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Dawn singing reflects past territorial challenges in the winter wren

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Territory defence can be seen as a dynamic long-term process that involves some learning. For example, a resident may adjust its territory proclamation behaviour depending on its prior experience with territorial intruders. We investigated whether short territorial challenges could have long-lasting effects on the singing behaviour of male birds. We used song playbacks to simulate intrusions into autumn territories of male winter wrens, *Troglodytes troglodytes*, shortly after dawn and compared male singing behaviour immediately before and 1 day after the simulated intrusion. As in many other bird species, unchallenged male wrens tended to sing more songs before than after sunrise. One day after a simulated intrusion, however, this pattern was much more pronounced. Males significantly increased their song output before sunrise, but maintained or even reduced song output after sunrise. This result suggests that dawn singing before sunrise is particularly important for territory defence. On the day after the intrusion, the start of dawn singing varied less between males, although the average starting time remained the same. Our findings suggest that a territorial challenge can influence singing behaviour almost 24 h after the intrusion. The amount and timing of birdsong, as a preventive territorial proclamation, can thus be adjusted to past territorial challenges.

The males of many bird species rely on a territory to acquire and to hold limited resources such as mates, food or shelter (Armstrong 1956; Davies & Houston 1984; Ydenberg & Krebs 1987; Tobias 1997). Territories are therefore vigorously defended against intruding rivals (Stamps 1994; Switzer et al. 2001), and the use of territorial song can be both sufficient and necessary to expel intruders (Krebs 1977; McDonald 1989; Nowicki et al. 1998). Male songbirds also sing in contests with simulated territorial intruders, and the playback of song within a subject's territory has been used in many experimental studies on the function of singing strategies (Naguib 2005). Simulated intrusions by unfamiliar rivals, however, may also have profound long-term effects: females have been shown to eavesdrop on song contests between their mate and a simulated intruder and, depending on the performance of their mate, to visit other males and to engage in extrapair copulations on the days after the intrusion (Otter et al. 1999; Mennill et al. 2002).

So far, experimental studies on how simulated intrusions affect the behaviour of male birds have concentrated on short-term responses. For example, males adapt their singing strategy in a contest with a simulated intruder depending on the immediately preceding experience they have had with an intruder (Naguib 1999; Peake et al. 2002). For long-term tenure of a territory, learning processes seem to be important (Switzer et al. 2001). Residents can not only learn to distinguish between intruding neighbours and strangers (Temeles 1994), but may also adjust their level of aggression in response to the strangers' long-term behaviour: dynamic modelling of territory defence suggests that residents' behaviour in territorial contests depends on whether individual strangers are expected to intrude repeatedly or only once (Switzer et al. 2001). However, territorial signalling also occurs in the absence of an immediate territorial threat. Birdsong may be seen as a general territorial proclamation and a first line of defence (Catchpole & Slater 1995), and the occurrence of such territory defence behaviour is suggested to depend on the level of intruder pressure (Davies & Houston 1984; Switzer et al. 2001). We would therefore predict that the amount and timing of birdsong, as a preventive territorial proclamation, is adjusted to past territorial challenges.

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We investigated whether simulated territorial intrusions can have long-lasting effects on the males' territorial song, which in many species has a peak at dawn (Staicer et al. 1996). During the breeding season, singing at dawn is often related to the behaviour of females, so researchers have concluded that singing before sunrise has a strong intersexual component, that is, be addressed mainly to females, or serve to guard a fertile female. For example, the dawn chorus may be longest or start earliest during the fertile period of females (Mace 1987; Cuthill & Macdonald 1990; Welling et al. 1995); furthermore, fertile female superb fairy-wrens, *Malurus cyaneus*, visit extrapair mates shortly before sunrise (Double & Cockburn 2000) and fertile female great tits, *Parus major*, interact vocally with their mates during the dawn chorus (Gorissen & Eens 2004). In other studies, however, dawn singing was less influenced by the reproductive behaviour of females and was interpreted to have a strong intrasexual component, that is, be addressed mainly to males, and to serve to defend the territory (Slagsvold et al. 1994; Amrhein et al. 2004a; Liu 2004; Kunc et al. 2005). For example, nonterritorial male nightingales, *Luscinia megarhynchos*, prospect territories almost exclusively during the hour before sunrise (Amrhein et al. 2004b), which is consistent with the hypothesis that dawn singing of resident males is necessary to defend the territory against territory-searching rivals (Kacelnik & Krebs 1983).

In this study, we avoided an immediate influence of reproductive behaviour on song output by investigating autumnal dawn singing in the winter wren, *Troglodytes troglodytes*. In this small passerine, only the males defend territories and sing territorial song, and pair bonds are formed only during spring courtship and mating (Armstrong 1955; Dallmann 1987; Cramp 1988). However, unlike most other European songbirds, resident male wrens in mild climates are territorial and sing at dawn throughout the year (Armstrong 1955; Cramp 1988).

Wrens on their autumn migration are most likely to be caught in mist nets at dawn or shortly after dawn (Glutz von Blotzheim 1985). Since wrens migrate at night (Cramp 1988), this may indicate that, like territory-prospecting nightingales (Amrhein et al. 2004b), they settle at resting places around sunrise, or that they prospect the area at dawn after arriving at night (Martin 1990). If singing before sunrise is important to announce territory occupancy to prospecting or migrating males, we predicted an earlier start of dawn singing or an increase in song output before sunrise after the bird has experienced a territorial challenge. After sunrise, however, the risk that an intruder has settled in the territory may be highest, and territory defence strategies other than singing could become more useful. Therefore, a territorial challenge may differentially influence song output before and after sunrise. In addition, optimality models predict a change in singing patterns around sunrise, as increasing light levels make activities such as foraging more profitable (Hutchinson 2002). We therefore simulated territorial intrusions in autumnal wren territories 1 h after sunrise and compared how the resident males changed their song output before and after sunrise the next morning, almost 24 h after their territory was challenged.

METHODS

General

We conducted the study between 3 October and 5 November 2004 at the Petite Camargue Alsacienne in the Upper Rhine Valley in France, 10 km north of Basel, Switzerland. In lowlands such as this study site, with mild winters, resident male wrens defend territories and sing throughout the year (Armstrong 1955; Glutz von Blotzheim 1985; Cramp 1988). Females, however, do not defend territories and do not sing territorial song (Armstrong 1955; Dallmann 1987). Wrens do not form strong pair bonds, and resident males are solitary outside the breeding period, except for nights with harsh weather conditions when they may roost communally (Cramp 1988). During October, male wrens have an autumn peak of singing activity, and the diel peak of singing is shortly after the males leave their roosts at dawn (Armstrong 1955; Cramp 1988). At the study site, about 50 males were present during our field work. We selected our subjects to be out of earshot of each other, and checked their territories once a week to verify that they were occupied throughout the autumn field season.

Equipment and Song Recording

We created playback stimuli from clear recordings that were made during the autumn field season at the study site, from territorial males out of earshot of the playback sites. We recorded song at dawn, less than 10 m from the males, using a Sennheiser ME66/K6 directional microphone and a Sony WM-D6C tape recorder. We digitized songs at 44 100 Hz and 32 bit using Audacity 1.2.2 for Macintosh (http://audacity.sourceforge.net). From each recorded male, we selected at random 10 songs that were normalized to the peak amplitude. For each playback tape, we used songs from a different male. On the playback tape, we inserted about 400 ms of silence between songs, so that we could use the pause button of the tape recorder to release the songs one by one during interactive playback. Songs were played from a Sony WM-D6C through a Blaupunkt GTA 250 amplifier connected via a 25-m cable to a Canton Plus X loudspeaker.

Playback and Data Collection

Playbacks were conducted on 12 territorial wrens. In two territories, however, there was a singing intruder present before or during playback, and those two trials were abandoned. In the remaining 10 territories, we collected data during two consecutive mornings. The observation periods for the individual subjects were distributed throughout the month of field work, and observation periods did not overlap between subjects. On the first day, as a control period with unchallenged birds, we observed each subject for 2 h, starting 1 h before sunrise. We noted each song and the corresponding position of the bird. In the third hour of observation, we broadcast a playback of 3 min starting 1 h after sunrise.

The playback songs were broadcast from a loudspeaker placed at a height of about 1.5 m within the subject's singing territory. We adjusted playback volume by ear and used the same settings for all playbacks so that sound amplitude was standardized across trials. The playback was repeated 30 min later with the same order of playback songs, to simulate a fairly persistent intruder. Each subject thus received a total of 6 min of playback and a mean ± SD of 38 ± 6 playback songs (about 6 songs/min). One of the subjects did not respond vocally during both song playbacks, and two subjects responded vocally only during the first or the second playback, respectively, although one of them was seen next to the loudspeaker during both playbacks. The nine subjects that responded vocally sang in total a mean ± SD of 24 ± 14 songs during the 6 min of playback. In each playback, we first simulated an intruder singing at a natural rate of about 5–6 songs/min (Dallmann 1987); once the subject started to sing, we interactively overlapped a mean ± SD of 37 ± 9% of its songs, to simulate a moderately aggressive intruder (Naguib et al. 2004). On the second day, we observed the subjects for 2 h, starting 1 h before sunrise and following exactly the same data collection protocol as on the first day, but we left out the third hour of observation, in which the playback had taken place on the first day.

Data Analysis

This study was designed to compare song output before and after sunrise. The minute of sunrise (as given at www.sunrisesunset.com for Basel, Switzerland) was defined a priori as a cutoff point in the analysis, since the dawn chorus of birds is usually defined as taking place before sunrise (Staicer et al. 1996). Males of many species often become relatively quiet around sunrise (Staicer et al. 1996; Hutchinson 2002), and this was also the case with seven of our 10 subjects (although they did not always pause exactly at sunrise). Alternatively, we could have defined dawn singing to end individually, and independently from actual sunrise time, for example with a pause or a sudden drop in song output. However, three wrens continued to sing after sunrise without pausing, and, as suggested by Hutchinson (2002), this pattern also changed within individuals from day to day (two wrens singing continuously only on the first day and one only on the second day). Defining an individual end of dawn singing would thus have been at least as arbitrary as taking sunrise as a cutoff point for all of the males (for a discussion of the difficulties with comparing dawn singing routines within and between individuals, see Hutchinson 2002).

Most subjects paused once or twice for several minutes before or after sunrise. An interpretation of song rates (number of songs/min) is not straightforward for these individuals, and their song rates would also be difficult to compare with individuals that sang more continuously. As our measure of song output, we therefore chose the total number of songs sung during the periods before and after sunrise.

To analyse the data we used SPSS 11 for Macintosh (SPSS Inc., Chicago, IL, U.S.A.). Values are reported as means ± SD, and tests are two tailed. Unless otherwise noted, all sample sizes are $N = 10$.

RESULTS

The 10 wrens started to sing at dawn 23.0 ± 8.9 min before sunrise on the first day and 23.7 ± 4.1 min before sunrise on the second day. Thus, the average start of dawn singing was similar before and after playback. However, the onset of dawn singing varied less on the second day (variance ratio test for paired samples, Zar 1996: $t_8 = 3.39$, $N = 10$, $P = 0.009$). One day after playback, early birds started to sing later, and late birds started to sing earlier (Fig. 1).

Generally, the first wrens started to sing 32 min before sunrise (Fig. 1). To examine whether singing before and after sunrise was influenced differentially by playback, we analysed the song output for all subjects for 32 min before sunrise and 32 min after sunrise.

As predicted, the song output before sunrise was influenced by the previous day's simulated territorial intrusions (Fig. 2a). On the first day, the 10 wrens sang 41 ± 19 songs before sunrise, whereas after playback, on the next day, they sang 47 ± 19 songs (paired *t* test: $t_9 = -3.03$, $P = 0.01$). This increase by, on average, six songs corresponded to a proportional increase of 21 ± 25%.

The song output after sunrise was less clearly influenced by playback (Fig. 2b). The wrens sang 23 ± 16 songs after sunrise on the first day and 16 ± 19 songs after sunrise on the second day, but this decrease was not significant (paired *t* test: $t_9 = 0.98$, $P = 0.35$). However, the pattern was largely influenced by one bird that sang excessively after sunrise on the second day (Fig. 2b; the nine remaining wrens sang 23 ± 17 songs after sunrise on the first day and 11 ± 9 songs on the second day; paired *t* test: $t_8 = 2.98$, $P = 0.02$).

In consequence, while the 10 wrens showed a tendency to sing more songs before than after sunrise on the first day (41 ± 19 and 23 ± 16 songs, respectively; paired *t* test: $t_9 = 2.11$, $P = 0.06$), this difference was even stronger on the day after playback (47 ± 19 and 16 ± 19 songs, respectively; $t_9 = 4.36$, $P = 0.002$).

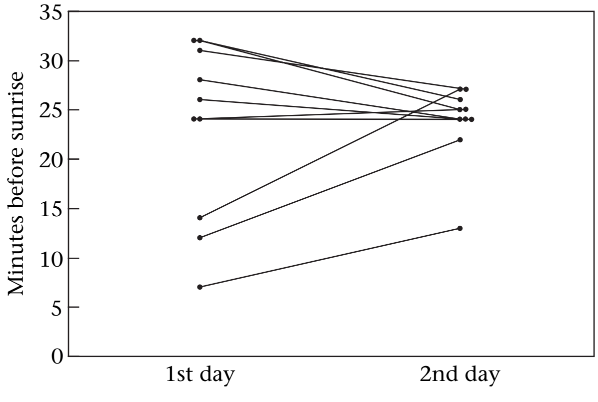

Figure 1. Start of dawn singing (minutes before sunrise) by 10 male wrens, shortly before an intrusion was simulated by playback in a male's territory (first day) and on the next morning, 1 day after the intrusion was simulated (second day).

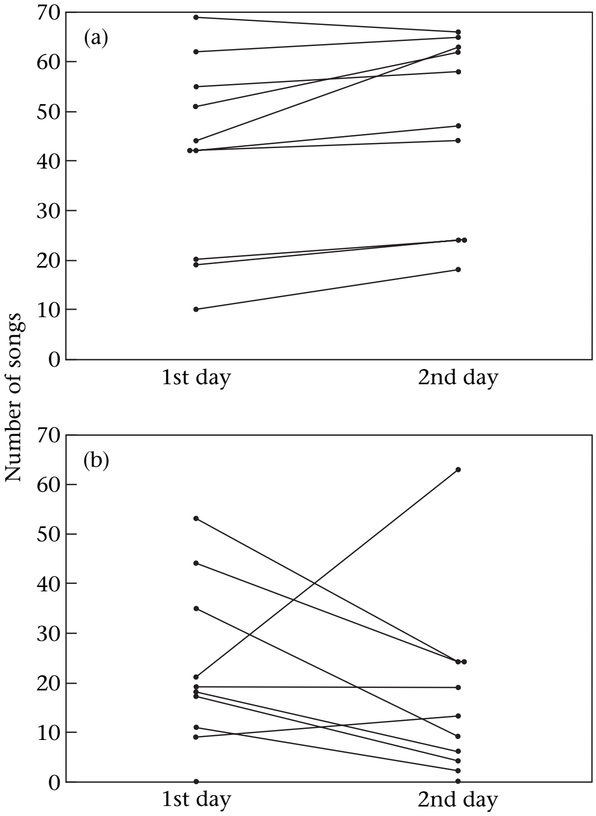

Figure 2. Song output (a) before and (b) after sunrise. Number of songs sung by 10 male wrens in 32 min before/after sunrise, shortly before and 1 day after an intrusion was simulated in a male's territory.

Wrens that, before sunrise, sang many songs on the first day also sang many songs on the second day (Fig. 2a; Pearson correlation: $r_8 = 0.95$, $P < 0.001$). For the 32 min after sunrise, the same correlation was not significant ($r_8 = 0.33$, $P = 0.34$; after omitting the bird with the exceptionally high after-sunrise song output: $r_7 = 0.78$, $P = 0.01$; Fig. 2b). Birds that started to sing earlier than others before playback also started to sing earlier on the day after playback ($r_8 = 0.68$, $P = 0.03$; Fig. 1). However, although on the first day earlier-starting birds sang more songs before sunrise than later-starting birds ($r_8 = 0.78$, $P = 0.008$), the same correlation was not significant on the second day ($r_8 = 0.52$, $P = 0.12$), indicating that after the simulated intrusion, song output before sunrise was less dependent on starting time. For the first day, we found no significant influence of observation date during the field season on start of singing before sunrise ($r_8 = 0.53$, $P = 0.12$), number of songs before sunrise ($r_8 = 0.21$, $P = 0.57$) and number of songs after sunrise ($r_8 = -0.08$, $P = 0.84$); for the second day, too, the same correlations were not significant (all $P > 0.32$).

DISCUSSION

One day after a territorial intrusion was simulated by song playback, male wrens sang more songs before sunrise, and the onset of dawn singing varied less, than the morning before playback. These findings suggest that the wrens remembered the territorial intrusions for almost 24 h and changed their dawn singing behaviour in response to past territorial challenges.

Resident male wrens are known to defend their territories vigorously even in midwinter, but an established territory owner may be expelled by a bold intruder at any season of the year (Armstrong 1955, 1956). For a male wren in an autumn territory, it therefore seems reasonable to reinforce territory defence after an intrusion by a stranger. With our playback, we intended to simulate territory-prospecting males that intrude and settle in a territory shortly after sunrise (Amrhein et al. 2004b). We found that wrens responded to the intrusion by reinforcing their usual singing pattern: the next morning, before sunrise, they sang even more songs than they did before the intrusion, but after sunrise they maintained their relatively low song output or even sang fewer songs than before the intrusion.

The increase in singing activity before sunrise is consistent with the hypothesis that resident males sing at dawn to defend their territory and to advertise territory ownership to males prospecting territories before sunrise (Kacelnik & Krebs 1983; Staicer et al. 1996; Amrhein et al. 2004b). Furthermore, in nocturnally migrating species such as the wren and the nightingale, prospecting or migrating males may settle around sunrise (Glutz von Blotzheim 1985; Martin 1990; Amrhein et al. 2004b). This is in line with our finding that resident wrens, with the exception of one outlier, seemed to decrease their song output after sunrise. Given that, after sunrise, intruders could already be present in the territory, territory defence strategies other than singing may then be more useful. Resident wrens could silently patrol their territory boundaries or search their territory for possible intruders. Male great tits, *Parus major*, for example, spend a higher proportion of time travelling between food patches and less time feeding after a territorial intrusion, thereby investing more heavily in territorial vigilance (Ydenberg & Krebs 1987). An alternative explanation would be that, before sunrise, male wrens rely on singing to defend their territory because light levels are too low to chase an intruder effectively. A gradually increasing profitability of chasing or patrolling could cause a switch from singing to patrolling after sunrise (Hutchinson 2002). The need to forage after a period of singing, as was implied in the model by Hutchinson (2002), could also cause a decrease in song output after sunrise.

Our results indicate that a behaviour such as singing that may act as a preventive territorial proclamation (Catchpole & Slater 1995) is adjusted to territorial challenges that occurred as long as 24 h ago. Territory defence can be seen as a dynamic long-term process that involves some learning (Switzer et al. 2001). The male wrens in this study altered their singing behaviour differentially before and after sunrise, following a territorial intrusion shortly after sunrise. Residents thus seem to have learned from experience and may have anticipated the hour of possible future intrusions. Alternatively, wrens may increase song output before sunrise after any territorial intrusion, regardless of the hour of the day it occurred. It would therefore be interesting to investigate how residents react to intruders that vary, for example, in the time of day they intrude. Further research could also be done on the defence of breeding territories as opposed to the autumn territories that were used in this study, or on the influence of differences in quality between residents (Hyman et al. 2004).

In male wrens, the rank order of individuals with regard to song output and the start of singing was remarkably constant from day to day, and the large differences between subjects were partly maintained also after the intrusion. This is in line with previous findings that dawn singing reliably indicates the quality of males (Otter et al. 1997; Poesel et al. 2004). An alternative explanation would be that in individual territories, consistent environmental factors differentially influence the behaviour of residents (Hyman et al. 2004). For example, singing patterns such as starting time at dawn could be influenced by the behaviour of territorial neighbours (Liu 2004). We found that the onset of dawn singing varied less between male wrens on the day after an intrusion, although this finding was tested a posteriori and should be verified in subsequent studies. The dawn chorus can be seen as an interactive communication network (Burt & Vehrencamp 2005), and one function of this network could be to defend the territories against intruders cooperatively (Elfström 1997; Naguib et al. 2004). In that case, territorial neighbours might synchronize their starting time of dawn singing in response to an intrusion. For future studies, the analysis of long-term changes in singing behaviour could be a tool for investigating how different intruders using different singing strategies are perceived by a resident. Such studies could also take the behaviour of territorial neighbours into account.

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