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Effects of Rapid Broadband Trills on Responses to Song Overlapping in Nightingales

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Abstract

In communication, animals often use complex signals with different traits carrying different information. In the song of some songbirds, both trills and song overlapping signal arousal or the readiness to escalate a contest in male-male interactions, yet they also differ inherently from each other. Song overlapping is restricted to interactions and has a clear directive function as the songs are timed specifically to the songs of a counterpart. Trills, however, can be used without opponents actively singing and do not have such a directional character unless when combined with directed traits. This difference raises the question whether trills can enhance the agonistic function of song overlapping when being used simultaneously. Here, we exposed male nightingales (*Luscinia megarhynchos*) prior to pairing to overlapping playback treatments differing in the presence or absence of rapid broadband trills. Males responded differently to the two playback treatments suggesting that song overlapping and rapid broadband trills have some synergistic effects. Consequently, the separate or simultaneous use of trills and of song overlapping may allow males to adjust information encoded in their singing on a fine scale. Furthermore, males that remained unpaired throughout the breeding season responded differently to the playbacks than did subsequently paired males, emphasizing the implications of differences in territory defence behaviour on males subsequent pairing success.

In competition over resources such as mates, space, or food, animals signal aspects of their motivation and their quality to rivals. Signals often are complex, with different traits carrying different information (Bradbury & Vehrencamp 1998; Rowe 1999; Searcy & Nowicki 2005). In birdsong, some signaling traits such as the timing of songs and the use of specific patterns can be varied independently, raising questions about how the combination of independent singing traits effects the overall signal value.

Two distinct strategies of song timing have received specific attention: song alternating (i.e., starting a song in the silent interval between two songs of the opponent) and song overlapping (i.e., starting the song while the opponent is singing a song). Generally, song overlapping has been shown to be a directed agonistic signal (despite recent misconceptions; Searcy & Beecher 2009), whereas song alternating has been shown to be more moderate (Dabelsteen et al. 1997; Naguib 1999; Mennill & Ratcliffe 2004; Hall et al. 2006). To adjust responses to an opponent, a bird may also use specific songs (Falls et al. 1982) or song patterns such as trills, i.e., rapid repetitions of identical elements (Todt & Naguib 2000). Due to physical constraints in song production, a singer is limited in the ability to sing trills with a high element repetition rate while at the same time using elements with a broad frequency bandwidth (Westneat et al. 1993; Podos 1996, 1997). Thus, trills are considered to act as an honest signal reflecting male quality that can function in female choice (Vallet et al. 1998; Ballentine et al. 2004). Furthermore, songs containing trills have been shown to be used and perceived as an agonistic signal in male–male interactions (Illes et al. 2006; Kunc et al. 2006; Schmidt et al. 2008; Kort et al. 2009).

Songs with trills and song overlapping thus appear to be valued similarly by rivals, but nevertheless they differ inherently in their ability to signal arousal in different contexts. Song overlapping can be used exclusively in vocal interactions, i.e., when the rival is singing. Songs with trills, however, can be used as signal of arousal or quality even when the opponent is not singing. Moreover, by timing the onset of a song to that of an opponent's song, males can direct the agonistic intention of song overlapping to this specific opponent. In contrast, songs with trills, like other structural song traits, do not have such an inherent directional function, unless combined with directed singing traits. These contrasting characteristics of song overlapping and songs with trills raise the question about whether their combination has enhancing effects in male–male interactions. Overlapping an opponent's song and additionally using songs with trills may well enhance the overall signal value, as trills could obtain a strong directive function when being added to song overlapping, and together they may act as a stronger agonistic signal. Yet, except for studies on song matching, when a male replies with the same song pattern as sung by the opponent (Catchpole & Slater 2008), little is known about the effects of combining the specific timing of songs with agonistic structural song patterns (Mennill & Ratcliffe 2004).

Here, we tested responses of male nightingales (*Luscinia megarhynchos*) to nocturnal overlapping playback that did, or did not include songs with rapid broadband trills. Nocturnal playbacks enable quantifying vocal responses without additional effects by spatial movements, and nocturnal vocal responses have been shown to predict territorial behavior during the day (Schmidt et al. 2007). We predicted a stronger vocal response by subjects receiving the overlapping treatment with rapid broadband trills compared to subjects receiving the overlapping treatment alone. Since responses do not only depend on the motivation and quality of the singing rival, but also on the motivation or quality of the subject (Kunc et al. 2006; Schmidt et al. 2006), we further tested whether the males' subsequent pairing success was reflected in responses to playback. We expected male nightingales that successfully attracted a female to respond stronger to playback than males that remained unpaired throughout the season.

Methods

Study Site and Subjects

The playback experiment was carried out between 18 April and 2 May 2007 in the nature reserve Petite Camargue Alsacienne (France) in the Upper Rhine Valley, 10 km north of Basel (Switzerland). Here, about 240 singing male nightingales settle in a study area of approx. 18 sq km, and up to half of the males may remain unpaired throughout the season (Amrhein et al. 2007).

In our study site, nightingale territories are characterized by dense bushes and groves that border pathways, open fields or grasslands and often are in close proximity to rivers or streams. Thus, territory boundaries usually are well defined by the habitat. Playbacks were conducted only in territories that were sufficiently isolated so that close neighbors would not interfere with the playback.

Males usually cease singing at night after pairing, whereas unpaired males continue nocturnal singing throughout the breeding season (Amrhein et al. 2002, 2004; Roth et al. 2009). To map the presence and the singing activity of all male nightingales in the study area, we conducted standardized census rounds at midnight and at dawn throughout the breeding season (10 April to 20 May 2007). Thus, we were able to distinguish between paired and unpaired males (bachelors) by judging from the presence or absence of prolonged nocturnal singing in an occupied territory (Amrhein et al. 2002, 2004, 2007). All playbacks were conducted before males had attracted a female. Of the 41 playback subjects, 21 males ceased singing at night later in the season and were considered as subsequently paired males. The other 20 males sang nocturnal song throughout the breeding season and were considered to have remained unpaired. The first male nightingale was heard on 11 April 2007, and each subject had been singing for at least three nights before the playbacks were carried out.

Playback Stimuli

For the 41 playback stimuli we used nocturnal song recordings from 41 male nightingales. Song was recorded with a Sony TC-D5M or WM-D6C tape recorder (Sony Ltd., Tokyo, Japan) and a Sennheiser ME66/K6 microphone (Sennheiser electronic GmbH, Wedemark, Germany) between 2003 and 2007 and digitized with Cool Edit 2000 (Syntrillium Software Cooperation, Phoenix, AZ, USA, sampling frequency: 44.1 kHz, resolution: 16 bit). For each set of playback stimuli, 20 different song types were selected from one male using the sound analysis software Avisoft SASlab Pro 4.4 (R. Specht, Berlin, Germany). For the first treatment group, we randomly chose 10 song types containing rapid broadband trills for each playback (Fig. 1a, b). Rapid broadband trills used for playback had a bandwidth of 9643 ± 2648 Hz (mean ± SD; measured at −20 dB) and an element repetition rate of 12 ± 3 elements/s. The remaining 10 song types were chosen randomly from songs without rapid broadband trills (Fig. 1c, d) with the constraint that each playback contained one to four whistle songs (Fig. 1e, f), i.e., songs that started with non- or only slightly modulated whistles (Naguib et al. 2002; Kunc et al. 2005). For the second treatment group, we proceeded similarly with the difference that none of the stimulus songs contained songs with rapid broadband trills. Even though the combined duration of the 20 songs tended to differ between treatments because songs containing trills tend to be longer than other songs (overlapping playback with trills: 62 ± 5 s (mean ± SD); overlapping playback without trills: 58 ± 7 s; Welch *t*-test; $t_{36.0} = 1.93$, $p = 0.062$), the subjects' responses were not significantly affected by the duration of stimulus songs (effects of duration of stimuli when included in the statistical models as a covariate: all $p > 0.19$).

Each song was normalized in peak amplitude using Cool Edit, to standardize the playback amplitude across trials. We arranged playback songs randomly, but the first of the 20 playback songs did not contain rapid broadband trills. For playback we used the software Syrinx PC version 2.3s (J. Burt, http://www.syrinxpc.com) installed on a Toshiba Satellite notebook (S2210CDT; Toshiba Corporation, Tokyo, Japan), in order to play each song separately. The notebook was connected to a Blaupunkt MPA2 amplifier (Blaupunkt GmbH, Hildesheim, Germany) and a Canton Plus X passive speaker (Canton Elektronik GmbH & Co. KG, Weilrod, Germany). Sound pressure of the stimulus songs was adjusted to 90 dB at 1 m distance measured with a Brüel & Kjær precision SPL meter 2223 (C-weighing, fast response), which is within the range of the sound pressure of singing males (Brumm 2004).

Playback Protocol

All trials took place at night, between 2345 hours and 0340 hours CEST. All males were singing at the onset of playback. Each male received one of the two treatments (bachelors: overlapping with trills n = 11 and without trills n = 9; subsequently paired males: overlapping with trills n = 10 and without trills n = 11).

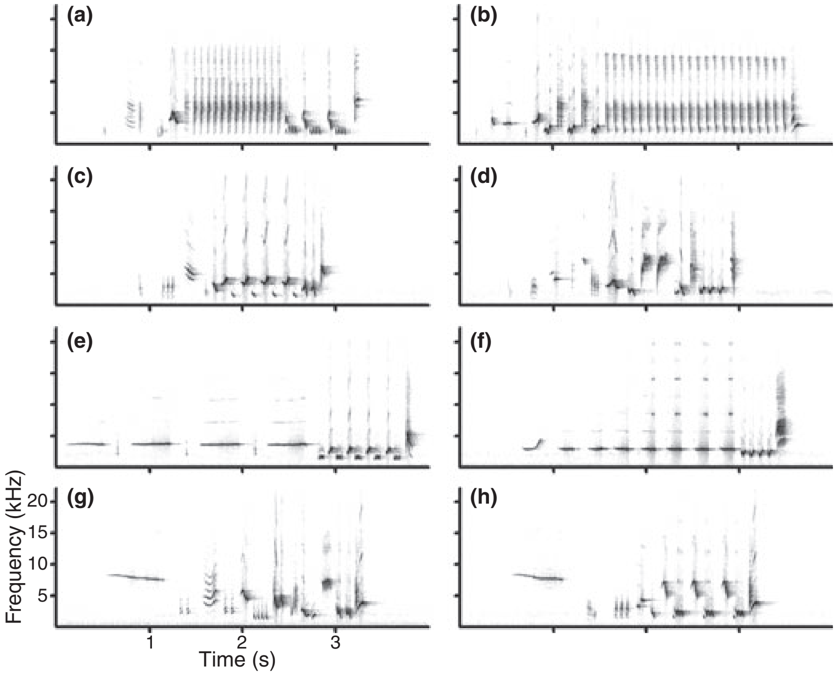

Fig. 1: Sound spectrograms of nightingale songs containing rapid broadband trills (a and b), of songs without such trills (c and d), of whistle songs (e and f) and of songs with initial whistles (g and h).

Stimuli songs overlapped almost all of the subjects' songs, and there was no significant difference between treatments in the number of songs that were overlapped by playback (treatment with trills: 95 ± 5% (mean ± SD); treatment without trills: 92 ± 8%; Welch *t*-test: $t_{36.5} = 1.49$, $p = 0.15$).

To simulate a newly arrived opponent, stimulus songs were broadcasted from well outside the subjects' territories, at a distance of about 30 m from the subjects' nocturnal song posts. The loudspeaker was positioned on a tripod at a height of 1.5 m on open fields bordering the territories.

Stimulus songs were obtained either from recordings made out of earshot from the respective focus males in the year we made the present study, or from recordings made in previous years in territories other than the territories chosen for the experiments. Thus, a subject most likely was unfamiliar with the male whose songs were used for playback. Subjects' song was recorded either with a Marantz PMD 660 or a Marantz PMD 670 digital solid state stereo recorder (Marantz Corporation, Kenagawa, Japan) and a Sennheiser ME66/K6 microphone. On the second channel, we recorded the playback songs with a microphone of the same kind.

Response Measures and Statistical Analysis

We measured males' singing during three time periods; before the playback, during the playback, and after the playback. All analyzed periods were of equal duration as the period of the actual playback and did not differ significantly between treatments (overlapping playback with trills: 117 ± 30 s per period (mean ± SD); overlapping without trills: 124 ± 34 s per period; Welch *t*-test; $t_{23.8} = 0.94$, $p = 0.36$). Similar to previous playback experiments, males occasionally interrupted their singing, leading to intersong intervals that differed markedly from the mean pause duration of silent intervals between two songs of nocturnal song (Naguib 1999; Mennill & Ratcliffe 2004; Schmidt et al. 2006). We therefore decided to analyze singing interruptions separately by defining intersong intervals as interruptions if they were longer than the mean + 1 SD of silent intervals between two songs of normal nocturnal song (Naguib & Kipper 2006). Accordingly, intersong intervals that were longer than 6.1 s were considered to be singing interruptions.

In response to playbacks or in other contexts of apparent arousal, nightingales often add high-frequency whistles of low amplitude at a frequency window of approx. 6 to 8 kHz before the actual song begins. We refer to these whistles as 'initial whistles'. Initial whistles differ from the ordinary whistles of whistle songs (Fig. 1e, f) in that the initial whistles are always sung at very high frequencies and are usually not repeated (Fig. 1g, h; Naguib et al. 2002; Kunc et al. 2005). Yet, initial whistles have not been quantified in previous experiments. On the rare occasions in which initial whistles were repeated up to three times, males used significantly longer silent intervals between the initial whistle elements compared to whistle elements of ordinary whistle songs (initial whistles: 725 ± 390 ms (mean ± SD); ordinary whistles: 205 ± 34 ms; Welch *t*-test; $t_{11.1} = 4.61$, $p < 0.001$). Moreover, initial whistles often were added to a series of successive songs whereas ordinary whistle songs are rarely sung in immediate succession.

For analysis, we used the following song parameters as response variables: (1) percentage of songs with initial whistles, (2) number of singing interruptions, and (3) percentage of songs containing rapid broadband trills. We defined rapid broadband trills based on the definition we used for stimulus trills (see above). We used percentages instead of absolute numbers of songs because percentages account for the number of songs sung by a subject. We did not analyze total duration of singing interruptions, because total duration was highly positively correlated with number of interruptions (Spearman rank correlation; $r_S = 0.99$, $n = 41$, $p < 0.001$). The other analyzed song parameters did not correlate significantly in any of the three playback periods (Spearman rank correlations; all $p > 0.05$).

In the period before playback, males receiving different treatments did not differ significantly in the use of the three song parameters (Welch *t*-tests; all $p > 0.24$). However, before playback, bachelors sang more songs with rapid broadband trills than subsequently paired males (Welch *t*-test; $t_{37.6} = 2.47$, $p = 0.018$). Males differing in subsequent pairing status did not differ in the use of initial whistles and the number of singing interruptions before the playback (Welch *t*-tests, all $p > 0.088$).

Data analysis was done using R 2.8.1 (R Development Core Team 2008). To assess if the playback affected singing differently depending on treatment and pairing status, we used generalized linear models (GLM) for each of the three response variables, by analyzing singing during and after playback separately using the 'glm' function in R. As factors we included playback treatment, subsequent pairing status, and their interaction. To control for variation in male singing behavior prior to playback, we included the song parameter for the time period before the playback as a covariate. Percentage of songs with initial whistles and percentage of songs with trills were fitted with a Binomial error distribution. Number of singing interruptions was fitted with a Poisson error distribution. For model simplification we used backward selection following Crawley (2007). We removed non-significant ($p > 0.05$) terms from the maximal models starting with the interaction. We selected models based on likelihood ratios between alternative models. For all likelihood ratio tests, the degrees of freedom were df = 1. We visually checked homogeneity of variance and normality of error using plots of standardized residuals against fitted values and of quantiles of residuals against quantiles from a Normal distribution.

Results

Effects of Playback Treatment

Males increased the percentage of songs with initial whistles in response to both overlapping playback treatments (Fig. 2a). During playback, males did not differ in use of songs with initial whistles between the playback treatments (Table 1). However, after playback, males sang a higher percentage of songs with initial whistles in response to playback with rapid broadband trills than to overlapping playbacks without trills (Table 1; Fig. 2a).

Males generally decreased the number of singing interruptions during playback and interrupted their singing less frequently in response to playback with rapid broadband trills than to playback without trills (Table 1; Fig. 2b). After playback, however, males that received the overlapping playback with trills interrupted their singing more often than males that received the playback without trills (Table 1; Fig. 2b).

Males increased the percentage of rapid broadband trills in response to both treatments (Fig. 2c). During playback, males sang more songs with rapid broadband trills in response to overlapping playbacks with rapid broadband trills than in response to overlapping playback without trills (Table 1; Fig. 2c). After playback, males that received different treatments did not differ in the use of trills (Table 1; Fig. 2c). Males' responses during and after playback also was reflected in the way they were singing before playback (Table 1).

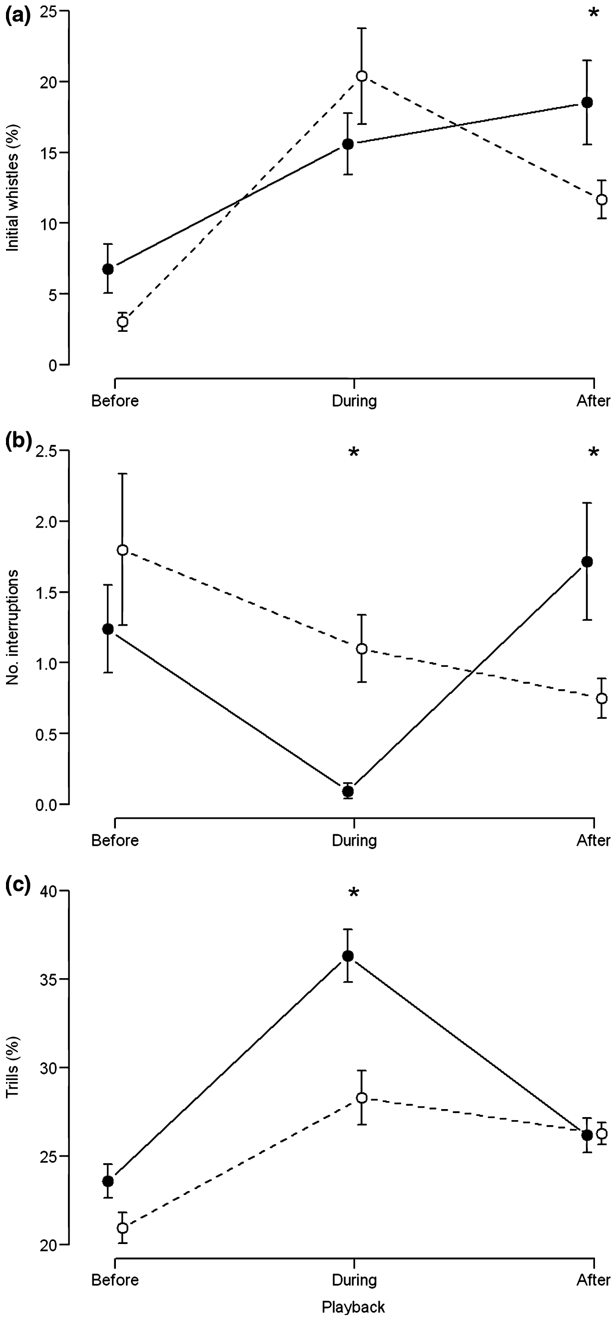

Fig. 2: Effect of playback treatment on the response variables (a) percentage of songs containing initial whistles, (b) number of singing interruptions, and (c) percentage of songs containing rapid broadband trills before, during and after playback. ● treatment with trills (n = 21), ○ treatment without trills (n = 20). Shown are mean ± SE. *Significant ($p < 0.05$) main effects of treatment of the generalized linear models (during and after playback; see Table 1).

Effects of Pairing Status

During playback, bachelors sang more songs with initial whistles than did subsequently paired males regardless of playback treatment (Table 1; Fig. 3a). Moreover, males responded differently to the playback treatments depending on their subsequent pair-

Table 1: Results of generalized linear models on three song parameters (percentage of initial whistles, number of song interruptions and percentage of trills) during and after playback, with treatment (songs with trills vs. songs without trills) and subsequent pairing status (paired vs. unpaired) as fixed effects and singing behavior prior to playback (song parameter before) as covariate

		Initial whistles (%)		No. interruptions		Trills (%)	
GLM		LR	p	LR	p	LR	p
During playback	Treatment	3.24	0.072	20.49	<0.001	6.12	0.013
	Pairing status	7.82	0.005	1.56	0.21	<0.01	0.97
	Song parameter before	32.38	<0.001	8.02	0.005	4.92	0.027
	Treatment × pairing status	15.64	<0.001	0.72	0.40	1.34	0.25
After playback	Treatment	25.07	<0.001	7.92	<0.005	0.03	0.87
	Pairing status	3.25	0.070	12.65	<0.001	4.51	0.034
	Song parameter before	51.10	<0.001	3.50	0.061	10.07	0.002
	Treatment × pairing status	1.71	0.19	0.41	0.52	0.12	0.73

GLM, generalized linear model. LR are likelihood ratios between alternative models, and all degrees of freedom are df = 1.

ing status (interaction treatment x pairing status; Table 1). During playback without trills, bachelors sang a higher percentage of songs with initial whistles than did subsequently paired males (bachelors: 29 ± 9% (mean ± SE); paired males: 16 ± 5%). During playback containing trills, however, bachelors and subsequently paired males did not differ strongly in the use of songs with initial whistles (bachelors: 15 ± 5%; paired males: 13 ± 4%). After playback, there was no significant difference in the use of songs with initial whistles between bachelors and subsequently paired males (Table 1; Fig. 3a).

During playback, subsequently paired males and bachelors interrupted their singing similarly often (Table 1; Fig. 3b). After playback, however, bachelors interrupted their singing more often than did subsequently paired males (Table 1; Fig. 3b).

Subsequent pairing status did not have an effect on the use of rapid broadband trills during playback as both increased the number of trills (Table 1; Fig. 3c). After playback, however, bachelors sang more songs with rapid broadband trills than did subsequently paired males (Table 1; Fig. 3c).

Discussion

The experiments show that males differed in their vocal responses to the two playback treatments, indicating that the combination of song overlapping and trills had some enhancing effects. Furthermore, males that later in the breeding season successfully attracted a female responded differently to playback than did males that remained unpaired.

The increase of songs containing rapid broadband trills during playback is in line with a previous study (Kunc et al. 2006) and supports the agonistic function of rapid broadband trills (Illes et al. 2006; Schmidt et al. 2008). Furthermore, the higher percentage of songs containing rapid broadband trills during playback with such trills indicates that males differentiated between the two treatments. This response, on an immediate level, may have been caused by vocal matching of the category 'songs with rapid broadband trills'. In agonistic interactions, males often match an opponent's song type (Krebs et al. 1981; Beecher et al. 2000) or certain song parameters such as the frequency (Otter et al. 2002) or specific song components (Burt et al. 2002; Anderson et al. 2005), and thus direct their singing to an opponent. Consequently, the higher percentage of songs with trills during playback containing such trills could suggest that males perceived the playback with trills as more threatening than the overlapping playback without trills.

Surprisingly, males responded to playback by singing on average with fewer interruptions than before the playback, rather than with more interruptions, as found in previous studies (Naguib & Kipper 2006; Schmidt et al. 2006). Singing with many interruptions has been interpreted as signaling arousal and as a strategy to avoid being overlapped by singing more irregularly (Naguib 1999). Our findings may be taken to suggest that arousal is not necessarily reflected by singing with many interruptions *per se*, but that a change in singing may equally well fulfill this function. A change in singing interruptions may be advantageous especially in cases where males sing with comparatively many interruptions, like males did here before playback, as further increasing interruptions would result in very low song rates. Signaling arousal by a change in singing could have benefits as it directly signals a change in state that may have more information content than the absolute level of a singing behavior. Absolute levels

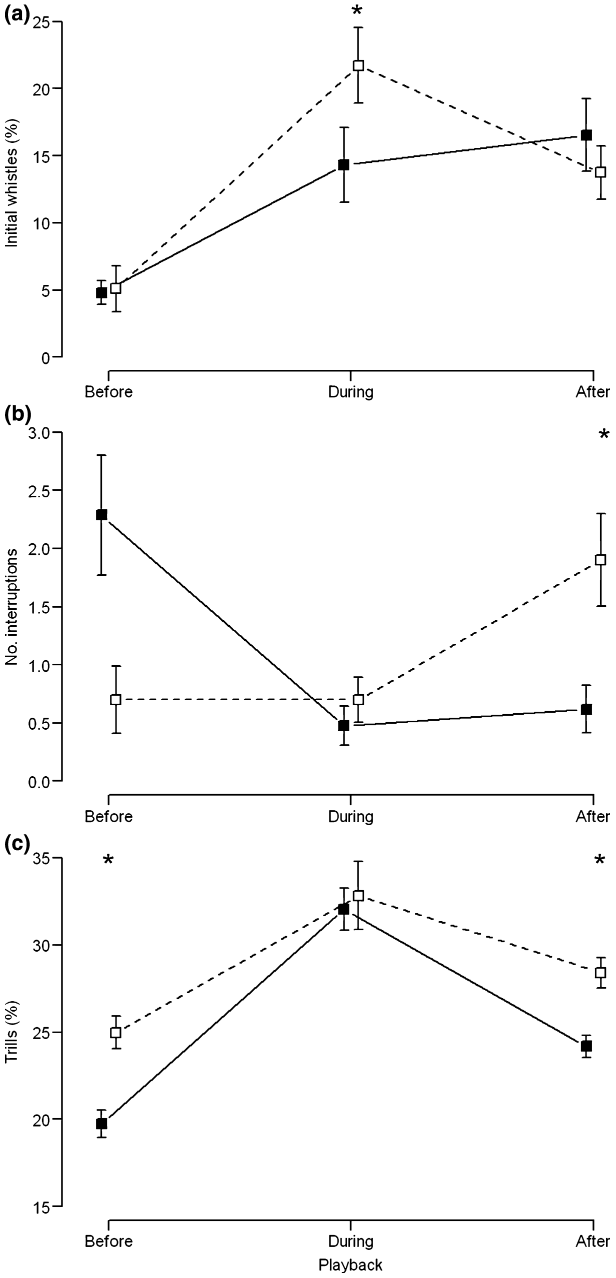

Fig. 3: Effect of subsequent pairing status on the response variables (a) percentage of songs containing initial whistles, (b) number of singing interruptions, and (c) percentage of songs containing rapid broadband trills before, during and after playback. ■ subsequently paired males (n = 21), ☐ bachelors (n = 20). Shown are mean ± SE. *Significant ($p < 0.05$) main effects of pairing status of the generalized linear models (during and after playback; see Table 1) and of Welch *t*-tests (before playback).

could sometimes be more difficult to interpret for a receiver in traits that vary substantially across males or contexts. Fewer singing interruptions during playback with trills than during playback without trills then would suggest that males perceived the playback treatment with combined agonistic stimuli as a more threatening signal than the overlapping playback without trills. Yet, the opposite effects in the use of interuptions during and after playback leaves an inconsistent pattern, so that one has to remain cautious in drawing strong conclusions based on the way subjects interrupted their singing.

Males sustained a high percentage of songs with initial whistles only after overlapping playback containing rapid broadband trills. This high percentage of songs with initial whistles suggests that the combination of overlapping and rapid broadband trills has stronger persisting effects after the playback than has overlapping alone. Due to the low amplitude of the initial whistles, they may be functionally similar to 'soft songs' that are considered as agonistic signal during intraspecific interactions (Searcy & Nowicki 2006; Anderson et al. 2008). Soft songs may be adaptive during vocal interactions because their low amplitude reduces the ability of other eavesdropping individuals to intercept the signals (McGregor & Dabelsteen 1996; Naguib et al. 2004). The use of low frequency whistles may even expand this function since adding such structural song patterns does not constrain the overall long-range function of the regular loud song.

The signal function of song overlapping is confined to vocal interactions, addressing a specific opponent, whereas trills can be used at any time. Consequently, the use of rapid broadband trills may not fully fulfill a directed agonistic function unless when used in a context in which the receiver is specified, such as during song matching or in combination with song overlapping. Such combinations may allow males to direct the information coded in rapid broadband trills at a specific opponent. However, the opposing courses of the number of interruptions during and after playback remain difficult to interpret.

The results further revealed that males' singing strategies differed depending on their subsequent pairing status. Bachelors sang more songs containing rapid broadband trills before and after playback than did subsequently paired males. Given the agonistic effect of songs with trills in nightingales (Kunc et al. 2006; Schmidt et al. 2008), these findings suggest that bachelors were more aroused even when not challenged by an opponent. Possibly, bachelors are less competitive and thus have a higher baseline level of arousal when claiming their territory. This conclusion is supported by the high number of singing interruptions bachelors used after playback, as singing with many interruptions is considered to reflect a high level of arousal (Naguib & Kipper 2006). The finding that bachelors generally sang more songs with trills than subsequently paired males further suggests that rapid broadband trills in nightingales may not be a signal of male quality that is used by females in their choice of mates, as was shown in other species (Draganoiu et al. 2002; Ballentine et al. 2004).

Taken together, the differences in response to the two treatments suggest that adding rapid broadband trills to song overlapping does have some enhancing effect on the signal value. However, given the opposite effects of interruptions during and after playback, we are reluctant to overstate such enhancing effects for the combined signal. Because trills, other than song overlapping, can also be effective during non-interactive situations, the use of trills may be a more general demonstration of male arousal, with stronger consequences even beyond the cessation of an interaction. In contrast, song overlapping, which is suitable only during direct interactions, may rather signal directed arousal or short-term motivation. Overall, the experiment suggests that the combination of the two agonistic signals has enhancing effects during agonistic male–male interactions to some extent and may allow males to vary signal content on a fine scale.

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