THE ROYAL SOCIETY
biology letters

Non-territorial nightingales prospect territories during the dawn chorus

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Recd 22.09.03; *Accptd* 29.10.03; *Published online* 10.12.03

Male songbirds usually sing when they have occupied a territory, but the territory prospecting of non-territorial males is more elusive and has been rarely studied. Here, we simulated newly arriving, non-territorial males by translocating unmated male nightingales (*Luscinia megarhynchos*) to our study site. We show that territory prospecting of translocated males was largely confined to the hour before sunrise. The radio-tagged males made extensive excursions visiting several singing males at dawn, but after dawn they remained stationary outside occupied territories. As in many other songbird species, dawn was also the time when resident males sang the most. These results suggest that non-territorial male nightingales use the dawn chorus to assess singing residents or territory occupancy. For resident males, dawn singing may be important to announce territory occupancy to prospecting males and may thus play a role in territory maintenance.

Keywords: dawn chorus; non-territorial males; floaters; radio tracking; *Luscinia megarhynchos*

1. INTRODUCTION

The hour before sunrise is a time of peak singing activity in the males of many bird species (Staicer *et al.* 1996). Intensified singing during this dawn chorus has been hypothesized as serving to attract a mate (McNamara *et al.* 1987), to guard a fertile female (Mace 1987; Welling *et al.* 1995) or to defend the territory against rival males (Kacelnik & Krebs 1983). Given that birds must, for any of those reasons, spend some part of the day singing, dynamic modelling has further demonstrated that environmental factors could generate a dawn peak of singing (McNamara *et al.* 1987; Hutchinson *et al.* 1993; Hutchinson 2002). Reviewing the hypotheses on the dawn chorus, Staicer *et al.* (1996) have pointed out that mate attraction or mate guarding cannot explain why, in many bird species, dawn singing extends well beyond the fertile period of females or is unaffected by male mating status. For example, in the socially monogamous nightingale (*Luscinia megarhynchos*), both mated and unmated males show high singing activity at dawn until late stages of the breeding cycle (Amrhein *et al.* 2004). Such singing patterns are consistent with the hypothesis that song serves to defend the territory against rival males. Krebs (1977) demonstrated, by removing males and replacing them with loudspeakers, that broadcasting song delays reoccupation of territories in the great tit (*Parus major*). Krebs suggested that song has a role in territory maintenance and that non-territorial males use song to assess the occupancy of an area. Kacelnik & Krebs (1983) then argued that, if territory prospecting by non-territorial birds peaks at dawn, this could reinforce the need to sing at dawn for resident males. In their study on the great tit, however, Kacelnik & Krebs (1983) present data on invasions by potential settlers only for the hours after dawn.

In several bird species, non-territorial individuals are common. They are generally referred to as ‘floaters’ and have been shown to visit breeding territories regularly (Smith 1978; Zack & Stutchbury 1992). Also in highly territorial species, there are often many non-breeding males (Ligon 1999). Non-breeding males may defend a territory, but after a certain time desert it to settle somewhere else. Newly arriving, territory prospecting males may be another territorial threat to residents. It is, however, difficult to observe non-breeding or newly arriving males in the short time period when they actually search for a place to settle. One way to investigate the spatial behaviour of such floaters is to translocate birds from one area to another. This procedure serves to control for the subjects’ settlement status and to exclude familiarity with local territories. To date, translocations have been used to investigate female mate sampling behaviour (Dale *et al.* 1990; Bensch & Hasselquist 1992). Here, we applied the same method to study male territory sampling behaviour. We observed translocated radio-tagged nightingales throughout the day and found that they prospected territories almost exclusively at dawn, when resident males had their peak of singing activity.

2. MATERIAL AND METHODS

(a) *General*

The translocated males were released during the breeding season of 2002 at the Petite Camargue Alsacienne in the Upper Rhine Valley in France, where we had surveyed about 50 nightingale territories per year since 1994 (Amrhein *et al.* 2002). The capture site was 70 km to the north of the release site. At both sites, we monitored territories and mating status of all males throughout the breeding season. We ascertained the males’ mating status by observing their nocturnal singing behaviour, because it is only unmated males who sing regularly at night for a prolonged period (Amrhein *et al.* 2002, 2004). At the release site, we controlled the identity of males and the presence of females or floaters by regularly mist-netting throughout the season; the first males arrived on 12 April, and the females settled between 20 April and 8 May.

(b) *Translocation*

From 16 April to 2 June 2002, we translocated 13 male nightingales at intervals of 4 ± 2 days (mean ± s.d.) between translocations of a male. For translocations, we captured unmated males and glued radio-transmitters to their back feathers. We released the birds at about 10.00, within 4 hours of capture, and tracked all translocated males continuously during their first 2 days at the release site. We used telemetry equipment by Titley Electronics, Australia: three element Yagi antennae, Regal 2000 receivers and LT1 transmitters (equipment mass of 0.9 g = 4.1% of the average mass of our subjects).

(c) *Singing activity of resident males*

From 15 April to 9 June 2002, we made five rounds of inspection at the release site each day. Singing activity of a male is expressed as the proportion of rounds on which it was heard singing (Amrhein *et al.* 2002, 2004). Rounds followed a fixed route of 4500 m; we changed the direction of the rounds from day to day, and the duration of each round was 1 hour. The dawn round started 1.25 hours before sunrise. The morning round started at 09.00 (CEST). The afternoon round started at 14.00, the dusk round at sunset and the nocturnal round at midnight. For statistical analysis, we normalized the proportional data by applying an Anscombe transformation (Zar 1996).

DOI 10.1098/rsbl.2003.0133

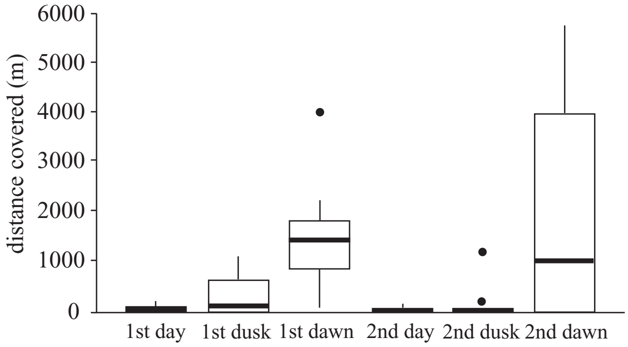

Figure 1. Diel pattern of movements of non-territorial male nightingales. For their first 2 days after translocation to the study site, movements of 13 radio-tagged males are given as the number of metres covered per hour (second dawn: $n = 9$). Boxes are median and 25th and 75th percentiles, whiskers are non-outlier ranges and dots are outliers. The first day is from releasing time at about 10.00 until before dusk. The lengths of the movements varied depending on time of day (Friedman test, $n = 9$, d.f. = 5, $p = 0.002$), with a burst of movement during the dawn chorus in the hour before sunrise.

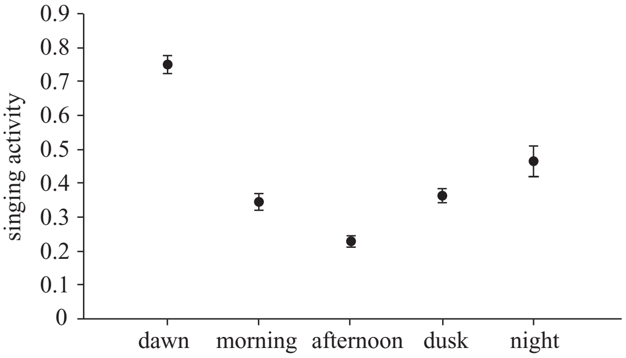

Figure 2. Mean (± s.e.) singing activity of 43 resident male nightingales, based on five rounds conducted on the study site each day throughout the breeding season. Singing activity of a male is expressed as the proportion of rounds on which it was heard singing. The probability of encountering a male nightingale singing was highest at dawn (repeated-measures ANOVA, $F_{4,168} = 53.67$, $p < 0.001$).

3. RESULTS

(a) *Translocation*

During the day, the translocated males remained almost stationary (figure 1). In the first dusk after translocation, seven out of the 13 males made short excursions with a length of 650 ± 410 m (mean ± s.d.) and a duration of 20 ± 4 min, starting 9 ± 5 min after sunset. No movements were observed during the night. It was only at dawn that most males made significant movements (figure 1). During the first dawn, two translocated males moved 30 and 120 m, respectively, and spent most of the time singing outside the territories of resident males. Eleven translocated males that only exceptionally sang covered 1700 ± 900 m in 54 ± 25 min and stopped moving 15 ± 11 min before sunrise. The lengths of dawn trips did not change as the season progressed (linear regression, $F_{1,11} = 0.04$, $p = 0.84$). During the first dawn trip, the 11 males visited 5 ± 3 occupied territories, often sitting close to the singing resident, and spent more time stationary inside occupied territories (25 ± 15 min) than outside (14 ± 9 min; Wilcoxon signed ranks test, $Z = -1.96$, $n = 11$, $p = 0.05$). Eight translocated males that visited both mated and unmated residents spent more time per visit in territories where a female was present (6.8 ± 1.9 min) than in territories of unmated males (3.8 ± 1.8 min; Wilcoxon signed ranks test, $Z = -2.1$, $n = 8$, $p = 0.04$). After dawn, males spent more daylight hours outside than inside occupied territories (Wilcoxon signed ranks test, $Z = -2.17$, $n = 13$, $p = 0.03$). During the second dawn we followed nine males, six of which again made excursions with a length of 3100 ± 2340 m. Eleven translocated males left the release site after 2–5 days and returned to the site of capture; two males settled in unoccupied territories that they had visited during a dawn or dusk trip.

(b) *Behaviour of resident males*

We monitored the singing activity of 43 resident males. The probability of encountering a resident nightingale singing was highest at dawn and lowest in the afternoon (figure 2). Out of 43 resident males, 21 males (49%) remained unmated and sang regularly at night in addition to diurnal song. All unmated males were territorial for some part of the breeding season. However, 11 unmated males left their territories after 6–46 days (33 ± 12 days) and were observed in other parts of the study site. One of those floating males was radio-tagged and showed similar behaviour to the translocated males. On 23 May, it sang at dawn in a previously unoccupied territory until 24 min before sunrise, when it moved 600 m to the border of an occupied territory and stayed stationary for the rest of the day.

4. DISCUSSION

We found that translocated male nightingales moved around extensively at dawn, rather than at other times of the day or night. During those dawn movements, the translocated males visited several resident males, but after dawn they remained stationary outside occupied territories. Dawn was also the time that resident males sang most.

Our study was intended to simulate non-territorial, newly arriving males that prospect an unfamiliar area. Although the translocation procedure may have influenced the birds in many ways, we do not expect that the dawn peak of activity can be attributed solely to adverse effects of the handling. Furthermore, a resident, not translocated floater showed similar behaviour. Yet we do not know when the translocated birds decided whether to stay at the release site or to return to the capture site; both the males that returned and the males that stayed may have prospected the area on the search either for a territory or simply for a place to rest. Whichever is the case, however, their territory prospecting behaviour remains interesting. During their dawn trips, the translocated birds apparently were attracted by singing residents, since they intruded territories and approached the singing males. These intrusions may have served to assess singing males or territory quality; the presence of a female could also have been of interest, since translocated males spent more time in territories of mated than of unmated males.

Most striking, however, is that territory prospecting was largely confined to the hour when resident males sang the most. The causes and implications of this correlation remain speculative at present. It may well be that both singing and territory prospecting had their peaks at dawn owing to environmental factors that favour these behaviours above foraging (Hutchinson 2002). However, the coincidence of the behaviours could also be of some adaptive value. Dawn seems to be the best hour for territory prospecting, since this time was when most residents sang. By contrast, the probability of encountering a resident male announcing its territory was lower at other times of the day and was biased at night when only unmated males regularly sing (Amrhein *et al.* 2002). Non-territorial males may therefore use the dawn chorus to assess singing residents or territory occupancy. For resident males, dawn singing may be important to drive non-territorial males into unoccupied areas and thus to maintain the territory. At the release site, several unmated residents left their territories and moved around after being territorial for a certain time. This could explain why territorial nightingales sing at dawn throughout the breeding season (Amrhein *et al.* 2004). There is evidence for a general territory maintenance function of song in the thrush nightingale (*Luscinia luscinia*), a close relative of the nightingale: Göransson *et al.* (1974) showed that, after removal of resident males, day-round broadcasting of song delays reoccupation of territories.

We suggest two ways to explore further the territory maintenance hypothesis of dawn singing. First, speaker replacement experiments could test whether song broadcast at dawn delays reoccupation of a territory for longer than song broadcast at other times of the day (Staicer *et al.* 1996). Second, the territory prospecting behaviour of non-territorial males could be incorporated in dynamic programming models of singing and foraging behaviour. The observation that non-territorial males were attracted by dawn singing suggests that resident males should reduce their dawn singing when their females reach peak fertility. Indeed, some studies showed that dawn singing has a shorter duration or a lower volume during the fertile period than afterwards (Pärt 1991; Rodrigues 1996), and mated nightingales reduce their dawn singing activity during the period before egg-laying commences (Amrhein *et al.* 2004). Outside the fertile period, however, singing for territory maintenance and territory prospecting may be shown to be mutually enhancing and thereby to stabilize the pattern that territorial males have a peak of song at dawn.

Acknowledgements

The authors thank H. Altrichter, C. Eikenaar and M. Weerheim for assistance in the field, and P. Korner and two anonymous referees for comments on the manuscript. Permissions were given by the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris. The research was funded by the Swiss Association Pro Petite Camargue Alsacienne, the Swiss Foundation Emilia Guggenheim-Schnurr and the Deutsche Forschungsgemeinschaft (NA 335/4).

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