Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales

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Animal communication often occurs in communication networks in which multiple signalers and receivers are within signaling range of each other. In such networks, individuals can obtain information on the quality and motivation of territorial neighbors by eavesdropping on their signaling interactions. In songbirds, extracting information from interactions involving neighbors is thought to be an important factor in the evolution of strategies of territory defense. In a playback experiment with radio-tagged nightingales *Luscinia megarhynchos* we here demonstrate that territorial males use their familiar neighbors' performance in a vocal interaction with an unfamiliar intruder as a standard for their own response. Males were attracted by a vocal interaction between their neighbor and a simulated stranger and intruded into the neighbor's territory. The more intensely the neighbor had interacted with playback, the earlier the intrusions were made, indicating that males eavesdropped on the vocal contest involving a neighbor. However, males never intruded when we had simulated by a second playback that the intruder had retreated and sang outside the neighbor's territory. These results suggest that territorial males use their neighbors' singing behavior as an early warning system when territorial integrity is threatened. Simultaneous responses by neighboring males towards unfamiliar rivals are likely to be beneficial to the individuals in maintaining territorial integrity. *Key words:* communication networks, eavesdropping, *Luscinia megarhynchos*, radio-tracking, territory defense. *[Behav Ecol 15:1011–1015 (2004)]*

Male songbirds commonly settle in neighborhoods in which other territorial males are a fundamental component of the environment in which signaling and territorial behavior has evolved. To adaptively defend resources in such an environment, it is necessary to gather information about competitors. Such information can be obtained by attending to signals and signaling strategies used for individual territorial advertisement (Catchpole and Slater, 1995) or by eavesdropping specifically on signaling interactions (McGregor and Dabelsteen, 1996). Attending to signaling interactions can allow bystanders to extract information on relative differences among competitors by direct comparison and thus is thought to be of primary social importance in optimizing strategies of territory defense. Recent research has shown that songbirds extract information from vocal interactions between two simulated strangers. Experiments on nightingales *Luscinia megarhynchos* (Naguib and Todt, 1997; Naguib et al., 1999) and great tits *Parus major* (Peake et al., 2001, 2002) showed that males extract information from asymmetries in the timing of songs and use this information adaptively by responding more vigorously to the more dominant singer. In female birds, long term effects of such eavesdropping have been documented in black-capped chickadees *Poecile atricapillus*, which seem to use information gathered by eavesdropping on male-male interactions in reproductive decisions (Mennill et al., 2002). Studies on fish also have shown that eavesdropping exists in other taxa using different signaling modalities (Earley and Dugatkin, 2002; Oliveira et al., 1998). Thus, eavesdropping appears to be a general pattern of information gathering in animal communication (Johnstone, 2001; Whitfield, 2002).

McGregor and Dabelsteen (1996) pointed out that songbirds that eavesdrop on interactions between a neighbor and an unfamiliar rival should use the neighbor's performance as a measure to assess the unfamiliar rival. Yet, evidence for eavesdropping by male songbirds on singing interactions has been derived from territorial males being confronted with interactions between two simulated strangers. A more naturalistic approach to communication networks is to consider singing contests involving a territorial male and the effects this contest has on neighbors. Neighbors constitute a vital part of the environment in which territorial strategies have evolved and in which an individual attempts to maintain territorial integrity. However, effects of singing contests on neighbors are difficult to assess, since eavesdropping neighbors may remain silent but react with movements within and between territories. Previous studies used radio telemetry to show that male songbirds have activity ranges larger than their singing territory and that forays into neighboring territories are common (Chandler et al., 1997; Naguib et al., 2001; Pitcher and Stutchbury, 2000).

Here, we report an experiment on male songbirds in which we used playback experiments combined with radio-tracking techniques to study effects of territorial intrusions on neighboring males. We tested the specificity with which male territorial nightingales respond to simulated intrusions by strangers into a neighboring territory. We investigated how such a response depended on (1) the neighbor's performance during a vocal interaction with the intruder and (2) the subsequent behavior and location of the intruder, i.e., whether or not it had been expelled from the neighbor's territory.

Figure 1
Experimental setup. Experiment 1: A resident male (M1) was challenged by playback. Singing responses and spatial movements of a neighbor (M2) were surveyed by radiotracking. Experiment 2: Part 1 equals playback 1. In part 2 we simulated the intruder by a second playback from outside the territory to have withdrawn two min after the simulated intrusion had ended.

Experiment 1

M1   M2

Experiment 2

Part 1

M1   M2

Part 2

M1   M2
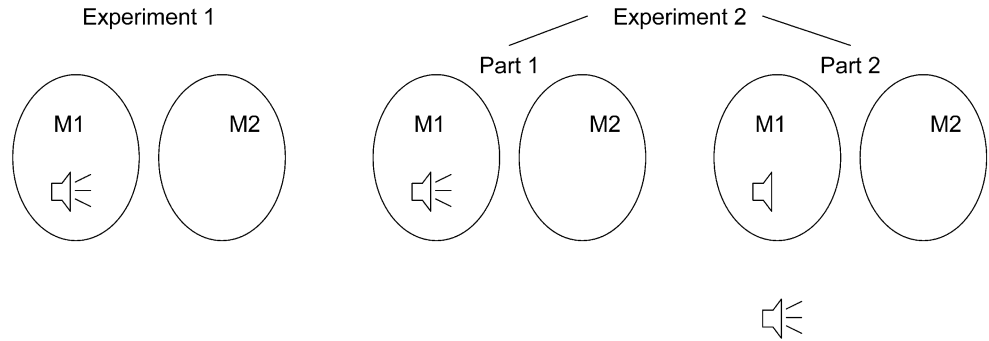
METHODS

Study area and general radio-tracking procedures

We conducted the playback experiments on 15 territorial males and 19 territorial neighbors in April and May 2002 and 2003 on a well-studied population of territorial nightingales at the Petite Camargue Alsacienne in France, 10 km North of Basel, Switzerland (Amrhein et al., 2002). The first singing males were heard on 12 April (in 2002) and 13 April (in 2003), and the first females arrived on 20 April in both years. We caught nightingales soon after arrival on the breeding ground and attached radio tags (0.9 g, Titley Electronics, Australia) to their backs. We removed the radio tags about three weeks later. As radio-tracking equipment we used three-element Yagi antennas (Biotrack LTD, UK and Titley Electronics) and Mariner M-57 (Mariner Radar LTD, UK) and Regal 2000 (Titley Electronics) receivers. We applied standard tracking procedures by recording the location and distance of a subject based on signal strength, variation in signal strength, habitat structure, sight of the subject, and its singing behavior. The fragmented habitat additionally provided reliable cues about the location of a subject. We followed movements of males from as much distance as possible, usually about 20 m distance, to minimize disturbance, and we had no indication that our presence or movements affected the subjects' spatial behavior or singing behavior. To determine borders of singing territories, we tracked all tagged neighbors ($n = 19$) and most ($n = 9$) resident males that received the playback for at least seven hours each on the days prior to playback. During those tracking and observation sessions, we recorded every two minutes the location of the focal bird on a detailed map of the study site and marked whether or not it was singing. Out of the 15 resident males that received the playback, six males were not radio-tagged, but we observed them for the same period and marked all singing locations on a map.

Immediately before onset of the playback, the tagged neighbors were tracked for 30 min, and in cases in which playback subjects were radio-tagged, we also tracked them for the same period. When playback ended, we continued to track the tagged birds for 30 min. During and after the playback sessions, all movements of the neighbors were continuously followed and their changes in locations were recorded on the map. When males approached in the vicinity of a territorial boundary, we positioned ourselves along the line of the territory boundary such that we could determine with high accuracy whether or not a male trespassed a territory boundary. For data analysis, we used SPSS 11.5.1. All given statistical tests are two-tailed. Averages are given as mean ± SE.

Playback experiments

Playbacks were conducted on 15 male territorial nightingales from 26 April to 9 May 2002 (experiment 1) and 26 to 29 April 2003 (experiment 2), after territories had been occupied for several days and after most females had settled. Playback tapes were created from clear recordings made with a Sennheiser ME66/K6 directional microphone (Sennheiser electronic GmbH, Germany) from less than 10 m distance of 15 color-ringed males in 2001, within the local population at sites out of earshot from the playback sites. We digitized songs at 44,100 Hz and 16 bit on a PC and used Cool Edit (Syntrillium Software Cooperation, USA) to generate playback tapes. We selected at random 20 different song types from each male (male nightingales have song repertoires of 160–240 song types; Hultsch and Todt, 1981). All files used from one male were normalized at once to the peak amplitude using Cool Edit so that natural variations in sound level among the different song types were conserved on each playback tape. We recorded songs on a tape with about 400 ms silence between songs, which allowed us to release songs one by one using the pause button so that we could play songs manually at a normal singing rate and then could switch to an interactive playback once the resident that received the playback had started to sing. Each male received a playback with songs recorded from a different male.

We simulated the strangers' intrusions by playbacks, conducted on 15 territorial males with one ($n = 11$) or two ($n = 4$) radio-tagged neighbors. In the cases of two radio-tagged neighbors (two cases in each year), both were radio-tracked during the experiments. Playbacks were never conducted on the same day on which we had captured and radio-tagged a male involved in the experiment. Seven males received one playback simulating an intruder, to test whether or not neighbors would respond in relation to the performance of the challenged resident during playback (experiment 1; Figure 1). For eight males, we used a dual playback approach in which we first simulated an intrusion (as in experiment 1) and 2 min after the end of the playback we repeated the playback from outside the territory (and outside any neighboring territory) using a second set of the same equipment and playback songs (experiment 2; Figure 1). The aim of the second playback in experiment 2 was to test whether or not a neighbor's response was contingent on the location of the intruder, i.e., whether or not the stranger had been expelled from the territory. In two cases (one in each experiment) we used the same two males reciprocally, once as a neighbor and once as a playback subject, with at least one day between the two experiments.

Songs were played from a Sony WMD6 or a Sony TC-D5M tape recorder (Sony Ltd., Japan) through a Blaupunkt MPA 2
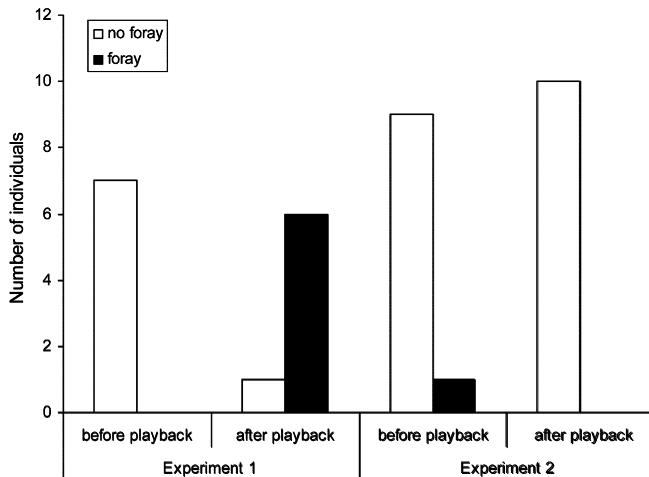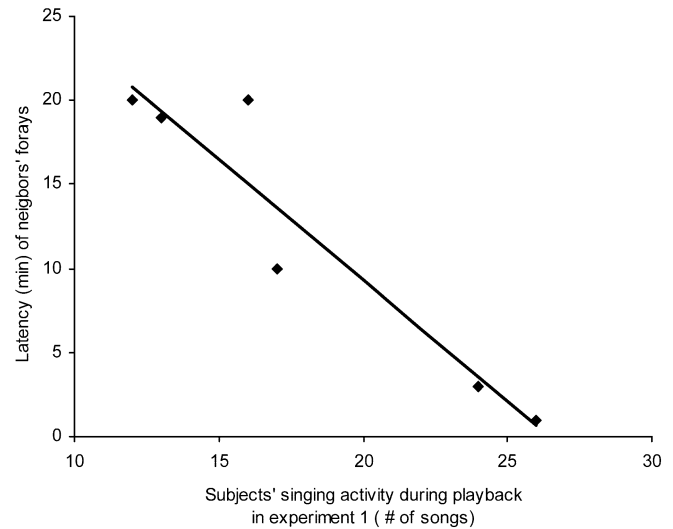
Figure 2
Number of radio-tracked males that forayed within the 30 min before and after playback into the territory in which the intrusions were simulated.

Figure 3
Linear regression of the latency by neighbors to intrude in the playback territory on the residents singing activity during playback (experiment 1). The more the challenged resident had been singing during playback, the earlier the neighbor intruded its territory.

amplifier (Blaupunkt GmbH, Germany) connected via a 25 m cable to a Canton Plus X loudspeaker (Canton Elektronik GmbH, Germany). The loudspeaker was placed at a height of 1.5 to 2 m within the subject's singing territory. The loudspeaker inside the territory of the male that received playback was placed at 20 ± 3 m from its territory boundary with the neighbor that was radio-tracked and 39 ± 5 m from that neighbor's territorial boundary ($n = 19$). In the second playback in experiment 2, the loudspeaker was placed outside any territory and about 25 m outside the territory in which the intrusion had been simulated, but within hearing range of the radio-tagged neighbor (56 ± 12 m from its boundary). At the onset of playback the territory owners were 33 ± 8 m away ($n = 12$, as for some resident males the exact location at the onset of playback was not known) from the loudspeaker but inside their territory. Neighbors ($n = 18$) also were inside their own territories at the onset of playback and were 81 ± 7 m away from the loudspeaker. The distance of neighbors from the loudspeaker at the onset of playback that simulated the intrusion did not differ between the two experiments ($U = 29$, $p = .35$, $n_1 = 9$, $n_2 = 10$; Mann-Whitney U test).

Songs were played at a rate of nine songs/min and a peak amplitude of 86 dB as measured at 1 m prior to playbacks (Brüel & Kjær precision SPL meter 2233; Brüel & Kjær, Denmark). Once the resident male that received the playback started to sing, we first alternated songs with him and then simulated a moderately aggressive intruder by overlapping $23 \pm 4\%$ of the number of a resident male's songs (Langemann et al., 2000; Naguib, 1999). We used standard loop playback with the same 20 songs used in the simulated intrusion, respectively, at a natural rate of 9 songs/min for playback from outside the territory.

RESULTS

Challenged by simulated territorial intrusions, all except two resident males that had received the playback approached the loudspeaker and counter sang with playback (binomial test, $p = .007$, $n = 15$). The playback also elicited singing by 17 out of the 19 radio-tracked neighboring males (binomial test, $p = .001$). In experiment 1, i.e., the playback broadcast only from inside the territory, neighbors intruded into the threatened territory after the playback had ended (Figure 2). This happened in all six cases in which the resident male counter

sang with the playback (binomial test, $p = .03$, $n = 6$). The more a challenged resident had been singing during the playback, the earlier the neighbor intruded his territory (Figure 3; linear regression, $r^2 = .89$, $F_{1,4} = 35.58$, $p = .004$). Neither the number of songs overlapped by the playback, the song rate of the interactively played songs, nor the song rate by the subject after playback had a significant influence on the neighbors' latency to intrude (all $r^2 < .4$, all $p > .16$, linear regressions). Neighbors did not make longer forays when subjects had sung more songs during playback ($r^2 = .45$, $F_{1,4} = 4.13$, $p = .122$, $n = 6$, linear regression). Foray duration was 10 ± 4 min. Neighbors started moving towards playback with a latency of 4 ± 2 min and intruded into the playback territory 12 ± 4 min after onset of playback. They intruded by 15 ± 5 m into the territory in which the intrusion was simulated.

In the experiment simulating first an intrusion and two min later a retreat of the intruder (experiment 2), all except one resident that were challenged by playback were singing during the first and during the second playbacks. During the second playback, three subjects resumed singing in direct response to this second playback, four subjects still had been singing since the first playback, and one subject that also did not sing during the first playback started to sing only after the second playback had terminated. All except one of the 10 neighbors that were radio-tracked sang during the first playback and five also sang during the second playback. Three neighbors approached the boundary shared with the male that had received the playback but the other seven neighbors did not approach. The song rate by resident males in response to the simulated intrusions into their territory (experiment 1 and part 1 of experiment 2) did not differ between the two experiments ($U = 17.5$, $p = .24$, $n_1 = 7$, $n_2 = 8$; Mann-Whitney U test). In contrast to experiment 1, no neighbor intruded into the territory of the male that had received the playback (Figure 2; binomial test, $p = .008$, $n = 8$). Males thus intruded only when there was no evidence that the simulated intruder had withdrawn from the territory (Fisher's Exact test, $p = .001$, $n = 15$).

DISCUSSION

Male nightingales intruded into their neighbor's territory after we had simulated an intrusion by a stranger into that neighbor's territory. The more their neighbor had been singing during the interaction with the simulated intruder, the earlier males intruded. This indicates that territorial males eavesdropped on the vocal contest between their neighbor and the intruder and used their neighbor's performance as a standard for their own response. These male's spatial movements depended on the location of the stranger, as males did not intrude into their neighbor's territory when we had simulated the unfamiliar intruder as having withdrawn from that territory.

Our finding that songbirds eavesdropped on interactions in their neighborhood confirms the findings of previous studies on this topic (Naguib and Todt, 1997; Naguib et al., 1999; Peake et al., 2001, 2002). Moreover, our results expand on these findings by showing that males use their neighbors' performance during a singing interaction with an unfamiliar intruder as a standard for their own response. This had been predicted to be a key factor in the evolution of eavesdropping in communication networks (McGregor and Dabelsteen, 1996), but had not yet been tested empirically. The studies on male eavesdropping mentioned above have focused on singing responses and conspicuous approaches to singing contests between two simulated strangers. We here document that information obtained through eavesdropping can result in subtle reactions such as intrusions into a neighboring territory, complementing previous findings on female responses to male vocal interactions (Mennill et al., 2002; Otter et al., 1999). In contrast to previous findings that high song rates more effectively keep out neighboring males in nightingales (Naguib et al., 2001), the radio-tagged neighbors here intruded earlier the more the resident males had been singing during the contest. Thus, the consequence of male song as a keep-out signal appeared to be reversed in a situation in which eavesdropping males were responding to a singing contest between their neighbor and a non-territorial stranger.

Males intruded into their neighbor's territory only when we had not simulated the unfamiliar rival as having withdrawn, i.e., when no information was given on the subsequent location of the stranger. One possible explanation is that males intruded to be in better position to locate the stranger. Intrusions, thus, may have functioned to obtain more information on the situation at close range. Unfamiliar non-territorial males, as they often sample several territories subsequently, may represent a prevalent threat for any territorial male in the neighborhood, (Amrhein et al., 2004). Intrusions into neighboring territories, as observed in our experiment, may thus serve in defending the own territory against unfamiliar non-territorial males. Alternatively, males may have intruded into their challenged neighbor's territory to exploit its distraction by the playback and to investigate its territory. However, this seems to be a less important function of an intrusion, given that males have ample opportunities to foray into their neighbor's territory in less intense and presumably risky situations. Being detected during an intrusion can be costly in terms of physical injuries and in terms of challenging long-term mutual relations (Godard, 1993). If resident males are alerted already by an intrusion of a stranger, costs of intrusions by neighbors are likely to be particularly high. Thus, males seem to intrude only in a situation when they have no information about the fate of the stranger. Any further information obtained during a foray in this situation is presumably highly valuable. Strangers that are expelled and then sing outside a territory still can be a threat to the status quo of territorial integrity, but this threat is not as directly linked to the neighboring territory.

The general singing responses by neighboring males in both experiments raise broader issues on adaptive strategies in the evolution of territorial behavior in neighborhoods and of decisions of territorial settlement. Singing responses by both the challenged subjects and their neighbors are likely to increase the probability of repelling an intruder from the neighborhood, regardless of whether this is an evolved mutualistic strategy or a side-effect of defending the own territory. Newly arriving males seeking to establish a territory may be more likely to avoid sites where they have to expect resistance by several established territory holders. Thus, neighbors in territorial systems could benefit from each other not only by decreasing the territorial interference (Godard, 1991; Stoddard, 1996), a benefit known as the 'dear enemy effect', but also by using each other as early warning systems (Eason and Stamps, 1993) and as mutual border guards when the status quo of territorial integrity is threatened. These considerations emphasize that neighbors are likely to play an important role in the evolution of strategies in territorial settlement.

Taken together, our study emphasizes that territorial defense and territorial settlement have to be viewed from a broader perspective that takes into account neighboring individuals and their behavior (Stamps, 1994; Stamps and Krishnan, 2001; Naguib 2004). Integrating playback experiments with radio-tracking procedures may pave the way for further insights into the evolution of territorial strategies and the significance of eavesdropping in communication networks.

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