



Distance-dependent responses by eavesdroppers on neighbour–stranger interactions in nightingales

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ARTICLE INFO

Article history:

Received 26 August 2011

Initial acceptance 25 October 2011

Final acceptance 20 December 2011

Available online 8 February 2012

MS. number: 11-00677

Keywords:

birdsong

communication network

conditional behaviour

eavesdropping

Luscinia megarhynchos

neighbour–stranger interaction

nightingale

In communication networks, territorial neighbours often regulate social relations using long-range signals. However, such relations may be affected when unfamiliar third parties threaten the territorial integrity of the neighbourhood. We investigated responses of vocally interacting nightingales, *Luscinia megarhynchos*, that were successively challenged by simulated rivals prospecting the neighbourhood. Using playback experiments, we tested whether territorial behaviour of males is affected differently dependent on whether their neighbours were challenged with aggressively or moderately singing rivals and whether information from the observed interaction is being used in subsequent encounters with the simulated prospector. Males sang more moderately the closer they were to a neighbour that was threatened by an aggressively singing rival. When challenged themselves, these males then discriminated between rivals depending on how they had previously interacted with their neighbour. Thus, males condition their vocal behaviour on their neighbour's situation and use information from neighbour–stranger interactions in future decision making. These findings reveal that in social networks, rivals' behaviour and distance to neighbours matter, emphasizing the importance of considering multiple individuals and their spatial relations when assessing the functions of territorial signalling.

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In many animal species, males establish and defend a territory throughout the reproductive season. As a consequence, males engage in repeated signalling interactions with their neighbours and thus form communication networks (McGregor 2005). Within those networks, familiar neighbours often behave less aggressively towards each other than towards strangers, a behavioural strategy that is also referred to as the dear-enemy effect (Fischer 1954; Godard 1991). Reducing aggression towards familiar neighbours once boundaries are established can be beneficial, as such behaviour reduces residents' expenditure in time and energy, as well as the risk of injury in frequent escalated encounters. Moreover, settling adjacent to familiar neighbours has been shown to enhance reproductive success (Beletsky & Orians 1989). In contrast, reducing aggression towards neighbours can also be costly, because defecting neighbours may benefit at the cost of a cooperative neighbour (Earley 2010). Moreover, quality-indicating traits have also been shown to affect behaviour of residents (Poesel et al. 2007). Consequently, males in communication networks face a trade-off

between behaving competitively and cooperatively with their neighbours (Godard 1993; Hyman 2002; Olendorf et al. 2004; Akcay et al. 2009).

Often, social networks involve third parties, so called audiences, that eavesdrop on others' interactions without actively interfering (Matos & Schlupp 2005). Audiences may affect the mutual relations between neighbours, and, indeed, several studies have shown that interacting individuals behave differently depending on the presence and the kind of an audience (Doutrelant et al. 2001; Earley & Dugatkin 2002; Freed-Brown & White 2009; Milner et al. 2010). However, not only may an audience affect the way others interact, but the audience itself can use information obtained by observing differences in signalling behaviour between the interactants. For instance, territorial songbirds that attend to interactions between unfamiliar conspecifics have been shown to perceive rivals that are dominant over others as more threatening (Naguib & Todt 1997; Naguib et al. 1999; Peake et al. 2001; Mennill & Ratcliffe 2004a; Illes et al. 2006; Fitzsimmons et al. 2008).

Another situation arises when third parties actively interfere with interacting neighbours (Connor 2010), such as in an attempt to establish a territory within an existing neighbourhood. Territory-seeking rivals that are new to a neighbourhood prospect different

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territories of a neighbourhood (Amrhein et al. 2004a), and thereby may challenge the territory holders. Territory holders can be expected to benefit from attending to challenges of novel rivals in the neighbourhood before actively being challenged themselves, as they could use this information in subsequent encounters with those rivals. Research on territorial singing has shown repeatedly that males in communication networks attend to each other's vocal interactions (Peake 2005; Naguib et al. 2011). However, it remains unclear whether territorial males also use information they could have obtained by eavesdropping on previous interactions between familiar neighbours and unfamiliar rivals in subsequent encounters with the same rivals (but see McGregor et al. 1997 for a preliminary experiment on this topic). Likewise, only little is known about how social relations between neighbours change when one of them is being challenged by a stranger (Detto et al. 2010; Milner et al. 2010). Understanding how neighbour relations are affected by territorial challenges of unfamiliar others, however, is an integral component in understanding the benefits of territorial neighbourhoods. A challenge to any territory holder may have consequences for the whole neighbourhood, as established relations will change if new rivals succeed in settling, to the cost of others (Mesterton-Gibbons & Dugatkin 1992; Naguib 2005; Connor 2010). Thus, males in communication networks may benefit from behaving conditionally on the situation of the neighbour (Naguib et al. 2004; Amy et al. 2010). For instance, behaving less aggressively when a neighbour is challenged by a threatening rival may enable the neighbour to focus on that rival and thus increase the probability of maintaining the stability of the neighbourhood. On the assumption that established neighbours benefit from preventing a novel rival settling too close, neighbours may interact with each other differently during any such external threat, to signal strong mutual relations to others. Such neighbour relations and how they are affected by territorial challenges of third parties are a central feature in territorial systems, yet they have not received attention in experimental research on communication networks.

Another important aspect for the strength of mutual relations in social networks is the distance between interactants. Assessing the distance to conspecifics can be important for discriminating between intruding and nonintruding rivals and as such the threat that a rival poses (Naguib et al. 2000; Naguib & Wiley 2001). Yet, distance is also important for discriminating between rivals singing from different distances outside territory boundaries (Simpson 1985; Sprau et al. 2010a). In a field experiment on Carolina wrens, *Thryothorus ludovicianus*, in which territorial neighbours were housed in cages at different distances, Simpson (1985) showed that neighbours switched song types and matched songs with neighbours more frequently at close range, suggesting that distance between neighbours strongly affects vocal behaviour and therefore social relations. Moreover, distance may affect not only territorial behaviour of interacting individuals but also that of eavesdroppers. Because territory-seeking rivals often prospect different territories (Amrhein et al. 2004a), close males that eavesdrop on their neighbours defending their territory against such prospecting rivals may behave less aggressively in order to minimize the probability of being the next target.

In the present study, we tested the effect of neighbour–stranger interactions on the behaviour of eavesdropping neighbours when they are challenged subsequently, as well as on the subsequent interactive behaviour between the two neighbours. We recorded nocturnally singing interactions between nightingales, *Luscinia megarhynchos*, and subsequently challenged the interactants one by one with aggressively and moderately singing unknown rivals. In the first playback, songs of one of the neighbours were either overlapped or alternated with playback songs, whereas in the second playback, the playback songs were alternated with the

songs of the other neighbour. Compared to song alternating, song overlapping has been shown in previous studies to elicit characteristic and often aggressive responses (see Searcy & Beecher 2009; Naguib & Mennill 2010 for discussion on this topic). We here investigated two aspects of eavesdropping on neighbour–stranger interactions. First, we tested whether neighbour–stranger interactions affect singing behaviour of eavesdropping males dependent on whether the neighbour is challenged by a more or less aggressively singing rival. Assuming that neighbours seek stable neighbourhoods, we expected eavesdroppers to behave less aggressively when their neighbours are threatened by aggressive rivals and thus to behave conditionally upon their neighbours' situation. Second, we tested whether males use information gathered during eavesdropping on neighbour–stranger interactions, when being challenged themselves by the same strangers. We expected males to respond more aggressively when they had already observed the rival being aggressive towards their neighbour.

METHODS

Study Site and Subjects

The experiments were conducted between 13 April and 2 May 2009 in the nature reserve Petite Camargue Alsacienne, France (47°37'20 N, 7°32'13 E). In this area of approximately 18 km², about 200 male nightingales occupy territories characterized by dense scrub (Amrhein et al. 2007). Usually, these territories are located along rivers or streams, pathways, grasslands or open fields. Thus, most territory boundaries are well defined by the habitat.

Male nightingales sing for many hours at night once they have arrived on the breeding grounds. Males then usually cease nocturnal song upon pairing, whereas bachelors continue to sing at night throughout the breeding season (Amrhein et al. 2002, 2004b; Roth et al. 2009). Thus, nocturnal singing activity allows us to distinguish between paired and unpaired males ('bachelors'); up to half of the males in our study area can remain unpaired throughout the breeding season (Amrhein et al. 2007). By conducting standardized census rounds at midnight and at dawn, we were able to determine the subsequent pairing status of males used for the experiments (for details of the methods see Amrhein et al. 2002). Playbacks were conducted when males were still unpaired.

For the experiments, we selected 30 dyads of interacting males (i.e. a total of 60 males). To reduce interference with neighbouring males in the vicinity, interacting males were either the only singing males in audible range, or they were further away from other singing males than twice the distance between the interacting males. Males' nocturnal songposts during interactions were a mean \pm SD of 100 \pm 78 m apart (range 33–180 m; as measured after mapping the nocturnal songposts of males on detailed maps of the area). There was no significant difference in neighbour distance between the two treatment groups (mean neighbour distance overlapping treatment: 104 \pm 103 m; mean distance alternating treatment: 96 \pm 46 m; Welch *t* test: $t_{19,39} = 0.29$, $P = 0.77$). Experiments were conducted only after both interacting males had been singing for at least three consecutive nights. Thus they had settled and had sufficient time to become familiar with each other prior to the experiments. We walked regular routes several times a day through the study site and monitored male nightingales' preferred nocturnal song perches to confirm that interacting males were the same individuals over the observation period.

Playback Stimuli

Stimulus songs used for playback experiments were taken from nocturnal song recordings of 30 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, U.S.A., sampling frequency: 44.1 kHz; resolution: 16 bit). Playbacks were obtained from recordings made in territories differing from the territories chosen for the experiments and we also did not use recordings obtained from neighbouring territories. Thus, a subject was most probably unfamiliar with the male whose songs were used for playback. Stimuli were made using the sound analysis software Avisoft SASlab Pro 4.4 (R. Specht, Berlin, Germany). All stimuli were composed of 20 randomly chosen songs from the nocturnal recordings, and stimulus songs were randomly arranged for the experiments. Each song was normalized in peak amplitude using Adobe Audition (Adobe Audition 1.0, Adobe Systems Inc., San Jose, CA, U.S.A.) to standardize the playback amplitude across trials. Sound pressure of the stimulus songs was adjusted to 90 dB at 1 m distance measured with a Voltcraft digital sound level measuring meter SL-300. This sound pressure is within the range of the sound pressure of singing nightingales (Brumm 2004).

Playback Protocol

Nocturnal dyadic vocal interactions between two neighbouring birds were recorded throughout the experiment using a Marantz PMD 660 digital solid state stereo recorder and two Sennheiser ME66/K6 directional microphones, each recording one of the two singing neighbours. After we had recorded the singing interaction for 15 min, one of the birds received one of two playback treatments ('neighbour A', Fig. 1); playback songs were either alternated with the subject to simulate a more moderately singing unfamiliar rival ($N = 15$; mean \pm SD; overlapped songs: $1.1 \pm 1.9\%$), or playback songs overlapped those of the challenged male, simulating a more aggressive rival ($N = 15$; overlapped songs: $76.7 \pm 11.0\%$). Then 15 min after the termination of the playback, the other neighbour ('neighbour B', Fig. 1) received an alternating playback, simulating the same rival that had previously been used on the 'neighbour A'. After the second playback, singing interactions between both males were recorded again for another 15 min. Because we standardized the number of songs for all playbacks, total playback durations of the first

playback were shorter for the overlapping treatment than the alternating treatment (mean \pm SD; overlapping treatment: 129 ± 22 s; alternating treatment: 157 ± 41 s, Welch t test: $t_{21,79} = 2.25$, $P = 0.035$). During the second playback, all 'neighbours B' (Fig. 1) received the same alternating playback treatment, and thus the playback duration did not differ significantly between the two treatments (previously overlapping playback: 161 ± 26 s; previously alternating: 158 ± 5 s; Welch t test: $t_{26,55} = 0.38$, $P = 0.71$).

The position of the loudspeakers was carefully chosen to ensure that both interacting males could hear the broadcast songs while at the same time ensuring that the playback was directed at the recipient and not the eavesdropper (Fig. 1). Playbacks were broadcast from 20 m from the males' nocturnal songpost, outside the territory boundary on adjacent open fields. Distances were measured using a Leica DISTO A5 laser distance meter (Leica Geosystems, Munich, Germany).

All trials took place at night, between 2350 and 0330 hours CEST. Because nightingales change their songpost only rarely at night, nocturnal playbacks allowed us to standardize the distance between males' songposts and the playback loudspeakers. In this study, none of the males changed their nocturnal songpost during the experiments.

For the playbacks, we played each song (wav file) separately using a Creative Zen digital player (Creative Labs Ltd, Dublin, Ireland). Thus, we were able to alternate and overlap subjects' songs, and ensured that no song was played twice. The digital player was connected to a Foxpro FX5 speaker (Foxpro Inc., Lewistown, PA, U.S.A.) positioned on a tripod at a height of 1.5 m on the open fields.

Response Measures and Statistical Analysis

We measured nine different song parameters of all males (Appendix Table A1): (1) song rate (songs/min), (2) song duration (s), (3) pause duration (s), (4) number of singing interruptions, (5) total duration of interruptions (s), (6) latency between the end of the song of one neighbour until the start of the song of the other neighbour (s), (7) percentage of songs males used to overlap their neighbours, (8) percentage of song type matches, and (9) percentage of songs with rapid broadband trills. As in previous studies (Naguib 1999; Mennill & Ratcliffe 2004b; Schmidt et al. 2006; Sprau et al. 2010a, b), males occasionally interrupted their

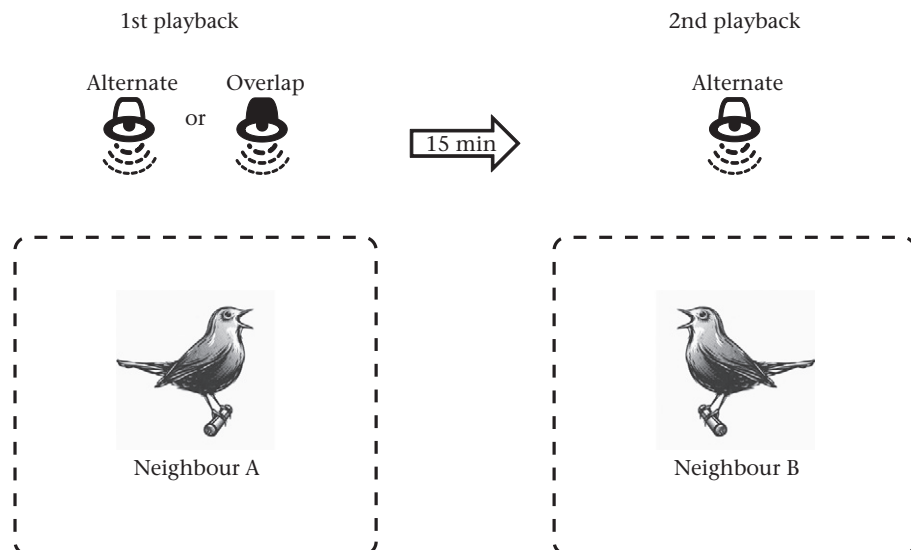


Figure 1. Playback set-up. In the first playback, neighbours A received either an overlapping ($N = 15$) or an alternating playback ($N = 15$). Then 15 min later, neighbours B ($N = 30$) received only an alternating playback from a second loudspeaker, simulating the same rival. Dashed lines indicate territory boundaries. For further details see text.

singing, leading to intersong intervals that differed substantially from the mean duration of all silent intervals. We therefore decided to analyse singing interruptions separately from the regular pause durations by defining singing interruptions as silent intervals that were longer than the mean + 1 SD of all pauses measured in the 15 min before the playback (Naguib & Kipper 2006; Sprau et al. 2010a, b). Accordingly, silent intervals that were longer than 4.75 s were considered as singing interruptions. Pauses were considered as silent intervals that were shorter than 4.75 s. Songs were defined as containing rapid broadband trills when trills in the terminal part of the song had a frequency bandwidth larger than 5000 Hz (measured at -24 dB from the peak in a power spectrum) and an element repetition rate faster than 8.5 elements/s (Naguib et al. 2008). Song type matching was defined as singing the same song type the interacting bird had just sung (Kipper et al. 2006; Sprau & Mundry 2010).

For analysis of the responses to playback, we used the song parameters measured within a period of 2.5 min before and after the playback (which corresponds to the average duration of all periods during playback, i.e. 2.51 ± 0.35 min), as well as the entire period during playback. Data were analysed using R 2.10.1 (R Development Core Team 2009). With the nine song parameters we performed a principal components analysis (PCA) over the entire duration of the experiment (i.e. before, during and after the playback) to summarize males' responses with the fewest possible composite variables. Several of the song parameters were highly correlated, and the PCA reduced these into fewer noncorrelated variables (Stamps & Krishnan 2001). We used components with eigenvalues greater than 1 to explain variation in response to the playbacks (Stamps & Krishnan 2001). The PCA was conducted using the *rda* function in R (package *vegan*, version 1.17-4), and significance of PC scores was determined using the broken-stick method with the function *PCA.significance* (package *BiodiversityR*, version 1.4.2). The principal component analysis generated two PC scores that explained 56% of the total variance and 55% of the variance using the broken-stick method (Appendix Table A2). All temporal song parameters (i.e. song rate, song duration, pause duration, number and duration of interruptions, latency to start a new song, and song overlapping) had high loadings in the first PC score (PC1), whereas all structural song parameters (i.e. song type matches, rapid broadband trills) had high loadings in the second PC score (PC2, Table A2).

The two principal components were then taken as reflecting temporal (PC1) and structural responses (PC2) in singing, and were used as response variables for linear mixed-effect models (LMM) using the *lme* function in R (package *nlme*, version 3.1-97). In all models we included three fixed factors as predictors: treatment (alternating or overlapping), future pairing status (paired or bachelor) and playback period (either before and during or before and after). We ran two different sets of LMMs in which we either tested for changes in response from before to during the playback (i.e. the fixed factor playback period consisted of the levels 'before' and 'during') or from before to after the playback (i.e. the fixed factor playback period consisted of the levels 'before' and 'after'). Playback periods during and after the playback were tested separately (while in both cases also accounting for the playback period before), to obtain a clearer picture of the male's responses. Distance between the two neighbours was fitted as a continuous variable, and we further included the PC score of the neighbour as a covariate, to test whether singing of the neighbour would affect the singing of the analysed male. Full models included the two-way interactions treatment * pairing status, treatment * playback period, pairing status * playback period and distance * playback period. If treatment affected vocal behaviour of males we expected treatment * playback period interactions to be significant. As each male was

measured twice (before and during/after the playback), individual was taken as a random effect. One of the 30 trials was excluded because of technical problems during field work. One male stopped singing before the second playback and thus could not be included in the analysis. We removed nonsignificant ($P > 0.05$) terms from the models starting with the least significant interaction (Crawley 2007). The model assumptions for all final models were tested by visual inspection of residuals plotted against fitted values (Quinn & Keough 2002).

RESULTS

Responses to the First Playback

Males that were challenged by the first playback ('neighbour A', Fig. 1) responded differently to the two playback treatments. Males showed an increase in PC1 scores (temporal song parameters) when they were overlapped, indicating that they sang with higher song rates, longer songs, shorter pauses and with fewer and shorter interruptions (Table 1, neighbour A first PB; Fig. 2). Irrespective of playback treatment, the challenged males tended to show an increase in PC1 scores also after playback (Table 1, neighbour A first PB). After playback, challenged males also tended to show an increase in PC2 scores (structural song parameters), indicating that they tended to sing more songs with rapid broadband trills and matched more songs of their neighbours, compared to before playback (Table 1, neighbour A first playback).

During playback, 'neighbours B' (Fig. 1) that could eavesdrop on the interaction between the subject and the playbacks did not show significant changes in PC scores (temporal and structural song parameters) depending on playback treatment, period, distance or subsequent pairing status during the playback (Table 1, neighbour B first playback). There was also no main effect of treatment and playback period on vocal behaviour of eavesdroppers after playback; and no effect of the interaction between treatment and period that we expected to be significant. However, after playback, neighbours changed their singing behaviour depending on playback treatment and on the distance to the challenged males (treatment * distance interaction; Table 1, neighbour B first playback; Fig. 3). With decreasing distance to the playback subject, neighbours sang with lower PC1 scores (temporal song parameters) when the subject was overlapped, but sang with higher PC1 scores when the subject received an alternating playback.

Not only was vocal behaviour of both neighbouring males directly affected by the playback, but both males also affected each other's singing. Males adjusted their temporal and structural singing behaviour to that of their neighbours, as shown by the significant effects of the covariate PC scores of the neighbour on males' singing (neighbour; Table 1, neighbour A and B first playback).

Responses to the Second Playback

When challenged themselves in the second playback, the previously eavesdropping males ('neighbours B', Fig. 1) differed in temporal song parameters (PC1 scores) depending on which playback treatment their neighbours ('neighbours A', Fig. 1) had received, and on the distance to that neighbour (treatment * distance interaction; Table 1, neighbour B second playback). With increasing distance to their neighbours, males responded to playback with higher PC1 scores when their neighbours were overlapped previously, but sang with lower PC1 scores when neighbours had received an alternating playback (Fig. 4a). Distance to neighbours also affected the way males changed their response from before the experiment to during the second playback

Table 1

Results from linear mixed-effect models (LMM) with PC1 (i.e. compound temporal parameters) and PC2 (i.e. compound structural parameters) as response variables and playback treatment, future pairing status, playback period (before and during or before and after), and distance to the neighbour as well as their two-way interactions as predictors

Response	Predictor	PC1				PC2			
		During		After		During		After	
		LR	P	LR	P	LR	P	LR	P
Neighbour A first playback	Treatment	2.62	0.11	1.51	0.22	3.22	0.07	0.30	0.58
	Pairing	0.40	0.53	0.92	0.34	2.52	0.11	0.58	0.45
	Period	3.40	0.07	3.47	0.06	0.89	0.35	3.52	0.06
	Distance	\	\	0.20	0.65	\	\	0.002	0.97
	Neighbour	\	\	8.34	0.004	\	\	5.55	0.02
	Treatment*pairing	0.03	0.85	0.10	0.75	0.93	0.34	0.53	0.47
	Treatment*period	4.19	0.041	1.47	0.22	3.14	0.08	0.70	0.40
	Treatment*distance	\	\	0.54	0.46	\	\	0.01	0.94
	Period*distance	\	\	0.33	0.57	\	\	1.34	0.25
Neighbour B first playback	Treatment	0.99	0.32	0.11	0.74	0.001	0.97	0.97	0.32
	Pairing	0.03	0.86	<0.001	0.96	0.05	0.82	0.94	0.33
	Period	1.14	0.28	0.11	0.74	1.65	0.20	1.38	0.24
	Distance	1.25	0.26	1.80	0.18	<0.001	0.99	0.97	0.33
	Neighbour	0.92	0.34	6.62	0.01	10.56	0.001	9.29	0.002
	Treatment*pairing	0.62	0.43	0.31	0.58	2.69	0.10	3.59	0.06
	Treatment*period	0.81	0.37	0.15	0.70	0.05	0.82	0.50	0.48
	Treatment*distance	2.54	0.11	4.61	0.03	0.13	0.72	0.48	0.49
	Period*distance	2.92	0.09	0.99	0.32	0.73	0.39	0.002	0.96
Neighbour B second playback	Treatment	0.02	0.90	0.36	0.55	0.06	0.80	0.10	0.75
	Pairing	0.01	0.94	0.08	0.77	0.01	0.94	0.87	0.35
	Period	6.89	0.01	1.08	0.30	0.71	0.40	0.13	0.72
	Distance	0.03	0.86	0.54	0.46	0.10	0.75	0.02	0.88
	Neighbour	5.85	0.02	12.02	0.001	9.99	0.002	2.03	0.15
	Treatment*pairing	6.78	0.01	1.90	0.17	0.01	0.92	0.002	0.97
	Treatment*period	<0.002	0.99	0.72	0.40	0.02	0.90	0.04	0.84
	Treatment*distance	5.11	0.02	1.47	0.22	0.22	0.64	0.07	0.79
	Period*distance	5.94	0.01	3.40	0.07	1.98	0.16	0.06	0.80

The vocal behaviour of the neighbour (PC scores) was included in the model to test whether neighbours affected each other. LR are likelihood ratios between alternative models and all *df* = 1. Significant variables are indicated in bold.

(period * distance interaction; Table 1, neighbour B second playback). Whereas males showed an increase in compound temporal song parameters (PC1) with increasing distance to their neighbours before the experiment, they showed a decrease in PC1 scores when they were challenged themselves by these rivals (Fig. 4b). Also this

analysis showed that males adjusted their temporal and structural singing behaviour to that of their neighbours as represented by the covariate PC score of the neighbour (neighbour; Table 1, neighbour B second playback).

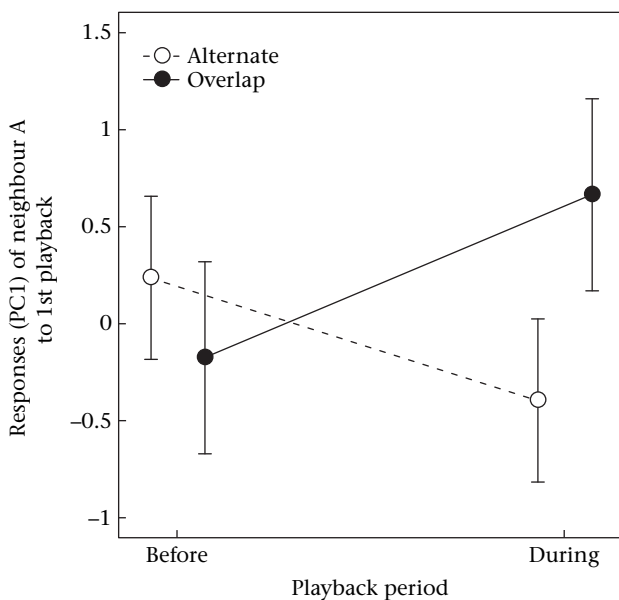


Figure 2. Effects of playback treatment and period (before or during playback) measured as composite temporal song parameters (PC1) on challenged males ('neighbours A') singing during the first playback. Means are shown ± SE.

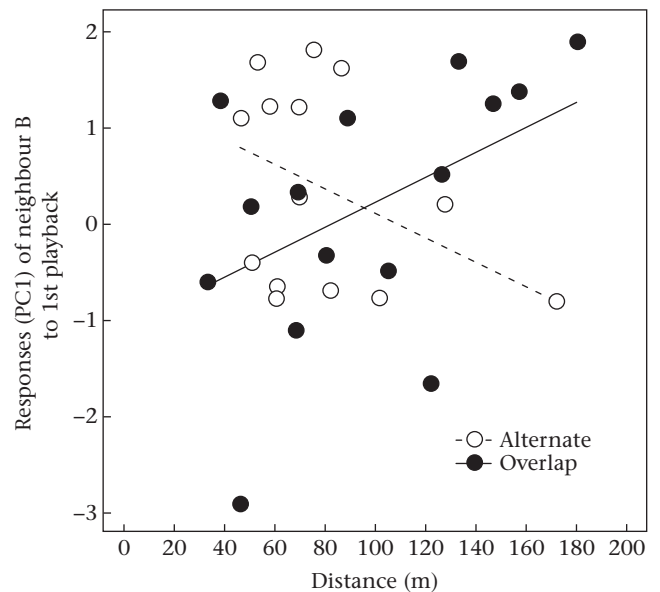


Figure 3. Effect of playback treatment and distance between neighbours measured as composite temporal song parameters (PC1) on males that eavesdropped on neighbour-stranger interactions ('neighbours B') after the first playback. Removal of the outlier (bottom left) still leads to a significant interaction between treatment and distance (LR = 4.03, *P* = 0.045).

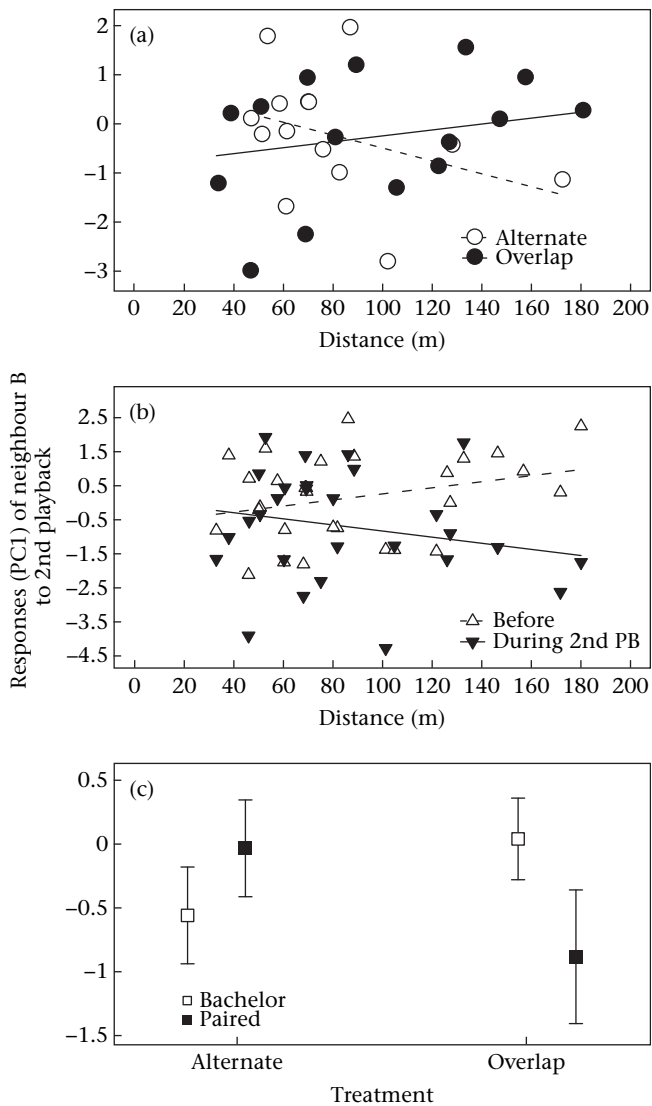


Figure 4. Effects on composite structural song parameters (PC1) used by males that were challenged during second playback ('neighbours B') of (a) playback treatment and distance between neighbours, (b) distance between neighbours and playback period on temporal song parameters (PC1), and (c) treatment and pairing status. Means are shown \pm SE.

Moreover, subsequently paired males and bachelors responded differently depending on the playback treatment their neighbour had received previously. Subsequently paired males sang with higher PC1 scores (temporal song parameters) than bachelors, thus responded more strongly, when their neighbours had received an alternating playback, but with lower PC1 scores when their neighbours were overlapped (treatment \times pairing interaction; Table 1, neighbour B second playback; Fig. 4c).

DISCUSSION

The experiments reveal that playback treatment (i.e. song overlapping and song alternating) affected the vocal response of males that received the playback, and, dependent on the distance to the neighbour, also the vocal response of males that could eavesdrop on these neighbour-stranger interactions. Moreover, when eavesdroppers were challenged themselves by the same simulated stranger, their responses depended on whether the rival had

previously behaved more or less aggressively towards their neighbour and on distance to that neighbour. These experiments show that eavesdropping territorial males adapt their vocal behaviour to the situation of their neighbours when they are challenged and use information gathered during neighbour-stranger interactions in future decision making.

Males that were challenged with the overlapping treatment in the first playback showed an increase in compound temporal song parameters, indicating that they sang with higher song rates, longer songs, shorter pauses, and with fewer and shorter interruptions than those males that were challenged with the alternating treatment. These findings show that the response of the challenged males depended on the simulated rivals' vocal behaviour, and suggest that overlapping playback was considered as more threatening (Mennill & Ratcliffe 2004b; Hall et al. 2006; Naguib & Kipper 2006; Schmidt et al. 2006). Even though playback treatment itself did not have the expected effect on the behaviour of males that could eavesdrop on their neighbours interacting with the simulated rivals (i.e. there was no significant treatment \times playback period interaction), treatment did affect vocal behaviour of eavesdroppers in a distance-dependent way. Close eavesdroppers sang more moderately after their neighbours were challenged with an aggressively singing rival. These findings suggest that males attended to others' interactions and thus support findings of studies that simulated interactions between two strangers (Naguib & Todt 1997; Naguib et al. 1999; Peake et al. 2001; Mennill & Ratcliffe 2004a; Illes et al. 2006; Fitzsimmons et al. 2008; Amy & Leboucher 2009). Naguib et al. (2004) further showed that eavesdropping nightingales use interactions of their neighbours with unfamiliar strangers as a yardstick for their own response. Conditioning behaviour on the situation of the neighbour may be adaptive, as it may stabilize the neighbourhood. One possibility for eavesdroppers to help maintain the integrity of the neighbourhood in threatening situations is to behave aggressively. Increased aggression, however, could also be perceived by challenged neighbours as an additional threat against themselves so that they would have to decide whether to reply to the neighbour or the unfamiliar rival. Consequently, behaving less aggressively when neighbours are at risk of losing their territory against others may be another strategy to stabilize the neighbourhood, because decreased aggression could enable challenged neighbours to focus on defending their territory.

The findings that males behaved less aggressively towards close neighbours may be taken to suggest that neighbours form defensive coalitions (Getty 1987; Mesterton-Gibbons & Sherratt 2009). Neighbours can benefit from building such defensive coalitions, as they would not have to renegotiate a new dear-enemy relationship with an unknown rival that acquired the territory of a familiar male, especially since these new rivals may also be stronger than a displaced male (Backwell & Jennions 2004; Detto et al. 2010). In general, influences of third parties on social relations between neighbours, as documented here, are still poorly understood (Naguib et al. 2004; Akçay et al. 2010; Amy et al. 2010). Thus, our findings showing that territorial males condition their vocal behaviour on their neighbours' situation provide new insights in social regulations between neighbours in communication networks.

The less aggressive behaviour of territorial males towards close neighbours that were challenged by aggressive rivals, however, may not only be advantageous for the stability of the neighbourhood. Behaving less conspicuously when neighbours are challenged by rivals may also be beneficial for the males themselves, as they may well expect to be challenged by the same rivals in subsequent encounters. Territory-seeking males that are new to a neighbourhood have been shown to prospect other territories in succession (Amrhein et al. 2004a). Therefore, males in communication

networks may have to use anticipatory strategies to avoid too much attention, such as behaving less aggressively when an aggressive rival challenges a neighbour. Such anticipatory behaviour may then also explain why playback treatment affected eavesdroppers' vocal behaviour not only during the first but also during the second playback. Males discriminated between rivals that had previously interacted aggressively or moderately with their neighbours, when they were challenged themselves by the same simulated rivals, even though rivals did not differ in their challenging behaviour. Even though we cannot exclude that males' singing during the second playback resulted from long-term consequences of the first playback, such possibly persisting discriminative behaviour also indicates that males extract information from singing interactions involving their neighbour and this affects their subsequent responses according to the threat an unfamiliar rival imposed on the neighbour. Similar two-loudspeaker experiments on great tits, *Parus major*, showed that males responded more strongly to intruders that had previously been more dominant in interactions with another rival than to intruders that were less dominant (Peake et al. 2001, 2002; Peake 2005). Two-loudspeaker experiments, simulating interactions between two unknown rivals, most probably reflect situations early in the season when not all territories are occupied. Later in the season, when the first territories have been established, males will most often be exposed to song of neighbouring individuals. In a recent study on song sparrows, *Melospiza melodia*, Akcay et al. (2010) showed that territory owners attend to simulated intrusions of familiar neighbours into another neighbour's territory, and use that information during subsequent interactions with these defecting neighbours. At such later stages of the breeding season, late-arriving males that are still nonterritorial may yet constitute a different situation, because information gathering and processing includes both familiar and unfamiliar conspecifics. Our experiments simulated this latter situation and thus they complement previous findings by showing that resident males also use information on challenging strangers that had previously been interacting with familiar neighbours. Such coordinated behaviour may well be adaptive, as it can reduce costs for residents in defending and maintaining resources against any newly arriving male attempting to establish a territory.

The distance-dependent response of eavesdroppers to simulated rivals could be further affected by variation in signal amplitude at the position of the receiver. Close neighbours, and also playback at the position of a close neighbour, are presumably perceived by the focal bird as being louder. This is important, because it has been shown that territorial songbirds react more strongly towards rival males singing high-amplitude songs (Brumm & Ritschard 2011; Ritschard et al. 2012). On the assumption that nightingales can assess the distance to their neighbours (as well as to the playback) by ear, as has been shown in other songbird species (Naguib & Wiley 2001), they should have information about the actual distance and thus also about the source level of the songs.

Similar to previous studies (Kunc et al. 2006, 2007; Schmidt et al. 2006, 2008), in the present study subsequently paired males and bachelors responded differently to playback. However, response behaviours between subsequently paired males and bachelors did not differ when males directly experienced the different playback treatments, but only when they experienced rivals that had previously behaved aggressively or moderately during interactions with their neighbours. These findings suggest that information gathered from eavesdropping on interactions also affects paired males and bachelors differently. Extending earlier findings showing that eavesdropping females can affect males' reproductive success (Otter et al. 1999; Mennill et al. 2002), our results suggest that singing responses of eavesdropping males can also predict subsequent reproductive success.

Taken together, our experiments reveal that territorial males' vocal behaviour depends upon their neighbours' situations and that they sing less aggressively when the territorial integrity of neighbours is being threatened. Such behaviour may well be adaptive as it may help stabilize established neighbourhoods. Our experiments also show that males integrate information on rivals obtained during previous encounters of these rivals with their neighbours and use that information in subsequent contexts. Thus, these findings provide new insights in information gathering and processing in communication networks and show how social relations of interacting neighbours are affected when audiences take action.

Acknowledgments

We thank Martin Lutsch, Christina Brendler, Laurent Emily, Peter Santema and Julia Wesley for assistance in the field and Joe Waas for discussions stimulating this experiment. The research was funded by the Swiss Association Pro Petite Camargue Alsacienne, the Treubel-Fonds and the Deutsche Forschungsgemeinschaft (Na 335/8).

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Appendix

Table A1

Descriptive statistics of the song parameters measured during 15 min before the experiments started

Song parameter	Mean	SD
Song rate (songs/min)	9.13	1.35
Song duration (s)	2.92	0.30
Pause duration (s)	3.35	0.45
Number of interruptions	17.40	16.43
Total duration interruptions (s)	119.08	129.18
Latency (s)	1.50	0.25
Song overlapping (%)	34.05	6.66
Song type matching (%)	2.47	3.00
Rapid broadband trills (%)	19.23	5.44

Table A2

Results of the principal components analysis of nine song parameters for 58 males, showing unrotated component loadings, eigenvalues, percentage of total variance and broken-stick percentage explained by each component

Song parameter	PC1	PC2
Song rate (songs/min)	0.48	−0.10
Song duration (s)	0.66	−0.19
Pause duration (s)	−0.37	−0.14
Number of interruptions	−0.48	−0.12
Total duration interruptions (s)	−0.47	−0.11
Latency (s)	−0.46	−0.07
Song overlapping (%)	0.29	0.18
Song type matching (%)	0.05	0.88
Rapid broadband trills (%)	0.12	0.27
Eigenvalue	3.43	1.03
Percentage of variance	42.89	12.86
Broken-stick percentage	33.97	21.47

PC1 represents temporal song parameters and PC2 structural song parameters.