

Differential effects of moving versus stationary territorial intruders on territory defence in a songbird

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Summary

1. In territorial contests, not only acoustic or other signals, but also the movements of a territorial intruder are likely to influence the response of a resident.
2. We tested this movement hypothesis by simulating moving vs. stationary intruders into the territories of winter wrens *Troglodytes troglodytes*, using the same non-interactive song playbacks in both treatments.
3. Male winter wrens showed a different long-term singing reaction in response to a moving than to a stationary intruder.
4. One day after experiencing an intruder that was switching between three locations, residents started to sing earlier before sunrise, and they sang more and longer songs at dawn than before the intrusion.
5. Residents receiving the same playback from one location only reacted by starting to sing later relative to sunrise, and by singing fewer and shorter songs than before the intrusion.
6. We could not discriminate between the treatments when examining the short-term singing reactions during and immediately after the playbacks. However, our results clearly demonstrate an effect of the spatial behaviour of territorial intruders on the long-term territory defence of residents at dawn, about 24 h after an intrusion.
7. We argue that spatial behaviour of territorial intruders should be an integral part of the study of animal territory defence behaviour. Investigating long-term changes in territory defence at dawn is a sensitive tool for discriminating between different types of intruders.

Key-words: bird song, communication, dawn chorus, interactive playback, loser effect, simulated intruder, winner effect

Introduction

Many animals compete for resources such as mates, food or shelter by excluding competitors from a territory containing the resources (Davies & Houston 1984; Maher & Lott 1995). Invasions of a territory by an intruder often elicit aggressive responses from the resident. Responses can involve physical contact, but often are mediated by passive signals such as visual, acoustic, chemical or tactile cues (Bradbury & Vehrencamp 1998; Darden & Dabelsteen 2008). Theory predicts that territory owners adapt their level of aggression and their territory defence effort in response to intruders' behaviour (Switzer, Stamps & Mangel 2001; López-Sepulcre & Kokko 2005). For example, in a variety of animal species, residents have been shown to react differently depending on the types or numbers of intruders (Chapman & Kramer 1996; Desjardins

et al. 2008) and depending on the information content of the signals given by the intruders (López, Martín & Cuadrado 2004; Mucignat-Caretta, Cavaggioni & Caretta 2004; Stropa 2007). In studies on acoustic territory defence in songbirds, interactive song playbacks have been used to demonstrate that residents either react more aggressively or more cautiously when their songs are overlapped by a simulated singing intruder (Naguib & Kipper 2006; Osiejuk, Ratyńska & Cygan 2007). Only recently, playback studies on birds have started to take long-term influences of simulated intrusions on the behaviour of residents into account. For example, it has been shown that overlapping songs during a first simulated intrusion can affect the behaviour of the resident during a second intrusion simulated several hours or days later (Hall, Illes & Vehrencamp 2006; Schmidt *et al.* 2007). However, bird song often acts as a preventive territorial proclamation in situations in which there is no immediate territorial threat (Catchpole & Slater 2008). Territorial challenges are thus

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predicted to have long-term effects on general territory proclamation (Davies & Houston 1984; Stamps & Krishnan 2001; Switzer *et al.* 2001). Indeed, male winter wrens *Troglodytes troglodytes* have been shown to increase their singing activity during the dawn chorus 1 day after an intruder was simulated using interactive song playback (Amrhein & Erne 2006; Erne & Amrhein 2008).

In naturally occurring territorial contests, not only acoustic or other signals, but also the location of an intruder is likely to influence the response of a resident. In birds and mammals, studies have found that male residents react more vigorously towards songs or calls of an intruder when they are played back in the centre of a territory rather than at the edges (Giraldeau & Ydenberg 1987; Molles & Vehrencamp 2001; Darden & Dabelsteen 2008). Smith (1996) argued that in most playbacks using fixed speaker positions, a lack of movement by the simulated intruder actually impedes efforts to simulate truly natural interactions. In a study using three loudspeakers, Poesel & Dabelsteen (2005) simulated intruders overlapping the songs of male blue tits *Parus caeruleus* to varying degrees, while switching among the three locations and remaining either inside or retreating outside the territory. They found that blue tits followed the simulated intruders when they stayed inside their territories, and that residents used the combined information from both the singing and the spatial behaviour of the intruder. Also in studies on banded wrens *Thryothorus pleurostictus* (Molles & Vehrencamp 2001) and nightingales *Luscinia megarhynchos* (Naguib, Amrhein & Kunc 2004), interactive playback experiments were performed that simulated first an intrusion and then a retreat by the intruder from the territory. However, so far it has not been tested whether the movements by an intruder inside the territory, other signals held constant, can affect territory defence of residents.

In this study, we aimed to separate the effects of movements from the effects of song performance by territorial intruders on the singing behaviour of territorial songbirds. We used the same non-interactive playback stimuli simulating a stationary intruder or an intruder changing song posts within the territories of resident male winter wrens. To avoid an immediate influence of reproductive behaviour on song output of our subjects, we studied singing behaviour in autumn territories (Amrhein & Erne 2006). To investigate the short-term response to playback, as well as the effects on singing as a general territory proclamation, we surveyed singing behaviour of male winter wrens during and immediately after the simulated intrusion as well as during undisturbed dawn singing before the playback and on the next day, almost 24 h after the intrusion. Our aim was to test whether residents react differently to moving vs. stationary territorial intruders. According to Smith (1996), an intruder continuing to sing from the same location after the resident has approached may be an unnatural and confusing scenario for the resident defending its territory. We therefore predicted that the wrens would sing less intensely in response to the stationary intruder than to the intruder changing song posts.

Materials and methods

We conducted the study between 29 September and 9 November 2006 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. In this study site with mild winters, male wrens defend territories and sing throughout the year (Amrhein & Erne 2006; Erne & Amrhein 2008). Female winter wrens do not defend territories and do not sing territorial song (Armstrong 1955; Dallmann 1987). During our fieldwork, about 35–40 male wrens were present at the study site. We selected our subjects to be out of earshot of each other, and we distinguished between individuals on the basis of their well separated territories.

EQUIPMENT AND SONG RECORDING

To ensure that the playback stimuli were the same in both treatments, we used 10 loop playbacks with a fixed number of songs. Each playback tape was used in two different wren territories, once for each treatment. For each playback tape, we used clear song recordings from a different male that were made at the study site from males that were out of earshot from the playback subjects. We recorded songs in autumn at dawn, from less than 10 m distance to the males, using a Sennheiser ME66/K6 directional microphone (Sennheiser electronic GmbH, Wedemark, Germany) and a Sony WM-D6C tape recorder (Sony Ltd, Tokyo, Japan). We digitized songs at 44100 Hz and 32 bit using Audacity 1.2.2 for Macintosh (<http://audacity.sourceforge.net>). From each of the 10 recorded males, we selected at random 10 songs that were normalized to the peak amplitude. We randomly arranged copies of these 10 songs to one another to create a playback tape that was 7 min in duration (three times 2 min of song, with two pauses of 30 s). We simulated an intruder singing at a rate of six songs per min, which lies within the natural range of singing winter wrens (Dallmann 1987). In total, each subject received 6 min of playback and 36 playback songs, which corresponds to our earlier studies (Amrhein & Erne 2006; Erne & Amrhein 2008).

During playbacks, we played the songs from a Sony WM-D6C tape recorder through a Blaupunkt GTA 50 amplifier connected by three 25 m cables to three Canton Plus X loudspeakers. The three loudspeakers were placed in a triangle and were 15–20 m away from each other, at a height of about 1.5 m. The researcher was placed on a public trail, at about 25 m distance from the speakers, and did not move during the playbacks. We always positioned all three loudspeakers in the subject's territory, independently of the following treatment. Playback volume was adjusted by ear prior to playbacks, to match the natural sound level of a singing wren, and the same volume was then retained throughout the experiments. The singing reactions of the subjects were recorded with a Sennheiser ME66/K6 directional microphone and a second Sony WM-D6C tape recorder.

DATA COLLECTION

Playbacks were conducted on 20 territorial male wrens (10 for each treatment). Each trial with a subject ran for 2 days, and the observation periods did not overlap between subjects. Within the 42 days of the study, there were 2 days on which no observations were made (1 and 20 October). Observation periods were chosen independently of weather conditions, and we alternated between treatments from one subject to the next. On the first day, as a control period with unchallenged birds, we observed each subject for 90 min, from 45 min before sunrise until 45 min after sunrise. We recorded the sounds within the subject's territory during the full 90 min on tape, using the recording equipment mentioned above, and simultaneously noted

the number of songs sung by the subject. Between 45 and 55 min after sunrise, we installed the loudspeakers in the territory, and 60 min after sunrise we started the loop playback. For the treatment simulating a stationary intruder, we used one loudspeaker only that was selected at random from the three loudspeakers inside the subject's territory. For the treatment simulating a moving intruder changing song posts, we alternated between the three loudspeakers inside the territory: we started with the loudspeaker in the middle position, and after 2 min (i.e. after 12 playback songs), we used the pause of 30 s on the playback tape to switch to the next loudspeaker in counter-clockwise direction. Because we played back songs from the same recorded male during the three 2-min periods of playback, we consider it very likely that subjects perceived the songs as coming from a single intruder moving between three different locations rather than coming from three different intruders. We recorded the singing reactions of the subjects during the playback and during 7 min following the playback on tape and simultaneously noted the number of songs sung by the subject. On the second day, we recorded the sounds within the subject's territory again from 45 min before sunrise until 45 min after sunrise, following exactly the same data collection protocol as on the first day.

DATA ANALYSIS

As the dawn chorus of birds is usually defined as taking place before sunrise (Staicer, Spector & Horn 1996), the minute of sunrise (given at <http://www.sunrisesunset.com> for Basel, Switzerland) was defined *a priori* as a cut-off point in the analyses. Because we showed earlier that singing after sunrise is less clearly influenced by a previous territorial intrusion (Amrhein & Erne 2006; Erne & Amrhein 2008), we restricted our analyses to the period before sunrise. Our response variables were the number of songs sung before sunrise, the length of the songs and the start of dawn singing in minutes before sunrise. We further investigated song rate before sunrise (number of songs sung before sunrise divided by the number of minutes from start of singing until sunrise), and song rate during the playback and during 7 min immediately after the playback. For measuring song lengths, we used the software SYRINX version 2.6 h (John Burt, <http://www.syrinxpc.com>). Because we were interested in a comparison of long-term and short-term singing responses and because the tiny winter wrens were difficult to observe visually in the dense bushes, we did not analyse measures of physical approach to the loudspeakers during playback. For data analysis, we used R 2.7.1 (R Development Core Team 2008) and linear mixed effects models with the function `lme` in the package `nlme` (version 3.1–89). We included individual subject as a random factor with individual-specific intercepts; including also random slopes gave similar results, and in most cases random intercept models had a lower BIC (Bayesian information criterion) and were thus preferable. As fixed factors, we included census day (before playback vs. after playback) or playback period (during vs. immediately after playback) and kind of intruder (stationary intruder vs. intruder changing song posts). To account for possible seasonal effects, we included the observation day (1–42) as a covariate. In the mixed effects models on dawn singing behaviour, we used principal components (function `princomp`) as response variables rather than the original variables (see below). In the mixed effects models on the numbers and lengths of songs sung during the 6 min of song playback, we included the minute of playback as a continuous variable, and also added the quadratic term min^2 to test for possible curvilinear relationships. We selected models based on likelihood ratios (LR) between alternative models, and non-significant terms were removed from the models. For all LR

tests, the degrees of freedom were $\text{d.f.} = 1$. We visually checked homogeneity of variance and normality of error using plots of standardized residuals against fitted values and of quantiles of residuals against quantiles from a normal distribution. If necessary, song rates and song lengths were square root transformed. Values are reported as $\text{mean} \pm \text{SE}$, and all tests are two-tailed.

Results

LONG-TERM RESPONSE

The first wren started to sing 41 min before sunrise. The start time of singing and the number of songs sung before sunrise were correlated: on the first day (before playback), wrens that started to sing earlier also sang more songs before sunrise ($r_{18} = 0.74$, $P < 0.001$). Start time of singing and mean song length before sunrise were not significantly correlated ($r_{18} = -0.27$, $P = 0.24$) and neither were number of songs and mean song length ($r_{18} = -0.01$, $P = 0.98$). To obtain uncorrelated response measures, we made a principal component analysis on the three measures of dawn singing behaviour (Table 1). The first two components together accounted for 93% of the variance of the original variables. PC1 was a measure of song output before sunrise, whereas PC2 was related to mean song length before sunrise (Table 1).

In a linear mixed effects model on song output before sunrise (PC1), we did not find a seasonal effect (LR = 2.07, $P = 0.15$). The interaction between census day (before or after playback) and kind of intruder was significant (LR = 4.81, $P = 0.028$), indicating that on the day after playback, subjects changed their song output differently depending on the kind of intruder. When the simulated intruder had changed song posts, the wrens increased their song output before sunrise, but they decreased their song output when the intruder had been stationary (Fig. 1). Wrens increased the number of songs sung before sunrise by 5.5 ± 4.5 (mean \pm SE) songs when the intruder had changed song posts, but decreased the number of songs by -12.3 ± 6.9 songs when the simulated intruder had been stationary. On the day after playback, subjects that had experi-

Table 1. Principal component analysis on three measures of dawn singing behaviour in male winter wrens

	PC1	PC2	PC3
Songs before sunrise	0.71	0.22	0.68
Start of singing	0.71	-0.20	-0.68
Song length		0.96	-0.29
Proportion of variance	0.57	0.36	0.07
Cumulative proportion	0.57	0.93	1.00

PC1 and PC2 were used as response variables in further analyses. Loadings of variables that made an important contribution to the components are indicated in bold. High scores on PC1 indicate large numbers of songs sung before sunrise and an early start of singing (high song output); high scores on PC2 are mainly related to long song lengths.

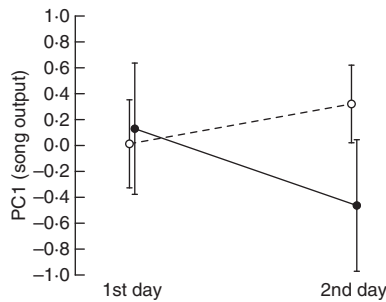


Fig. 1. Mean (\pm SE) scores on song output before sunrise (PC1; see Table 1) by male winter wrens, shortly before (first day) and 1 day after (second day) a playback was made simulating either an intruder changing song posts ($N = 10$; open circles and hatched line) or a stationary intruder ($N = 10$; full circles and solid line). High scores on PC1 indicate large numbers of songs sung before sunrise and an early start of singing.

enced a moving intruder started to sing 1.7 ± 1.4 min earlier, while those with a stationary intruder started singing -2.9 ± 1.9 min later.

Depending on the kind of intruder, the subjects also responded differently with respect to mean song length before sunrise (PC2; interaction between census day and kind of intruder: LR = 8.19, $P = 0.004$), but there was no seasonal effect on song length (LR = 1.99, $P = 0.16$). Wrens with a moving intruder increased mean song lengths from the first to the second day (3.26 ± 0.15 to 3.47 ± 0.17 s), while wrens with a stationary intruder reduced song lengths (3.81 ± 0.26 to 3.29 ± 0.24 s).

SHORT-TERM RESPONSE

Three subjects that received the playback simulating a stationary intruder did not vocally respond during the playback, but were seen next to the loudspeaker. All 10 subjects that received a playback simulating a moving intruder responded by singing and were seen to follow the switches from one loudspeaker to the next.

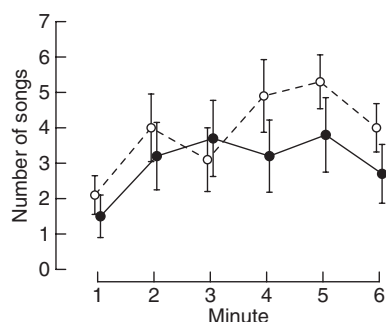


Fig. 2. Mean (\pm SE) numbers of songs sung by male winter wrens during 6 min of song playback simulating two kinds of intruders into their territory. After the first 2 min and after the second 2 min of song playback, there were pauses of 30 s duration without playback. Symbols and sample sizes are as in Fig. 1.

For the following analyses of song during the 7-min playback period, we omitted the two pauses of 30 s during which there was no playback. During the 6 min of song playback, the song rate of the 20 subjects was higher during the playback (3.46 ± 0.56 songs per minute) than during the song period before sunrise (1.37 ± 0.17 ; LR = 6.11, $P = 0.013$), while there was no overall effect of season on song rate during playback and before sunrise (LR = 0.45, $P = 0.50$). The song rate during playback was not found to correlate with the mean song length ($r_{15} = 0.04$, $P = 0.89$). For the short-term responses, we therefore analysed song rate and song length separately.

In a mixed effects model on the number of songs sung during the 6 min of song playback, the interaction between the squared minute of playback (min^2) and the kind of intruder was not significant (LR = 2.74, $P = 0.098$); note, however, that in the late stages of song playback, subjects with moving intruders tended to sing more than subjects with stationary intruders (Fig. 2). The main effect of playback treatment was not significant (LR = 0.66, $P = 0.42$), suggesting that faced with an intruder changing song posts, subjects did not generally sing more songs during playback than with a stationary intruder. However, the curvilinear temporal pattern was significant (min^2 : LR = 17.98, $P < 0.001$), reflecting the finding that in the beginning of the playback subjects increased their song rate, and at the end of playback slightly decreased song rate again (Fig. 2).

With respect to song length, neither the interaction of playback treatment with a curvilinear temporal pattern min^2 (LR = 0.43, $P = 0.51$), nor the main effects of treatment (LR = 0.008, $P = 0.93$) and min^2 (LR = 0.005, $P = 0.94$) were significant. However, song lengths tended to decrease towards the end of the playback (main effect of min: LR = 3.39, $P = 0.065$).

We also compared singing responses during the 7-min playback period (including the two pauses of 30 s) and during the 7-min period after playback. In a linear mixed effects model on song rate, we did not find a seasonal effect (LR = 0.33, $P = 0.56$). The interaction between playback period and kind of intruder was not significant (LR = 0.06, $P = 0.81$), indicating that subjects changed their song rate from during playback to after playback similarly if they had a contest with a moving intruder (3.93 ± 0.77 to 3.06 ± 0.65 songs per minute) or with a stationary intruder (3.09 ± 0.93 to 2.46 ± 0.89 songs per minute). Also the main effects of treatment (LR = 1.31, $P = 0.25$) and of playback period (LR = 2.13, $P = 0.14$) were not significant.

With respect to song length, we did not find a significant seasonal effect (LR = 0.81, $P = 0.37$). The interaction between playback period and kind of intruder was not significant (LR = 0.48, $P = 0.49$), indicating that subjects changed the length of their songs from during playback to after playback similarly if they had a contest with a moving intruder (3.01 ± 0.18 to 3.23 ± 0.29 s) or with a stationary intruder (2.99 ± 0.21 to 2.97 ± 0.28 s). Neither the main effects of treatment (LR = 0.16, $P = 0.69$) nor of playback period (LR = 0.27, $P = 0.60$) were significant.

Discussion

Male winter wrens showed a different long-term singing reaction in response to a simulated intruder that was moving and changing song posts than to a stationary intruder. One day after the intrusion, males experiencing a moving intruder started to sing earlier before sunrise, and they sang more and longer songs at dawn than before the intrusion. In contrast, males that had received a playback simulating a stationary intruder reacted by starting to sing later relative to sunrise, and by singing fewer and shorter songs than before the intrusion.

Because the playback stimuli were the same in both treatments, the differential reactions of territory owners were evidently caused by the spatial behaviour and not by the individual song characteristics of the intruders. Our study thus demonstrates that spatial behaviour of territorial intruders provided some kind of information that caused residents to adjust their long-term territory proclamation behaviour. Earlier studies suggested that simulating intruders to retreat from the territory causes different reactions by territorial males than when song playback is broadcast from inside the territory only (Molles & Vehrencamp 2001; Naguib *et al.* 2004; Poesel & Dabelsteen 2005). The present results indicate that also movements of simulated intruders inside the territory itself can alter the signal value of the playback. As proposed by Smith (1996), switching of speaker positions should thus be incorporated as an alternative method in studies using interactive song playbacks. In the established standard procedures of interactive playback, the dynamic switching of song stimuli that are broadcast from fixed speaker positions has greatly increased our understanding of animal communication strategies. Switching between speaker positions while keeping song stimuli constant, as demonstrated in this study, should be a promising new method to investigate territorial behaviour of animals.

Although we clearly demonstrated an influence of the spatial behaviour of intruders on singing behaviour of winter wrens in the following morning, the interpretation of the differential singing responses in our subjects seems currently less straightforward. If a moving intruder represents a more natural scenario of an intrusion (Smith 1996; Molles & Vehrencamp 2001), the subjects increasing their song output in response to the moving intruder may have reacted in a more normal way, while the stationary intruders may have been perceived as a less natural and therefore less threatening experience. Increased dawn singing performance by the subjects experiencing a moving intruder could then be interpreted as an increased effort in territory defence in the face of a greater territorial threat. In line with this hypothesis, De Kort *et al.* (2009) recently found that banded wrens sang with a higher song rate in response to intruders singing with a higher performance. This explanation, however, cannot account for why we found that subjects experiencing stationary intruders actually decreased their song output. The decrease in song output was about double as large compared to the increase when the intruder had changed song posts,

which is a typical ratio in effect size between the so-called loser and winner effects after aggressive encounters (Rutte, Taborsky & Brinkhof 2006). An alternative explanation could thus be that residents perceived an intruder that was stationary and persisting during a relatively long period of 7 min as if they had lost the vocal contest. Contrarily, an intruder changing song posts could then be interpreted as a winning experience; in this case, the resident may have perceived the intruder as having reacted to its territory defence effort by changing song posts and by avoiding the resident. According to the self-assessment hypothesis on the winner effect (Rutte *et al.* 2006), the resident subjects could have gained information about their own relative fighting ability during the playbacks. Because dawn singing is likely to reflect the quality of males (Otter, Chruszcz & Ratcliffe 1997; Poesel, Dabelsteen & Pedersen 2004; Amrhein & Erne 2006), subjects then might have adapted their dawn singing behaviour to their own perceived quality, by increasing singing when they had won, and by decreasing singing when they had lost the song contest.

In our earlier experiments on winter wrens (Amrhein & Erne 2006; Erne & Amrhein 2008), we used the same number of playback songs and the same total playback duration as in this study; yet, although songs were played back from one position only, the subjects had reacted by increasing rather than decreasing song output before sunrise on the next morning. We argue that this different reaction can be explained by the fact that we used interactive song playbacks in the earlier studies, and that playbacks were split into two 3 min sessions with a half hour pause between the two parts of the playback. This suggests that interacting with a resident via overlapping some of its songs (earlier studies) or via switching between song posts (present study) may actually lead to similar reactions by the resident, which could be tested in future experiments.

Interestingly, we only found weak evidence that in the short term, during the actual song contests, residents sang more songs when confronted with moving intruders. Also in their singing reactions in the minutes after playback, subjects did not show significant differences in song rate or song length depending on the spatial behaviour of the intruder. It is of course difficult to compare the results on song performance for the restricted time periods during and immediately after playback with the results on the more lengthy periods of undisturbed dawn singing. However, such a comparison seems to demonstrate that, given our sample sizes, investigating long-term changes in dawn singing had greater statistical power to discriminate between our treatments than investigating short-term song responses to playback.

Based on our findings, we argue that spatial behaviour of territorial intruders should be an integral part of the study of animal territory defence behaviour. Further studies are needed to unravel the signal value of movement patterns by territorial intruders. At least in the winter wren, long-term changes in dawn singing behaviour seem to be a sensitive tool when investigating the effects of simulated territorial intrusions on territory defence.

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