influence of playback treatment, i.e. whether the simulated rival overlapped or alternated with

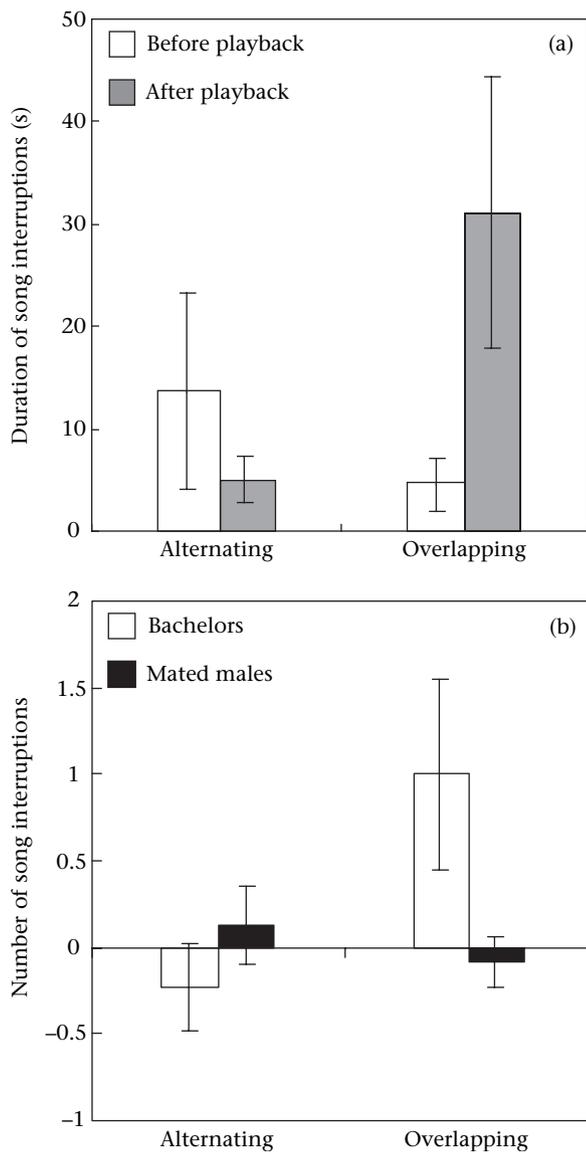


Figure 3. (a) Duration of all singing interruptions ($\bar{X} \pm \text{SE}$) within 10 min before playback and within 10 min after playback depending on playback treatment. (b) Difference between the number of singing interruptions after and before playback ($\bar{X} \pm \text{SE}$) for subsequently unmated and mated males depending on playback treatment. Negative values indicate fewer, and positive values more, interruptions after than before playback.

the subjects' songs. Compared to the time before playback, males interrupted their singing for significantly longer after they had been overlapped by playback than they did after playback songs had alternated with them. Furthermore, those males that remained unpaired throughout the breeding season interrupted their singing significantly more often after the song-overlapping treatment than after the song-alternating treatment. In contrast, subsequently mated males showed a similar number of singing interruptions, regardless of whether their songs had been overlapped by playback. These males increased their song rate more than did bachelors, regardless of playback treatment. Furthermore, subsequently mated males, which prior to playback sang fewer songs containing rapid trills than did bachelors, tended to increase the use of such songs after playback and sang as many as did bachelors, which did not vary the use of trills.

The increased duration of singing interruptions after being overlapped by a simulated opponent is in line with previous findings (Naguib 1999; Mennill & Ratcliffe 2004b; Naguib & Kipper 2006) and supports the hypothesis that song overlapping is a signal of aggression in male–male vocal interactions (Dabelsteen et al. 1996, 1997; Langemann et al. 2000; Mennill & Ratcliffe 2004b). These studies focused on the singing strategies of males responding during playback to the perceived level of aggression of a simulated opponent. Expanding on these findings, our results show that singing interruptions persisted even after playback had terminated, i.e. when residents could not localize the rival. The persistence of singing interruptions after a song contest supports the idea that singing irregularities in response to overlapping playback are not necessarily only the result of avoiding being overlapped, but rather more generally reflect male arousal as a consequence of being challenged or intimidated by a threatening opponent.

In our study, bachelor males interrupted their singing significantly more often after being overlapped than after alternating playback, whereas subsequently mated males kept the number of singing interruptions more constant across playback treatment. This suggests that subsequently mated males did not differentiate between an aggressive and a moderate opponent, whereas bachelors did. Thus, bachelors may be more intimidated by an aggressively singing opponent. However, the small, albeit significant, difference in the absolute number of interruptions raises the question whether these differences reflect biologically relevant differential response strategies of subsequently mated and unmated males, an issue that requires further study.

To increase song rate, a male can either shorten his songs or reduce the pauses between two songs, the latter being the most common pattern in songbird species (Catchpole & Slater 1995), including the nightingale (Naguib 1999; Kunc et al. 2005). Our study revealed that only those males that attracted a social mate later in the season sang at higher rates after playback, regardless of playback treatment. Furthermore, they increased the percentage of songs with trills to the same level as bachelor males after playback, although this was not quite significant. Changes in song output are often discussed in the

Table 1. Changes in singing behaviour elicited by playback treatment (overlapping versus alternating) on subsequently mated and unmated male nightingales as identified by general linear models

Dependent variable	Treatment		Mating success		Interaction	
	$F_{1,38}$	P	$F_{1,38}$	P	$F_{1,38}$	P
Overall effect	2.23*	0.058	2.95*	0.017	3.28*	0.010
Duration of interruptions	6.03	0.019	1.13	0.30	0.04	0.85
Number of interruptions	2.15	0.15	0.25	0.62	4.52	0.040
Percentage of trilled songs	0.07	0.79	3.88	0.056	1.09	0.30
Percentage of whistle songs	1.85	0.18	2.01	0.16	0.19	0.67
Song rate	0.03	0.87	5.53	0.024	0.21	0.65
Pause duration	0.002	0.96	8.93	0.005	0.22	0.64
Song duration	0.11	0.75	0.02	0.90	1.36	0.35

Changes were calculated as differences during 10 min after and 10 min before playback.

* $F_{7,32}$ in the overall analysis.

context of constraints and performance limits acting, for instance, on song rate (Alatalo et al. 1990; Wasserman & Cigliano 1991; Collins 2004) or the production of trills (Podos 1996, 1997; Ballentine et al. 2004; Podos & Nowicki 2005). Our finding that only males that sang at higher rates after playback became paired could be taken to suggest that an increase in singing activity may reflect male condition or quality. On the other hand, the same males, although they sang more trills in response to playback, sang a similar percentage of trills after playback as did bachelor males. Thus, differences between males were reflected more in temporal patterns of song and the change in use of trills in response to playback than in the absolute number of songs containing trills.

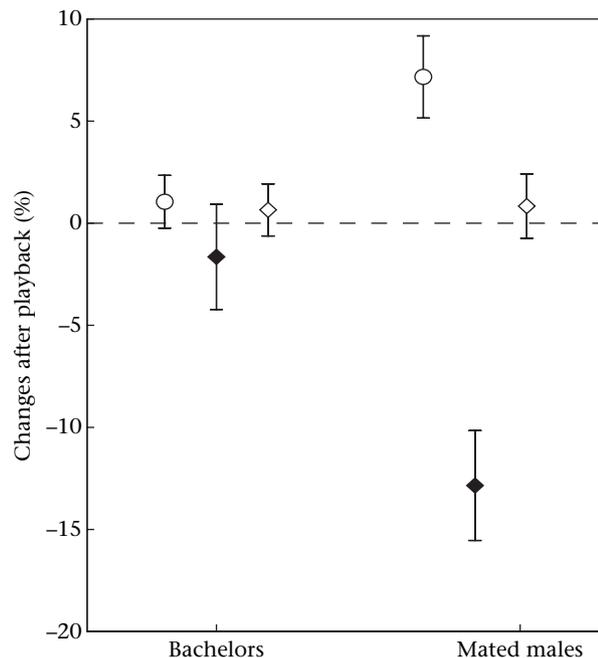


Figure 4. Relative increase (positive values) or decrease (negative values) of nocturnal singing within 10 min after playback compared to 10 min before playback; mean values \pm SE of the song rate (\circ), the pause duration (\blacklozenge), and the song duration (\diamond) are shown separately for bachelors and males that attracted a social mate.

The lack of a differential use of whistle songs is in line with the idea that whistle songs are used as long-range signals (Richards 1981; Todt & Naguib 2000) which are important in female choice (Hultsch 1980; Kunc et al. 2005), rather than being used in close-range vocal contests between males.

Another link between increased performance and aspects of male quality involves the time for which the subjects had already held a territory on the day they received the playback. The value of the territory is likely to increase with time of residency so that males holding a given territory for longer may be more willing to defend it (Davies & Houston 1981; Krebs 1982; Beletsky & Orians 1987; Stamps 1987; Jakobsson 1988; Tobias 1997; Forstmeier 2002). In addition, the time of residency on the day of playback depends on the date on which the males arrived from migration. The differences in response to playback by subsequently mated and bachelor males

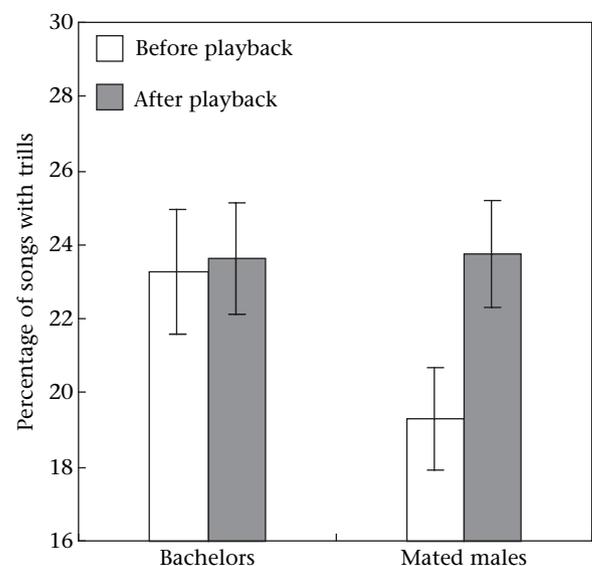


Figure 5. Percentage of songs ($\bar{X} \pm$ SE) containing trills within 10 min before playback and within 10 min after playback with respect to the males' future pairing success.

might have been affected in part by such differences in time of residency. However, an early arrival on the breeding ground may also indicate a male's quality (Forstmeier 2002), and early arriving males in our study population of nightingales are more likely to attract a social mate (Amrhein et al. In press).

Regardless of the mechanisms underlying changes in male song output in response to playback, the singing performance of males after the song contests predicted future pairing success of the singers. These results expand on a previous study by Kunc et al. (2006), which revealed that a male's subsequent pairing success is reflected in the temporal pattern of his song relative to a simulated noninteracting opponent during a vocal interaction. This information on the males' future pairing success may be conveyed not only to the opponent within a dyadic interaction, but also to eavesdropping conspecifics in a communication network. There is accumulating evidence that males assess the level of aggression of rivals from male–male interactions (Naguib et al. 1999, 2004; Peake et al. 2001, 2002; Mennill & Ratcliffe 2004a). Based on our findings, we hypothesize that males also obtain information on their rivals' future mating success from singing interactions. Recently, paired female black-capped chickadees, *Poecile atricapillus*, have been shown to eavesdrop on male singing interactions and to base their choice of extrapair copulations on the performance of their mates in vocal contests (Mennill et al. 2002, 2003). Our results expand on these findings by showing that even at the very beginning of the breeding season, i.e. prior to mating, females could eavesdrop on singing interactions of males and prefer the male that sings more vigorously as a social mate. Thus, direct male–male interactions (Kunc et al. 2006), as well as the singing performance after a song contest, may well be important for female choice during the early stages of the breeding cycle in nightingales. Whether females use information obtained by eavesdropping when choosing a social mate remains to be shown. If they do, they may impose an indirect selection pressure on males to interact vocally with each other, if only those males that perform well in intrasexual conflicts are preferred by females (Wiley & Poston 1996; Naguib 2005).

In conclusion, our study supports previous findings that time-specific patterns in song contests, namely song overlapping versus song alternating, signal socially relevant information, as overlapped males sang more irregularly after contests than did males that were not overlapped. Furthermore, we showed that differences between males as indicated by their subsequent pairing success were reflected in singing responses to challenges posing different levels of threat. Elevated singing after a vocal interaction even at the beginning of the breeding season predicts future mating success, and thus may be used by conspecifics in a communication network to assess the singer's condition or quality.

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