

Communication across territory boundaries: distance-dependent responses in nightingales

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In communication, vocal signals are often used for long-range signaling. Yet, little experimental evidence is available on the role of territorial signals across territory boundaries and their effectiveness at different propagation distances. In many songbird species, song overlapping and rapid broadband trills are used and perceived as agonistic signals, yet they differ in their propagation distance. Trills degrade quickly over distance, suggesting that their agonistic function may decrease faster over distance than that of song overlapping. Here, we tested whether different signaling distances of a rival affect singing responses of a territorial male and whether such distance effects differ when a rival uses rapid broadband trills or song overlapping. We exposed male nightingales (*Luscinia megarhynchos*) to songs of simulated rivals broadcast from 2 distances outside their territories. Each subject was exposed either to a moderate alternating playback without trills or to an agonistic playback, that is, to an alternating playback with trills or to an overlapping playback without trills. Irrespective of the treatment, males sang more songs containing trills in response to near than to far playback. As expected, males responded more strongly to the 2 agonistic treatments than to the moderate treatment. However, males did not clearly decrease responsiveness to playback containing trills broadcast from afar. This indicates that trills maintain their agonistic function even at distances at which information encoded in frequency bandwidth is degraded. Taken together, our results show that information encoded in signals used for resource maintenance is important also in communication across territory boundaries. *Key words*: bird song, distance effects, interactive playback, song overlapping, trill, vocal interactions. [*Behav Ecol* 21:1011–1017 (2010)]

In competition over resources and mates, animals often use sexually selected signals that propagate over long ranges. Efficient propagation of signals highly depends on the signals' spectral characteristics as well as on habitat characteristics and the distance between sender and receiver (Wiley and Richards 1978; Forrest 1994; Naguib and Wiley 2001; Parris 2002). One of the key model systems for the study of sexually selected signals is vocal communication, often highlighted for its long-range signaling capacities in various taxa such as insects (Römer 1993; Greenfield 1994), anurans (Ryan 2001; Schwartz et al. 2002; Bee 2008), birds (Catchpole and Slater 2008; Brumm and Naguib 2009), and some mammals (Janik 2000; Wich and Nunn 2002).

The territorial function of birdsong has been a textbook example for vocal long-range signaling and has mainly been studied using playback experiments that broadcast songs from within the territory to simulate an intruding rival (McGregor 1991; Searcy and Nowicki 2005). Yet, territorial intrusions occur only rarely as males more commonly interact over long ranges across territorial boundaries presumably to prevent such intrusions (Krebs 1977; Nowicki et al. 1998). However, surprisingly little is known about the general function of birdsong at different distances beyond territory boundaries (Fitzsimmons et al. 2008). This applies even more so to the effectiveness of functionally similar signal components that differ strongly in their efficiency to transmit information over distance.

Vocal signals are usually characterized by temporal and structural traits (Gerhardt 1994; Todt and Naguib 2000). To temporally adjust the onset of a song to that of a rival, males can either overlap the songs of a counterpart (i.e., starting a song before a rival has terminated its song) or alternate with the songs of a rival (i.e., 2 interactants take turns in singing). Empirical evidence suggests that song overlapping is perceived and used as an aggressive signal, whereas alternating with the songs of a rival has been shown to be perceived as less aggressive and thus a more moderate signal (Dabelsteen et al. 1996; Mennill and Ratcliffe 2004; Hall et al. 2006; Amy et al. 2010; see Searcy and Beecher 2009 and Naguib and Mennill 2010, for a recent discussion on this topic). Rapid broadband trills are an example for a structural song trait with specific information content for females (Draganoiu et al. 2002; Ballentine et al. 2004) and males (Illes et al. 2006; Schmidt et al. 2008). Similar to song overlapping, songs containing trills are often used during agonistic encounters (Illes et al. 2006; Cramer and Price 2007; DuBois et al. 2009). The production of trills is physically constrained by the motor apparatus (Podos 1997), and males face a trade-off between singing trills with a wide frequency bandwidth and at the same time using a high element repetition rate. Thus, singing songs with rapid broadband trills is considered as an honest signal reflecting male quality (Podos 1997; Ballentine et al. 2004; Illes et al. 2006).

In nightingales (*Luscinia megarhynchos*), songs containing rapid broadband trills are used more during agonistic close-range interactions compared with undisturbed singing (Kunc et al. 2006; Schmidt et al. 2006, 2008; Sprau et al. 2010), possibly because broadband trills face strong spectral degradation and thus are not suitable in long-range communication (Naguib 2003; Naguib et al. 2008). As the propagation

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characteristics of rapid broadband trills and song overlapping differ, song overlapping and songs with rapid broadband trills might be used and perceived differently depending on the communication distance.

Here, we studied distance-dependent vocal responses of male nightingales to nocturnal interactive playbacks broadcast from 20 to 50 m outside the subjects' territorial boundaries. To examine whether trills and overlapping are assessed differently at different distances, we used 3 playback treatments: alternating playback without rapid broadband trills, alternating playback with rapid broadband trills, and overlapping playback without rapid broadband trills. We expected males to respond more strongly to near than to far playback and also to respond more strongly to the agonistic treatments (alternating with trills and overlapping) than to the more moderate treatment (alternating without trills). Because of the degradation of trills, we specifically expected males to decrease responsiveness to far playback containing songs with rapid broadband trills more strongly than to overlapping playback without trills.

MATERIALS AND METHODS

Study site and subjects

Playbacks were conducted on male nightingales in the Petite Camargue Alsacienne (France) between 19 April and 3 May 2008. This nature reserve is located in the Upper Rhine Valley, 10 km north of Basel (Switzerland) and accommodates about 240 male nightingales in an area of approximately 18 km² (Amrhein et al. 2007). In this area, nightingales settle in territories characterized by dense scrubs and groves alternating with more open areas. In most cases, territories are located along rivers or streams, pathways, grasslands, or open fields. Thus, territory boundaries usually are well defined by the habitat.

Playback stimuli

Stimulus songs used for playback experiments were taken from nocturnal song recordings of different male nightingales made between 2004 and 2007. Nocturnal 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) and digitized with Cool Edit 2000 (Syntrillium Software Cooperation, Phoenix, AZ, sampling frequency: 44.1 kHz, resolution: 16 bit). Songs used for playback were obtained from recordings made in territories that were out of hearing range from the territories chosen for the experiments. Thus, a subject most likely was unfamiliar with the male whose songs were used for playback.

To test for distance-dependent effects of rapid broadband trills and of song overlapping, each subject received one of 3 different playback treatments. Each subject received the given treatment from 2 distances; near and far (see below). Two of the treatments contained stimuli considered to be more aggressive: in the first treatment, playback songs alternated with the songs of the subject and additionally included rapid broadband trills. Songs of the second agonistic treatment lacked trills but overlapped the songs of the subject. In the third, more moderate, treatment, stimulus songs were alternated with the songs of the subject but did not include rapid broadband trills. The stimuli were constructed using the sound analysis software Avisoft SASlab Pro 4.4 (R. Specht, Berlin, Germany). A playback stimulus was composed of 20 randomly chosen songs from nocturnal recordings of one of 60 recorded males. For the alternating treatment with trills, we randomly chose 10 songs containing rapid broadband trills and 10 songs lacking those trills. Trills used for playback had a bandwidth of

9643 ± 2648 Hz (mean ± standard deviation [SD]; measured at -20 dB) and an element repetition rate of 11.7 ± 3.5 elements/s (Figure 1a,b). For playback, we arranged songs randomly with the constraint that the first of the 20 playback songs never contained rapid broadband trills. The total durations of all 20 songs did not differ significantly between the 3 treatments (alternating without trills: 70 ± 3 s [mean ± SD]; alternating with trills: 70 ± 3 s; overlapping without trills: 70 ± 5 s; analysis of variance: $F_{2,57} = 0.02$, $P = 0.87$). Each song was normalized in peak amplitude using Cool Edit. Sound pressure of the stimulus songs was adjusted to 90 dB at 1 m distance measured with a Brüel and Kjær precision SPL meter 2223 (C-weighting, fast response), which is within the range of the sound pressure of singing male nightingales (Brumm 2004).

Playback protocol

We conducted the playbacks on 30 male nightingales before they were paired to females. Pairing dates were determined by surveying nocturnal song each night throughout the study period, and males usually stop nocturnal song on pairing (Amrhein et al. 2002, 2004). Males were randomly allocated to one of the 3 treatments, with equal sample sizes for each treatment (alternating without trills: $N = 10$, alternating with trills: $N = 10$, overlapping without trills: $N = 10$).

In order to test for an effect of distance on responses to the different playback treatments, each male received one playback broadcast from a distance of 20 m (near) and a second playback with songs from another recorded male from a distance of 50 m (far) as measured from the subjects' nocturnal song posts, with a pause of 10 min between playbacks. Playback order was balanced within treatments (i.e., per treatment 5 subjects received the far playback first and 5 males received the close playback first). All trials took place at night, between 2315 and 0320 h Central European Summer Time. Distances were measured using a Leica DISTO A5 laser distancemeter (Leica Geosystems, Balgach, Switzerland). To assure that both distances fell well outside males' territories and were consistent across trials, we only used subjects that were singing from a bush or vegetation patch bordering the open field from which the playbacks were broadcast. Previous studies showed that territorial males respond vocally to simulated rivals singing from open fields at night (Schmidt et al. 2006, 2007; Sprau et al. 2010).

Rapid broadband trills lose most information that is encoded in frequency bandwidth within the first 32 m (Naguib et al. 2008). We thus chose 20 and 50 m as playback distances because those distances would lie within and outside the range of strongest frequency bandwidth degradation, respectively. By choosing 20 m as the closest distance, we minimized the risk that males would cease singing or shift away the nocturnal song post. Even though trills will already be degraded to some extent at 20 m, we expected the differences in playback distance to be large enough to result in perceived differences in frequency bandwidth. In this study, none of the males changed their nocturnal song post during the experiments. Playbacks were conducted only with males that were sufficiently isolated so that close neighbors would not interfere with the playback (distance to nearest neighbor singing at the time of the playback: 141 ± 58 m [mean ± SD]; distances were measured using ArcGIS 9.3, Esri Inc., Redlands, CA). In 2008, distance to nocturnal song posts of the nearest neighbors in the entire study area ranged from 44 to 197 m and in some cases, distance to the nearest nocturnally singing neighbor was shown to be even closer than 32 m (Naguib et al. 2008).

For the playbacks, we used a Creative Zen player (Creative Technology Limited, Singapore) connected to a Blaupunkt MPA2 amplifier (Blaupunkt GmbH, Hildesheim, Germany)

and a Canton Plus X passive speaker (Canton Elektronik GmbH & Co. KG, Weilrod, Germany) positioned on a tripod at a height of 1.5 m. Songs were individually stored as wave files and played separately by the experimenter to allow an interactive mode of either alternating with the songs of a subject or overlapping the subject's songs. The songs of the subjects were recorded with a Marantz PMD 660 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 separate Sennheiser ME66/K6 microphone.

Response measures and statistical analysis

We analyzed the song of the subjects preceding, during, and after the playbacks. All time periods used for analysis were of the same duration as the actual playback (alternating playback without trills: 139 ± 12 s [mean \pm SD]; alternating playback with trills: 141 ± 37 s; overlapping without trills: 115 ± 14 s). In order to determine how males responded to playback relative to undisturbed song, we calculated changes in singing from before to during as well as to after playback, by subtracting values of the measured song parameters before playback from the values obtained during and after playback. In contrast to previous experiments (Kunc et al. 2006, 2007; Schmidt et al. 2006, 2008; Sprau et al. 2010), pairing status was not included in the analysis due to the unequal distribution of subsequent pairing success of the subjects (unpaired males: $N = 4$; paired males: $N = 23$; unclear pairing status: $N = 3$).

Of the 30 males, playbacks with 2 subjects were removed from the data analysis because of technical difficulties with the playback equipment (one of these males received the alter-

nating treatment without trills and one the alternating treatment with trills). For the remaining 28 males, we analyzed the following 4 song parameters: 1) percentage of songs with rapid broadband trills, 2) pause duration between songs (s), 3) percentage of songs with initial whistles, and 4) number of singing interruptions. We chose these song parameters as they had been shown previously to reflect treatment differences in playbacks on nightingales (Naguib 1999; Naguib and Kipper 2006; Schmidt et al. 2006, 2008; Sprau et al. 2010). We did not include song overlapping by the subject as response variable as it was very rare given the interactive nature of the playback. As each song was played during or directly after the offset of a subjects' song, it was rarely possible for subjects to overlap the playback songs. Songs were defined as containing rapid broadband trills based on the same criteria used for the playback stimuli (see above). Initial whistles were defined as high frequency and low amplitude whistles that are often added to the beginning of songs (Figure 1) (Sprau et al. 2010). Males occasionally interrupted their singing, leading to intersong intervals that differed from the typical duration of all silent intervals. We therefore analyzed singing interruptions separately from pause duration by defining singing interruptions as silent intervals that were longer than the mean $+1$ SD of all pauses (Naguib and Kipper 2006). Accordingly, silent intervals that were longer than 6.2 s were considered as singing interruptions and not as pauses.

Data were analyzed using R 2.9.2 (R Development Core Team 2009). For each of the 4 response measures, we used a linear mixed model (LMM) using the lme function in R (package lme4, version 0.99875-1). We included treatment and playback distance as fixed factors. We accounted for the repeated sampling of the same individuals at the 2 distances by including subject as a random factor. As each male received

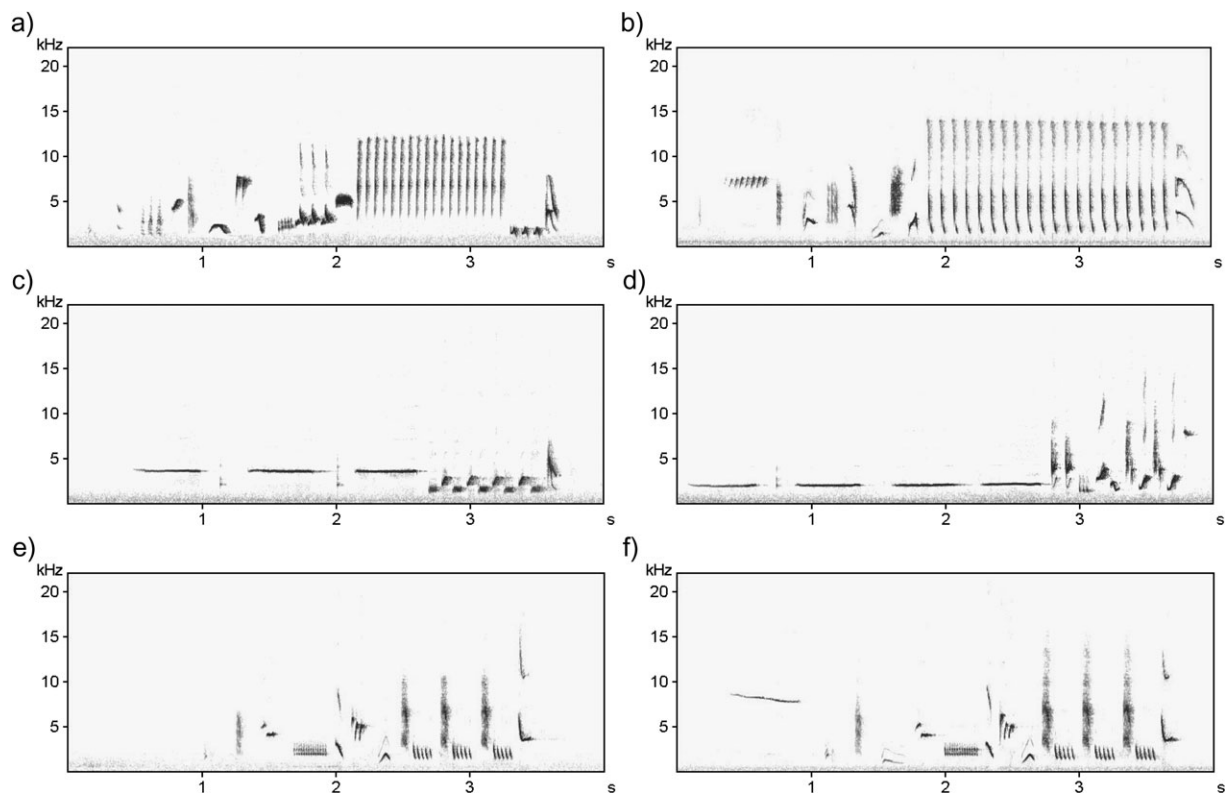


Figure 1
Sound spectrograms of different nightingale songs. Shown are 2 typical examples for songs with rapid broadband trills (a and b), whistle songs (c and d) and one song without initial whistle (e), and one song with initial whistle (f).

the same treatment from the 2 different distances, we also included order (i.e., whether playbacks were first broadcast from the close or the far distance) as a fixed factor. Maximal models included all possible interactions between the fixed factors. For model simplification, we used backward selection following Crawley (2007). We removed nonsignificant terms from the maximal models, starting with the 3-way interaction. 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

Playback distance affected male responses as subjects increased the number of songs containing trills more strongly during near than during far playbacks (LMM; distance: likelihood ratio LR = 10.43, degrees of freedom [df] = 1, $P = 0.001$; Figure 2a). The main effect of distance was not significant for the other 3 singing responses during playback (all $P > 0.59$; Figure 2b–d). Playback distance also had persistent effects as subjects increased the number of songs with initial whistles more strongly after near than after far playbacks (LR = 8.23, df = 1, $P = 0.004$; Figure 3c). The main effect of distance was not significant for the other 3 singing responses after playback (all $P > 0.18$; Figure 3a,b,d).

During playback, males also responded differently with respect to playback treatment. Subjects increased pause duration in response to the moderate playback (alternating playbacks lacking trills) but decreased pause duration in response to both treatments simulating a more aggressive rival, that is, during alternating playback containing trills and during overlapping playback without trills (treatment: LR = 14.91, df = 2, $P < 0.001$;

Figure 2b). The main effect of treatment was not significant for the other 3 singing responses (all $P > 0.19$; Figure 2a,c,d). After playback, the main effect of treatment was not significant for any of the 4 singing responses (all $P > 0.17$).

Playback order did not significantly affect subjects' response behavior during playback (all $P > 0.17$). After playback, however, subjects decreased pause duration (order: LR = 6.69, df = 1, $P = 0.01$; Figure 3b) and increased the number of songs sung with initial whistles (order: LR = 6.69, df = 1, $P < 0.001$; Figure 3c) more strongly to playbacks that were presented first at close range. The main effect of order was not significant for the percentage of trills and the number of interruptions ($P > 0.19$; Figure 3a,d).

During playback, males significantly varied pause duration with distance depending on playback treatment (interaction treatment \times distance, LR = 7.18, df = 2, $P = 0.027$; Figure 2b). Males that received the overlapping treatment without trills decreased pause duration more strongly in response to near than to far playback. However, males receiving the alternating playback containing trills decreased pause duration similarly in response to playbacks broadcast from both distances (Figure 2b). Males did not significantly vary the other 3 response parameters during and also none of them after the 3 playback treatments in a distance-dependent way (interactions treatment \times distance: during playback: all $P > 0.21$; Figure 2a,c,d; after playback: all $P > 0.07$).

After playback, subjects significantly varied the number of trills with distance depending on playback order (interaction distance \times order: LR = 3.96, df = 1, $P = 0.047$; Figure 3a). Subjects decreased trills from first to second playback when the first playback was broadcast from near. However, subjects maintained singing with many trills also after the second playback, when the first playback was broadcast from far. None of

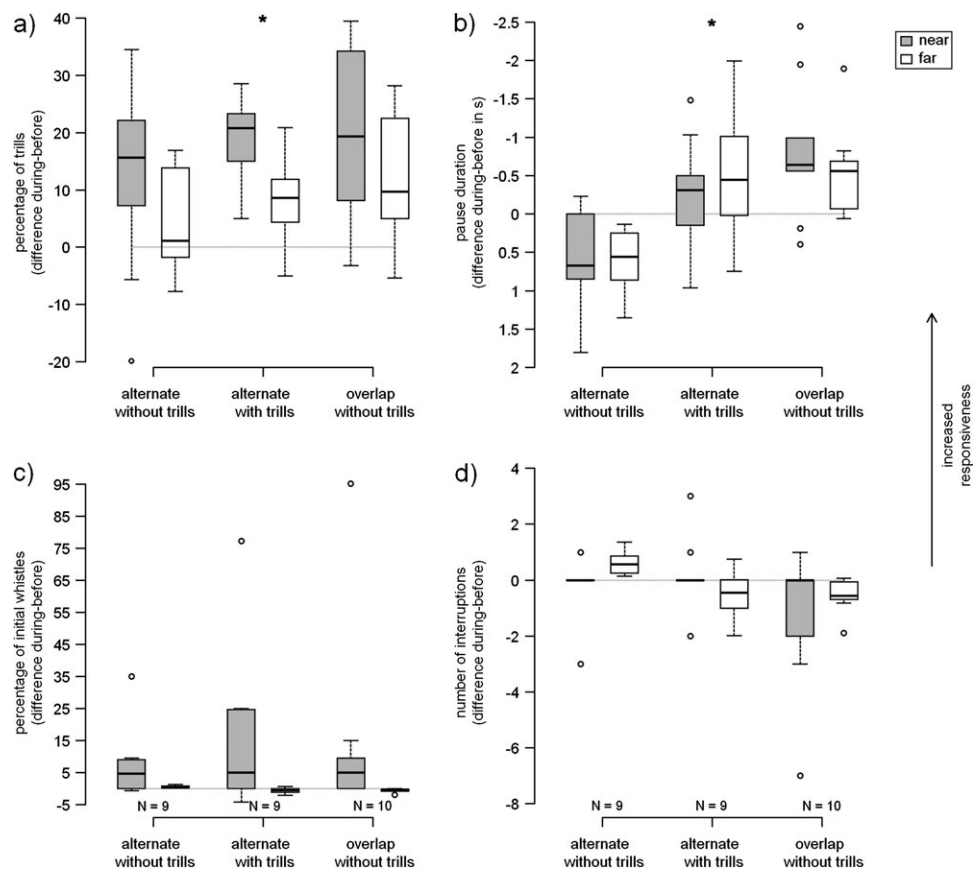
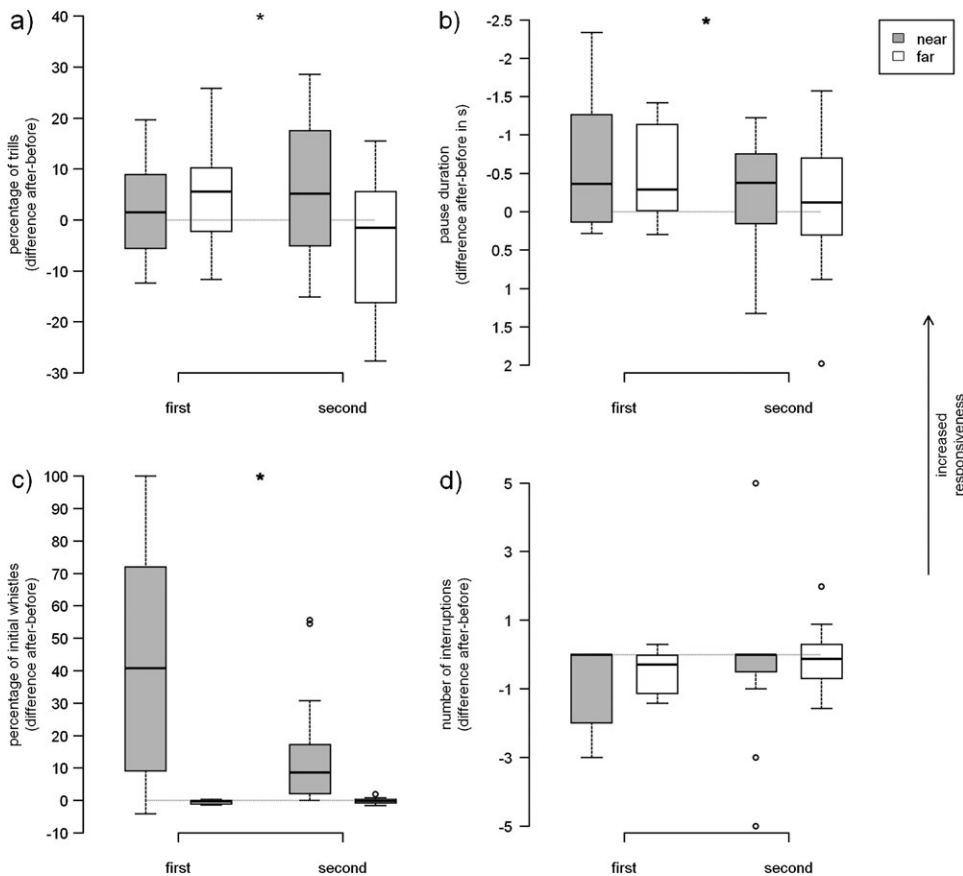


Figure 2

Effects of distance and treatment on (a) songs with rapid broadband trills, (b) pause duration, (c) songs with initial whistles, and (d) number of interruptions during playback. Gray bars represent responses to near playback (20 m) and white bars to far playback (50 m). Zero values indicate no difference in singing, and positive values indicate an increase during playback compared with before playback. Stars indicate a significant main effect of distance in (a) and a significant interaction distance \times treatment in (b).

**Figure 3**

Effects of playback order (i.e., whether playback from near or far was presented first or second) and distance on (a) songs with rapid broadband trills, (b) pause duration, (c) songs with initial whistles, and (d) number of interruptions after playback. Gray bars represent responses to near playback (20 m) and white bars to far playback (50 m). Zero values indicate no difference in singing, and positive values indicate an increase during playback compared with before playback ($N = 28$). Stars indicate a significant main effect of order in (b) and (c) and a significant interaction effect distance \times order in (a).

the other interactions between distance and order neither during nor after playback was significant (all $P > 0.23$). Also the interaction between treatment and order was not significant for any of the song parameters (all $P > 0.18$).

DISCUSSION

The experiments show that male nightingales responded more strongly to near than to far playback broadcast from outside their territory. Males sang more songs containing rapid broadband trills and songs containing initial whistles in response to near than to far playback. Males also sang with shorter pauses and thus with higher rates in response to the 2 agonistic treatments (song overlapping and rapid broadband trills) compared with the moderate playback (alternating without trills). Moreover, depending on playback treatment, males varied pause duration differently for the 2 distances. However, the effect of distance was not stronger in males that received rapid broadband trills than for males that received overlapping playback, as we had expected.

The stronger increase in the use of songs containing trills during near than during far playback shows that distance matters even beyond territorial boundaries. As trills are used more in close-range interactions (Kunc et al. 2006) and elicit strong vocal and spatial responses (Illes et al. 2006; Schmidt et al. 2008), they are considered to signal arousal and to be used as aggressive signal in male–male interactions. Consequently, our findings suggest that nearer rivals are perceived as being more threatening than more distant rivals. This conclusion is further supported by the more frequent addition of initial whistles to songs after being confronted with playback broadcast from near as initial whistles are considered an aggressive close range signal similar to “soft songs” (Sprau et al. 2010).

Surprisingly, distance-dependent responses to rivals outside territory boundaries have rarely been addressed experimentally. In a recent study, territorial black-capped chickadees (*Poecile atricapillus*) responded to simulated dyadic interactions outside their breeding territory. Moreover, males in adjacent territories responded stronger than more distant males, indicating similar effects of distance as shown here (Fitzsimmons et al. 2008). Yet, most playback experiments either simulated intrusions (e.g., McGregor 1991; Searcy and Nowicki 2005) or broadcast song from one standardized distance near (e.g., Brindley 1991; Godard 1991; Fitzsimmons et al. 2008) or very far from the territory boundary (Simpson 1985). Here, we show that also different distances are assessed when rivals are singing from outside the territory boundary, expanding on previous arguments that distance to rivals can be used to distinguish intruders from non-intruders (Naguib and Wiley 2001). In our study, however, males not only responded differently to simulated rivals singing from different distances but also changed their vocal behavior depending on whether a rival first was simulated from far and then from near or vice versa. These findings on distance effects complement recent studies showing that also spatial movements of rivals affect territorial defense by residents (Poessel and Dabelsteen 2005; Amrhein and Lerch 2010) and their neighbors (Naguib et al. 2004), emphasizing the dynamics of signaling in territorial systems. Taken together, our results highlight the distance-dependent function of song traits, where information needs to be gathered over different distances between singing males.

The difference in pause duration further shows that males responded more strongly to the alternating playback with trills and to the overlapping playback than to the alternating playback without trills. Decreases in pause duration in response to overlapping playbacks had been shown previously (e.g.,

Schmidt et al. 2006) and may be partly explained by song overlapping pushing males to shorten pause duration. Yet, given that males shortened pauses similarly in response to also the other agonistic treatment (alternating with trills), the experimental song overlapping alone cannot fully explain the strength of this effect. Unexpectedly, males did not differ in the number of singing interruptions or in use of initial whistles between the different treatments, as was shown in earlier studies (Naguib and Kipper 2006; Sprau et al. 2010; but see Schmidt et al. 2006 who also did not find such an effect). Consequently, such differential results could suggest that territorial responses such as the use of singing interruptions or songs with initial whistles often depend more individually on different signaling strategies.

In addition to testing general effects of playback distance on responses, our study was specifically designed to test whether the agonistic function of trills is distance dependent, given their rapid degradation with distance. Even though the interaction between distance and playback treatment was significant with respect to pause duration, the direction of this effect was unexpected as males reacted differently to the 2 agonistic treatments at the near distance but similarly at the far distance. We had expected males to respond similarly to the 2 agonistic treatments at near distance and to decrease responsiveness to playbacks containing trills with increasing distance much stronger than in response to the overlapping playbacks. The other response measures (songs with rapid broadband trills, songs with initial whistles, and number of interruptions) also did not vary distance dependently with treatment. Thus, males appear to have assessed the arousal of rivals, expressed in the use of trills, even without receiving the full information encoded in the frequency bandwidth that is strongly degraded at 50 m (Naguib et al. 2008). Consequently, frequency bandwidth alone cannot be the critical trait to elicit the strong responses also at far distances, unless trills were already degraded substantially after 20 m, a possibility we cannot rule out based on the current data. Yet, it is also possible that males extract information from other song parameters such as repetition rate or from the remaining bandwidth they are able to hear, allowing them to roughly assess the source frequency bandwidth of the trill without being able to actually hear the full bandwidth.

An interesting finding is that the subjects sang more rapid broadband trills in response to the near than to the far playbacks. In the light of the strong response of subjects to playback songs with trills perceived from far, we thus found a mismatch between the context in which males used trills and the context and intensity in which they responded to such trills sung by a rival. Such contrasting findings shed new light on the use and assessment of signals important for competition over resources. Assessing agonistic motivation of distant rivals and responding adequately presumably will be adaptive as it increases the probability that the rival will not approach closer. Yet, active use of rapid broadband trills that degrade easily with distance may not pay until a rival is close, suggesting that trills may function to define a repelling area and warn approaching rivals to retreat without getting involved in costly physical fights.

Taken together, our findings provide new insights into distance-dependent effects of song across territory boundaries and thus highlight the importance of song as a long-range signal in communication networks. Distance dependent use of easily degradable signal traits may enhance the territorial function of a signal as it facilitates distance assessment at close range so that perceiving high-frequency components of the signals may be used to assess the risk for an escalation of a contest. Our results also suggest that signal traits such as trills do not necessarily lose their general function when presumed key

components become degraded over distance by environmental transmission. The integration of signaling distance, signal use, and receiver response to signal traits highlights the complexity of territorial signaling.

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